Effects of interannual weather on understory plant traits in old-growth beech forests

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Abstract:
We aimed to estimate the effects of annual mean temperature and precipitation on understory plant traits and trait diversity in old-growth beech forests. We combined sub-canopy and open-field measurements from local weather stations with data on aboveground and belowground traits.
Relationships and potential confounding effects within the system were analysed using a causal model. The resulting statistical model estimated the response of traits to interannual weather fluctuations within a site, exploiting the longitudinal data from a 12-year monitoring program.
Overall, temperature effects were uncertain, while precipitation effects were more precisely estimated but small. Aboveground traits and trait diversity showed a positive response to temperature, while belowground traits a negative response to precipitation, highlighting the importance of considering distinct functional compartments and different sets of traits when assessing plant responses to environmental variability.
More than half of the variation in trait diversity occurred among neighbouring sub-plots, rather than among sites and years. This fine-scale heterogeneity suggests that micro-environmental factors and biotic interactions might have a larger effect on the coexistence of different functional strategies than broader-scale variation, environmental or otherwise.
We conclude that interannual weather variability, especially in precipitation amount, has limited effects on the functional properties of understory plant communities in undisturbed beech forests. However, this apparent functional stability may be threatened by more frequent climatic extremes or altered seasonal weather patterns.

Keywords:
Temperate forest, Beech forest, Weather, Sub-canopy, Temperature, Precipitation, Plant traits, Functional diversity, Causal inference, Bayesian models.

Introduction

What is the effect of weather on plant traits? Trait-based ecology promises to achieve a general understanding of community assembly and ecosystem functioning by focusing on

measurable phenotypic characteristics reflecting adaptations to abiotic and biotic factors (de Bello et al., 2025; Funk et al., 2017; McGill et al., 2006). Understanding how plant traits respond to environmental variation is therefore a central question. Trait-environment relationships have been widely investigated across large geographical scales (Bruelheide et al., 2018; Ordoñez et al., 2009; Wright et al., 2005), along environmental gradients (Dong et al., 2020), and over long timescales (Ordonez & Svenning, 2017). Many cross-sectional studies have examined the relationships between plant trait means and climate, particularly for leaf traits (Dong et al., 2020; Wright et al., 2005), with mean temperature and precipitation (Moles et al., 2014).

The focus on climate seems justified by the fact that variation in space and across geological timescales should be largest, but the response of plant traits to interannual weather variations has instead received less consideration. Weak relationships of traits with macroclimate (Bruelheide et al., 2018; Kambach et al., 2023) suggest the need to look at local conditions: effects of global change on plant communities are mediated by local environmental conditions and microclimatic buffering, especially in forest understories (De Frenne et al., 2021; Kemppinen et al., 2024). Indeed, a substantial amount of trait variation can occur at the local scale (Hevia et al., 2016; Kang et al., 2014). Investigating interannual variation in local weather may thus reveal responses that remain undetected when relationships are assessed across geographical gradients using long-term climatic averages.

Most studies of this kind are cross-sectional in nature, comparing sites with different geographical positions and conditions, in which relationships between traits and weather or climate can easily be confounded by unobserved geographic differences; additionally, these studies commonly employ gridded multi-year macroclimate as an explanatory variable (e.g. Bruelheide et al., 2018; Kambach et al., 2023; Moles et al., 2014; Padullés Cubino et al., 2021). Heilmeier (2019) considered evaluating the response of plant traits to the environment through the observation of gradients, capable of encompassing large scales and preserving biotic interactions and feedbacks but more susceptible to confounding, or through experimental approaches, which allow for a more mechanistic understanding of processes. This does not imply that ecologists interested in understanding effects and drivers are limited to experiments: the causal inference framework, which we adopt here, offers the possibility to make causal claims from observational data, under a set of assumptions which explicitly state the relationships involved in the system (Correia et al., 2026).

In this study, we focus on the understory of beech forests, one of the most widespread forest types in Europe, covering approximately 15 million hectares (Brunet et al., 2010), in their old-growth stage. Forest structure and canopy cover affect sub-canopy conditions, as well as buffer from external variations (De Frenne et al., 2021; De Lombaerde et al., 2022; Zellweger et al., 2020), thus an accurate assessment of these responses must take these differences into account by direct measurement or modeling of sub-canopy weather (Chelli, Bricca, et al., 2024; Haesen et al., 2021). Old-growth forests are deemed to provide a relatively stable habitat (Frey et al., 2016; Wolf et al., 2021), resulting in a selective and less diverse understory (Kermavnar & Kutnar, 2020; Ottaviani et al., 2019). At the same time, old-growth structural and canopy features are non-equilibrial (Nagel et al., 2014), and clear evidence in terms of interannual responses of understory plants to weather fluctuations alongside this stability is still lacking.

In forest understories, aboveground traits are the most widely analysed. There is an indication of a positive association of temperature with plant height, while evidence for specific leaf area (SLA) is contrasting. Relationships with other leaf traits and for precipitation seem weak (Maes et al., 2020; Padullés Cubino et al., 2021), although SLA may increase with precipitation or moisture availability (Amatangelo et al., 2014; Candeias & Fraterrigo, 2020). Beyond trait means, trait diversity provides complementary information on

the functional structure of plant communities. However, its relationships with climate remain comparatively understudied (see Andrew et al., 2021 for an example of geographic patterns in relation to climate). Studies of forest understories suggest that trait diversity can also vary with temperature and precipitation (Bricca et al., 2025), with an indication of an increase in diversity for size-related traits and a decrease for leaf economics traits with temperature, and weaker relationships with precipitation (Chelli, Bricca, et al., 2024; Padullés Cubino et al., 2021).

While aboveground traits are considered to represent tradeoffs in plant size and resource economics (Díaz et al., 2016), belowground clonal and bud bank traits inform on non-acquisitive functions such as persistence, spatial exploration, and regeneration after disturbance (Chelli, Klimešová, et al., 2024; Tumber-Dávila et al., 2026). At the same time, above- and belowground plant compartments may respond differently to climatic variation, since they are not coordinated and respond to distinct environmental constraints (Carmona et al., 2021; Chelli, Klimešová, et al., 2024; Klimešová et al., 2021). As a consequence, multifunctional, whole-plant approaches may provide a more comprehensive understanding of how plant communities respond to changing environmental conditions.

Refining the initial question, we thus ask what is the response of understory plant traits and trait diversity to interannual variation of local weather conditions, considering sets of aboveground and belowground traits. In particular, we focus on annual mean temperature (air and soil) and precipitation, variables that capture complementary aspects of the thermal and water environments experienced by plants (Moles et al., 2014). We leverage a 12-year panel dataset across four permanent forest monitoring sites, combining repeated observations with weather measurements from local stations both sub-canopy and open-field. By focusing on temporal variation within sites rather than on long-term climate averages, our study provides an opportunity for a more direct estimation of how interannual weather fluctuations influence plant functional characteristics, avoiding most of the confounding factors inherent in spatial comparisons.

Methods

Study area and data collection

The data for this study comes from four Italian old-growth (> 100 years since last logging, Campetella et al., 2020) beech forest (*Fagus sylvatica* L.) permanent monitoring sites, spanning a latitudinal range of 46–38°N (Figure 1). The two northern sites belong to the Alpine biogeographic region, the two southern sites to the Mediterranean one (Cervellini et al., 2020). Historical mean annual precipitation and mean annual temperature of the sites range between 1250–1900 mm and 5–10 °C, respectively, and the soils are slightly acidic overlain by a well-developed decomposing organic horizon (Campetella et al., 2020).
The four sites belong to the Level II of the ICP Forests network, surveyed over 12 years, from 2000 to 2011. Within this timespan, seven annual vegetation surveys were performed between June and August in 2000, 2001, 2002, 2005, 2006, 2008, and 2011. Species identity and cover (cm^2) were recorded for 100 non-adjacent 50 cm × 50 cm sampling units arranged in a grid inside a 50 m × 50 m plot area (Figure 1) for all vascular plants up to 1.3 m of height. The sites experienced no substantial anthropogenic disturbances (i.e., logging, deadwood removal, trampling) during the monitoring period, and are fenced to exclude grazing by large herbivores.

As part of the monitoring programme, weather variables, including air temperature, soil temperature, and precipitation, were measured both under the forest canopy (sub-canopy) and a short distance outside of it (open-field). Measurements followed the ICP Forests

Manual on Meteorological Measurements (Raspe et al., 2025). The weather data consists of monthly means obtained from daily values.

All data collected and used in this study are available from De Benedictis et al. (2026).

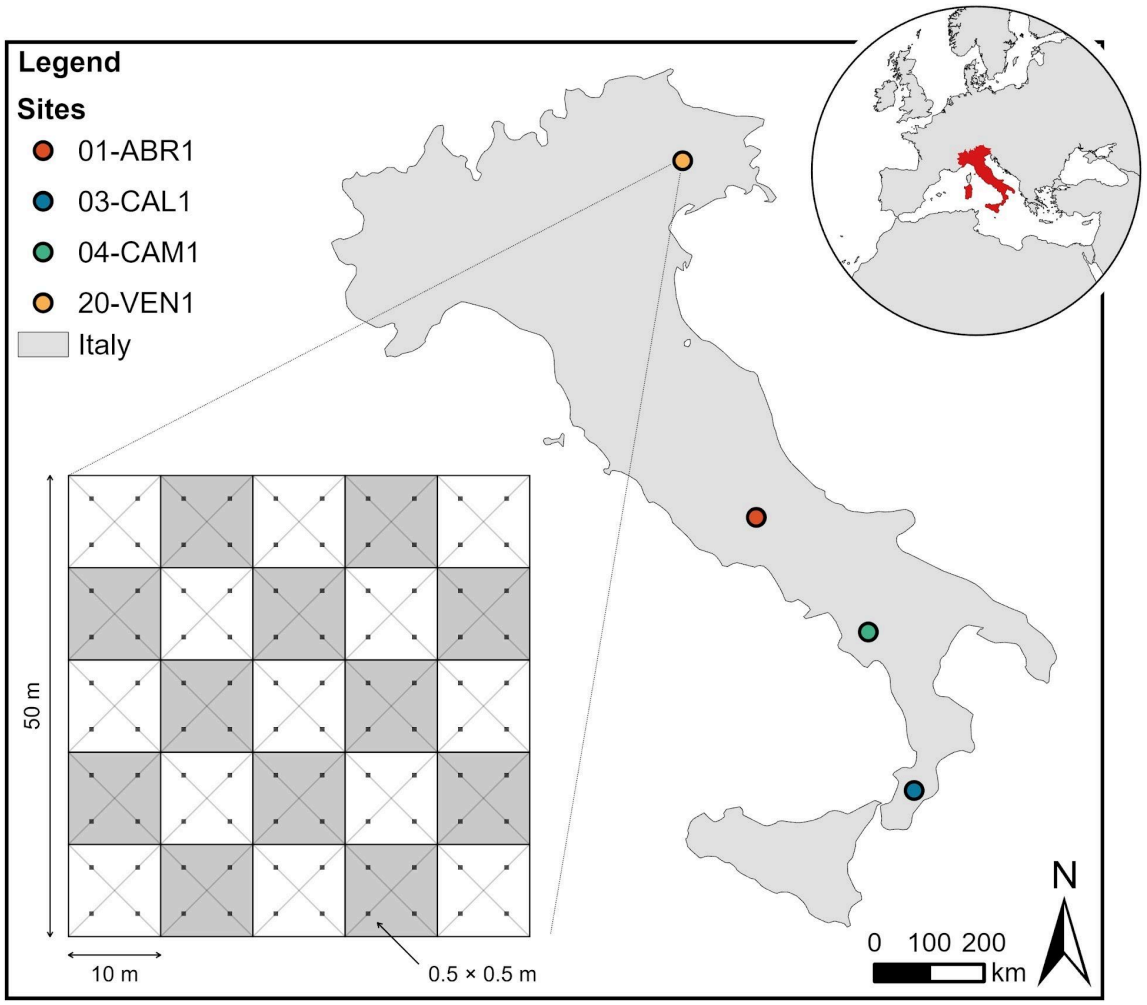


Figure 1. Location of the permanent monitoring forest sites and overview of the vegetation sampling design. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

Plant traits and trait diversity

We consider ten widely studied plant traits: six aboveground traits, and four belowground traits. The aboveground trait set includes leaf area (mm^2), leaf nitrogen per mass (mg/g), plant height (m), specific leaf area (mm^2/mg), stem specific density (mg/mm^3), and diaspore mass (mg). The belowground trait set includes bud bank size (including root-derived buds) and three clonal traits: multiplication rate, clonal lateral spread (cm/year), and persistence of connection (years).

Trait data for the 82 species was compiled from several sources, including measurements from specimens collected in proximity to the sites, other Italian forests, Diaz et al. (2022; 2022), CLO-PLA 3 (Klimešová et al., 2017), BROT 2.0 (Tavşanoğlu & Pausas, 2018), and the TRY database (Kattge et al., 2020): see the dataset for details. When trait information was missing, values from the most similar congeneric or the generic average were used (9.1% of the values); clonal traits were set at zero for non-clonal species, and clonal traits for

three species were scored from the interpretation of herbarium specimen pictures. After these steps, completeness was high (97.7% overall, 96.2% for aboveground traits, and 100% for belowground traits), thus no further gap-filling was performed. Specific sources for each value are described in the dataset.

The vegetation records include six ferns and two saprophytes, which represent completely different adaptations in regard to some traits: ferns have spores as diaspores, which cannot be measured reliably and are clearly distinct; saprophytes have no photosynthetic ability, so leaf traits and plant height, which are related to this process and competition for light, have a different meaning. For these reasons, both categories have been excluded for the calculation of trait diversity, and each from the analysis of those specific traits.

To reach a compromise between including small-scale heterogeneity and number of replicates on one hand, and stability in the estimation of trait diversity with a low number of species on the other hand, the sampling units were aggregated in groups of four into sub-plots, keeping sub-plots with at least four species. Thus, estimates of trait diversity are based on a non-contiguous 1 m^2 area (Figure 1), whereas estimates of cover-weighted trait values simply aggregate species cover across all sampling units.
After considering missing trait values and excluded categories, sub-plots (for trait diversity) and site-year combinations (for cover-weighted traits) were retained if the proportion of species cover with available traits was >80%.

Trait diversity was calculated with Rao's Quadratic Entropy (Rao, 1982) based on three distance matrices, two based on aboveground and belowground trait subsets, and a third which is an average of the former two (thus giving equal weight to the two trait subsets). The distance matrices were calculated with the Gower dissimilarity by the *FD* package (Laliberté et al., 2026), on traits transformed by the Box-Cox transformation with λ chosen by maximum likelihood. Instead of employing the raw trait diversity values, we calculated standardized effect sizes (FD-SES) by subtracting the mean and dividing by the standard deviation of 1000 randomizations: this controls for the dependence of quadratic entropy on species richness due to zero dissimilarities between conspecifics with species-level data (de Bello et al., 2016). The randomized values were obtained by permuting the distances between species pairs, considering only species occurring in that site in any year; this is consistent with the focus on within-site variation, and helps to further exclude differences in FD-SES due to different species pools and richness across sites.

Because species trait values are used, changes in community means and FD-SES depend on changes in species presence and abundance and are best interpreted as the result of species replacement or changes in relative abundance (Cornwell & Ackerly, 2009), rather than of intraspecific trait variation (Lepš et al., 2011; Palacio et al., 2025).

Weather data processing

Sub-canopy annual values were derived from the average (for temperature) or sum (for precipitation) of the 12 months preceding the survey (survey year), giving equal weight to each month, assuming the monthly coverage is sufficient. Weather data coverage for the surveyed years is incomplete, with missingness higher in some sites with respect to others (Appendix 1, part 4); in particular, sub-canopy weather was not measured in one site (04-CAM1), so it has not been considered in sub-canopy models. The percentage of missing monthly values before imputation was 17.8% for air temperature, 23% for soil temperature, and 26.2% for precipitation. We performed multiple imputation of 5 replicated datasets with fully conditional specification and predictive mean matching through the package *mice* (van Buuren & Groothuis-Oudshoorn, 2011): multiple imputation reflects the uncertainty of imputations in the variation between the imputed datasets (Blomberg & Todorov, 2025). This

uncertainty is transferred to the analysis model, which takes the imputations and pools estimates across them.

The probability of missingness depends on the site identity, so including this variable in the imputation model makes the missingness ignorable (Figure 2). For the imputation model and the analysis model to be congenial, the outcome variable should be included in the imputation (D'Agostino McGowan et al., 2024). This leads to a compromise, because the outcome (traits or trait diversity) has replicate measurements for each year and site (sub-plots), while the weather data is at the site-level, but has monthly measurements. Imputations are performed at the month level, even if annual values are of interest, because missingness is not homogeneous across months and it can lead to considerable bias in pre-averaged data. The chosen solution is to treat the outcome as time-invariant within each year (because the analysis model is at the year level), and to use the mean of the outcome as a site-level summary (because weather is a site-level variable). The imputation model further includes all available weather variables, both sub-canopy and open-field, and canopy cover. Only site-year combinations with observed data have been imputed, using sub-canopy and open-field measurements from all sites.

For open-field data (Appendix 1, part 4), which has more complete coverage, we used complete-case analysis, retaining survey years with all previous 12 months of data.

Graphical causal models

The identification of a causal effect requires the clear definition of a causal estimand (the quantity of interest) and the correct set of adjustment variables, even before the functional form of the statistical model is specified. Directed Acyclic Graphs (DAGs, Pearl, 2009) are an intuitive non-parametric graphical representation of the causal relationships within the system of interest, which summarize the necessary assumptions to recover the effect of interest (in this case, the effect of weather on understory plant traits). From these, the conditions under which an unbiased estimate is possible and an identification strategy logically follow (Arif & MacNeil, 2023; Dudney et al., 2025; Siegel & Dee, 2025), such as which variables should be adjusted for and which shouldn't in the statistical model.

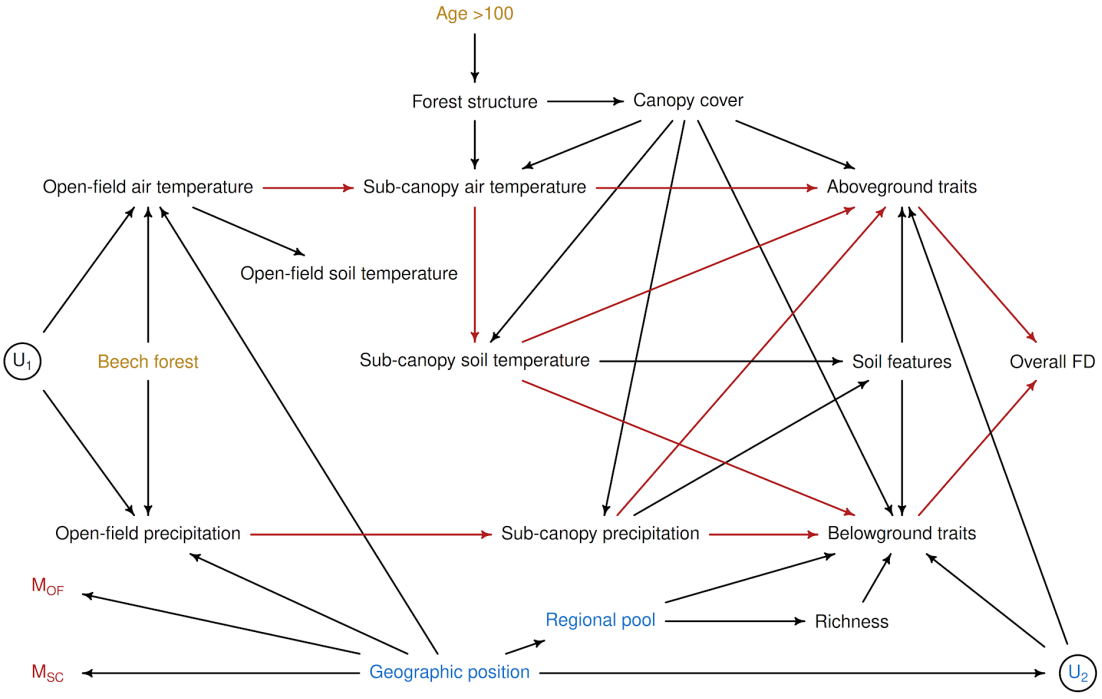


Figure 2. DAG representing the relationships between relevant variables in the system. Unobserved confounds (U_1, U_2) are circled; time-invariant confounds are shown in blue; selection variables, which restrict the field of observed conditions, are shown in yellow; variables which show what missing data depend on are shown in red (OF, open-field; SC, sub-canopy). Relationships which define causal estimands are highlighted in red.

In the Figure 2 DAG, we consider in turn specific sets of traits as the outcome, while the exposures are temperature (air and soil) and precipitation variables, either sub-canopy or open-field. The causal estimand is the total causal effect of said variables on trait diversity and community trait values.

According to the DAG, the effect of open-field weather on understory traits is mediated by sub-canopy conditions. We need not assume that temperature and precipitation are independent from each other, as it would not be in the case of heat waves and local weather anomalies, for example (U_1). The DAG also encodes that open-field soil temperature is not directly related to understory traits, unlike sub-canopy soil temperature. While soil temperature affects both aboveground and belowground traits, we assume that air temperature affects only aboveground traits.

The main confounding path between exposures and outcomes is through differences in the geographic position of sites, which result both in climatic differences in weather and in biogeographic differences in their regional species pools. We can also imagine that the geographic position affects plant traits in other ways (U_2). The key consideration is that these factors and geographic position do not vary within the considered timeframe, thus “within” estimators for panel data can be used to recover the causal effects, conditionally on the DAG and the absence of unobserved time-varying confounds (Byrnes & Dee, 2025). In practice, this means examining the effects of within-site weather variations on understory traits.
Forest structure plays a role in determining sub-canopy weather; while most structural features do not plausibly affect understory plant traits directly, canopy cover is a structural feature that might affect both traits and sub-canopy weather through its effect on light and rainfall interception (Padullés Cubino et al., 2021). For these reasons, it is considered a potential confound for all sub-canopy weather-trait relationships.
Edaphic features are another main determinant of understory plant traits (Candeias & Fraterrigo, 2020; Chelli et al., 2019). While geological substrate can be considered part of the time-invariant geographic features, soil chemistry (pH, carbon, nitrogen, phosphorus, etc.) is susceptible to change during the observed period, possibly at scales smaller than the plot area. Soil chemistry (Jager et al., 2015) and biota (Hahn et al., 2018; Orwin et al., 2010) can plausibly affect plant traits, and they are themselves affected by sub-canopy weather (Johnson & Martin, 2016), through for example effects of temperature on litter decomposition (Petraglia et al., 2019), of precipitation on organic carbon (Iavorivska et al., 2016) and nitrogen deposition, and on microbial biomass (Shi et al., 2018). These reasons place soil features as mediators, not confounders, of weather effects in Figure 2.

Statistical models

Bayesian models have been fitted to the data through the *brms* R package (Bürkner, 2017). Examination of the DAG with *dagitty* (Textor et al., 2016) indicates that the adjustment sets for the effects of open-field weather, aside from time-invariant confounds, require no other variable than the two weather variables (precipitation for temperature, temperature for precipitation), while sub-canopy models require to be adjusted for the confounding effect of canopy cover.

There are several ways to leverage longitudinal observational data to account for unobserved, time-invariant confounding (Dudney et al., 2025; Hamaker & Muthén, 2020): in

general, they separate the relationship between exposure and outcome in within-unit effects and between-unit effects; the latter represent a relationship confounded by between-unit differences in both variables, while the former should be free of confounding from variables that are stable within units (i.e., time-invariant). The method adopted here is the fixed-effects estimator, which absorbs all the variation between units in the outcome into site-specific intercepts. Alternative formulations have been tested (Appendix 1, part 5) and found to yield equivalent results, with the fixed-effects model being conceptually simpler, as well as more efficient and faster to sample.

It is reasonable to think that temperature and precipitation interact to affect traits (such as the combined effects of heat and drought, or evaporative cooling). Interaction terms pose an additional challenge to within-unit estimation, where the same "within-between" decomposition applies, resulting in interaction effects within sites, between sites, as well as across levels (Giesselmann & Schmidt-Catran, 2022), which means that the interaction must be built from group-centered variables after subtracting the site means, where the additional between-site variation in this centered interaction is absorbed by the site intercepts. The easier specification of these interaction terms with fixed-effects estimators is another reason they were preferred. Mean-centering of main effects in fixed-effects models is not necessary, because these effects already represent within-site effects net of site differences, but it has been performed anyway to improve model sampling by decorrelating intercept and slope parameters.

The above considerations result in model formulas of the kind:
$y \sim T_w + P_w + T_w : P_w + site$
Where the *w* subscript indicates within-site, mean-centered temperature and precipitation. Sub-canopy weather models additionally include percent canopy cover. According to the DAG (Figure 2), *T* is air temperature for open-field weather, aboveground traits, or overall trait diversity, while sub-canopy soil temperature is used for belowground traits.
The site factors have been coded with sum coding: this has the advantage that a value of zero represents the grand mean of the outcome across sites, allowing predictions for an average site other than for specific sites.

Weakly informative priors were used, together with prior predictive simulations (Appendix 1, parts 5, 6, 8), to constrain and regularize outcomes and effects within reasonable bounds (Gelman et al., 2013, 2017). This has been aided by scaling predictors by their approximate standard deviations, such that priors can be specified in terms of a change in predictors by that amount; the raw empirical standard deviations have not been used directly because they vary slightly between open-field, sub-canopy, across imputations and different subset of the data, so a representative value is used instead for consistency across models (2.5 °C for temperature, 600 mm for precipitation). FD-SES outcomes were not centered nor scaled, since this quantity has by construction an expectation of zero and a standard deviation of one. Trait outcomes have been scaled, but not centered, to keep them realistically bounded to positive values; instead, prior specification was aided by *brms* using the centered design matrix by default. Convergence was verified using trace rank plots, pairs plots of draws, and numerical diagnostics (Vehtari et al., 2021).

The data model family was assumed to be Gaussian for FD-SES, while for individual traits it was chosen based on substantive considerations for the specific trait and posterior predictive checks against the observed data. In most cases lognormal models were chosen, with the exception of stem specific density and bud bank size, which are Gaussian (Appendix 2, Table 1). For the three clonal traits, zero values have a special meaning, indicating that the species is not clonal: this is reflected in the use of hurdle-lognormal models, which correctly account for this distinction by modeling zeros separately, reflecting changes both in the proportion of clonal species and in the values of clonal traits.

Additionally, values of persistence of 4 should be interpreted as “4 years or more” (Klimešová et al., 2017); accordingly, these values have been treated as right-censored.

To infer effects on trait values at the community level, it is common to weigh species contributions by their cover proportions (Community-weighted mean, Violle et al., 2007). Instead of pre-averaging values at the site-year level, here species trait values were used directly, with averaging performed inside the model by regression weights. This allows for the inclusion of variation between coexisting species in the model and additional species information, such as whether such species is clonal or not and censored values, while obtaining equivalent inferences on the cover-weighted trait mean.

All data handling and statistical analyses were performed with R, version 4.6.1 (R Core Team, 2026). Further details about analysis steps, workflow and exploratory analyses are shown in the code notebooks, available as Supplementary material (Appendix 1).

Results

In most cases, there is substantial uncertainty regarding the effects of annual temperature and precipitation on both understory trait diversity and trait values (Figures 3–6). In general, effects of temperature are possibly large but uncertain, while effects of precipitation are better defined but weaker. The larger uncertainty is probably due to the smaller within-site variation of sub-canopy annual mean temperature compared to precipitation.

Aboveground trait diversity shows an indication of decreasing with temperature, while belowground and overall diversity do not (Figure 3). A decrease in trait diversity with precipitation is particularly evident for belowground traits (Figure 3f). Posterior predictions of conditional effects of weather help to put these results into context: a consistent change of at least 2° C in annual mean temperature and more than 1000 mm in precipitation within a site are required for a change in FD-SES of more than 0.5.

Cover-weighted traits show the same pattern of larger uncertainty for temperature than for precipitation effects. There is weak evidence of a decrease in leaf area (Figure 4a) and an increase in plant height (Figure 4c) with temperature, while diaspore mass (Figure 4e), leaf nitrogen per mass (Figure 5a) and specific leaf area (Figure 5c) seem to remain stable. It is hard to draw conclusions on temperature effects on stem specific density (Figure 5e) and belowground traits (Figure 6; a, c, e, g). Effects of precipitation are positive on leaf area (Figure 4b) and bud bank size (Figure 6b), negative for multiplication rate (Figure 6d), while they seem to be close to zero on other traits. The hurdle model components for clonal traits (Appendix 2, Figure 3) show that weather does not seem to affect the proportion of clonal species, but rather the values of clonal traits across clonal species.

Interactions between temperature and precipitation cannot be estimated with certainty in most cases (Appendices 2–5), but there is the possibility that simultaneous changes in one variable can drastically alter the effect of the other, even changing the sign of the relationship. This seems to be the case for specific leaf area (Appendix 4, Figure 5) and bud bank size (Appendix 4, Figure 7): in the former, a positive synergy between temperature and precipitation seems to underlie the lack of independent effects, in the latter a concomitant increase in precipitation could attenuate the negative effect of mean soil temperature, at the same time as the weak effect of precipitation can be modulated by temperature (Appendix 4).

Indirect open-field weather effects on trait diversity generally resemble those of sub-canopy weather (Appendix 2, Figure 1; Appendix 5), except for no indication of a decrease of aboveground trait diversity with temperature, and a stronger decrease in aboveground

diversity with precipitation, which is also reflected in the effect on overall diversity. We assessed the differences between open-field and sub-canopy air temperature and precipitation with correlations, ratio of standard deviations (SD), and major axis regressions on monthly data. Sub-canopy and open-field air temperatures are strongly correlated (r = 0.98), with similar dispersions (SD ratio 0.96) and a slope close to 1 (0.96); for precipitation, the correlation is lower (r = 0.78), there is less variation in sub canopy weather (SD ratio 0.82), and the slope is less than 1 (0.78) (Appendix 6, Table 1).

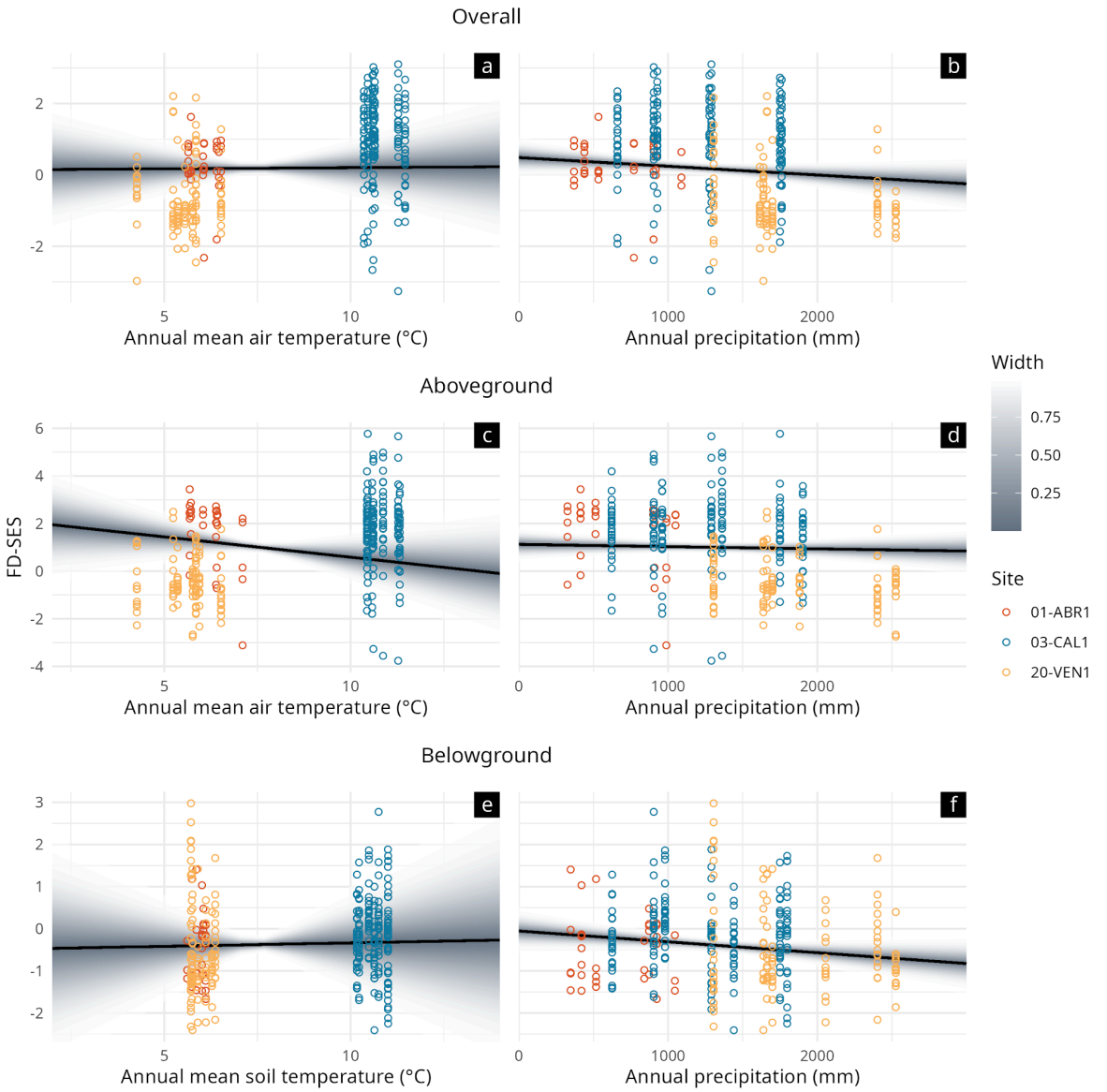


Figure 3. Posterior predictions of conditional effects for sub-canopy mean air temperature (a, c, e) and precipitation (b, d, f) on the expectation of overall (a, b), aboveground (c, d), and belowground (e, f) FD-SES, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width.

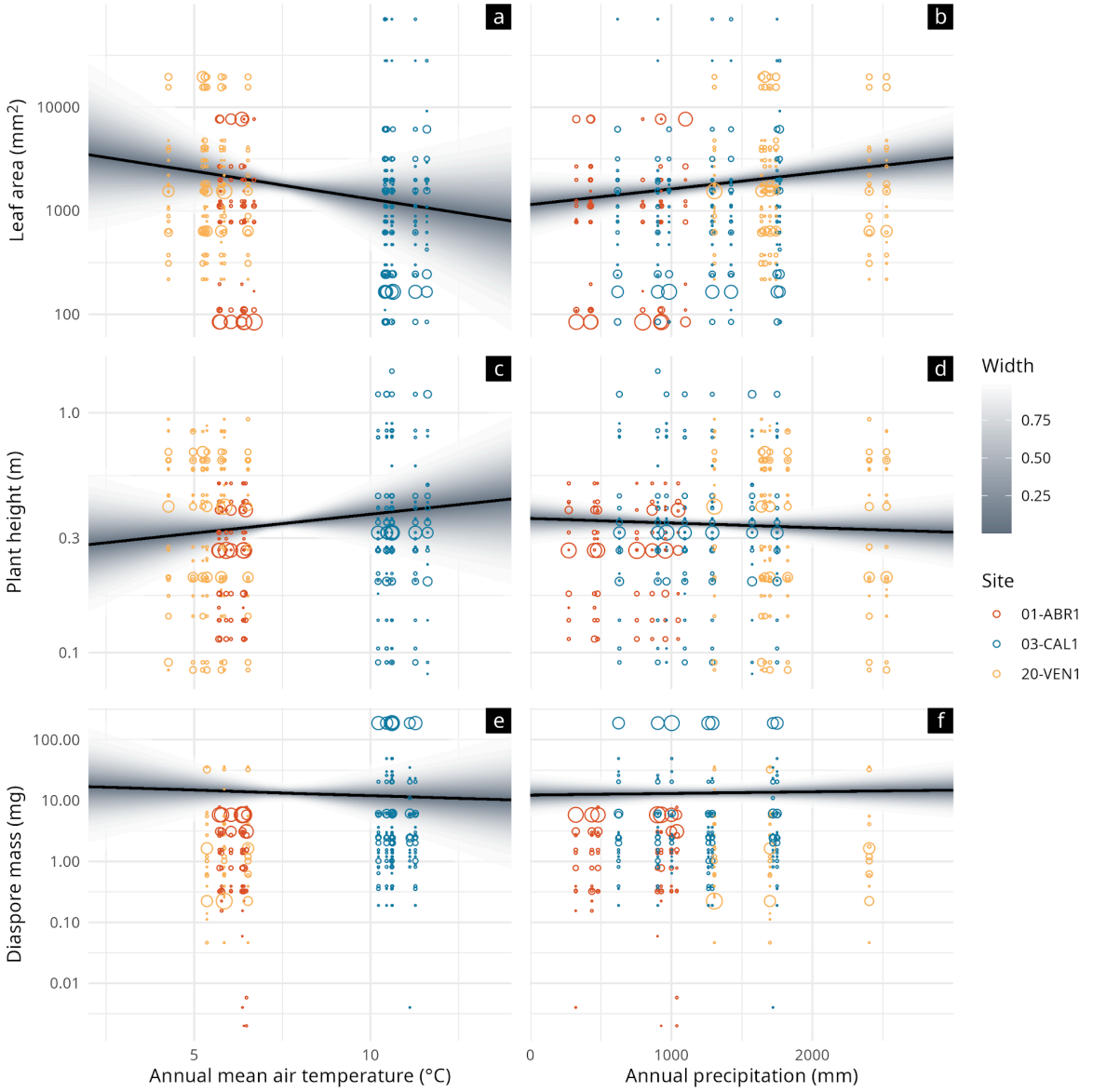


Figure 4. Posterior predictions of conditional effects for sub-canopy mean air temperature (a, c, e) and precipitation (b, d, f) on the expectation of leaf area (a, b), plant height (c, d), and diaspore mass (e, f), together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Point size is proportional to the relative cover of a species within a site and year.

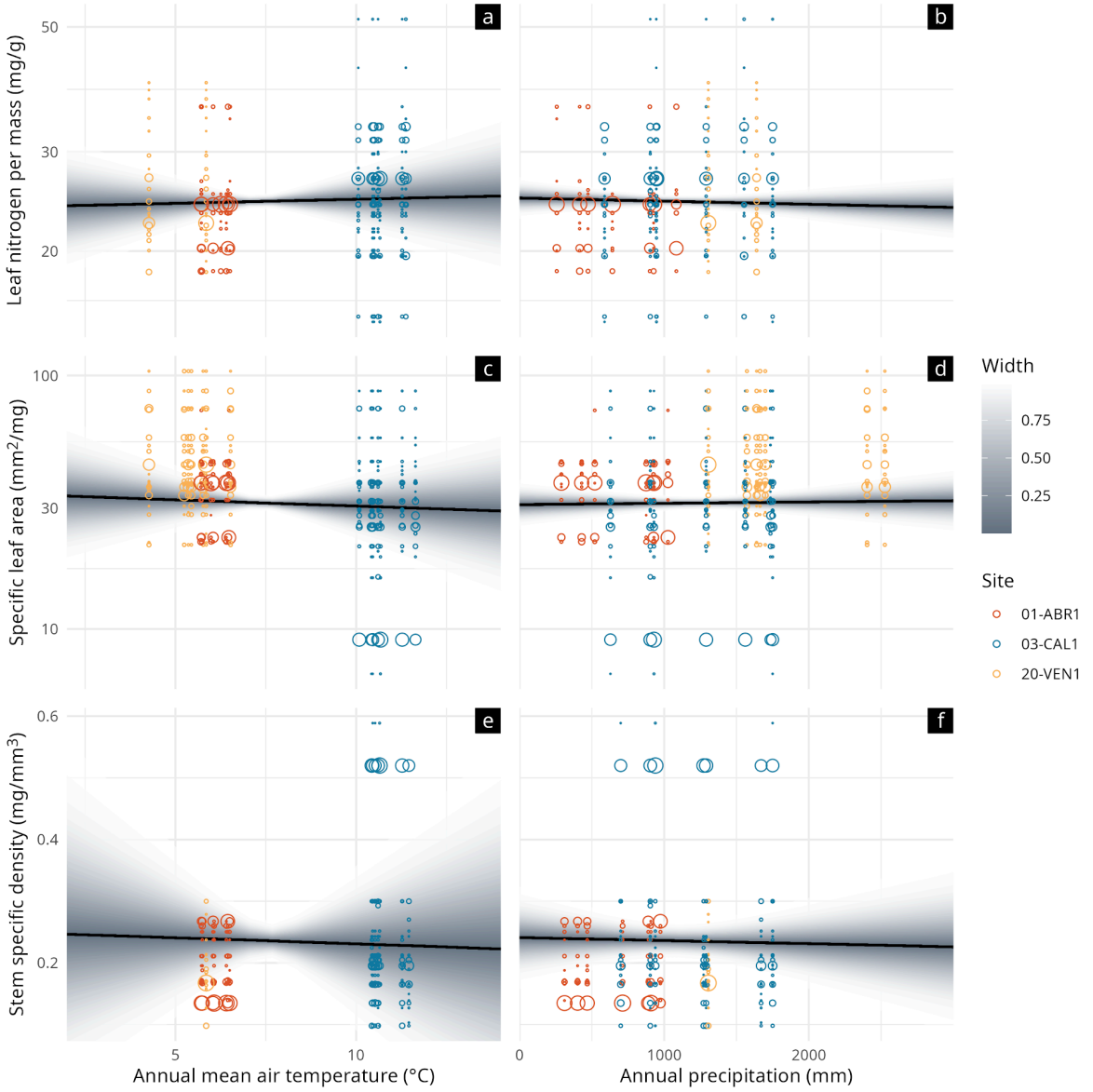


Figure 5. Posterior predictions of conditional effects for sub-canopy mean air temperature (a, c, e) and precipitation (b, d, f) on the expectation of leaf nitrogen per mass (a, b), specific leaf area (c, d), and stem specific density (e, f), together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Point size is proportional to the relative cover of a species within a site and year.

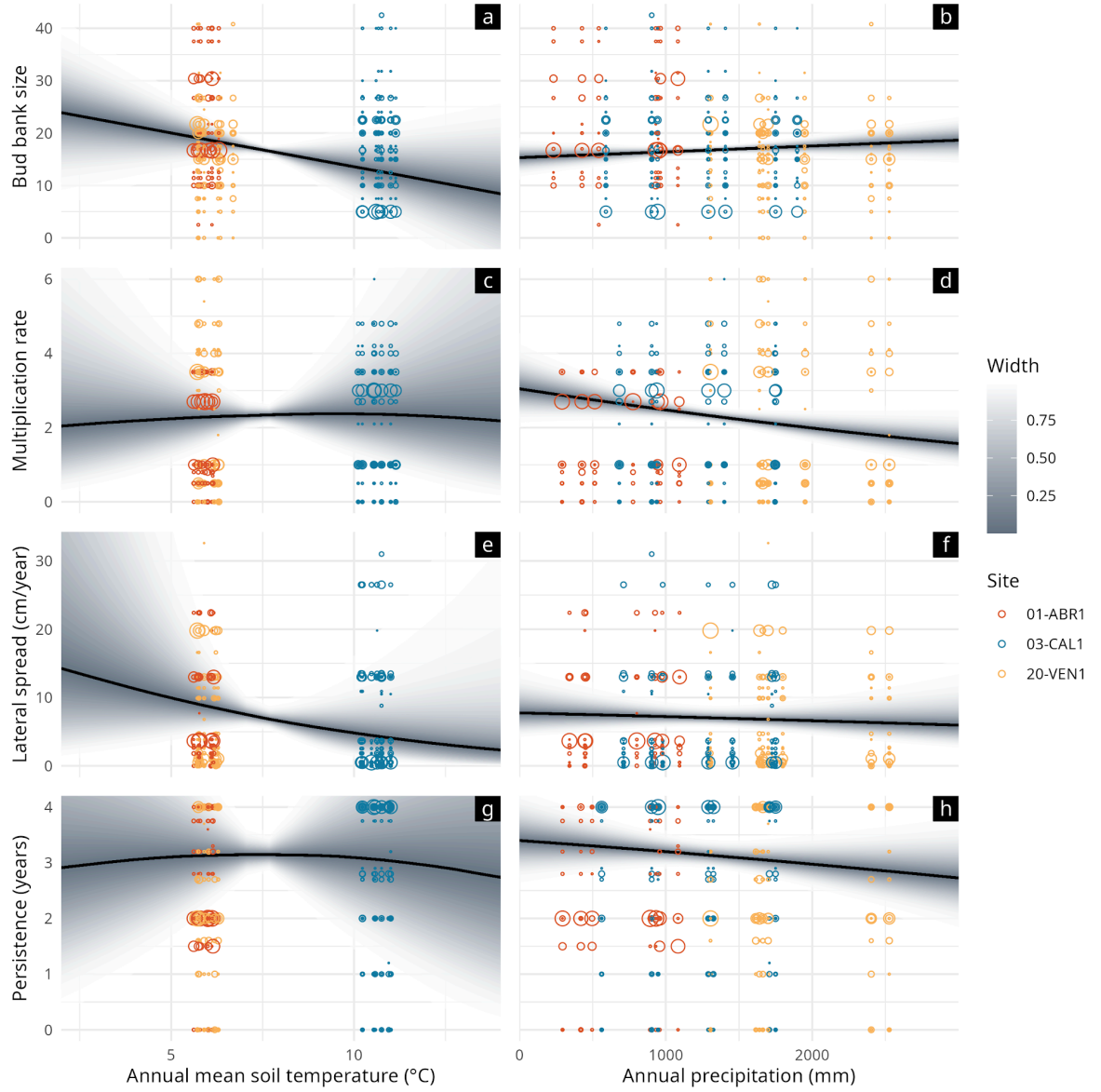


Figure 6. Posterior predictions of conditional effects for sub-canopy mean air temperature (a, c, e, g) and precipitation (b, d, f, h) on the expectation of bud bank size (a, b), multiplication rate (c, d), lateral spread (e, f), and persistence (g, h), together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width.

Discussion

“What is the effect of interannual weather on plant traits in old-growth beech forest understory” might seem a simple question, but we have shown that there are some challenges to overcome to try and find an honest answer. The complementary consideration of sub-canopy and open-field weather sheds light on the direct influence of environmental variation on understory traits, and on the capacity of the forest to buffer against external changes, respectively. Negligible effects of open-field or sub-canopy weather would support the view of old-growth forests as a stable ecosystem in terms of understory traits, whereas more substantial changes would warn against the vulnerability of this ecosystem to environmental changes. While we cannot confidently exclude larger effects of changes in air

and soil temperature, and interactions with precipitation, independent effects of precipitation seem generally small both on trait diversity and trait values (but for the latter see leaf area, Figure 4b; bud bank size, Figure 6b; multiplication rate, Figure 6d). Considering the magnitude of the predicted responses across the observed ranges of temperature and precipitation, our results suggest that interannual weather variability does not greatly impact the functioning of undisturbed temperate forest understories. However, this apparent relative stability should not be interpreted as evidence that these ecosystems are insensitive to climate change, particularly if future changes involve more frequent climatic extremes, or altered seasonal patterns of precipitation, not considered in our study.

The separate consideration of aboveground and belowground trait sets for functional diversity highlighted different responses that are not apparent when both compartments are considered together (i.e. overall, Figure 3). Specifically, the decrease of aboveground FD-SES with temperature is not apparent for belowground FD-SES, while aboveground FD-SES is not negatively affected by precipitation as belowground FD-SES.
Trait means were also affected in different amounts, but there is no clear separation between aboveground and belowground compartments. For instance, leaf area, an aboveground trait, shows a similar pattern to bud bank size, a belowground trait, while plant height shows an opposite response. It has been highlighted that the formation of bud-bearing organs comes at the expense of vertical growth (Midgley, 1996), so this result, if confirmed, could indicate a shift at the community level from a strategy of persistence to one of competitive ability with warmer and drier conditions (Appendix 4; Figures 2, 7). More broadly, these contrasting responses confirm that aboveground and belowground functional attributes may capture different dimensions of understory responses to climatic variability (Chelli, Klimešová, et al., 2024; Klimešová et al., 2021). This is particularly relevant when assessing ecosystem responses to global change, because changes in aboveground traits do not necessarily reflect concurrent changes in belowground strategies, and vice-versa.

The small, but usually negative, effects of precipitation on traits and trait diversity align with previous findings (Maes et al., 2020; Padullés Cubino et al., 2021), which seem to hold despite the differences between sub-canopy and open-field precipitation and the potential for confounding effects. Still, the indirect effects of open-field precipitation appear larger (Appendices 2–3) than those of sub-canopy precipitation; while differences between open-field and sub-canopy temperature are well documented (De Frenne et al., 2021), differences in precipitation might not only be due to canopy interception, but also to stemflow (Johnson & Martin, 2016). At the same time, soil moisture should be preserved more effectively by the forest microclimate regardless of the precipitation input. Estimating a total causal effect, such as that of weather on traits, makes no assumptions about the specific mechanisms through which this effect is exerted, such as indirect effects through humidity, soil biota, or litter.

Another interesting contrast was found between multi-year gridded climate from widely used sources such as WorldClim 2.1 (Fick & Hijmans, 2017) and CHELSA 2.1 (Brun et al., 2022), and the measurements from open-field stations averaged across the whole study period: while mean air temperature was similar, precipitation was severely lower in at least two sites in both gridded datasets (Appendix 6, Table 2). We do not know the extent of this bias, but leave this example as a warning about the use of these data sources, especially without modelling the contribution of local conditions (Frey et al., 2016).

The assessment of trait diversity at small scales shows that there is considerable variation among sub-plots experiencing the same weather conditions. To compare this to the variation among sites and years (due also to weather), the Bayesian R^2 (Gelman et al., 2019) of a model with an intercept for each site-year was calculated. The residual variance of sub-plots within site-years was large: 61% for overall, 55% for aboveground, and 79% for belowground trait diversity (Appendix 1, part 6). Previous studies have highlighted the importance of

small-scale soil heterogeneity in forests (Beck & Givnish, 2021; Helbach et al., 2022), which might explain a considerable part of this variation. Weather effects can be considered independently from these soil effects, as shown in Figure 2 and the corresponding Methods section; additionally, the permanent placement of sampling units within a plot ensures that the distribution of time-invariant micro-environmental features remains constant during the monitoring period.
In conclusion, the small-scale (sub-plots of four 0.25 m^2 sampling units) assessment of trait diversity shows that most of the variation is not explained by plot-scale (2500 m^2) factors, environmental or otherwise, that vary among sites and years, but rather it is variation among neighbouring sampling units at the same point in time. From a global change perspective, this finding opens the question of whether lasting small-scale heterogeneity may contribute to the persistence of contrasting plant strategies within communities under changing environmental conditions.

In this study, we narrowed our focus on mean annual temperature and annual precipitation, because of their widespread use in ecological studies (Moles et al., 2014), but we do not claim that they exert the strongest influence on understory plant traits. Other studies have considered climatic extremes and intra-annual variability (Chelli et al., 2019; Padullés Cubino et al., 2021; Vanneste et al., 2019), as well as spring or summer temperatures and winter growing degree days (Wolf et al., 2021); it is possible that these variables are more mechanistically related to understory responses. At the same time, we do not exclude that different traits or sets of traits might provide different or more informative results. Furthermore, it is possible that intraspecific variation is an important contributor to weather-induced trait changes, while we are considering changes due to species replacement and abundance differences. We therefore encourage further studies to investigate how seasonal weather patterns and climatic extremes in forest microclimates influence different functional compartments and traits, including intraspecific variation (Palacio et al., 2025).

Conclusion

This study represents an advancement in basic but fundamental questions about trait-environment relationships in forest understory plant communities, whose answers can be attempted from incremental knowledge. We cautiously limit external validity to undisturbed old-growth beech forests. It must be noted that beech forests in the Apennines (such as those in 01-ABR1, 03-CAL1, 04-CAM1; Figure 1) experience a warmer, drier climate and are spatially isolated from those of central Europe (Ottaviani et al., 2019).

It has been suggested to narrow the assessment of trait responses within habitat types (Kambach et al., 2023); while this contrasts with the goal of obtaining more general conclusions from traits, there are two reasons this would be effective: less opportunity for confounding and effect heterogeneity. Besides interactions resulting from mechanistic context dependence, the phenomenon can apparently arise from confounding factors, methodological, and statistical differences, such as the inclusion or not of covariates or different observed ranges of the variables (Catford et al., 2022). We address these points by transparently reporting the assumptions and the scientific reasoning behind the analyses, as well as presenting the results in a way that is easy to interpret. If contrasting results are found, this can be due to context dependence as much as to different analytical decisions.

An expanded dataset, both in temporal extent and in number of sites, can possibly resolve the large uncertainty around most effects. Attempting to reduce conclusions to binary summaries in the presence of large uncertainty has the potential to grossly overestimate the magnitude of the effects or even mistake their signs (Gelman & Carlin, 2014), thus we have chosen to present the results in a way that preserves their uncertainty.

Data availability statement

Data and code supporting the results in the paper are available at https://doi.org/10.5281/zenodo.24167466 and https://doi.org/10.5281/zenodo.24167182, respectively.

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Author contributions

Conceptualization: all authors. **Data Curation:** L.L.M.D.B. **Formal Analysis:** L.L.M.D.B. **Methodology:** L.L.M.D.B, C. P. C., E. T. **Project Administration:** R.C. **Software:** L.L.M.D.B. **Supervision:** S.C., R.C., C.P.C., G.C. **Visualization:** L.L.M.D.B. **Writing – Original Draft:** L.L.M.D.B., S.C. **Writing – Review & Editing:** all authors.

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Appendix 1: code notebooks

Available at
https://github.com/LucianoDeBenedictis/beech_weather_traits/tree/main/notebooks

Appendix 2: model coefficients and families

Trait diversity models use the identity link, while coefficients for most trait models are on the latent parameter scale, which is on the log-mean for lognormal models, while the hurdle coefficient uses the logit link function. Refer to the main text and Appendix 1, parts 6 and 8, for details.

Model	Family
Trait diversity	Gaussian, identity link
Leaf area	Lognormal, identity link (on log-mean)
Leaf nitrogen per mass	Lognormal, identity link (on log-mean)
Plant height	Lognormal, identity link (on log-mean)
Specific leaf area	Lognormal, identity link (on log-mean)
Stem specific density	Gaussian, identity link
Diaspore mass	Lognormal, identity link (on log-mean)
Bud bank size	Gaussian, identity link
Multiplication rate	Hurdle-lognormal, identity link on log-mean, logit on hurdle
Lateral spread	Hurdle-lognormal, identity link on log-mean, logit on hurdle
Persistence	Hurdle-lognormal, identity link on log-mean, logit on hurdle

Table 1. Summary of model families and link functions.

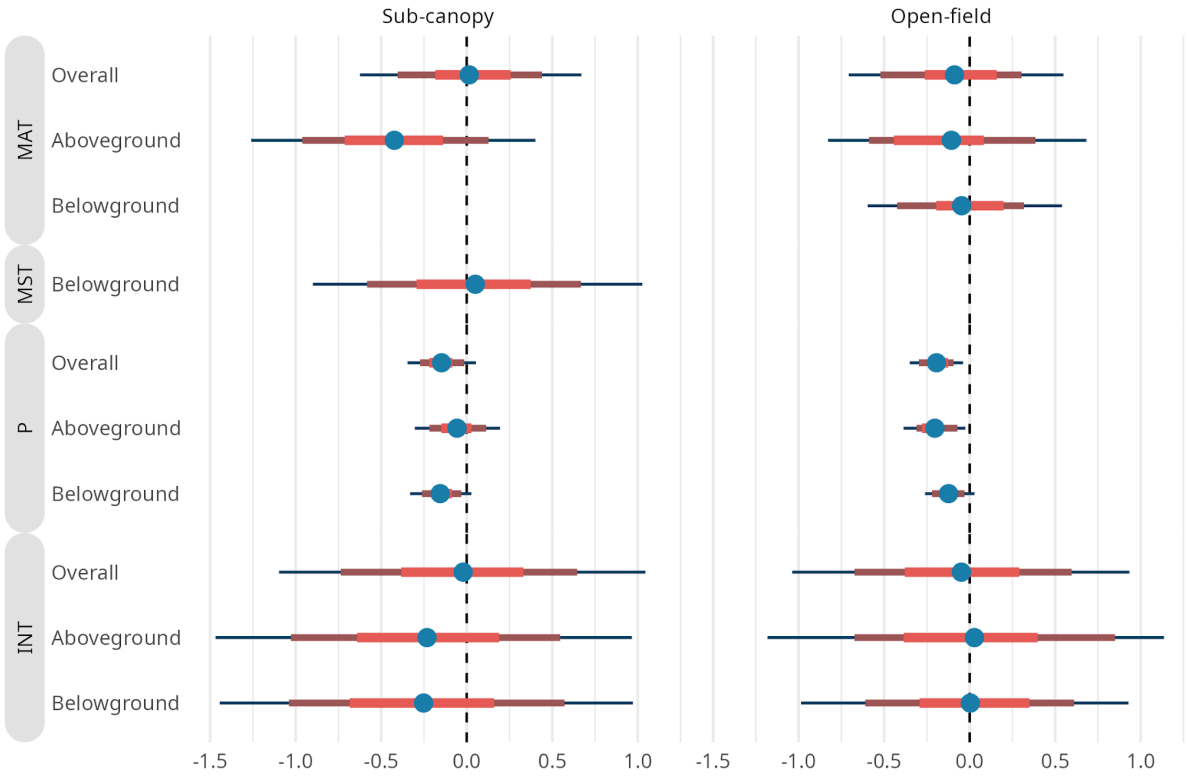


Figure 1. Model coefficients for trait diversity models. MAT: mean air temperature; MST: mean soil temperature; P: precipitation; INT: interaction.

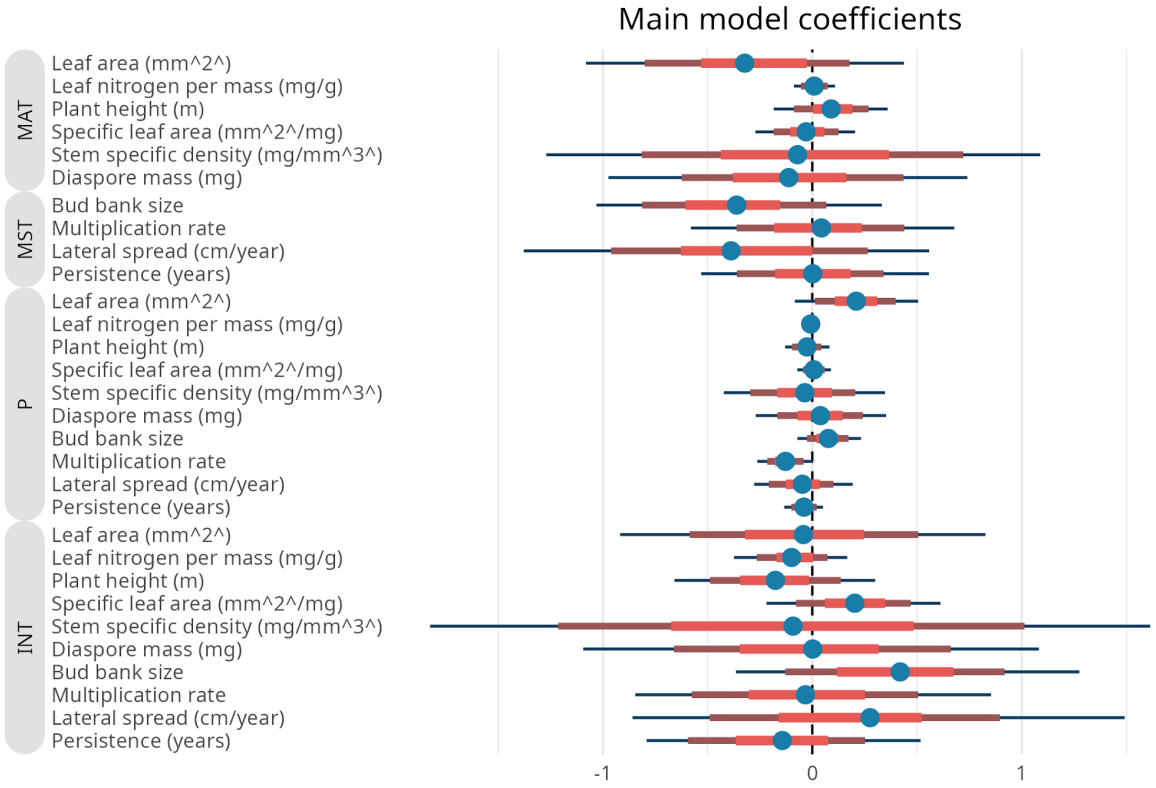


Figure 2. Model coefficients for the main part of trait mean models. MAT: mean air temperature; MST: mean soil temperature; P: precipitation; INT: interaction.

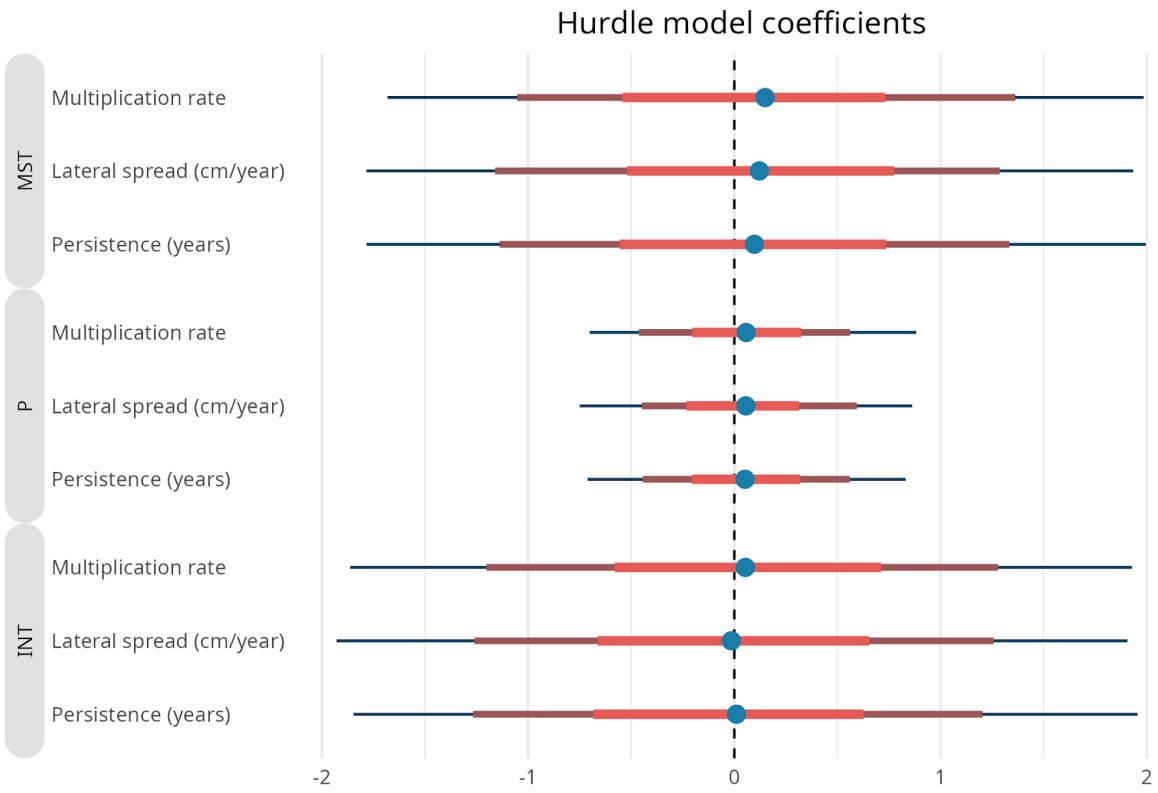


Figure 3. Model coefficients for the hurdle part of trait mean models. MAT: mean air temperature; MST: mean soil temperature; P: precipitation; INT: interaction.

Appendix 3: plots of sub-canopy trait diversity models with interactions

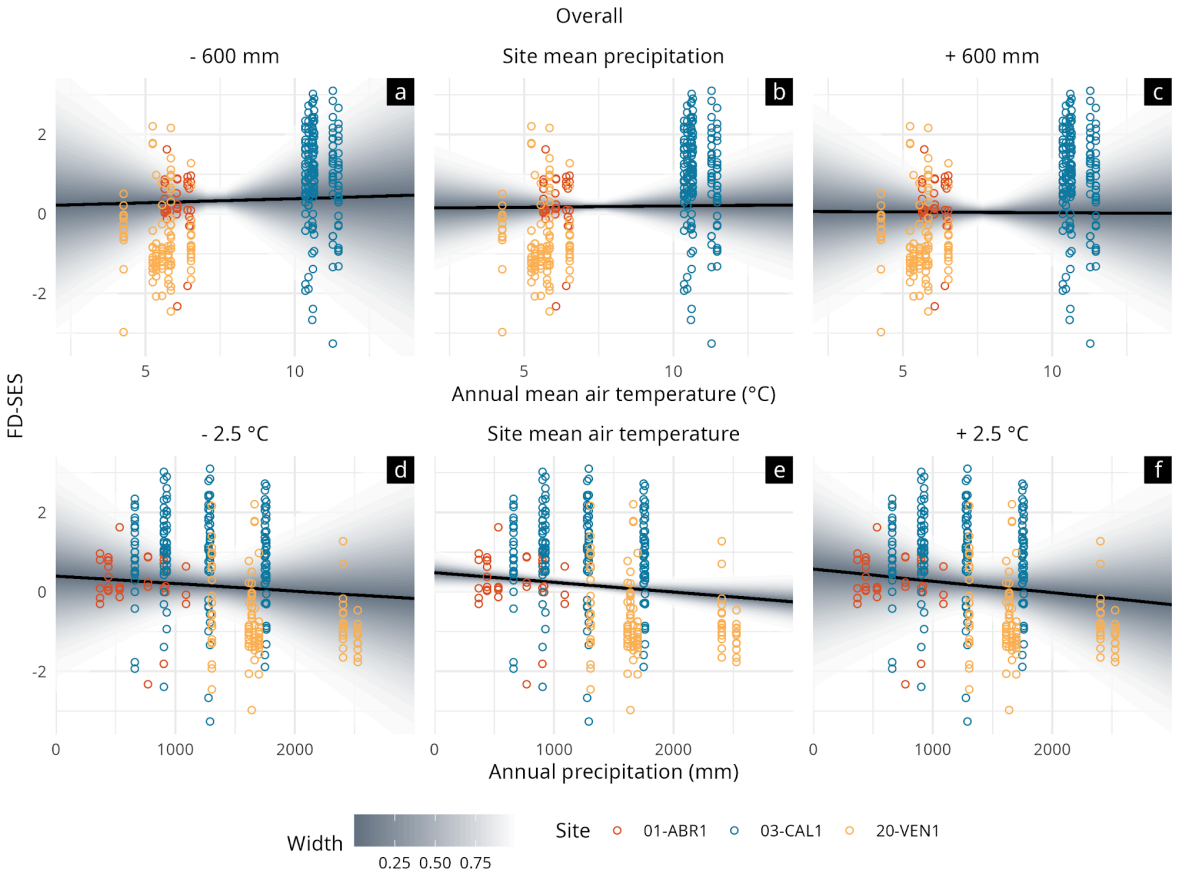


Figure 1. Posterior predictions of conditional effects for sub-canopy mean air temperature (a–c) and precipitation (d–f) on the expectation of overall FD-SES, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

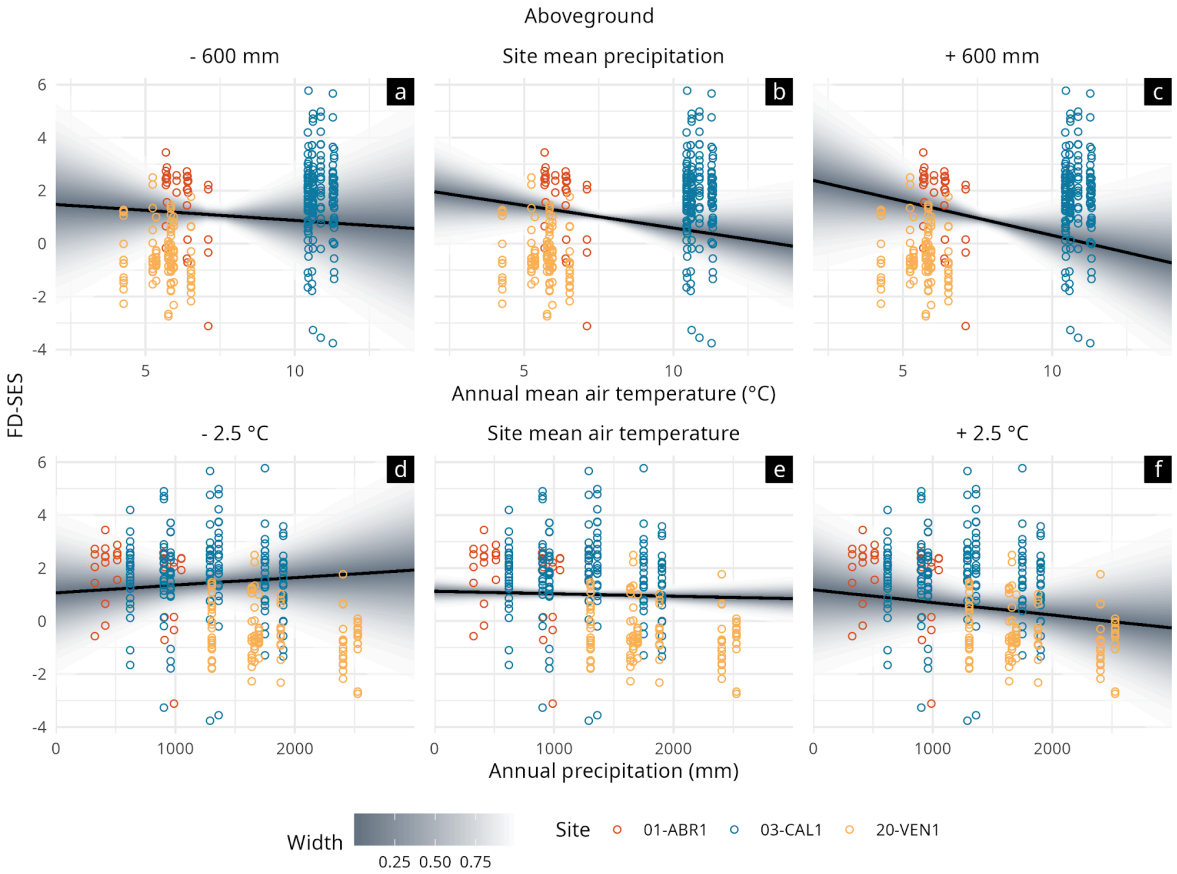


Figure 2. Posterior predictions of conditional effects for sub-canopy mean air temperature (a–c) and precipitation (d–f) on the expectation of aboveground FD-SES, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

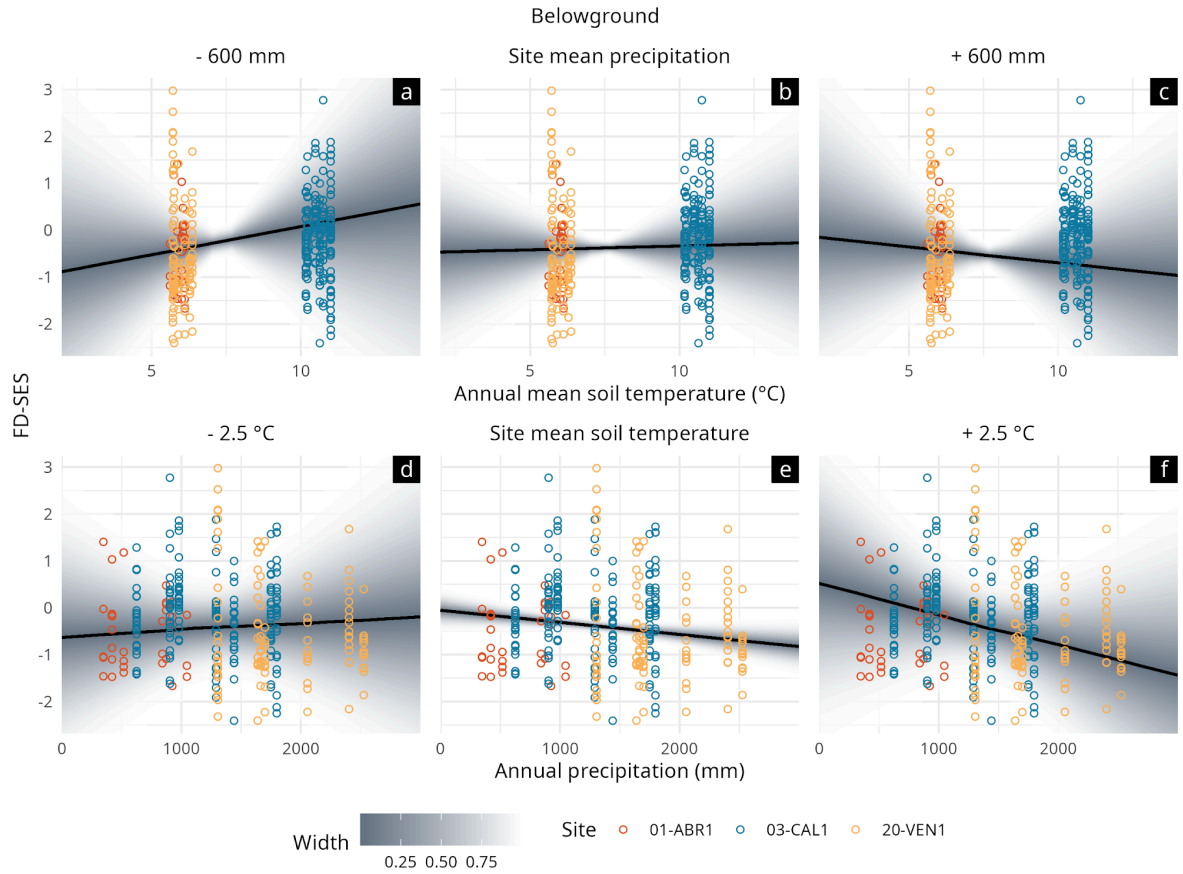


Figure 3. Posterior predictions of conditional effects for sub-canopy mean air temperature (a–c) and precipitation (d–f) on the expectation of belowground FD-SES, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

Appendix 4: plots of sub-canopy trait mean models with interactions

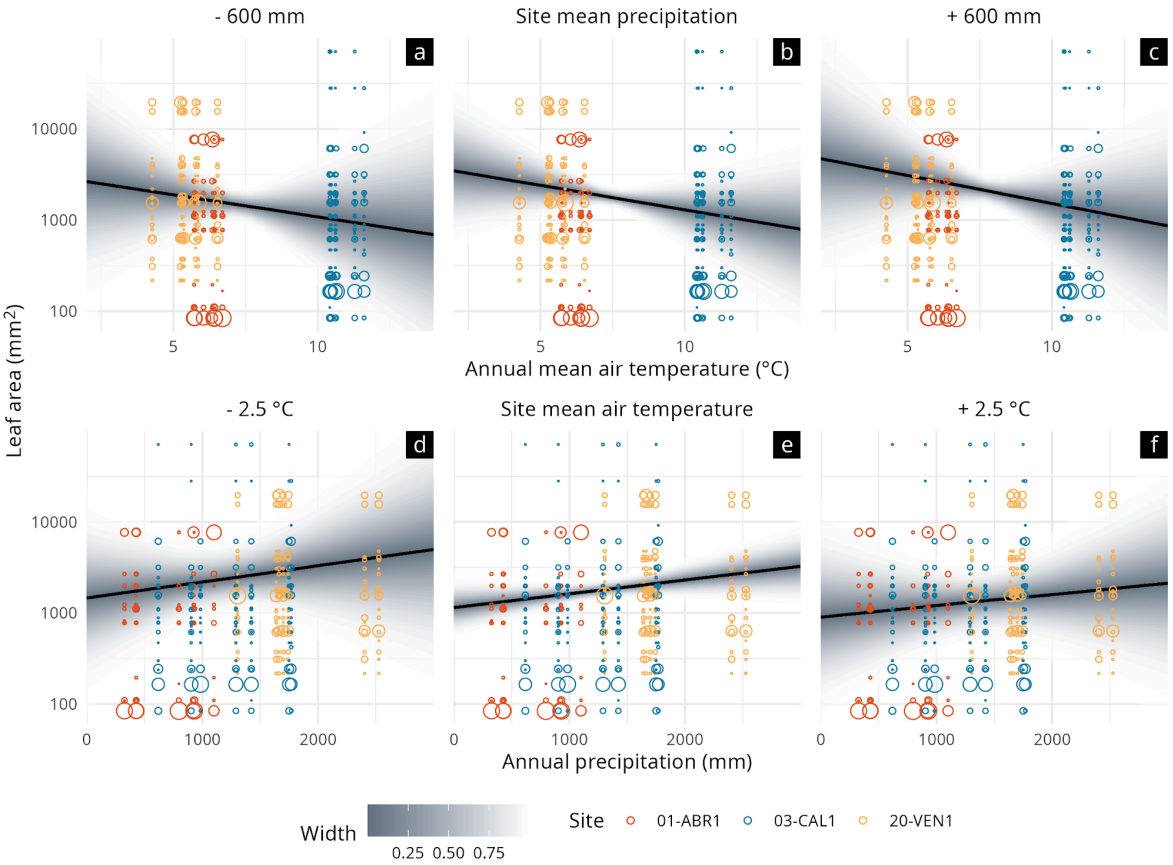


Figure 1. Posterior predictions of conditional effects for sub-canopy mean air temperature (a–c) and precipitation (d–f) on the expectation of leaf area, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Point size is proportional to the relative cover of a species within a site and year. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

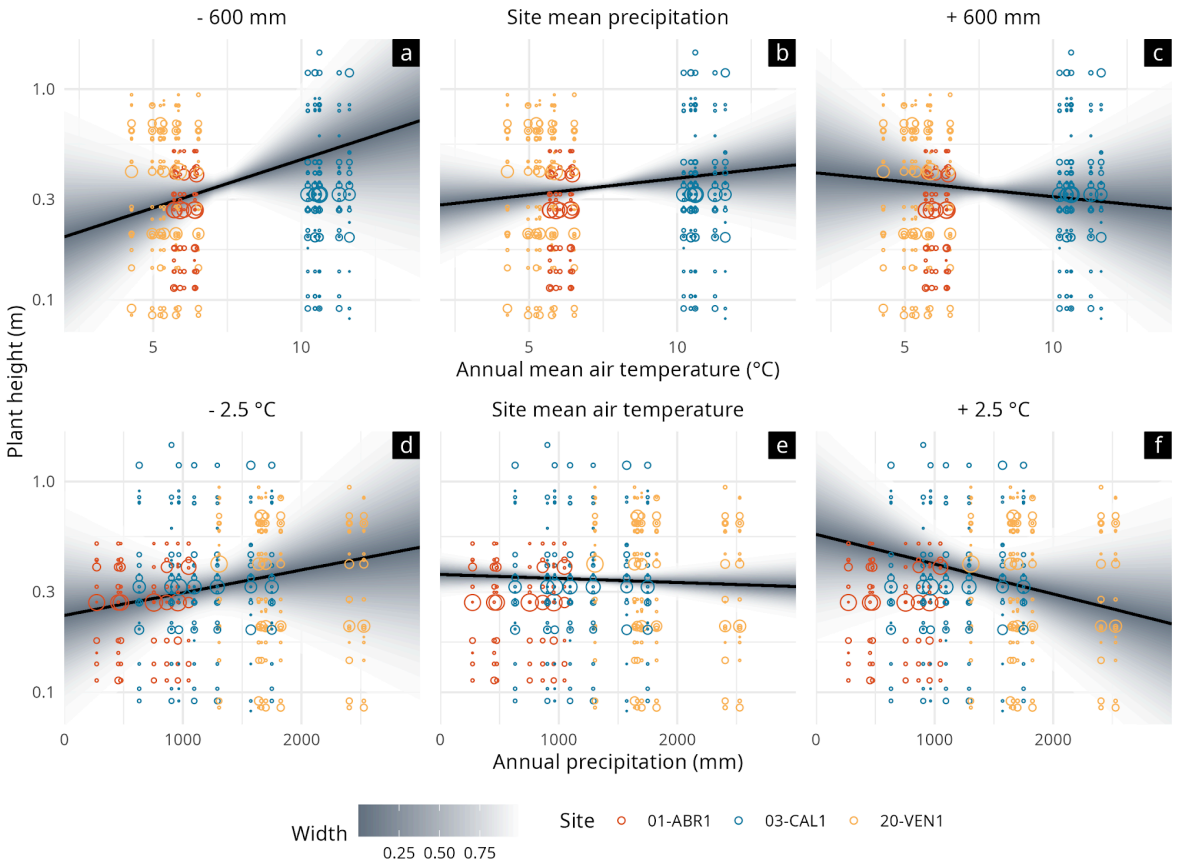


Figure 2. Posterior predictions of conditional effects for sub-canopy mean air temperature (a–c) and precipitation (d–f) on the expectation of plant height, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Point size is proportional to the relative cover of a species within a site and year. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

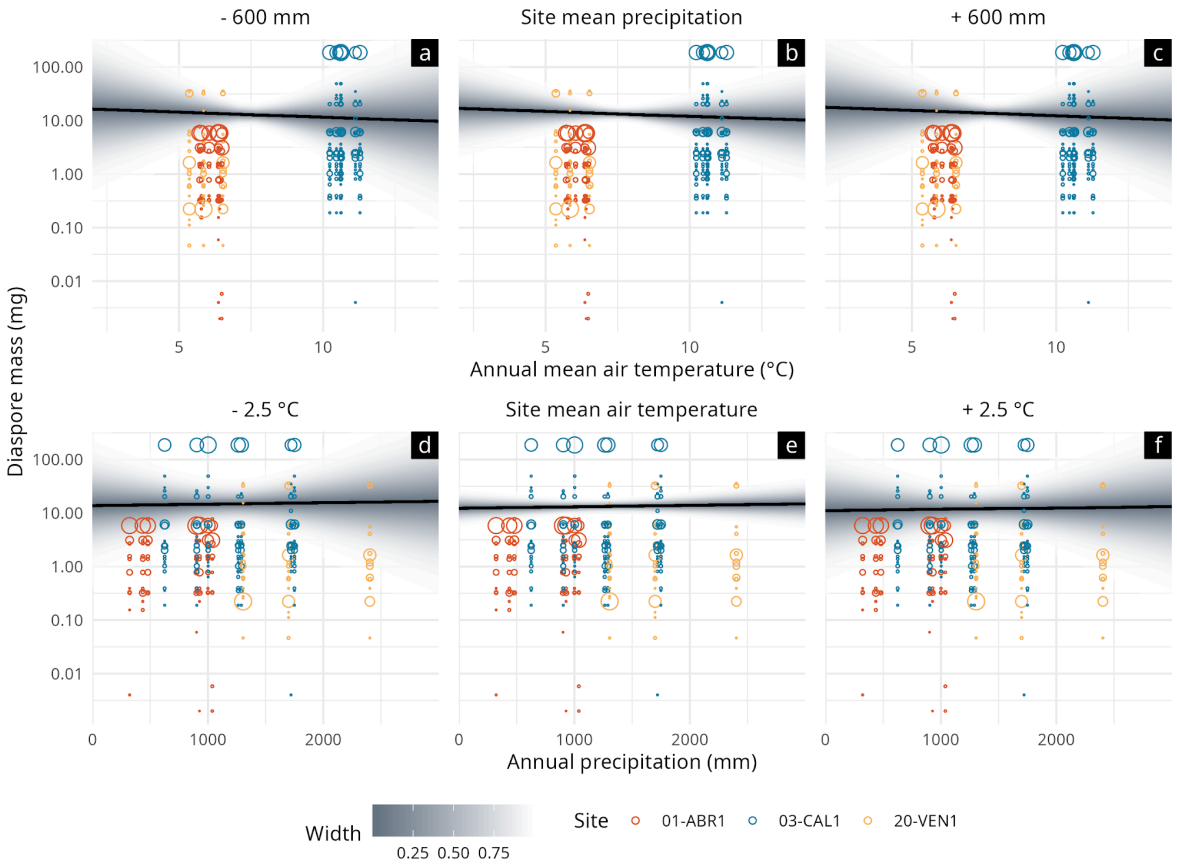


Figure 3. Posterior predictions of conditional effects for sub-canopy mean air temperature (a–c) and precipitation (d–f) on the expectation of diaspore mass, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Point size is proportional to the relative cover of a species within a site and year. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

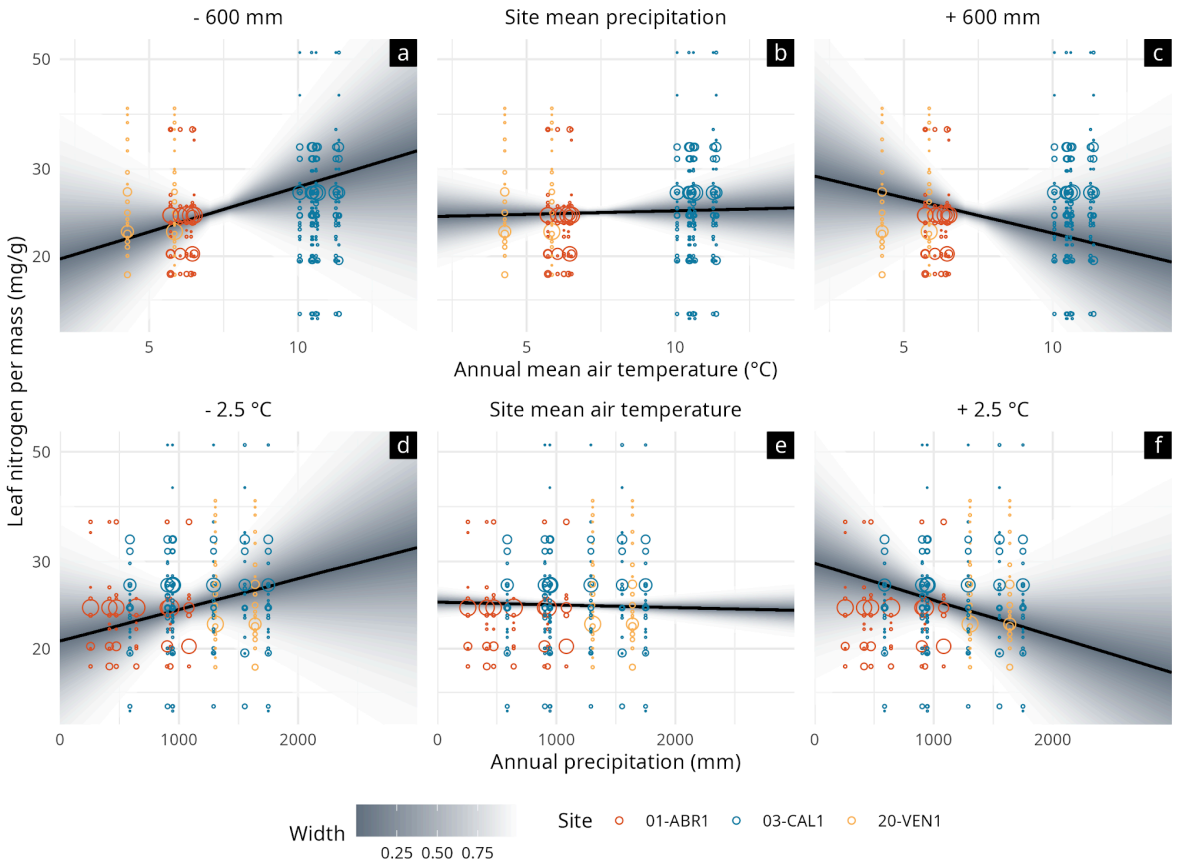


Figure 4. Posterior predictions of conditional effects for sub-canopy mean air temperature (a–c) and precipitation (d–f) on the expectation of leaf nitrogen per mass, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Point size is proportional to the relative cover of a species within a site and year. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

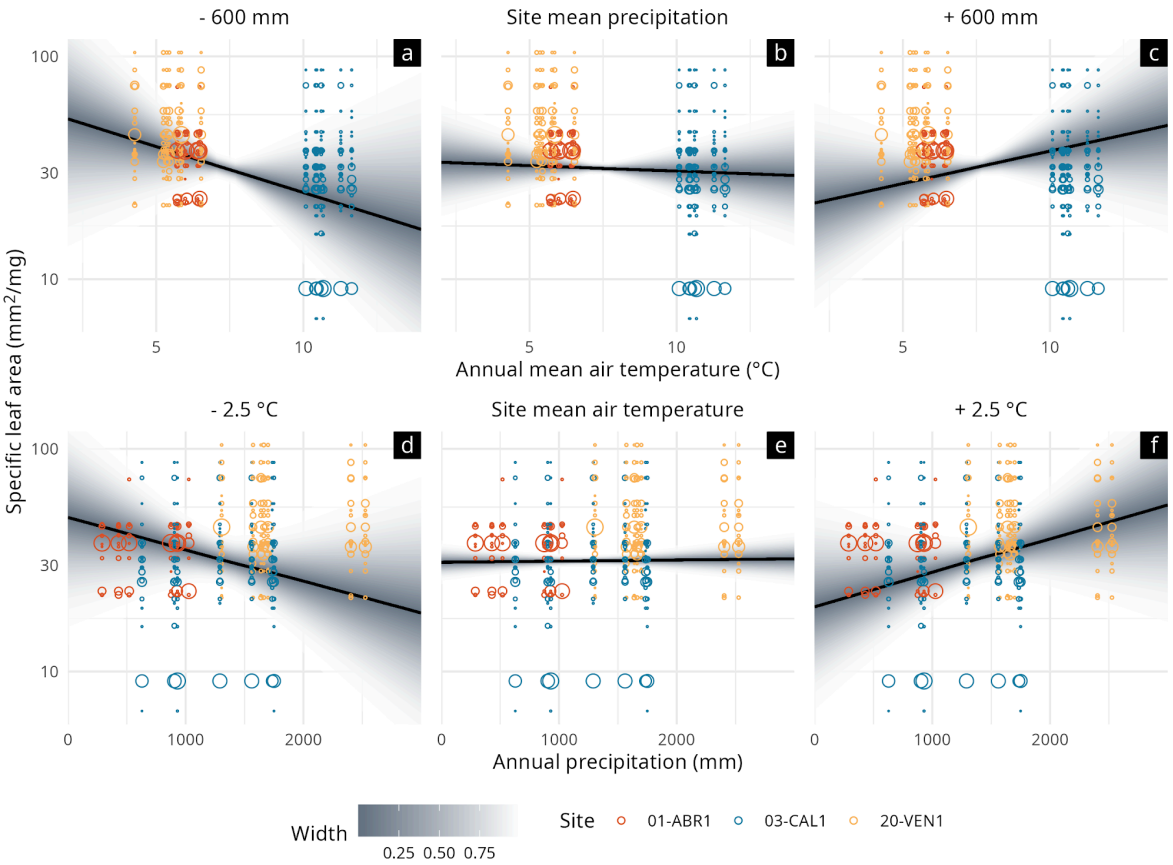


Figure 5. Posterior predictions of conditional effects for sub-canopy mean air temperature (a–c) and precipitation (d–f) on the expectation of specific leaf area, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Point size is proportional to the relative cover of a species within a site and year. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

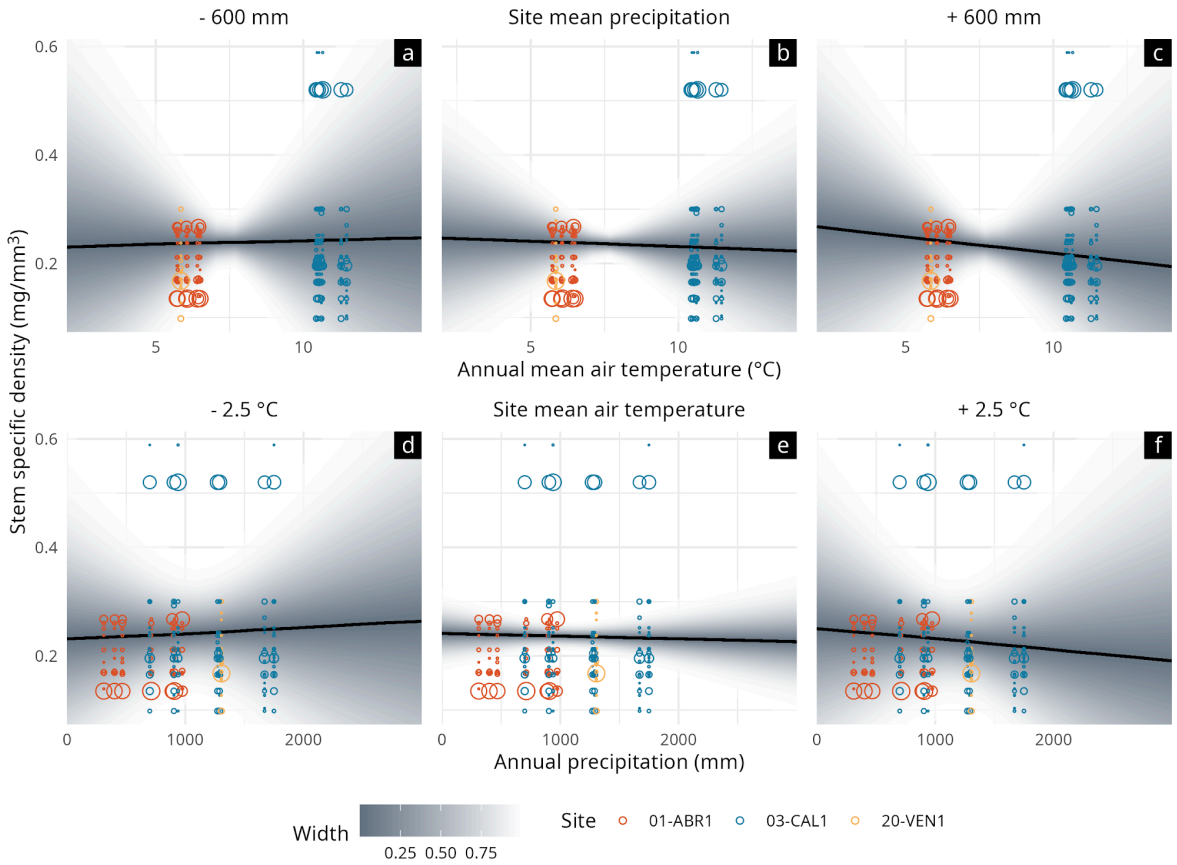


Figure 6. Posterior predictions of conditional effects for sub-canopy mean air temperature (a–c) and precipitation (d–f) on the expectation of stem specific density, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Point size is proportional to the relative cover of a species within a site and year. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

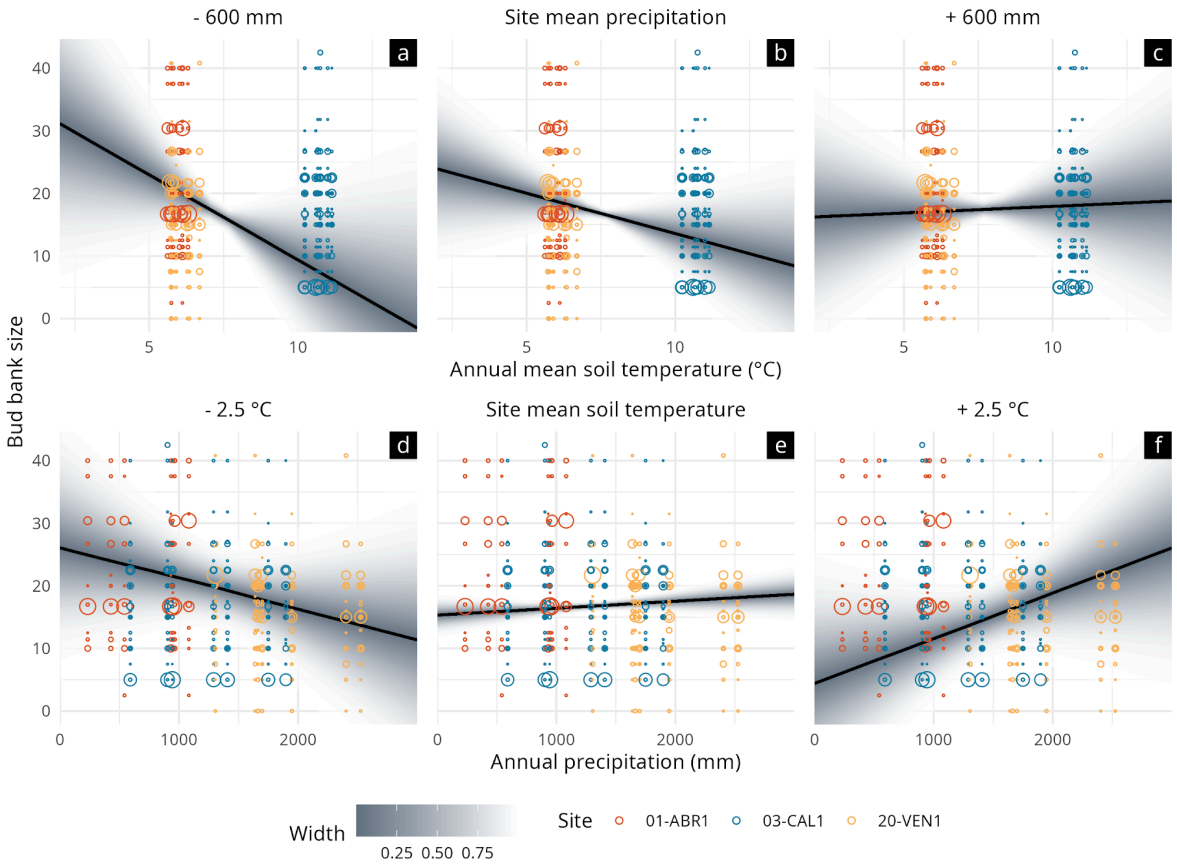


Figure 7. Posterior predictions of conditional effects for sub-canopy mean air temperature (a–c) and precipitation (d–f) on the expectation of bud bank size, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Point size is proportional to the relative cover of a species within a site and year. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

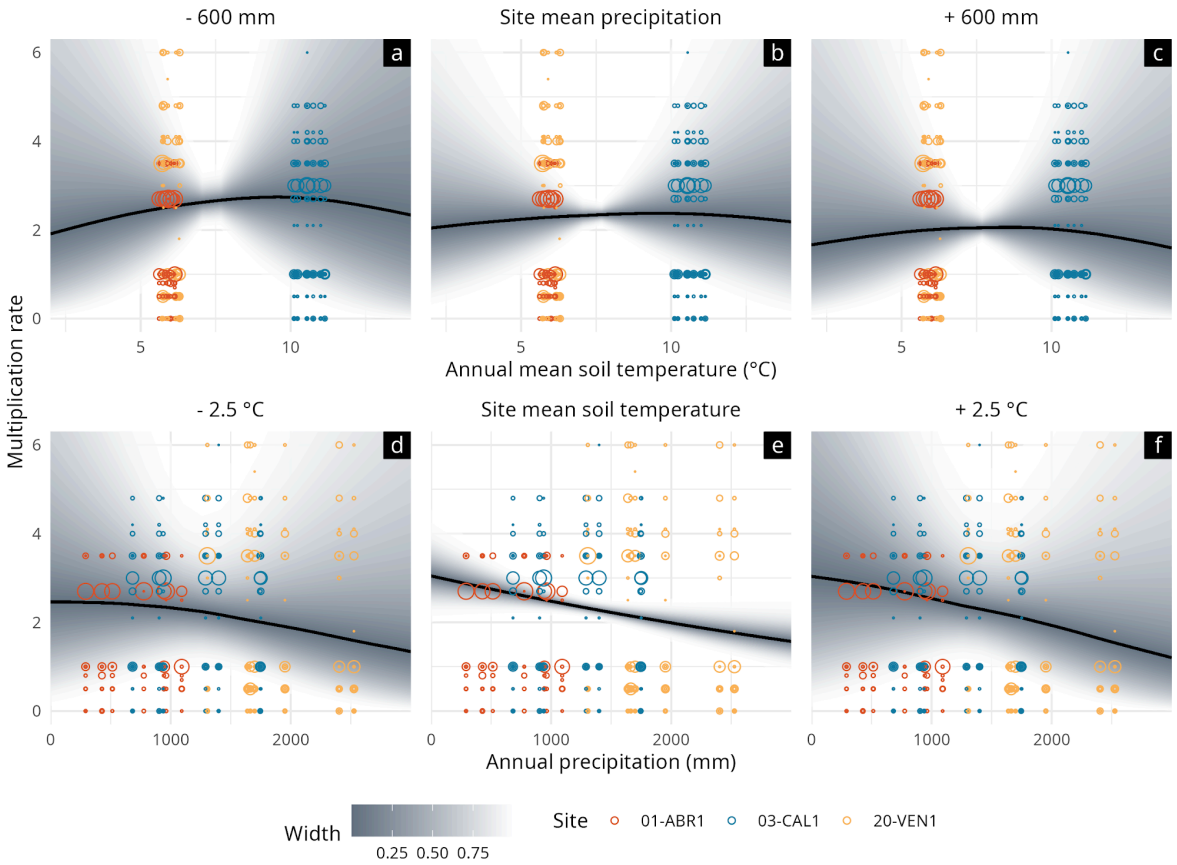


Figure 8. Posterior predictions of conditional effects for sub-canopy mean air temperature (a–c) and precipitation (d–f) on the expectation of multiplication rate, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Point size is proportional to the relative cover of a species within a site and year. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

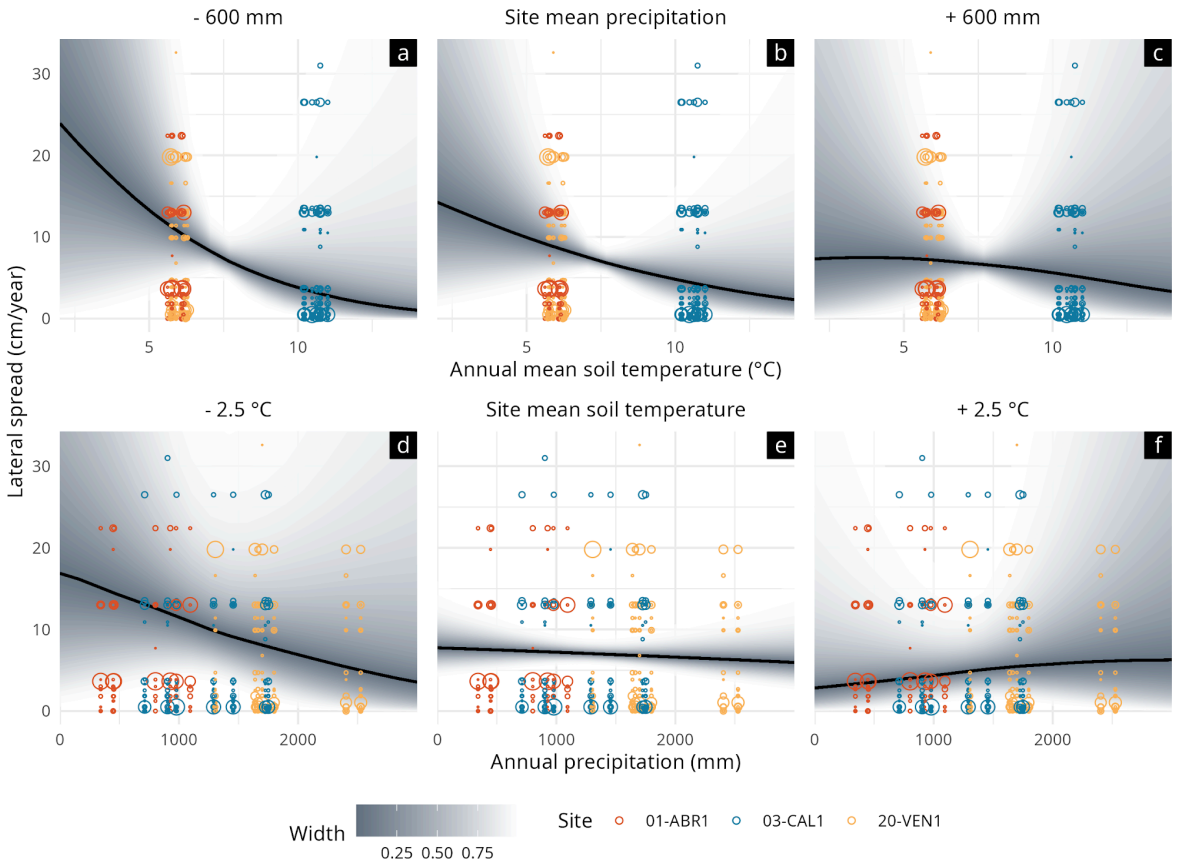


Figure 9. Posterior predictions of conditional effects for sub-canopy mean air temperature (a–c) and precipitation (d–f) on the expectation of lateral spread, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Point size is proportional to the relative cover of a species within a site and year. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

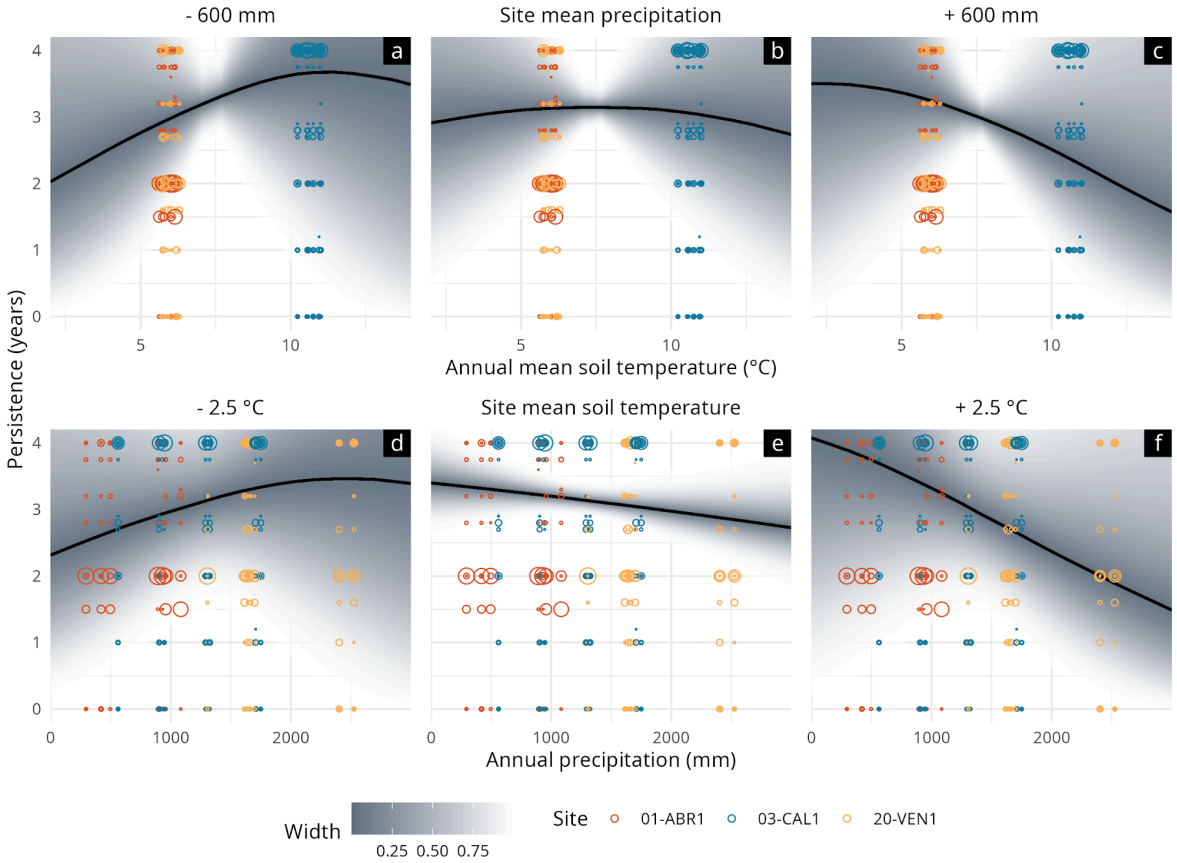


Figure 10. Posterior predictions of conditional effects for sub-canopy mean air temperature (a–c) and precipitation (d–f) on the expectation of persistence, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Point size is proportional to the relative cover of a species within a site and year. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

Appendix 5: plots of open-field trait diversity models with interactions

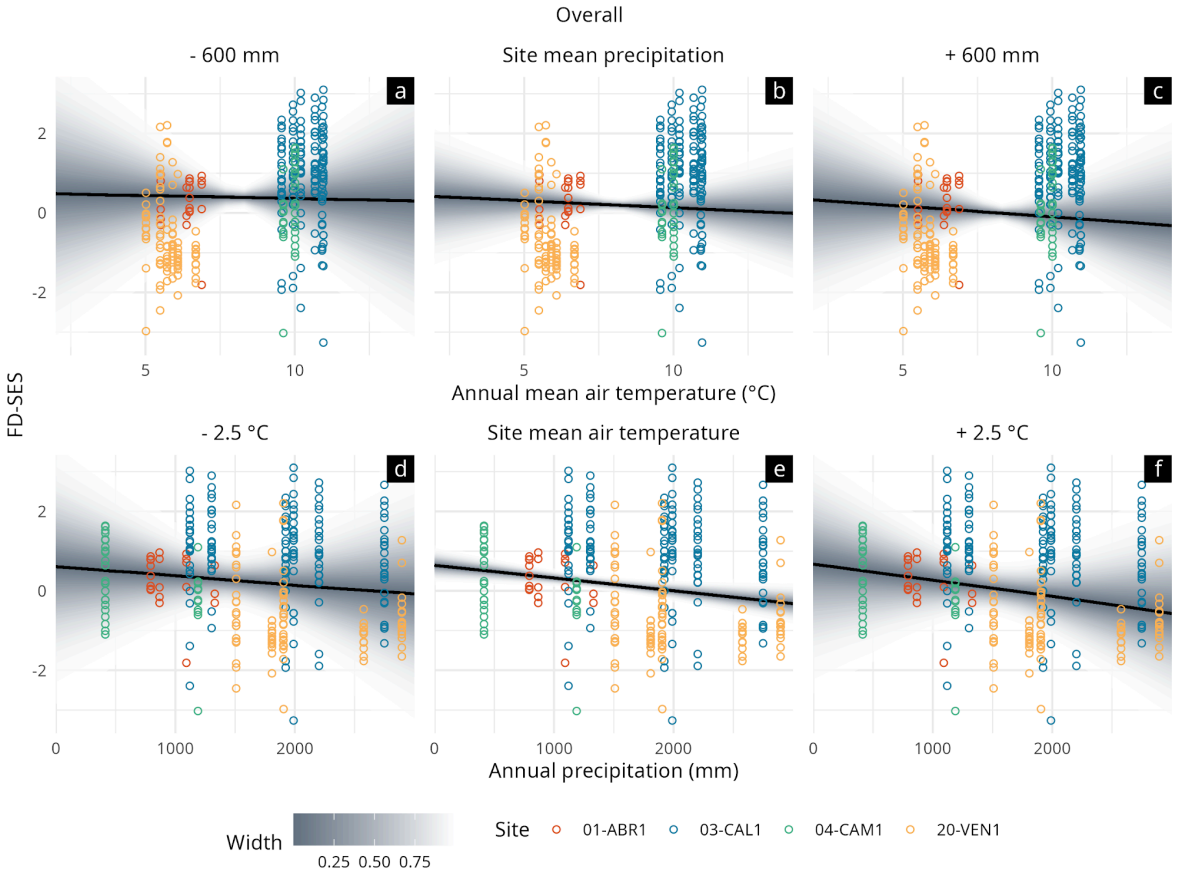


Figure 1. Posterior predictions of conditional effects for open-field mean air temperature (a–c) and precipitation (d–f) on the expectation of overall FD-SES, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

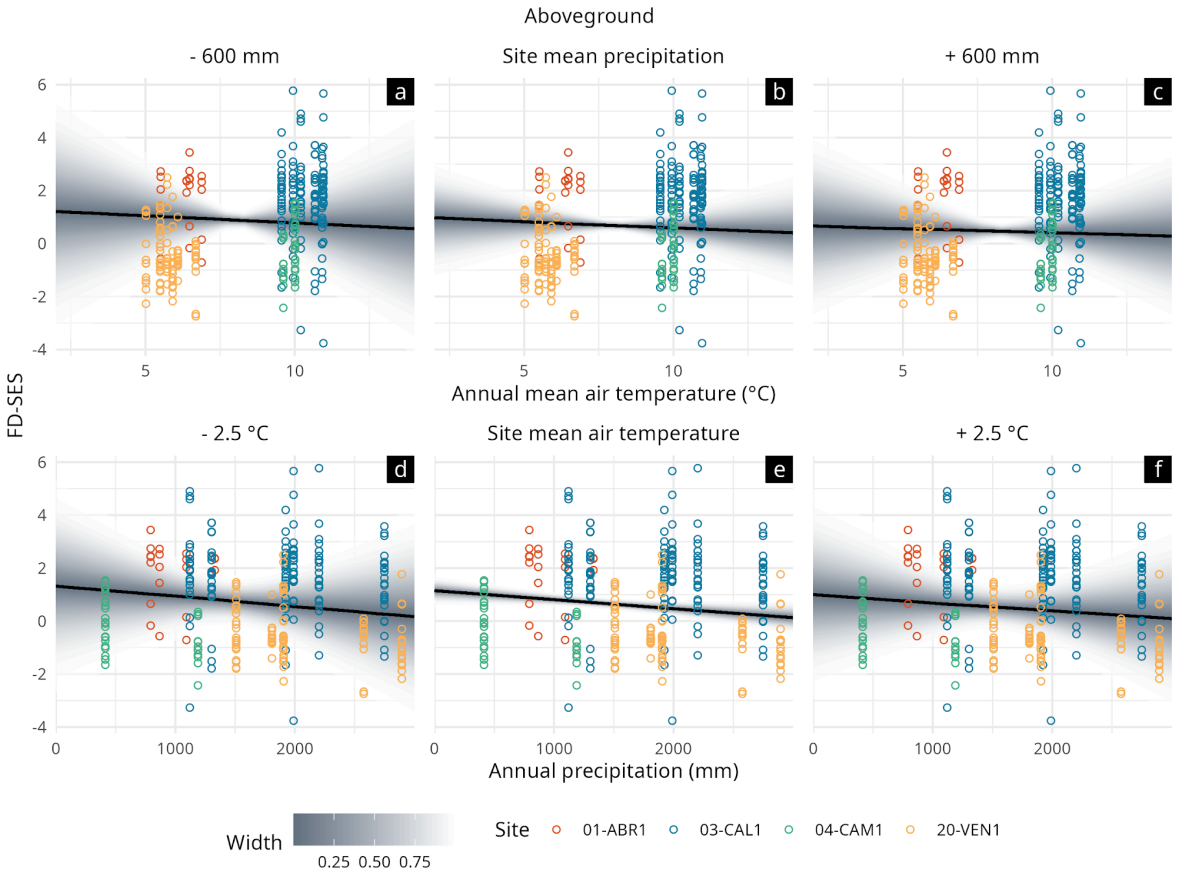


Figure 2. Posterior predictions of conditional effects for open-field mean air temperature (a–c) and precipitation (d–f) on the expectation of aboveground FD-SES, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

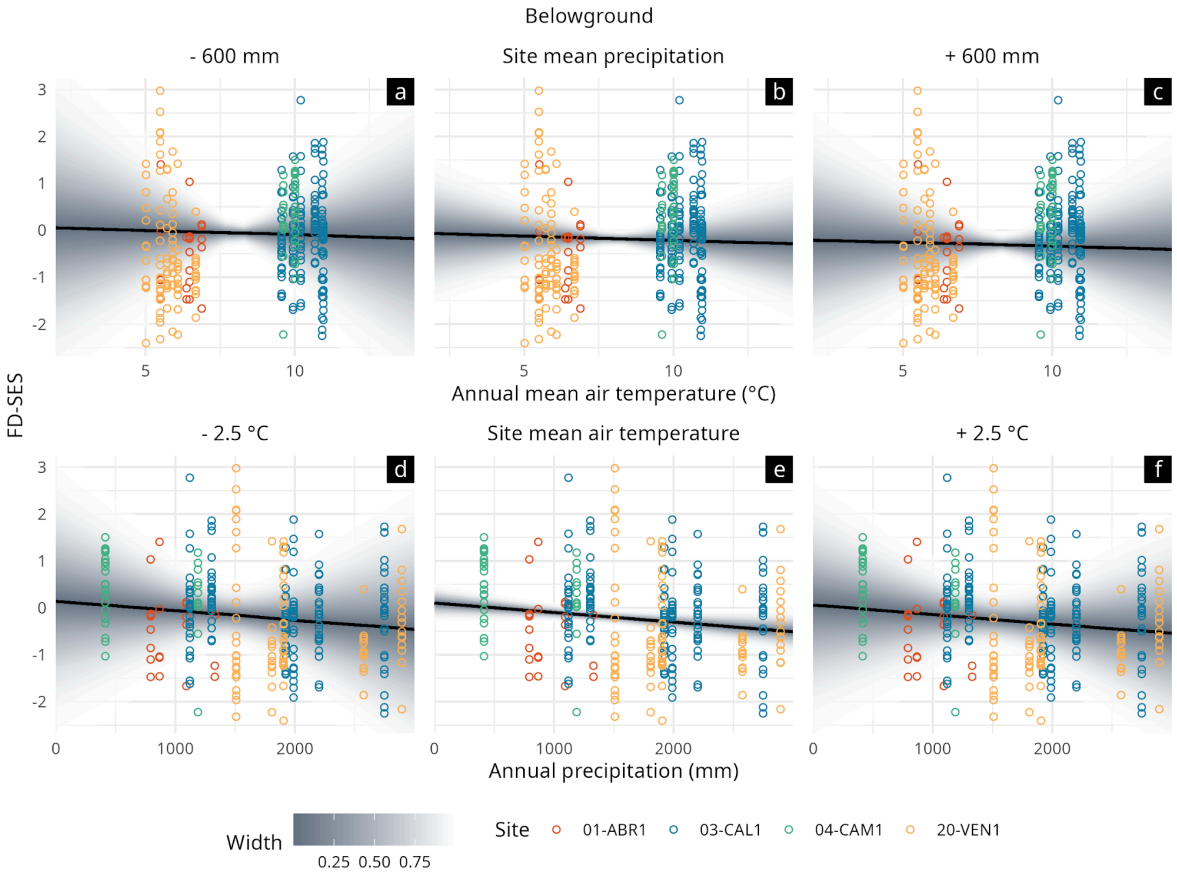


Figure 3. Posterior predictions of conditional effects for open-field mean air temperature (a–c) and precipitation (d–f) on the expectation of belowground FD-SES, together with data points. The predictions do not represent any specific site, but rather the effects of within-site variation for an average site. The solid black line corresponds to the posterior median, the grey shading to quantile intervals of increasing width. Interactions are shown as triptychs, with the other weather variable held at the site mean (b, e), one approximate standard deviation below (a, d), and one above (c, f).

Appendix 6: comparisons between weather and climate sources

	r	SD ratio	MA slope
Mean air temperature	0.98 (0.98–0.99)	0.96 (0.94–0.97)	0.96 (0.94–0.97)
Precipitation	0.78 (0.74–0.81)	0.82 (0.76–0.9)	0.78 (0.7–0.86)

Table 1. Correlations, standard deviation ratios (ITP/OFD), and major axis regression slopes between sub-canopy and open-field weather, for mean air temperature and precipitation.

Site	01-ABR1	03-CAL1	04-CAM1	20-VEN1
Longitude	13.58976	16.179124	15.428361	12.382952
Latitude	41.849678	38.426114	40.43414	46.057586
Annual mean temperature (°C) WorldClim	7.63	12.27	10.06	7.34
Annual mean temperature (°C) CHELSA	6.35	11.85	9.15	6.35
Annual mean temperature (°C) measured	6.48	10.4	9.73	6
Annual precipitation (mm) WorldClim	789	890	758	1069
Annual precipitation (mm) CHELSA	1178	1151	1059	1455
Annual precipitation (mm) measured	961	1879	1103	2108

Table 2. Comparison of gridded near current climate from WorldClim 2.1 (Fick & Hijmans, 2017) and CHELSA 2.1 (Brun et al., 2022) with open-field measurements, averaged across the monitoring period. WorldClim data refers to the period 1970–2000, CHELSA data to 1981–2010.

References

Brun, P., Zimmermann, N. E., Hari, C., Pellissier, L., & Karger, D. N. (2022). Global climate-related predictors at kilometer resolution for the past and future. *Earth System Science Data*, *14*(12), 5573–5603. https://doi.org/10.5194/essd-14-5573-2022

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086