

Virtual experiment with two species

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Intraspecific variability (IV) is often seen as an intrinsic property of individuals, associated with genetics, which is often considered as unstructured in space and time. Here, we investigated whether observed IV can result from the species responses to the spatial variations of the environment. Our hypothesis was that the individuals can be clones, i.e. have no genetic differences between them, and still have different measured attributes because the environment in which they strive varies, as shown in the previous analysis of a clonal dataset. The response of an individual results from the integrated effects of the environmental conditions which the individual has encountered during its life (local environmental variation, also called microsite effect) and its genetic features. Moreover, the differences between individuals due to environmental variation does not imply a broader overlap of the species niches. Therefore, this type of IV has no direct effect on species coexistence.

Here, we designed and conducted a virtual experiment that aims at illustrating that IV, or “individual effects,” can result from variation in unobserved environmental variables (Clark et al. 2007), therefore accounting for multidimensional species differences which cannot be observed on a few niche axes.

1 Perfect knowledge model: generating response values.

To do so, we first considered a “perfect-knowledge” model that depicts the ecological response (e.g. growth) of individual clones for two different species as a function of a set of environmental variables. This model represents the perfect knowledge of the process as it occurs in the field and thus includes no residuals:

$$Y_{ijt} = \beta_{0j} + \beta_{1j} * \ln(X_{1ijt}) + \beta_{2j} * X_{2ijt} + \dots + \beta_{Nj} * X_{Nijt} \quad \text{“Perfect knowledge model”}$$

where $1 \leq i \leq 500$ are the individuals ; $1 \leq j \leq 2$ are the species ; Y is a response variable, for instance growth ; X_1 to X_N are explanatory variables, for instance environmental variables, that can vary with time t ; and the $\beta_{k,i}$, $1 \leq k \leq N$ depict the species-specific responses to these environmental variables. As we consider clones, individuals of the same species respond the same way to environmental variables, and variation in Y among individuals within species is due to differences in the environment where each individual thrives.

The first explanatory variable was natural log-transformed to represent a log-log relationship as would be the relationship between tree growth and light for example.

We fixed the species parameters of the “Perfect knowledge model” as follows, using 10 environmental variables ($N=10$):

Parameters of species 1: $\beta_0 = 0.25$, $\beta_1 = 0.15$, β_2 to β_6 were chosen randomly between -0.05 and 0.05 and β_7 to β_{10} were chosen randomly between 0 and 0.05.

Parameters of species 2: $\beta_0 = 0.2$, $\beta_1 = 0.1$, β_2 to β_{10} were chosen the same way as for species 1.

The difference between the species is imposed by those parameters. Here, species 1 was more competitive on average thanks to its higher intercept (β_0) and response to the first environmental variable (β_1). The first environmental variable (X_1) has a higher weight in the computation of the response variable, as would be the most limiting factor for the response variable.

To account for intrinsic variability in our generated data, we added an IV in species parameters by sampling each individual parameter in a normal distribution centered on the species mean parameter and with a standard deviation of a quarter of the species mean parameter.

To represent the spatialised environment, we build a 2D matrix of dimension 500×500 for each environmental variable at a time t_0 , by randomly generating them with spatial autocorrelation. We here considered that all environmental variables were independent. Each variable was simulated by using the gstat R package (Pebesma 2004, Gräler et al. 2016), enabling to create autocorrelated random fields. A spherical semivariogram model was used for each of the ten environmental variables, with a mean of 0 for each explanatory variable (beta = 0), a sill of 1 (psill = 1) for each and a range of 50 (range = 50).

We then considered that Y had been measured at two times, t_0 and t_1 , for each individual as it would be under periodic forest plot censuses for instance. A pair of coordinates within this spatialised environment was randomly assigned to each of the 500 individuals. We considered that some of the environmental variables (light, temperature, humidity, nutrient availability for instance) had changed between t_0 and t_1 and others had not (slope, altitude for instance). For the first environmental variable which had a stronger impact on Y values and another randomly drawn environmental variable, we computed values at t_1 as $t_0 + \epsilon$, $\epsilon \sim \mathcal{N}(0, 0.1)$ (they randomly increase or decrease). For two other environmental variables randomly drawn, $X_{t_1} = X_{t_0} + |\epsilon|$, $\epsilon \sim \mathcal{N}(0, 0.1)$ (they increase) and for two other environmental variables, $X_{t_1} = X_{t_0} - |\epsilon|$, $\epsilon \sim \mathcal{N}(0, 0.1)$ (they decrease).

This led to two repeated measurements of Y for each individual of each species, i.e. 2000 values of $Y_{i,j,t}$, with $i = [1; 2]$; $j = [1, 50]$; $t = [t_0; t_1]$.

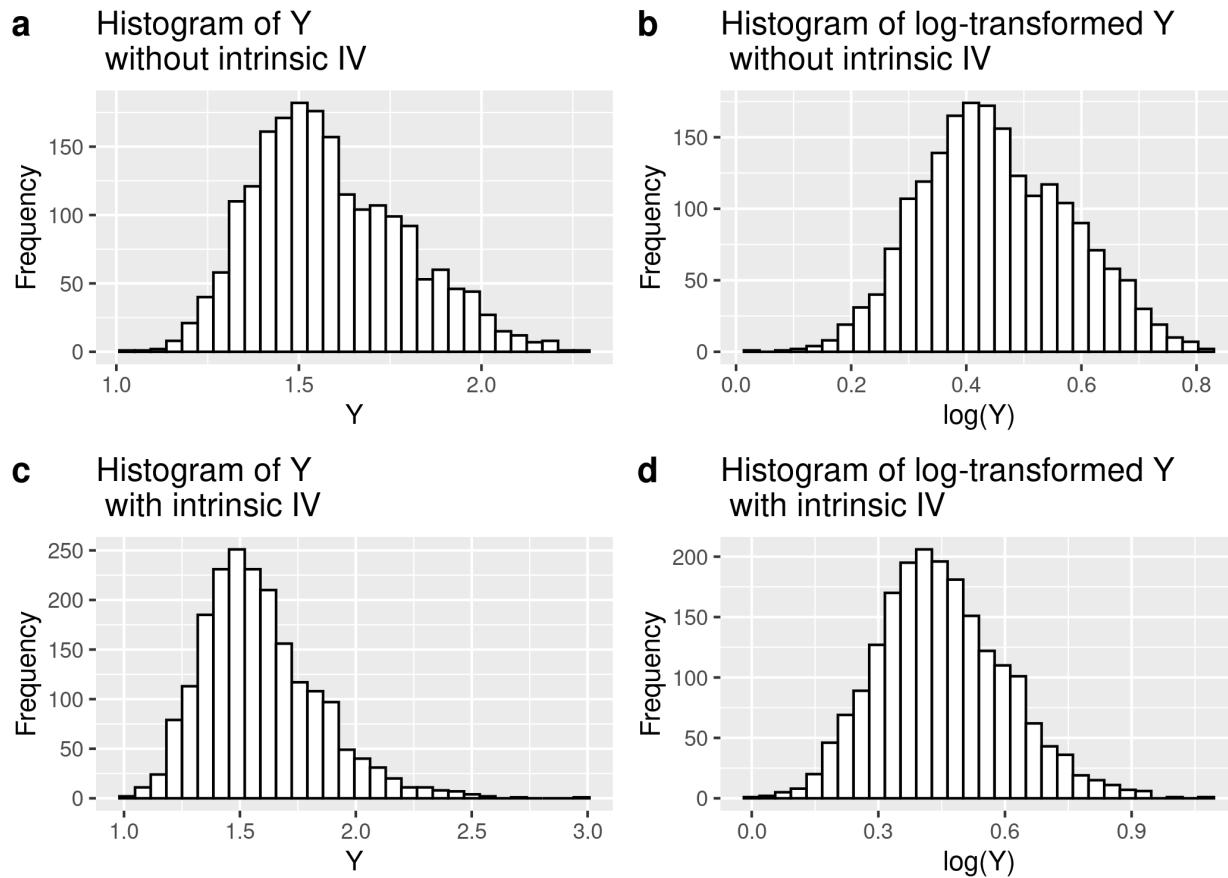


Figure S1.1: Histogram of raw and log-transformed Y with and without intrinsic IV

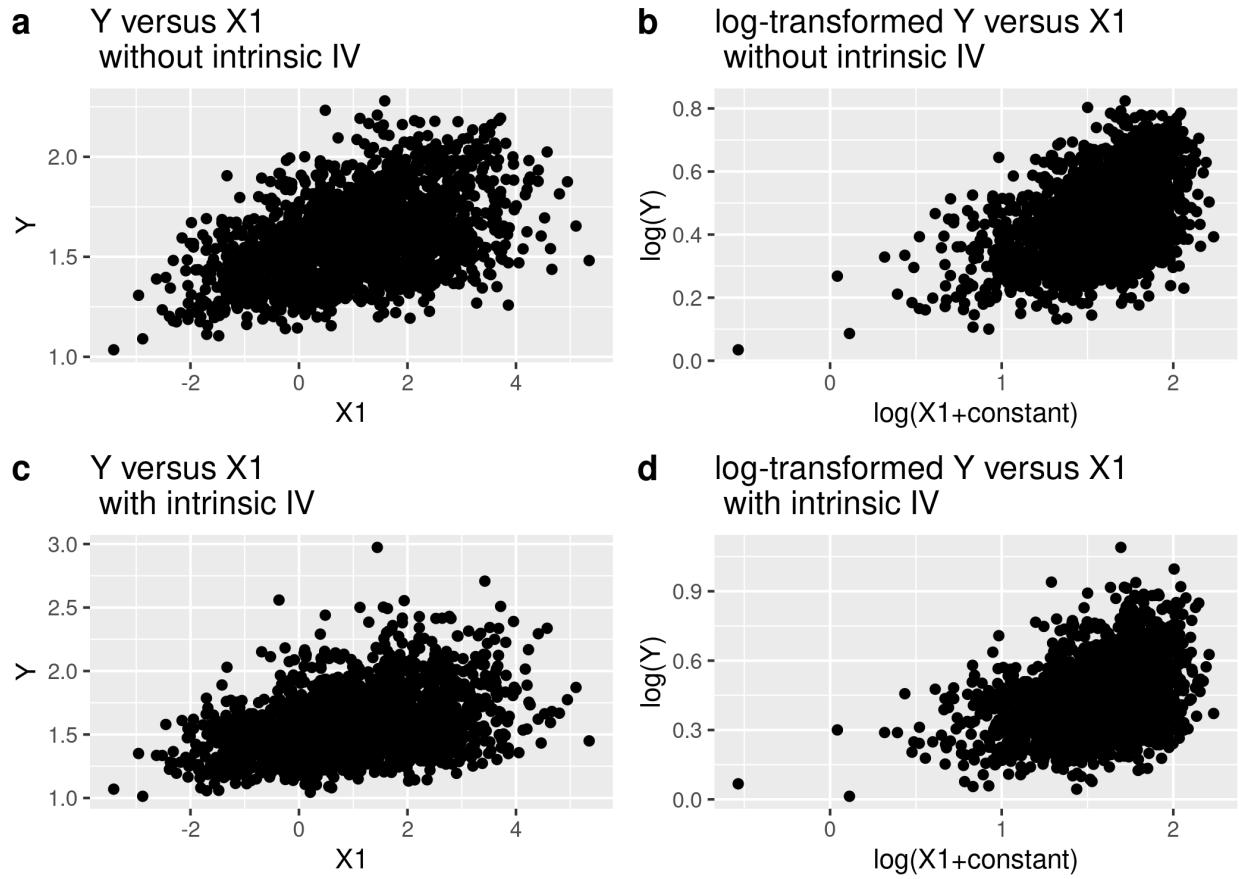


Figure S1.2: Raw and log-transformed Y versus X_1 plots with and without intrinsic IV

Figure S1.1 shows the distribution of the data and Figure S1.2 shows the relationship between the response Y and the environmental variable X_1 .

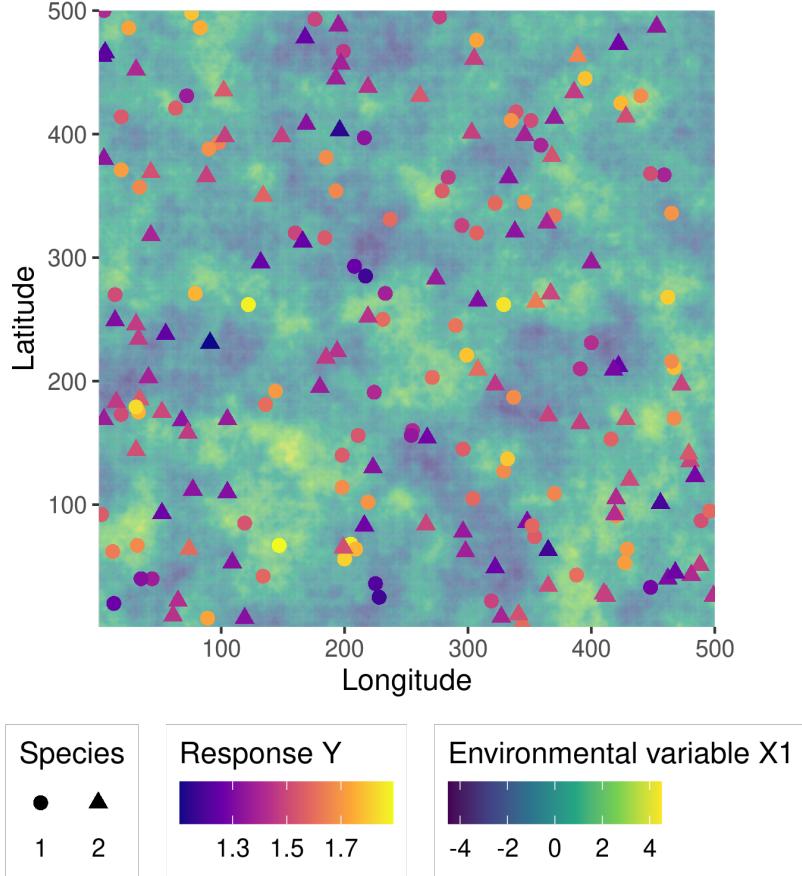


Figure S1.3: Virtual landscape representing X_1 and the individual with their respective Y value.

Figure S1.3 shows that microsite effects, which are the effects of the local multidimensional environment on the response variable, can result in local reversals of the competitive hierarchy between species. Indeed, the local outcome of competition can be opposite to the mean hierarchy: at one point of the space-time, an individual of Species 1 can overcome an individual of Species 2, whilst Species 1 is, on average, the fittest of the two species. Consequently, niche multidimensionality and variation of the environment in space allow the coexistence of Species 1 and Species 2.

2 Partial knowledge model: interpreting the response values with only one explanatory variable.

These two virtual datasets (with and without intrinsic variability) were then analysed with a “Partial knowledge model,” which represents the model derived by ecologists when using datasets derived from an incomplete characterisation of the environment: only a few variables (here only one, X_1) are actually measured and taken into account.

$$\ln(Y_{ijt}) = [\beta'_{0j} + b_{0i}] + \beta'_{1j} \ln(X_{1ijt}) + \varepsilon_{ijt}$$

“Partial knowledge model”

Priors:

$$\varepsilon_{ijt} \sim \mathcal{N}(0, V_j), j = [1, 2], \text{iid}$$

$$\beta'_{kj} \sim \mathcal{N}_2(0, 1), k = [0, 1], j = [1, 2], \text{iid}$$

$$b_{0i} \sim \mathcal{N}(0, V_{bj}), i = [1, 500], j = [1, 2], \text{iid}$$

Second level priors:

$$V_{bj} \sim t(3, 0, 2.5), j = [1, 2], \text{iid}$$

This model includes a random individual effect on the intercept (b_{0i}) to account for the variability among individuals within species. We ran this model twice, with the datasets generated with and without intrinsic IV. These models were fitted in a hierarchical Bayesian framework using the brms package (Bürkner 2017, Bürkner 2018) with 10,000 iterations, a warming period of 5,000 iterations and a thinning of 1/5, and 4 MCMC chains with different initial values. We obtained 1,000 estimates per parameter per MCMC chain.

We visualised the convergence and the results of the models thanks to trace and density plots.

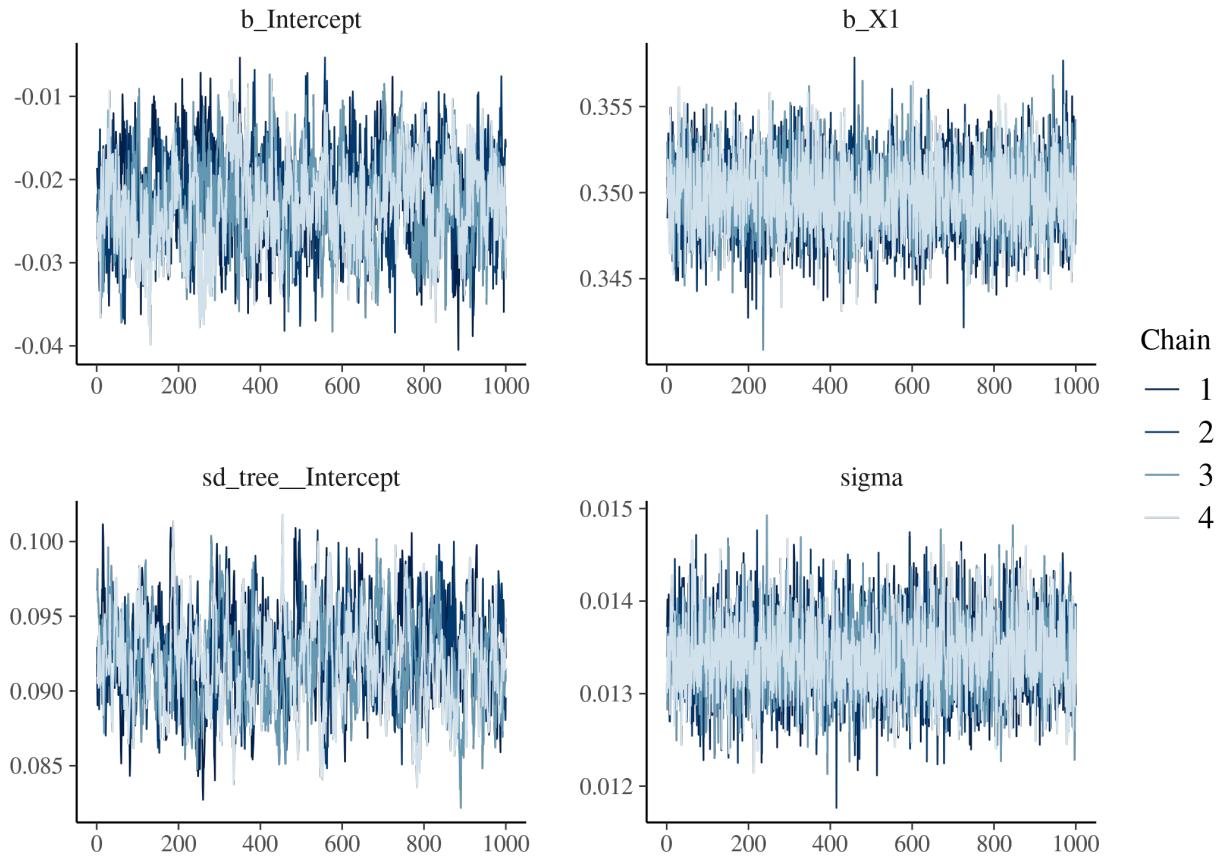


Figure S2.4: Trace of the posterior of the model for Species 1 without intrinsic IV

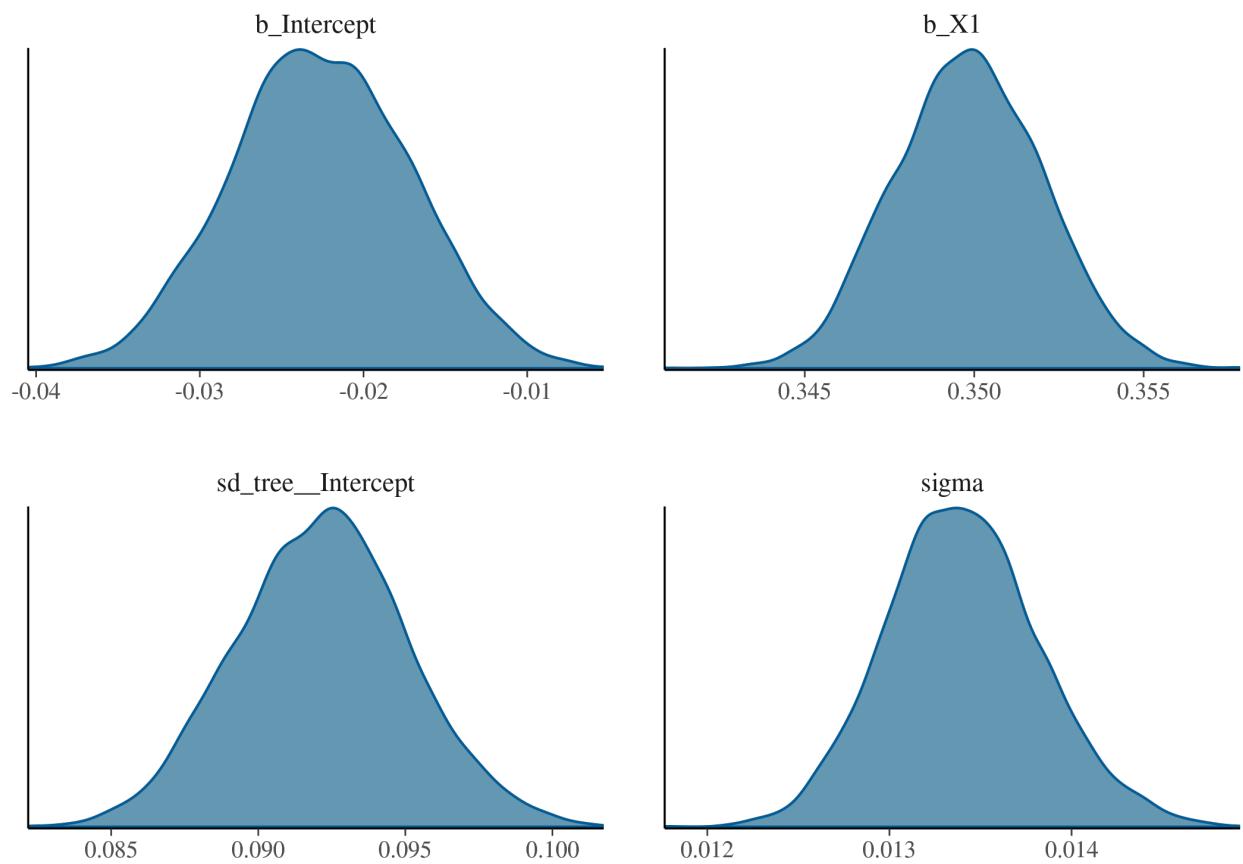


Figure S2.5: Density of the posterior of the model for Species 1 without intrinsic IV

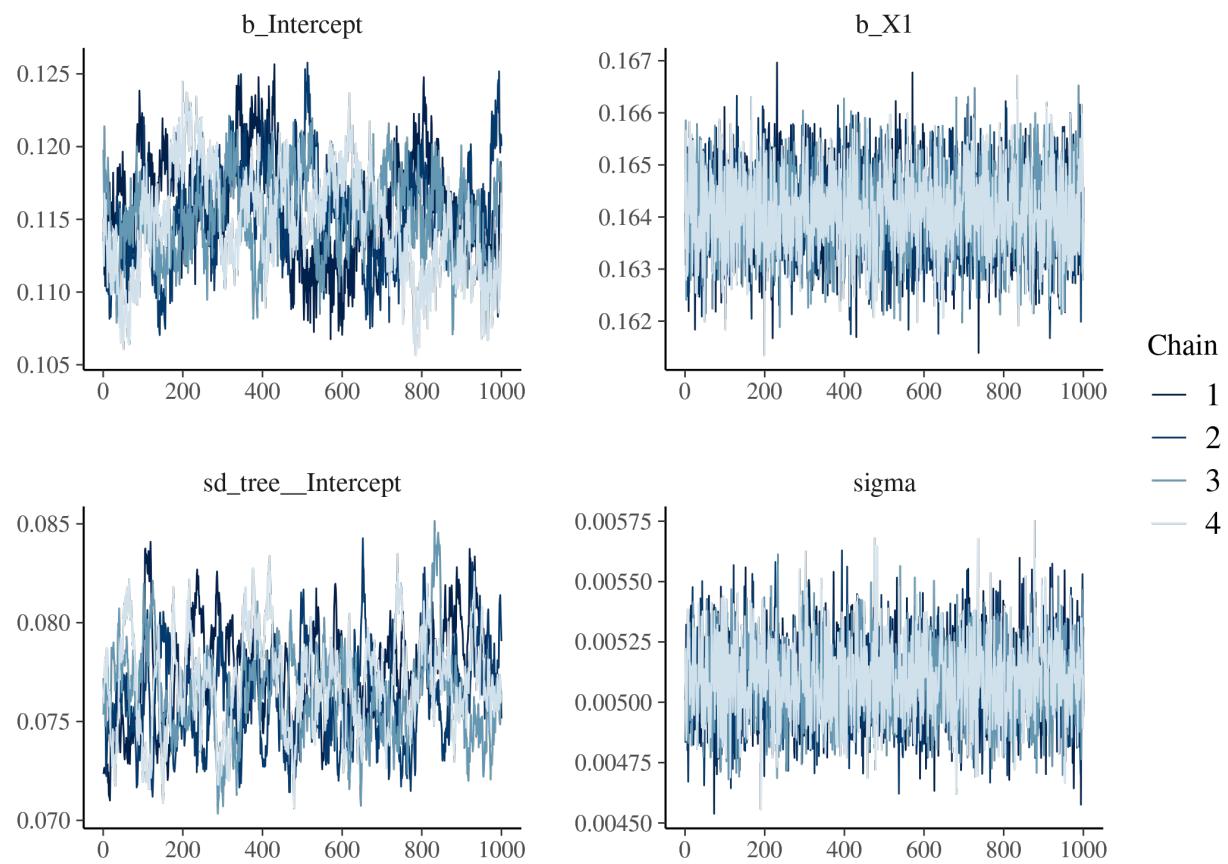


Figure S2.6: Trace of the posterior of the model for Species 2 without intrinsic IV

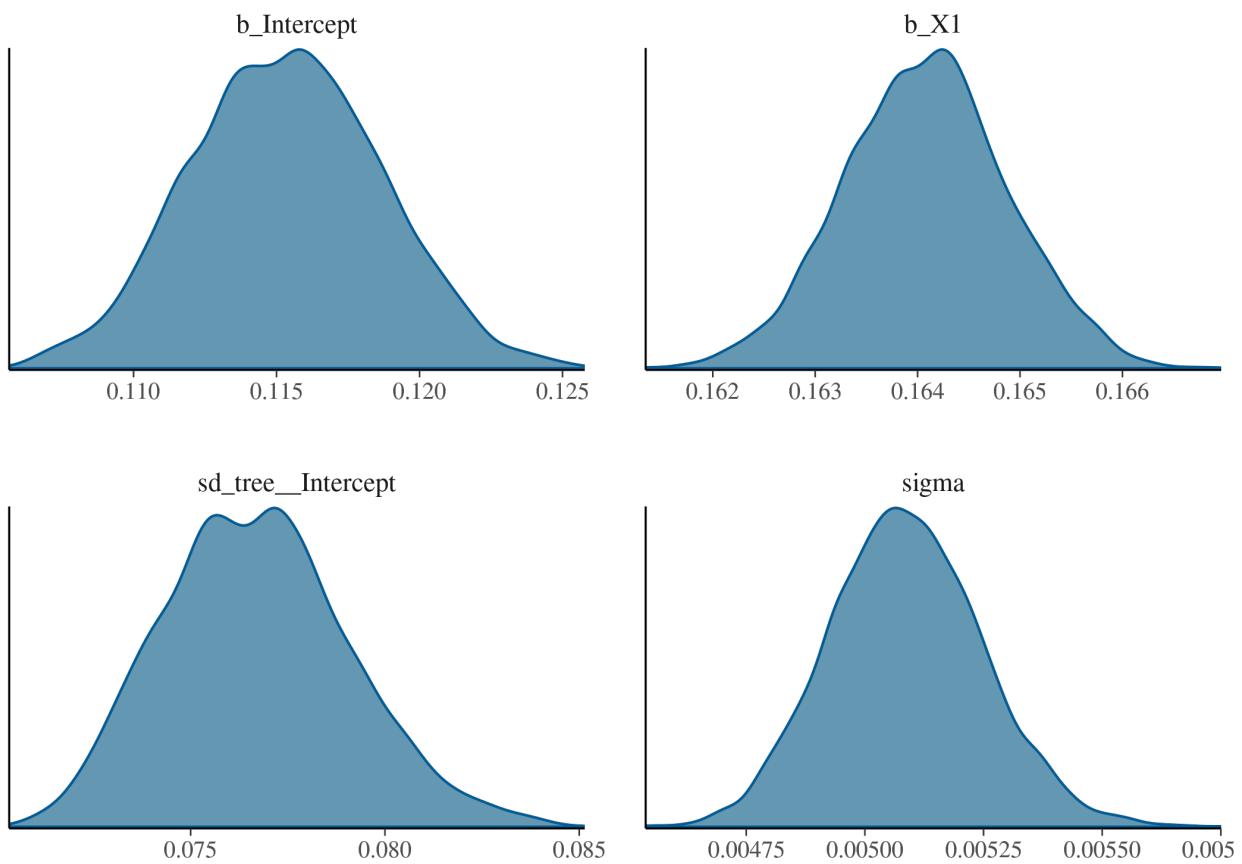


Figure S2.7: Density of the posterior of the model for Species 2 without intrinsic IV

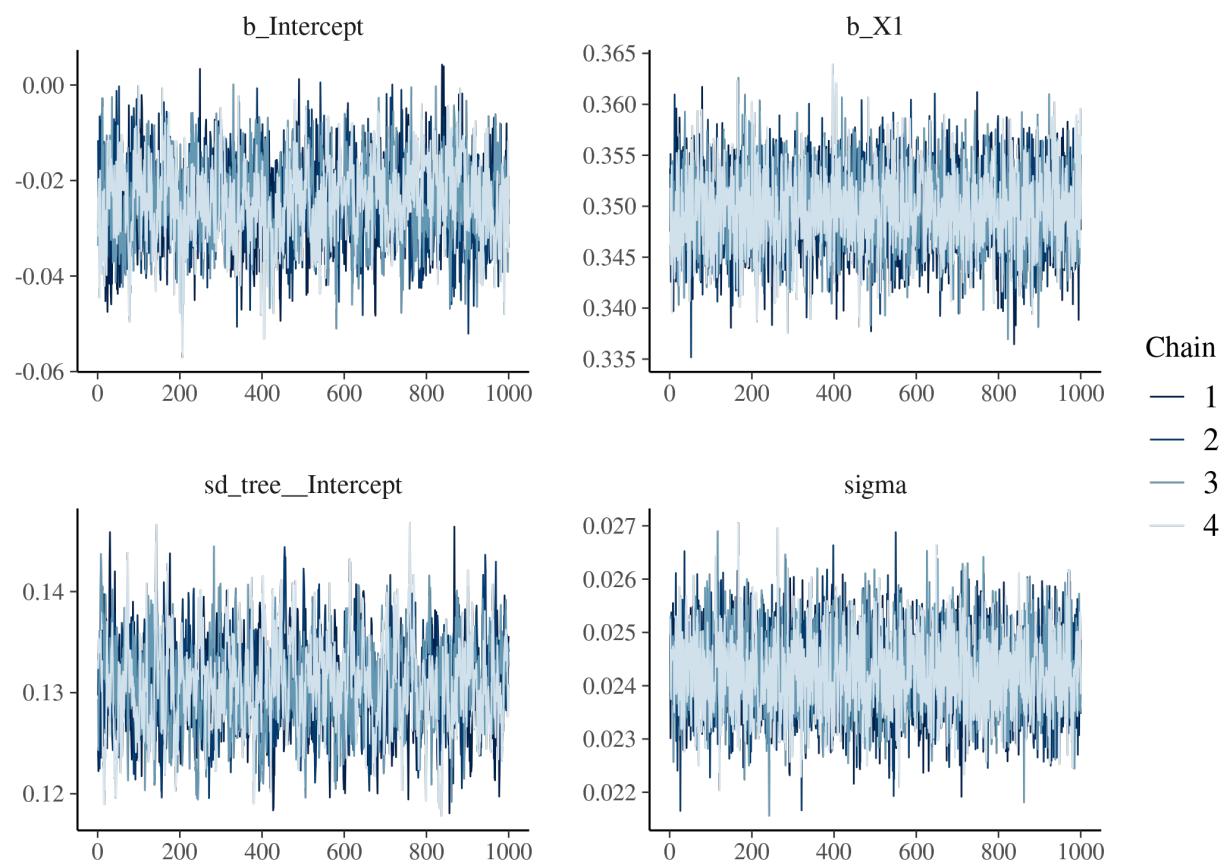


Figure S2.8: Trace of the posterior of the model for Species 1 with intrinsic IV

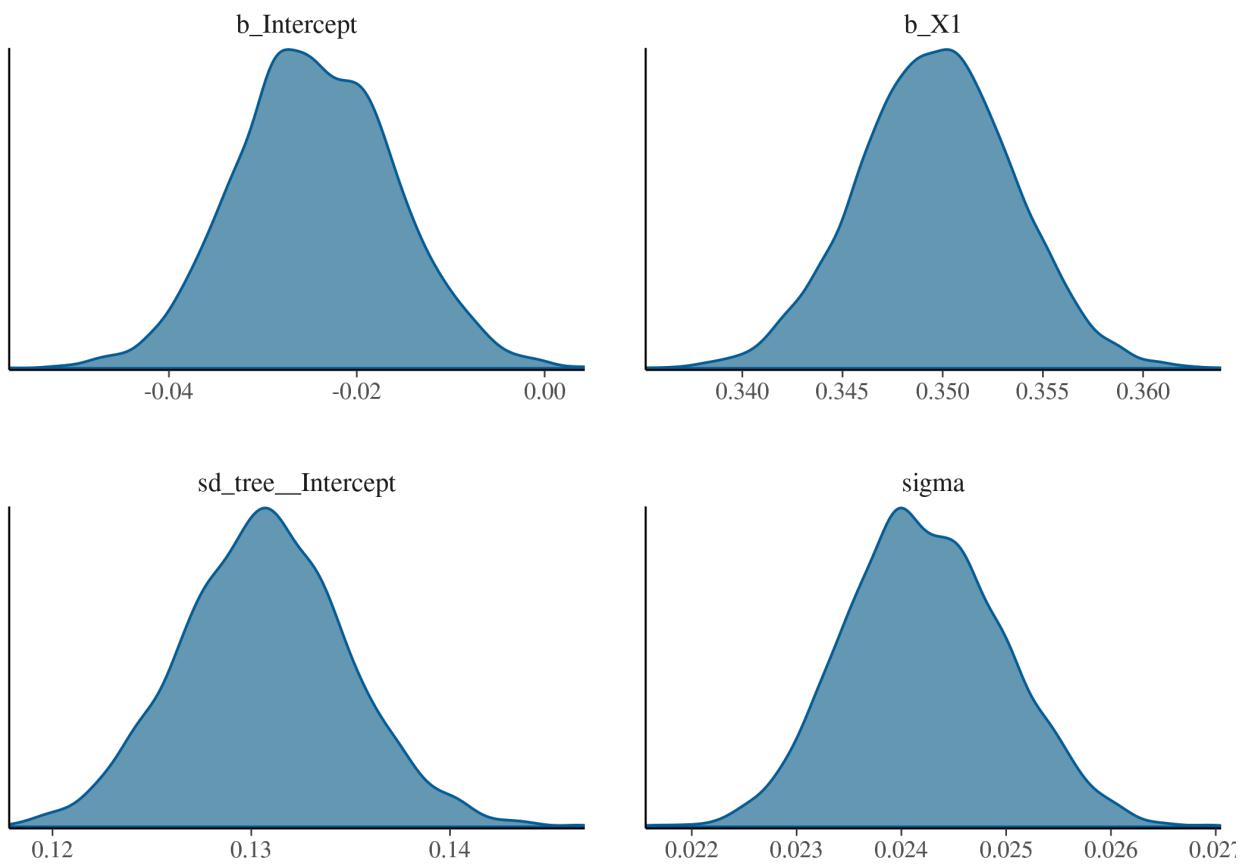


Figure S2.9: Density of the posterior of the model for Species 1 with intrinsic IV

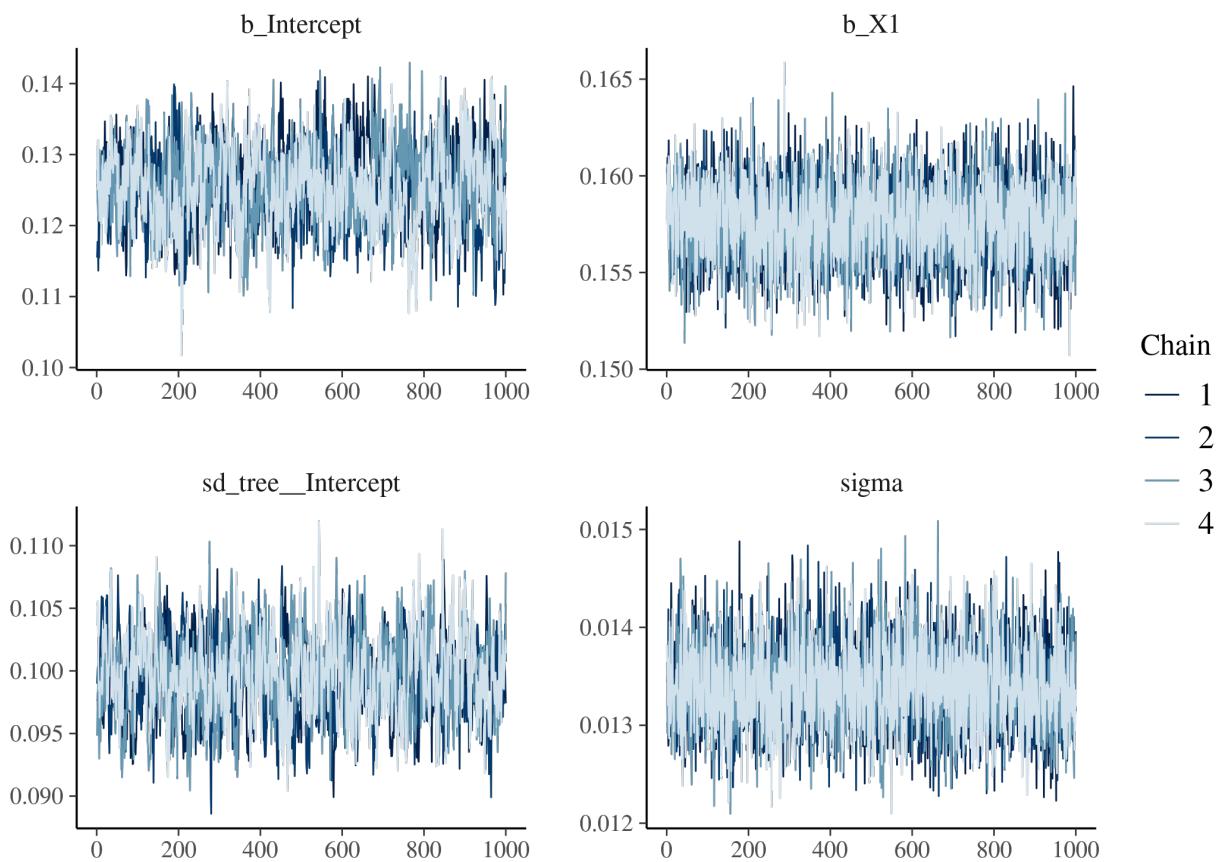


Figure S2.10: Trace of the posteriors of the model for Species 2 with intrinsic IV

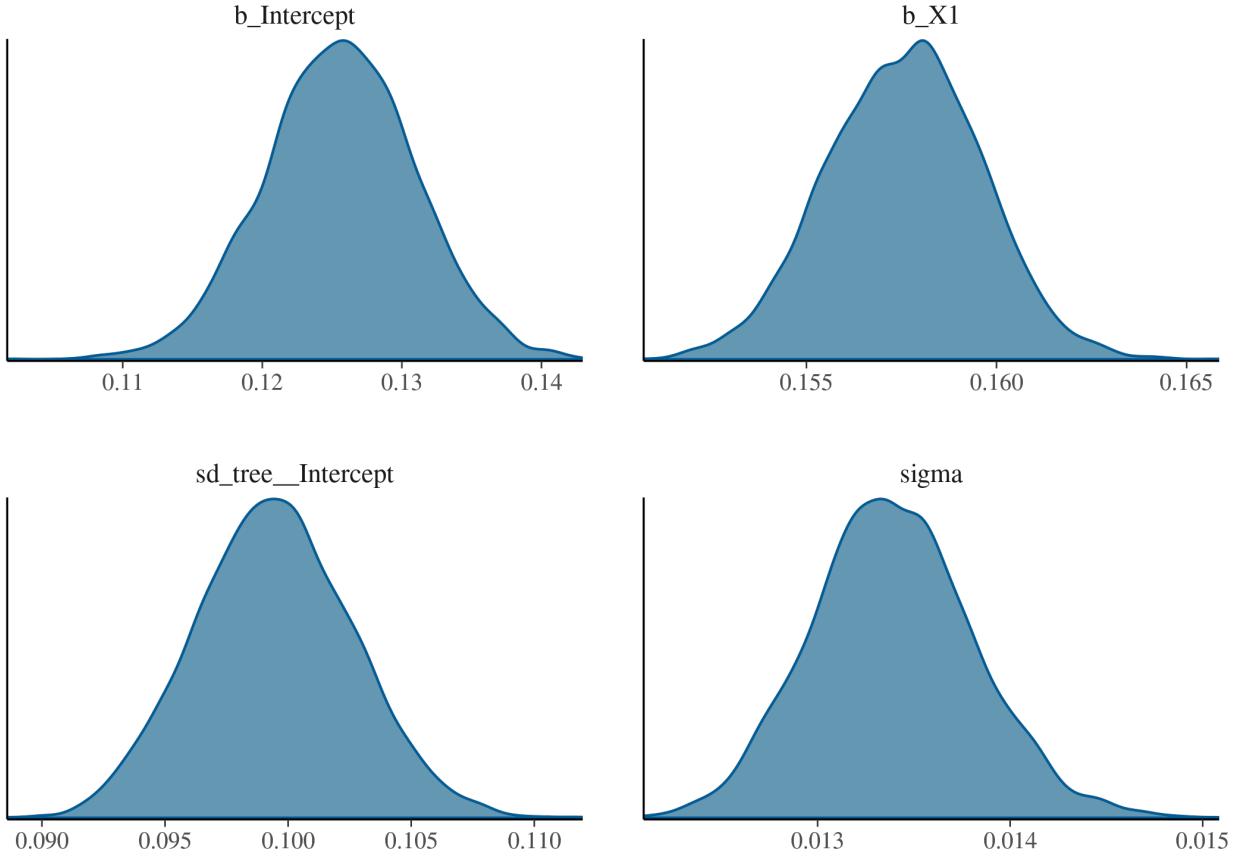


Figure S2.11: Density of the posteriors of the model for Species 2 with intrinsic IV

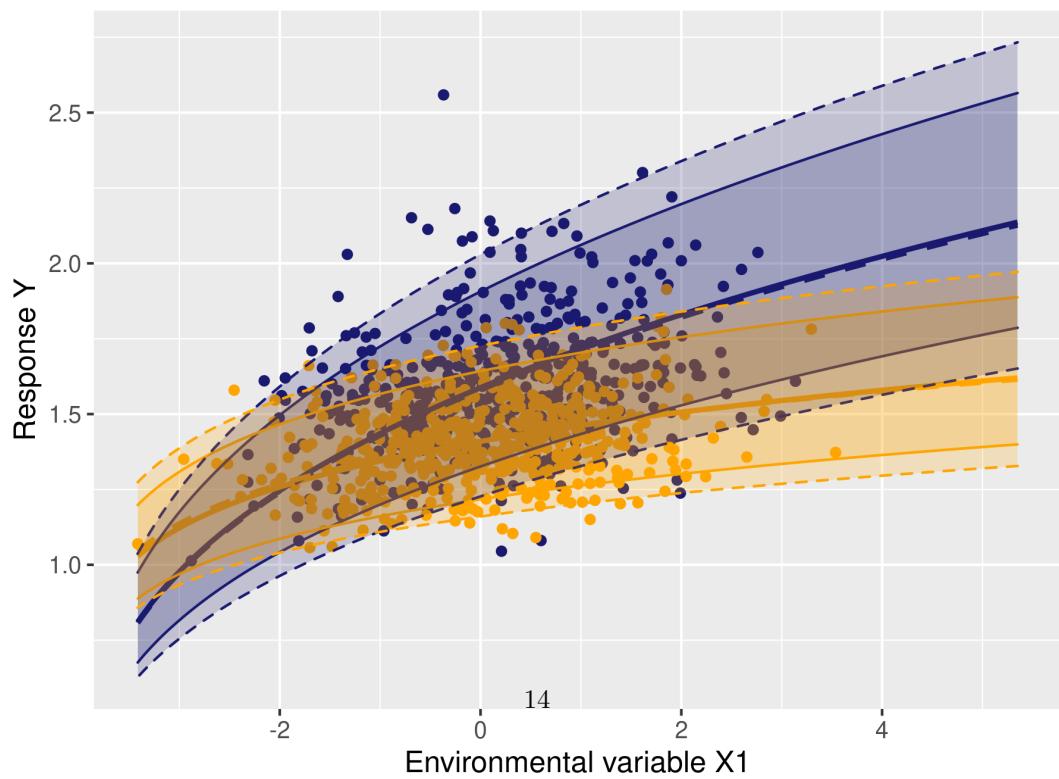
Table S2.1: Mean posteriors and their estimation error

| | β_0 | β_1 | V_b | V |
|-----------------------------------|-----------|-----------|---------|---------|
| Species 1 (no random IV) | | | | |
| Estimate | -2.3e-02 | 3.5e-01 | 9.2e-02 | 1.3e-02 |
| Estimation error | 5.5e-03 | 2.2e-03 | 2.9e-03 | 4.2e-04 |
| Species 2 (no random IV) | | | | |
| Estimate | 1.2e-01 | 1.6e-01 | 7.7e-02 | 5.1e-03 |
| Estimation error | 3.3e-03 | 8e-04 | 2.4e-03 | 1.6e-04 |
| Species 1 (with random IV) | | | | |
| Estimate | -2.4e-02 | 3.5e-01 | 1.3e-01 | 2.4e-02 |
| Estimation error | 8.4e-03 | 3.9e-03 | 4.2e-03 | 7.6e-04 |
| Species 2 (with random IV) | | | | |
| Estimate | 1.3e-01 | 1.6e-01 | 9.9e-02 | 1.3e-02 |
| Estimation error | 5.4e-03 | 2e-03 | 3.2e-03 | 4.2e-04 |

We inferred a high IV even in the absence of intrinsic IV (Table S2.1). Therefore, observed IV does not necessarily reveal intrinsic (mainly genetic) IV, but can also reveal hidden dimensions of the environment. We used the model parameters to plot the relationship between Y and X_1 accounting for intraspecific variability.

Table S2.2: Summary of the model's outputs

| | β_0 | β_1 | V_b | V |
|-----------------------------------|---------------------|-------------------|-------------------|-------------------|
| Species 1 (no random IV) | | | | |
| Estimate | -2.3e-02 | 3.5e-01 | 9.2e-02 | 1.3e-02 |
| Estimation error | 5.5e-03 | 2.2e-03 | 2.9e-03 | 4.2e-04 |
| 95% interval | -3.3e-02 - -1.2e-02 | 3.5e-01 - 3.5e-01 | 8.7e-02 - 9.8e-02 | 1.3e-02 - 1.4e-02 |
| R-hat | 1e+00 | 1e+00 | 1e+00 | 1e+00 |
| Bulk ESS | 3.6e+02 | 4.3e+03 | 4.7e+02 | 3.7e+03 |
| Tail ESS | 1.1e+03 | 3.9e+03 | 7.5e+02 | 3.8e+03 |
| Species 2 (no random IV) | | | | |
| Estimate | 1.2e-01 | 1.6e-01 | 7.7e-02 | 5.1e-03 |
| Estimation error | 3.3e-03 | 8e-04 | 2.4e-03 | 1.6e-04 |
| 95% interval | 1.1e-01 - 1.2e-01 | 1.6e-01 - 1.7e-01 | 7.2e-02 - 8.2e-02 | 4.8e-03 - 5.4e-03 |
| R-hat | 1e+00 | 1e+00 | 1e+00 | 1e+00 |
| Bulk ESS | 6.5e+01 | 4e+03 | 1.3e+02 | 3.6e+03 |
| Tail ESS | 1.8e+02 | 4e+03 | 3.8e+02 | 3.8e+03 |
| Species 1 (with random IV) | | | | |
| Estimate | -2.4e-02 | 3.5e-01 | 1.3e-01 | 2.4e-02 |
| Estimation error | 8.4e-03 | 3.9e-03 | 4.2e-03 | 7.6e-04 |
| 95% interval | -4.1e-02 - -7.8e-03 | 3.4e-01 - 3.6e-01 | 1.2e-01 - 1.4e-01 | 2.3e-02 - 2.6e-02 |
| R-hat | 1e+00 | 1e+00 | 1e+00 | 1e+00 |
| Bulk ESS | 8.5e+02 | 4e+03 | 8.7e+02 | 4.1e+03 |
| Tail ESS | 2.1e+03 | 4e+03 | 1.5e+03 | 3.8e+03 |
| Species 2 (with random IV) | | | | |
| Estimate | 1.3e-01 | 1.6e-01 | 9.9e-02 | 1.3e-02 |
| Estimation error | 5.4e-03 | 2e-03 | 3.2e-03 | 4.2e-04 |
| 95% interval | -4.1e-02 - 1.4e-01 | 1.5e-01 - 1.6e-01 | 9.3e-02 - 1.1e-01 | 1.3e-02 - 1.4e-02 |
| R-hat | 1e+00 | 1e+00 | 1e+00 | 1e+00 |
| Bulk ESS | 3.5e+02 | 4e+03 | 6.3e+02 | 3.9e+03 |
| Tail ESS | 1e+03 | 4e+03 | 1.4e+03 | 3.9e+03 |



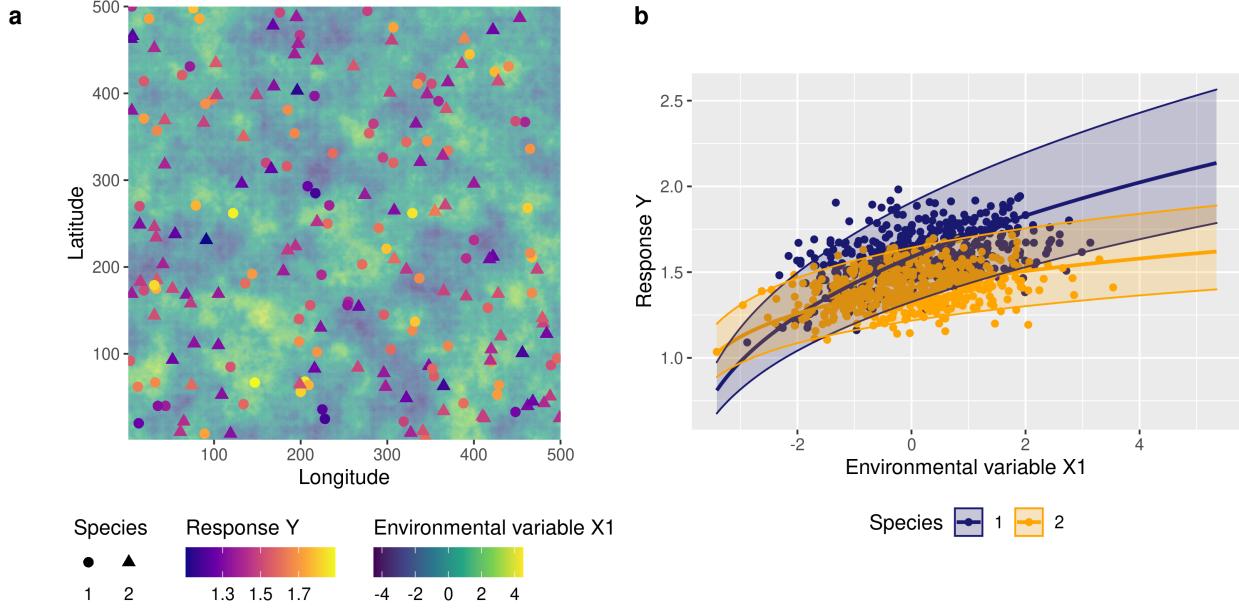


Figure S2.13: Response to an environmental variable and inferred intraspecific variability. (a) Positions of a sample of $I=600$ individuals from $J=2$ species in a landscape defined by a square grid of *CimesC* cells ($C=500$). The background color indicates the value of the environmental variable X_1 (e.g., light) on each cell at date t . The response (e.g., growth) of each individual, which depends on the environment within each cell (Eq. I), is also indicated by a color scale. (b) Response as a function of the observed environmental variable X_1 for the two species. Points represent the data $\{Y_{ijt}, X_{1,ijt}\}$. Thick lines represent the predictive posterior means for the two species. The envelopes delimited by two thin lines represent the 95% credible intervals of the predictive posterior marginalized over individuals (taking into account V_{bj}). The envelopes thus represent the intraspecific variability which is due to the $N - 1$ unobserved environmental variables.

In Figure S2.12 and panel a of Figure S2.13, the bold and solid (dashed) lines represent the mean rate of the response variable (e.g. growth) of Species 1 (blue) and Species 2 (orange) as computed with the parameters retrieved from the model without (with) intrinsic IV respectively. The plain lines represent the 95% interval of the posteriors from the model without intrinsic IV and the dashed lines show the 95% confidence interval of the posteriors from the model with intrinsic IV. Figure S2.12 shows that intrinsic IV simply increases the overlap between the response of Species 1 and Species 2.

Figure S2.13 represents the virtual landscape of X_1 and the corresponding individual response and the plot of Y versus X_1 (without intrinsic IV) next to each other, helping to visualise this virtual experiment.

In the model without intrinsic IV, the unobserved variation in the environment resulted in an important inferred intraspecific variability. The performances of the two species can intersect, which means that the competitive hierarchy among the two species can be locally reversed depending on the micro-environmental variation, offering opportunities for the coexistence of the two species in a variable environment.

3 Spatial autocorrelation of individual response

We then analysed the spatial structure of the response variable at the individual scale. We hypothesised that as environmental variables are spatially autocorrelated, and the response variable is the result of these variables, then the response variable should also be spatially autocorrelated. To test this, we computed Moran's I test. It is computed with the Moran.I function of the ape R package (Paradis and Schlie 2019).

Table S3.3: Results of the Morans's I test for both species separately and together.

| | Moran's I index | P-value |
|-----------------|-----------------|---------|
| Species 1 | 5.3e-02 | 0e+00 |
| Species 2 | 5e-02 | 0e+00 |
| All individuals | 3.4e-02 | 0e+00 |

Table S3.3 shows that the individual response variable is largely spatially autocorrelated. This is due to the spatial autocorrelation in the environmental variables. In this simple and controlled experiment, this seems natural. However, in a less controlled environment, detecting spatial autocorrelation in a response variable could be the sign of the spatial structure of the underlying environmental variables. Nonetheless, we acknowledge that the genetic structure of the population associated with limited dispersion for example could also lead to spatial autocorrelation in the response variable of the individuals, but this is likely to happen on a much larger geographical scale.

4 Similarity between conspecific individuals compared to heterospecific individuals and consequences for species coexistence.

Finally, we used semivariograms to visualise the spatial autocorrelation of the response variable and to test whether the individual response was more similar within conspecifics than within heterospecifics. The semivariograms were computed and modelled with the variogram and the fit.variogram functions of the gstat R package (Gräler et al. (2016)) respectively. The variogram models were spherical.

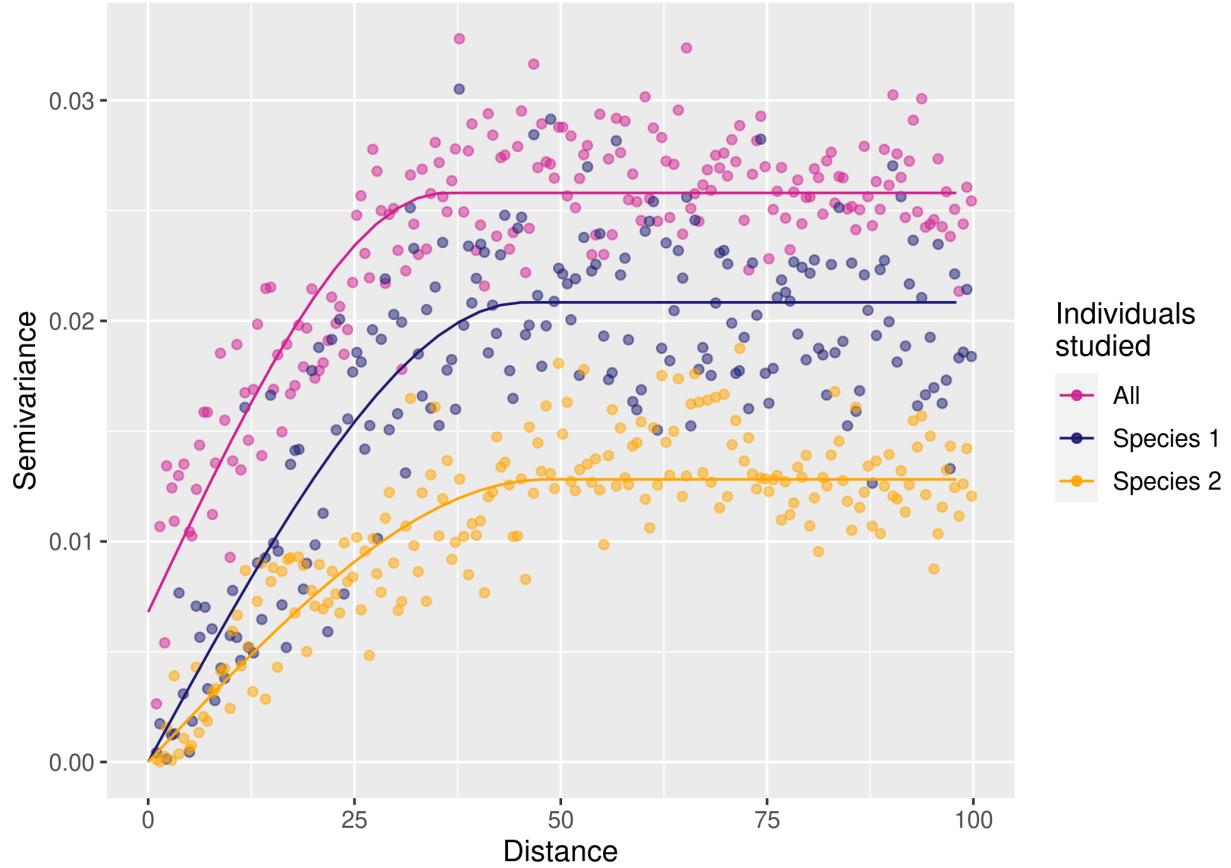


Figure S4.14: Spatial autocorrelation of response Y across individuals within and between species ($J=2$). This semivariogram represents the semivariance of the individual mean responses Y as a function of the distance between individuals. The increasing curves evidence spatial autocorrelation in Y (similar results using Moran's I test). The semivariance of all individuals taken together (purple curve) is higher than the semivariance of conspecifics for the two species (red and blue curves), which means that intraspecific variability is lower than interspecific variability.

As the semivariance between individuals of both species was higher than the semivariance between conspecifics (Figure S4.14), the individual response variable was more similar between conspecifics than heterospecifics.

5 Code implementation

The whole analysis is done using the R language (R Core Team 2021) in the Rstudio environment (RStudio Team 2021). The tables are made with the kableExtra package (Zhu 2021), the figures with the package ggplot2 (Wickham 2009), and the code uses other packages of the Tidyverse (Wickham et al. 2019) (dplyr (Wickham et al. 2021), magrittr (Bache and Wickham 2020)) and other R packages (here (Müller 2020), ggpibr (Kassambara 2020), sp (Pebesma and Bivand 2005, Bivand et al. 2013), ggnewscale (Campitelli 2021), gstat Gräler et al. (2016)). The pdf and html documents are produced thanks to the R packages rmarkdown (Xie et al. 2019, 2020, Allaire et al. 2020), knitr (Xie 2014, 2015, 2021) and bookdown (Xie 2017).

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