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# Climate variability and aridity modulate the role of leaf shelters for arthropods: a global experiment

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**Running title**: Climate and the role of refuge for arthropods

**Abstract**

Current climate change is disrupting biotic interactions and eroding biodiversity worldwide. However, species sensitive to aridity, high temperatures and climate variability might find shelter in microclimatic refuges, such as leaf rolls built by arthropods. To explore how the importance of leaf shelters for terrestrial arthropods changes with latitude, elevation, and climate, we conducted a distributed experiment comparing arthropods in leaf rolls vs. control leaves across 52 sites along an 11,790 km latitudinal gradient. We then probed the impact of short- versus long-term climatic impacts on roll use, by comparing the relative impact of conditions during the experiment versus average, baseline conditions at the site. Leaf shelters supported larger organisms and higher arthropod biomass and species

diversity than non-rolled control leaves. However, the magnitude of the leaf rolls' effect differed between long- and short-term climate conditions, metrics (species richness, biomass, and body size), and trophic groups (predators *vs.* herbivores). The effect of leaf rolls on predator richness was influenced only by baseline climate, increasing in magnitude in regions experiencing increased long-term aridity, regardless of latitude, elevation, and weather during the experiment. This suggests that shelter use by predators may be innate, and thus, driven by natural selection. In contrast, the effect of leaf rolls on predator biomass and predator body size decreased with increasing temperature, and increased with increasing precipitation, respectively, during the experiment. The magnitude of shelter usage by herbivores increased with the abundance of predators and decreased with increasing temperature during the experiment. Taken together, these results highlight that leaf roll use may have both proximal and ultimate causes. Projected increases in climate variability and aridity are therefore likely to increase the importance of biotic refugia in mitigating the effects of climate change on species persistence.

## 1. INTRODUCTION

Global temperatures, the frequency of extreme precipitation events and temperature variability are all increasing at unprecedented rates (IPCC Climate Change, 2014; Donat *et al.*, 2016; Bathiany *et al.*, 2018). Local climates are predicted to become warmer and drier, making these environments less suitable for species to thrive and affecting their distribution (De Frenne *et al.*, 2019; 2021). Such changes are leading to shifts in the geographic ranges and elevational or vertical distributions in order to adjust their physiological optima, sometimes resulting in species–environment mismatches (Vázquez *et al.*, 2017; Essl *et al.*, 2019; Trisos *et al.*, 2020, De Frenne *et al.*, 2021). Climate change exacerbates the threat to biodiversity when combined with other human-caused changes such as the intensification of forest management and logging.

To escape unfavourable conditions, terrestrial species often use microclimatic refuges (Scheffers *et al.*, 2014; Suggitt *et al.*, 2018; Pincebourde and Casas, 2019). Microclimatic refuges, created by a variety of habitat structural components – including plant architectural complexity, tree bark, cracks in deadwood, downed woody debris, leaf litter, and leaf shelters – reduce the exposure of their inhabitants to climatic fluctuations and extremes in surrounding habitats (Scheffers *et al.*, 2014; Suggitt *et al.*, 2018 Pinsky *et al.*, 2019). Such refuges can be particularly important to ectotherms (Pinsky *et al.*, 2019), including arthropods. Ectotherms depend on external energy to thermoregulate and are amongst the taxa most threatened by global change (García-Robledo *et al.*, 2016; Warren *et al.,* 2018; van Klink et al., 2020; Wagner, 2020; Wagner *et al.*, 2021). Therefore, the availability of these refuges may be a factor mitigating negative effects of climate change on arthropods.

Many structural refuges are the by-product of activity of organisms known as ecosystem engineers (Jones *et al.* 1997; Romero *et al.*, 2015). For instance, stem borers and bark beetles make stem and trunk galleries, gallers manipulate plant physiology to produce galls, and various arthropods (e.g., caterpillars, aphids, mites and thrips) build leaf shelters, such as leaf rolls and ties, thus providing refuge to many other plant-dwelling organisms in terrestrial ecosystems (Appendix S1; Lill and Marquis 2007; Wang *et al.,* 2012; Lima *et al.*, 2013; Vieira and Romero, 2013; Cornelissen *et al.*, 2015; Priest *et al.*, 2021; Pereira *et al.*, 2022). The role of leaf-rolling engineers as biodiversity amplifiers can be even stronger in dry seasons and extend to the entire plant. As a result, they may influence arthropod assemblages at various temporal and microspatial scales (Vieira and Romero, 2013; Pereira *et al.*, 2021). When abandoned by their creators, leaf shelters become available for other arthropods, as the leaves retain their rolled shape (Lima *et al.*, 2013; Vieira and Romero, 2013).

Similar to many other biotic interactions that are more important at lower latitudes (Schemske *et al.,* 2009), the beneficial effects of vertebrate and invertebrate ecosystem engineers appear to be particularly pronounced in the tropics, but also in arid regions regardless of latitude (Romero *et al.*, 2015). These latitudinal, regional (Romero *et al.*, 2015)

and temporal patterns (Lima *et al.*, 2013; Vieira and Romero, 2013; Novais *et al.,* 2018) suggest that climatic conditions may be a common driver of such beneficial interactions.

Large-scale patterns in climatic signatures have recently been investigated using standardized, replicated experiments, allowing us to distinguish the direct effects of climate from the indirect effects of latitude or elevation on biotic interactions (e.g., Callaway *et al.*, 2002; Roslin *et al.*, 2017; Romero *et al.*, 2018). Most of these macroecological studies have focused on antagonistic interactions, such as predation and competition. Although the importance of facilitative interactions among organisms is expected to increase under stressful conditions (Callaway *et al.*, 2002; He *et al.*, 2013; Romero *et al.*, 2015), no empirical studies to date have examined the impacts of current climate and climate variability, or predicted the impacts of future climates, on facilitative interactions at a global scale.

Although poorly understood, patterns in facilitative interactions may be determined by both short- and long-term climatic conditions. In terms of shelter use by arthropods, local arthropods may increasingly pack into protective spaces during spells of inclement weather. Such a response will be short-term and behavioural in nature, which is in line with the proximate causation notion (Mayr, 1961; Laland *et al.*, 2011). Yet, arthropods in areas characterised by more challenging conditions over time may eventually adapt to more widespread shelter use. This response will be long-term and evolutionary in character, which is in line with ultimate causation notion (Mayr, 1961; Laland *et al.*, 2011). To understand the consequences of current global change, it is important to distinguish the relative impact of these two factors. Here, we conduct a globally-distributed experiment, aimed at establishing the facilitative mechanisms provided by leaf-rolling ecosystem engineers. By providing artificially-constructed leaf shelters under different combinations of short- versus long-term climatic conditions, we aim to tease apart the relative impact of the two.

Reflecting the benefits of leaf rolls for arthropods to withstand inclement conditions, we hypothesized that species richness and biomass of arthropods within leaf rolls would increase with increasingly harsh climatic conditions, such as aridity (Maliva & Missimer,

2012). Reflecting a behavioural response, we expected an increasing diversity and biomass of arthropods with harsher conditions during the experiment. Reflecting the evolutionary history of the organisms involved, we expected increasing shelter use where baseline conditions are harsh, after accounting for conditions during the specific experimental period. We also expected species responses to climate to vary with trophic position and body size, both of which are known to influence the metabolic requirements of ectotherms (Daufresne *et al.,* 2009) and their ability to dissipate heat (Schmitz and Barton, 2014; Rubalcaba *et al.,* 2019) - both aspects of which are likely mitigated by shelter use. In particular, competition among predators could select for larger body size of species using the shelters. In addition, larger-bodied organisms typically require more favourable climatic conditions than their smaller prey (Petchey et al., 1999; Voigt et al., 2003; Brose et al., 2012). Finally, with continuing climate change, we predict changes in time to reflect current patterns in space, i.e., increasing dominance of larger-bodied predators in increasingly arid and climatically variable regions.

## 2. MATERIAL AND METHODS

To test our specific predictions, in 2017-2019 we conducted a global, coordinated experiment at 52 sites across an 11,790 km latitudinal gradient (from 45.8° S to 60.2° N, Fig. 1) and elevation spanning from 5 m to 2,900 m above sea level. To measure leaf roll occupancy, we recorded arthropods colonizing manually-rolled and control (unrolled) leaves. We then calculated the standardized mean difference (Hedges' d) between species richness, biomass and body size in rolled and on control leaves for each site. To test how current climatic conditions (i.e. weather during the specific experimental period) vs baseline climate (i.e., historical averages of three decades; Baker *et al.* 2016) influence shelter colonization, we investigated their effects as moderators (predictor variables) on the Hedges' d effect size. Finally, we provide geographical interpretations of climate change scenarios on the patterns of refuge use, and predict future changes in refuge use by projecting effect sizes to future (2070) climatic conditions at the study locations (Fig. 2).

### 2.1 Study sites

The 52 sites spanned diverse types of biomes, including tropical and temperate forests, xeric shrubland (caatingas), savannas, etc. and covered a wide range of combinations of short-versus long-term climatic conditions. Each experiment was conducted in the season of highest local arthropod activity (e.g., spring-summer and/or warm/wet conditions). We considered our sites spatially independent, as 94% of them were at least 500 km apart from each other. A detailed description of the sites, including environment, plant features and arthropods surveyed, is provided in Table S1, Table S2, Appendix S2, and in Pereira *et al*. (2022).

## 2.2 Global experiment and arthropod samples

Experiments at all 52 sites were conducted following a standardized protocol. Each experiment followed a randomized block design. For each site, we randomly selected 10 to 20 paired trees (hereafter, a pair of plants is referred to as a block). Paired plants within a block were at least 2 m apart. Blocks were at least 6 m apart from each other (Fig. 2). In most sites, the experiment was conducted using a single native plant species, typically the locally most common species. However, in some tropical forests, due to high species diversity and low relative density, we used different plant species among blocks, with plants within a pair always belonging to the same species. We used only broadleaf native plant species that did not exhibit any obvious type of indirect defence (e.g., domatia, extra-floral nectaries, glandular trichomes) (Romero and Koricheva, 2011).

One plant per block was randomly selected as a control plant, while the second plant was used for the leaf-rolling (shelter addition) treatment. On each plant, we selected 5-10 fully expanded leaves without obvious damage (hereafter referred to as 'sample unit'). Prior to the experiment, any arthropods present on experimental leaves were removed by hand. Then, the leaves of the treatment plant were rolled by hand from the adaxial to the abaxial surface across the leaf axis to form a cylinder approximately 0.6 cm in diameter (Fig. S1) to mimic shelters built by caterpillars - a phenomenon occurring in at least 17 moth and butterfly families, including Hesperiidae, Nymphalidae, Gelechiidae, Oecophoridae,

Lasiocampidae, Pyralidae, Gracillariidae, Tortricidae, Geometridae, Erebidae (Fitzgerald *et al.*, 1991; Fukui, 2001; Lill and Marquis, 2007). The leaf rolls were secured with a metal hairpin (see Fig. S1 and Vieira and Romero, 2013). In the control plants, 5-10 unrolled leaves were marked with a metal hairpin. Rolled and control leaves were exposed for 10 days in the field – this was deemed sufficient as previous bioassays showed that leaf shelters can be colonized very quickly (within 24 hours) (Vieira and Romero, 2013, Pereira *et al.*, 2021; G.Q. Romero, K. SAM, *pers. obs.*), and that species richness within leaf rolls reaches saturation within a few days (Vieira and Romero, 2013). Moreover, leaf abscission was observed in some plant species during the 10-day experiment (e.g., *Psychotria*, G.Q. Romero, pers. obs.), thus precluding experiments of longer duration. Maximum width of both control and rolled leaves was measured as an estimate of leaf size.

After 10 days of the experiment, we collected rolled and control leaves and stored them grouped by replicates and treatments; both control and rolled leaves were quickly placed into a zip-lock plastic bag and sealed. The leaves were either frozen for later sorting or immediately sorted to collect the invertebrates. We collected all the invertebrates visible to the naked eye (except mites) and stored them in ethanol. Mites could not be considered in the analysis, because identifying both mite taxa and feeding guilds is extremely difficult, with very few specialists worldwide. We identified the invertebrates to the lowest taxonomic level possible and classified them into morphospecies and feeding guilds (i.e., predator, parasitoid, herbivore, detritivore, omnivore; see Appendix S2). However, the sample size was only sufficiently large for separate analyses of predators and herbivores. Individual body size (dry body mass) was estimated from the dry mass (dried at 70°C for 24h) or by measuring total body length and then calculating the dry mass using published taxon-specific allometric equations (Hódar, 1996). Three dependent variables were used for the analyses: species richness, community biomass, and mean individual body size. As expected, total abundance explained much of the species richness ($R^2 = 0.78$, $F_{1,50} = 185.5$, P<0.001). Because of the small subsamples (5 to 10 leaves per plant), which would lead to highly stochastic results (Gotelli & Colwell, 2001), we were unable to determine rarefied species richness. Therefore, we focus our analyses on the number of species (richness) and assume that this is a product of increased overall abundance. Arthropod biomass represents the sum

of all individual body masses. Arthropod richness and biomass were weighted by the number of leaves sampled per plant (e.g., number of species per leaf), and average individual body size was calculated for each sampling unit by dividing the total biomass for each feeding guild (predator or herbivore) by the number of arthropods within that feeding guild - thus, the sample unit for body mass is the average mass per arthropod upon leaves.

To test for global gradients in the background occurrence of leaf rolls across the studied sites, we classified the frequency of natural rolls observed during the 10-day experiments on a scale from "never" (if we never saw caterpillar-created leaf rolls in their sites) through "occasionally" (if we saw one to two leaf rolls) to "often" (if we saw three or more leaf rolls in their sites). We found that leaf rolls were found "often" at 72.8% of the sites, "occasionally" at 15.1% of the sites, and "never" at 12.1% of the sites. These findings highlight that the frequency of natural leaf shelters is high at most sites studied. To test the assumption that shelter frequency is associated with precipitation, we ran a Generalized Linear Model (GLM) assuming a binomial error distribution, using the observed scores along the precipitation gradient ($PC1_{precipitation}$) as the predictor and natural shelter frequency (often vs. occasionally+never) as the response variable.

## 2.3 Climate, topography and productivity data

To (i) establish the relative impact of short- vs long-term climatic conditions on shelter use by arthropods, and (ii) thereby predict the effects of future climate variability on refuge usage (Fig. 1), we extracted site-specific information on the climate conditions prevailing during the experiment and on historical baseline climate (Baker *et al.*, 2016). For these purposes, we used the coordinates of each site to determine the identity of the surrounding grid square in the relevant climatic database (for the specific resolution per variable, see below).

Data on mean daily local precipitation, near-surface humidity, and temperatures during the 10-day experiment were extracted from the RNCEP database (Kemp *et al.,* 2012). The RNCEP database has a spatial resolution of 2.5 arc-minutes and a temporal resolution of 6 h (Kemp

*et al.,* 2012). We then used these data to calculate site-specific averages over the experiment. A detailed description of the variables is presented in Table S3.

Baseline climate data and topographic data were extracted from WorldClim (Fick and Hijmans, 2017) version 2 (http://www.worldclim.com/version2) and ENVIREM (Title and Bemmels, 2017) (https://envirem.github.io/). Bioclimatic variables from WorldClim and ENVIREM are averages of the years 1970-2000, and 1960-1990, respectively. For each site, we selected four variables for temperature (bio1, bio2, bio4, bio7), four variables for precipitation (bio12, bio14, bio15, Aridity), two variables for topography (TRI and topoWET), and one variable for site productivity (AnnualPET), following Romero *et al.*, (2018). A detailed description of the variables is presented in Table S3. WorldClim variables were extracted at 30 arc-second, 2.5 arc-minute and 10 arc-minute resolutions. The variables TRI and topoWET from ENVIREM were only available for resolutions of 30 arc-seconds. The variables Aridity and AnnualPET were extracted at resolutions of 30 arc-seconds and 10 arc-minutes, respectively. To establish whether variables measured at different resolutions could be used together, we compared the correlation structure among different resolutions and found them to be strongly correlated (Pearson correlation, r≥0.97), regardless of the type of variable and database (WorldClim and ENVIREM). Thus, we inferred that data measured at different scales were technically interchangeable.

Data on future climatic conditions were extracted from WorldClim version 2, using MIROC5 (RCP8.5) and CCSM4 (RCP8.5), as representing likely concentration pathways of $CO_2$ emissions projected for 2070 (Romero *et al.*, 2018). We focused our predictive analyses using bioclimatic variables solely from WorldClim, as future bioclimatic variables are not available in the ENVIREM databases. Since the bioclimatic variables were very strongly correlated between the MIROC5 and CCSM4 predictive climate models (Pearson correlation, r ≥ 0.98), we focused our analyses on the MIROC5 (RCP8.5) database.

## 2.4 Statistical analyses

*Effect size calculations*

While the experiment followed a standardized protocol across sites, sampling was performed by different researchers in different biomes. Therefore, we used a meta-analysis (meta-regression) approach to control for sampling bias (Gurevitch, 2013). The magnitude of the leaf shelter effect on arthropod community structure (measured as species richness, biomass and body size) was calculated at the site level (n = 52 sites) using Hedges' d (standardized mean difference; Rosenberg *et al.*, 2013) following the formula:

$$Hedges' \ d \ = \ \frac{Xe - Xc}{SDpooled},$$

where *Xe* and *Xc* are the mean community measures (dependent variables in Fig. 2A) for plants that had their leaves rolled and control plants, respectively, and *SDpooled* is the pooled standard deviation of the two groups. Positive effects indicate that leaf rolls had higher arthropod species richness, biomass or mean body size relative to the control leaves (Fig. 2A). Values around 0.2, 0.5 and 0.8 are considered small, medium and large effect sizes, respectively (Rosenberg *et al.,* 2013). Larger effect size values mean larger differences in occupation of rolled compared to control leaves.

*Moderators (predictors)*

To test our original predictions, we investigated the impact of different categories of moderators, including absolute latitude and elevation, as well as baseline climate, climate (weather) during the 10-day experiments, productivity (annualPET), topography (TRI, topoWET), and leaf size (width). Additional local moderators included available potential prey (abundance of herbivores) for predators, and abundance of predators on experimental leaves (control plus rolled) for herbivores (Fig. 2B).

To characterize local historical climatic conditions, we first reduced the dimensionality of the climatic data. Thus, we projected separately precipitation and temperature variables in multivariate space using principal component analysis (PCA, Fig. 2B) (Romero *et al.*, 2018).

The first axis of PCA for temperature variables (PC1$_{temperature}$) explained 78% of the total variance and was thus adopted as a gradient spanning from higher temperature variability to warming and lower temperature variability. Conversely, the first axis of PCA for precipitation variables (PC1$_{precipitation}$) explained 64% of the total variance and was used to represent a rainfall (dry to wet) gradient (Fig. 1) (Figs. S2-S3).

PC1$_{precipitation}$ included mean annual precipitation (bio12), precipitation of driest month (bio14), index of the degree of water deficit below water need (aridity) and precipitation seasonality (coefficient of variation) along the year (bio15) (Table S3). The only variable included to denote rainfall variability (bio15) did not contribute much to the PCA1 variance (Fig. S2). Therefore, PC1$_{precipitation}$ was interpreted as representing a rainfall gradient, which varied from arid (negative values, mostly explained by aridity) to wet conditions (positive values, mostly explained by bio12) (Fig. S2). Given that most arthropods are favoured by humidity within the observed range, sites characterized by higher PC1$_{precipitation}$ scores were then defined as being climatically more benign.

PC1$_{temperature}$ included mean annual temperature (bio1), mean diurnal range (bio2), temperature seasonality (bio4) and temperature annual range (bio7). For ease of interpretation, the signs of the original PC1$_{temperature}$ scores were multiplied by -1, thus producing a gradient from lower temperatures and higher temperature variability (negative values) to warmer sites with lower temperature variability (positive values). Sites defined as being thermally more variable were those characterized by higher intra-annual (e.g., bio4, bio7) or diurnal (e.g., bio2) variation in temperature (Fig. 1, Fig. S3).

*Meta-analysis*

We tested the effects of moderators on Hedges' d effect sizes using the rma function of the *metafor* (version 2.1-0) package (Viechtbauer, 2010) in the R environment (R Development Core Team, 2019). Prior to analyses, we examined outliers using diagnostic plots (Cook's distance), removing data points with a Cook's distance > 1. We visually checked normality of residuals using normal quantile–quantile (Q–Q) plots; our models showed appropriate

behaviour with respect to residuals and outliers. The overall effect size was determined by random-effects models and moderators were examined by mixed-effects models (Viechtbauer, 2010). Such mixed-effects models were obtained using a restricted maximum likelihood (REML) estimator, assuming random variation among replicates within a treatment (control or experimental), and fixed variation among treatments.

Effect sizes were considered statistically significant if their 95% confidence intervals did not overlap with 0. Some moderators were collinear (Fig. S4) and were thus removed from the models based on their variance inflation factor (VIF) (Zuur *et al.,* 2010). The removed moderators were Latitude, topoWET, and AnnualPET. All remaining moderators had a VIF < 2. The best-fitting linear models were then determined by backward selection (Fig. 2B); the best models retained were those that had the smallest Akaike Information Criteria corrected for small sample sizes, AICc (ΔAICc>2). AICc values were obtained using the *rma* function of the *metafor* package (version 2.1-0) (Viechtbauer, 2010). Null models (intercept effects only, i.e., no moderators included) were contrasted with models containing moderators plus the intercept. To test whether climate mediates antagonistic relationships between herbivores and predators, we included interactions between predator abundance and climate components in the full models for herbivore richness, biomass, and body size.

*Predicting temporal variations*

As our results indicated a stronger impact of long-term than short-term climatic conditions on predator richness, we used the associations between average, site-specific conditions and the changes in long-term climatic conditions predicted by climate scenarios to predict the effect of future climate change. For this purpose, we extrapolated the effect of ecosystem engineers on arthropods using the fitted models of effect sizes (Hedges' d) obtained at the experiment scale (step 3, Fig. 2C).

The magnitudes of the engineering effects on arthropod communities observed at each site and their association with climatic variables (see Table S3 for variable definitions) were tested using linear models (assuming a Gaussian error distribution). We used the function

*predict.lm* to obtain the predicted relationship between independent variables and the Hedges' d effect size (richness and biomass) (n = 52). Temperature (bio1, bio2, bio4, bio7) and precipitation (bio12, bio14, bio15) were included as independent continuous variables in separate models (see Table S3 for variable definitions). Here, we note that we used separate climatic variables rather than the principal component scores identified in our meta-analyses because the correlation structure among variables may shift with climate change. If such a shift occurs, the parameter predictions based on aggregate variables built from a specific covariance structure would be biased (Hadi and Ling, 1998).

For both temperature and precipitation climatic models most variables were collinear (see Figs. S2 and S3). We therefore first eliminated the influence of collinearity using the variance inflation factor, VIF (Zuur *et al.,* 2010). We then reduced the model through backward selection, retaining only the significant variables and those that improved the model fit (i.e., higher $R^2$ values). To produce maps providing a geographical interpretation of global ecological patterns, we adopted the approach of Tallavaara *et al.* (2018) and Gusmão *et al.* (2020). To model the current climate and scenarios projected to 2070, we adopted the approach of using rcp8.5 (MIROC5) as a general circulation model. We used graphical inspections (e.g., qq-plots, Cook's d, and influence) to check residual normality, homoscedasticity, and outliers, log-transforming the response variables when necessary. To reduce computational time, these predictions were made using variables at 10 arc-min resolution.

Model performance was tested using a *k*-fold cross-validation approach, which consists of splitting a dataset into k folds, where a fraction of the original dataset in each fold is randomly selected to fit a model and the other part used to measure the error of the model on unseen data. Each fold yields a measure of generalization error, and with the final performance measured as the average error across all k folds. A model with good generalization ability is the one in which the error on the unseen data is close to the error reported by the model in the data used to fit it (see details in Appendix S3, Fig. 2C).

## 3. RESULTS

### 3.1 Current interactions

Overall, predators, herbivores and the pooled arthropod assemblages including all feeding guilds (predators, herbivores, detritivores, parasitoids, omnivores) were strongly influenced by the presence of leaf rolls on plants (Fig. 3). Arthropod richness, biomass and mean body size were significantly higher in rolled compared to control leaves (as revealed by positive Hedges' d values, with 95% confidence intervals not spanning 0).

The effects of leaf rolls on pooled arthropod assemblages were found to be mediated solely by weather, specifically by the average temperature prevailing during the experiment (Table 1). The magnitude of the effect of leaf rolls on biomass and on the average body size of the pooled arthropod assemblages decreased with increasing temperature during the experiment (Table 1, Fig. 4).

The influence of climate on the response to the presence of leaf rolls varied between predators and herbivores. The effects of leaf rolls on predators were mediated solely by climate, but the effects of precipitation and temperature varied depending on the type of meteorological variable (weather during the experiment or baseline historic climate) and the particular predator metric examined (richness, biomass, body size). The magnitude of the effect of leaf rolls on predator richness increased with baseline, long-term aridity ($PC1_{precipitation}$, Table 1, Fig. 5a). In contrast, the effect size of leaf rolls on predator biomass and predator body size, respectively, decreased with increasing short-term (i.e. during the experiment) temperature, and increased with increasing short-term precipitation (Table 1, Fig. 5b,c). Predator biomass within leaf shelters and on control leaves was positively correlated with predator body size (shelter: r=0.82, df=45, t=9.6, P<0.001; control: r=0.94, df=38, t=16.6, P<0.001), but not with predator abundance (shelter: r=0.23, df=46, t=1.6, P=0.11; control: r=0.14, df=46, t=0.98, P=0.33).

In contrast to the effect of leaf rolls on predators, the positive effects of leaf shelters on the magnitude of the effect on herbivore richness and biomass decreased with mean

temperature during the experiment and increased on leaves with a higher abundance of predators, respectively (Table 1, Fig. 5). Herbivore biomass within leaf shelters and on control leaves was strongly positively correlated with the mean body size of the individuals (shelter: r=0.88, df=45, t=12.4, P<0.001; control: r=0.74, df=36, t=6.7, P<0.001), but not with their abundance (shelter: r=0.05, r=46, t=0.37, P=0.71; control: r=0.13, df=46, t=0.88, P=0.38). Average herbivore body size was 41% smaller than average predator body size (Fig. S5).

Other moderators such as latitude, elevation, ecosystem productivity, topography, and local average humidity during the experiment did not influence the effects of shelters on arthropods (Table 1).

In terms of the background occurrence of leaf rolls in the landscape, we found no association between the frequency of natural leaf rolls and climatic conditions ($PC1_{precipitation}$) of the studied sites (see Appendix S1).

### 3.2 Interactions under future predicted scenarios

The magnitude of the effect of refuge on predator richness is expected to increase by up to 33% in areas where baseline precipitation is predicted to decline (e.g., French Guiana and Mexico). In contrast, with increasing baseline precipitation predicted for sites in Europe, USA, and Borneo, the effects of refuge on predator species richness are expected to decrease by up to 25% (Fig. 6). Key bioclimatic variables reflecting precipitation (e.g., bio14) are predicted to be more variable over time in the study sites than key temperature variables (e.g., bio7) (Appendix S4).

### 4. DISCUSSION

Our results show that leaf rolls increase the leaf-level richness, biomass, and mean body size of arthropods from different trophic levels on all four continents where the experiments

were conducted. These results suggest that leaf rolls are used as structural refugia by arthropods. Both long-term climate and weather during the experiment were found to influence arthropod occupancy of leaf rolls, but the effects of climate differed by trophic level and by the specific community metric considered (richness, biomass, and body size). Importantly, long-term conditions have left a clear imprint on regional patterns of shelter use: as baseline aridity increased, more predator species used leaf shelters. In addition to the impact of historical climate, we found clear behavioural responses to specific conditions prevailing during the experiment: with increasing temperature during the experiment, the extent of shelter use by predator biomass, herbivore richness, and biomass and average body size of the full communities decreased. In addition, the effect size of shelter use by larger predators and herbivores, respectively, increased with increasing precipitation during the experiment and with predator abundance. Taken together, these findings pinpoint both short- and long-term climatic effects on shelter use by arthropods and highlight that the realised usage of leaf rolls can be traced to both proximate (weather during the experiment) and ultimate causes (historic climate) (see Laland *et al.*, 2011). As a proximate cause (i.e., short-term plasticity), predators and herbivores might gain protection against cold, heavy rain, and also predation, by colonizing leaf shelters. As an ultimate cause, natural selection appears to be driving predators' shelter use behaviour, revealed here by a greater number of predator species using shelters in locations that are predictably arid.

How aridity affects the evolution of refuge use by predatory arthropods remains to be experimentally established. It is likely that aridity may shape species diversity and composition within leaf shelters, as the refuges might be occupied by species sensitive to desiccation. Leaf shelters could provide them with local moisture via leaf transpiration and provide stable microclimatic refuges from long periods of drought. Such a mechanism might be revealed by future experiments with artificial rolls made out of non-transpiring versus transpiring materials.

In terms of specific adaptations to aridity, we note that the bioclimatic variables used to characterize long-term conditions at each site consist of both annual means and variances (Fick and Hijmans, 2017). If communities of predators experience higher climatic variability

and aridity during at least part of the year, then shelter use by predators might be favored by selection. This hypothesis is supported by the fact that increased precipitation over the duration of the experiment (average precipitation over 10 days) did not mediate the influence of shelters on predator richness, but surprisingly increased the incidence of larger predators on shelters. It is likely that large predators in particular, display higher competitive ability, and thus may rely on and dominate the refuges, especially during rain. Predators (e.g., spiders) are known to actively select sheltered microhabitats in harsh conditions and fire-prone environments (de Omena and Romero, 2010; de Omena *et al.* 2018). Therefore, we suggest that the behaviour of using leaf shelters might be an adaptive response to arid conditions.

In contrast to predators, herbivores showed no increase in shelter occupancy with increasing aridity. For them, shelter occupancy varied detectably only with the temperature prevailing during the experimental period, and with increasing frequency of predators on the plants. This difference among herbivores and predators may potentially be traced to a difference in resource use and nutritional physiology. Unlike many predators, herbivores can build their own refuges using plants (Pincebourde and Casas, 2019) and have access to a more predictable source of water from food (green leaves). Predators rely on more stochastic water sources (e.g., prey hemolymph), which depend on prey capture rates. Thus, it is likely that terrestrial predators are more sensitive to arid conditions than herbivores (Schmitz and Barton, 2014). Indeed, harsh climatic conditions are known to be especially detrimental to arthropods of higher trophic levels (Voigt *et al.,* 2003; Stireman *et al.*, 2005; Brose *et al.,* 2012; Schmitz and Barton, 2014; Vasseur *et al.*, 2014; Colinet *et al.,* 2015; Horne *et al.*, 2017) and predatory arthropod taxa exhibit differential susceptibility to desiccation (Edney, 2012). Conversely, herbivores might seek refuge from predators under more stable and favourable climatic conditions (Tvardikova and Novotny, 2012), where predation pressure on larger herbivores is often high (Romero *et al.*, 2018). It is therefore likely that herbivores use leaf shelters more as a refuge against natural enemies (Baer and Marquis, 2020) than for protection against aridity - this hypothesis might be further tested by adding a further treatment to the experiment proposed above, i.e., leaf rolls made of transpiring versus non-transpiring material, consisting of leaf rolls with apparatus preventing predator

occupancy, thereby allowing us to tease apart the respective benefits of shelter used for herbivores.

In terms of short-term, behavioural responses, the temperature conditions prevailing during the experiment were found to strongly affect the total community biomass, which ultimately correlated with body size inside the shelters (see Results). This suggests that larger organisms (especially predators), and more herbivorous species, use leaf shelter as protection from cold and tend to use leaf shelters proportionally less at sites which had warmer weather during the experiment. In fact, the negative Hedges' d effect sizes were observed mostly under warmer conditions (see Figs. 4 and 5). There are two possible explanations for this, which are not mutually exclusive. First, arthropods tend to be more active in warmer weather and move outside the refuge more often to forage for food (Schmitz and Barton, 2014; Speights *et al.*, 2017). Metabolic constraints under warmer conditions are higher for larger organisms (Brown *et al.* 2004), which tend to be more active in finding food outside of shelter (Barton & Schmitz, 2009). In addition, in warmer weather, leaf shelters may act as heating chambers, producing warmer microclimate conditions inside them (Caillon et al., 2014), thus forcing larger organisms to move outside the shelters. Heat transfer (or dissipation) is known to be reduced in larger organisms due to their smaller surface area-to-volume ratio (Horne *et al.*, 2017; Kühsel *et al.,* 2017), which poses a threat in warmer climates.

Because our experimental design involved sampling individual leaves, and not the entire plant, we were unable to conclude whether the overall reported effects are due to arthropod recruitment from outside to plants with shelters, or if shelter use represents a redistribution of arthropods already present on the plant. We tentatively suggest that both mechanisms might play a role in this system (Lill & Marquis, 2004). Furthermore, it still remains to be investigated whether the secondary colonizers are long-term residents of the leaf shelters, or whether they only use shelters during the day. Again, we suggest that both behavioral features may occur in the system, with certain taxa (e.g., spiders and ants) being more resident, and others (parasitoids, hemipterans) taking refuge in the leaf rolls for a shorter period of time. In addition, our results might be limited to more mobile arthropods, as 10-d

experiments might act to limit the abundances of those arthropods which recruit to shelters via oviposition (e.g., many herbivores). This will occur since the duration of the experiment is relatively short as compared to the time needed for eggs to hatch. Future controlled experiments would help to understand the dynamics of refuge occupancy by varying taxa, and how local climate and body size can moderate such occupancy.

Arthropods comprise over two-thirds of all terrestrial species and are key elements in intricate food webs. They provide valuable ecosystem services, such as biological control, nutrient cycling, bioturbation and pollination. Because arthropods are ectothermic and closely dependent on external energy, they are also among the organisms most acutely threatened by ongoing global changes (van Klink *et al.*, 2020; Wagner, 2020; Wagner et al. 2021; Nessel *et al.*, 2021). With the increasing frequency of extreme droughts and heat waves, terrestrial arthropod communities may become more dependent on suitable microclimates (Pinsky *et al.*, 2019). Understanding how arthropods cope with climate extremes is therefore central to improved conservation and mitigation strategies (Marquis *et al.*, 2019). Effective strategies should identify and maintain local conditions, such as structural habitat components (created by arthropods, or others, such as crevices in bark and leaf axils), which promote suitable microclimate, thus buffering against climatic adversity. Here we present evidence that leaf rolls created by ecosystem engineers might mitigate predicted increases in climatic adversity such as aridity. Our results suggest that body size and trophic position have a major influence on microhabitat use. Since the openings of leaf rolls are likely size-selective filters determining the range of body sizes of potential colonists, other shelter types are likely to show different responses due to their accessibility. We therefore call for further studies investigating the role of different physical structures, including size and shape, in climate change mitigations. Finally, as a direct projection from observed patterns, we predict that future changes in climatic conditions could alter the global pattern of shelter use by predatory arthropods, ultimately influencing patterns of both short-term plasticity and evolution. Ecosystem engineers are expected to become more important in the future, especially for predators and in sites where precipitation is expected to decrease. Increased future usage of shelters by predators might then alter predation risk on herbivores, and even strengthen intraguild predation pressure.

Our results point to larger predators as the dominant organisms using leaf shelters. This dominance likely results from higher competitive dominance and/or higher sensitivity to harsh climatic conditions, which are predicted to increase in frequency in the near future (IPCC Climate Change, 2014). The leaf shelters can act as refuges by mitigating climatic variation and harsh conditions, allowing predators to rapidly adjust their use of niche space according to their physiological tolerances. This result calls for further studies investigating direct measures of physiological benefits of shelter occupancy for a range of organisms, including the shelter builders (e.g., Trzcinski et al., 2021). The ability to forage from such shelters may still have a strong influence on their overall performance and on the overall imprint of climate on arthropod community change and behavioural adaptations. Increasing aridity may reduce the ability of these predators to forage and thus to perform important ecosystem services (Barton and Schmitz, 2009; Rosenblatt and Schmitz, 2016), such as biological control (Schmitz and Barton, 2014). Likewise, increasing refuge usage by predators is expected to displace herbivores into suboptimal microclimates under climate change (Barton and Schmitz, 2009). Asymmetric reliance on refuge use by predators and prey, and mismatch between predator and prey encounter rates, could lead to asymmetric extinctions of larger herbivores and predators (Clark *et al.,* 2020). Thus, the current patterns of climatic impacts on refuge use here observed, and their extension into the future strongly suggest possible ecosystem change. While the validity of these scenarios remains to be established, we hope that our study will be taken as a source of data-driven hypotheses to test, and as a blueprint for concrete experiments to be conducted. With this work, we have pinpointed an intersection between studies of ecosystem engineers and microclimatic impacts as an important avenue for future research on ecosystem functioning and community ecology.

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.

**Figure legends**

**FIGURE 1** Gradients of baseline precipitation (a) and temperature variability (b) projected across the globe. The colour gradients represent the first axis (PC1) of a principal component analysis of climatic variables. Negative values represented by light colours (greenish to yellow) denote unstable climatic conditions and arid regions, and positive values (dark, blue to purple colours) denote stable temperature and precipitation conditions. The main bioclimatic variables contributing to positive and negative values of the PC1 scores are presented below the colour gradient legends, along with their Pearson moment correlation coefficients, r, with PC1. Open circles indicate the study sites. See supplementary Table S3 for definitions of the bioclimatic variables.

**FIGURE 2** Schematic representation of the experimental design, effect size calculations (a), moderators, and analytical steps to achieve the results, including model selection (b). Construction of predictive maps, as well as cross validation to validate the maps (c).

**FIGURE 3** Effect sizes (Hedges' d) of ecosystem engineering on richness, biomass (standing stock) and body size of predators, herbivores and all surveyed organisms pooled together (predators, herbivores, detritivores, omnivores and parasitoids). Error bars represent 95% confidence intervals. Effects are considered significantly different from 0 if 95% confidence intervals do not cross 0.

**FIGURE 4** Effects of experiment temperature on effect size (Hedges' d) of community biomass (a) and average body size (b) of all surveyed organisms pooled together (predators, herbivores, detritivores, omnivores and parasitoids). Each dot represents a site.

**FIGURE 5** Effects of baseline historic precipitation stability ($PC1_{precipitation}$) on effect size (Hedges' d) of predator richness (a). Effects of experiment temperature ($^{o}C$) and precipitation (mm) on Hedges' d of predator community biomass (standing stock) (b), average predator body size (c), and herbivore richness (d). Effects of predator abundance upon leaves (# per leaf) on Hedges' d of herbivore biomass (e). Each dot represents a site.

**FIGURE 6** Difference in Hedges' d values between the future climate (2070) and baseline climatic effect size for predator richness. A value of zero (0) denotes no shift, whereas positive values imply an increased effect size, and negative values imply a decreased effect size. Predicted values for richness were based on precipitation of the driest month (bio14) and temperature annual range (bio7), respectively, assuming the RCP8.5 (MIROC5) global climate model (see Methods).

**TABLE 1** Best-fitted linear models, following backward selection, examining the effects of average local temperature, precipitation and humidity during the experiment, as well as baseline climate (i.e., $PC1_{precipitation}$, $PC1_{temperature}$), elevation, TRI and leaf size, on the standardized mean difference (Hedges' d) of total organisms (a), predators (b) and herbivores (c). Additional moderators for predators and herbivores included abundance of herbivores and of predators on experimental leaves, respectively. Full models for herbivores included interactions (abundance of predators:climate; abundance of predators:climate), but they were removed during backward selection procedure. Probabilities were calculated using Wald-type tests ($z$-test), and significant values are in bold. Empty cells (-) or omitted moderators denote moderators removed during backward selection procedure. Best-fitted models presented the smaller Akaike Information Criteria corrected for small sample sizes, AICc. Full versus reduced (final) models were discriminated using AICc. See Table S3 and Methods for variable definitions.
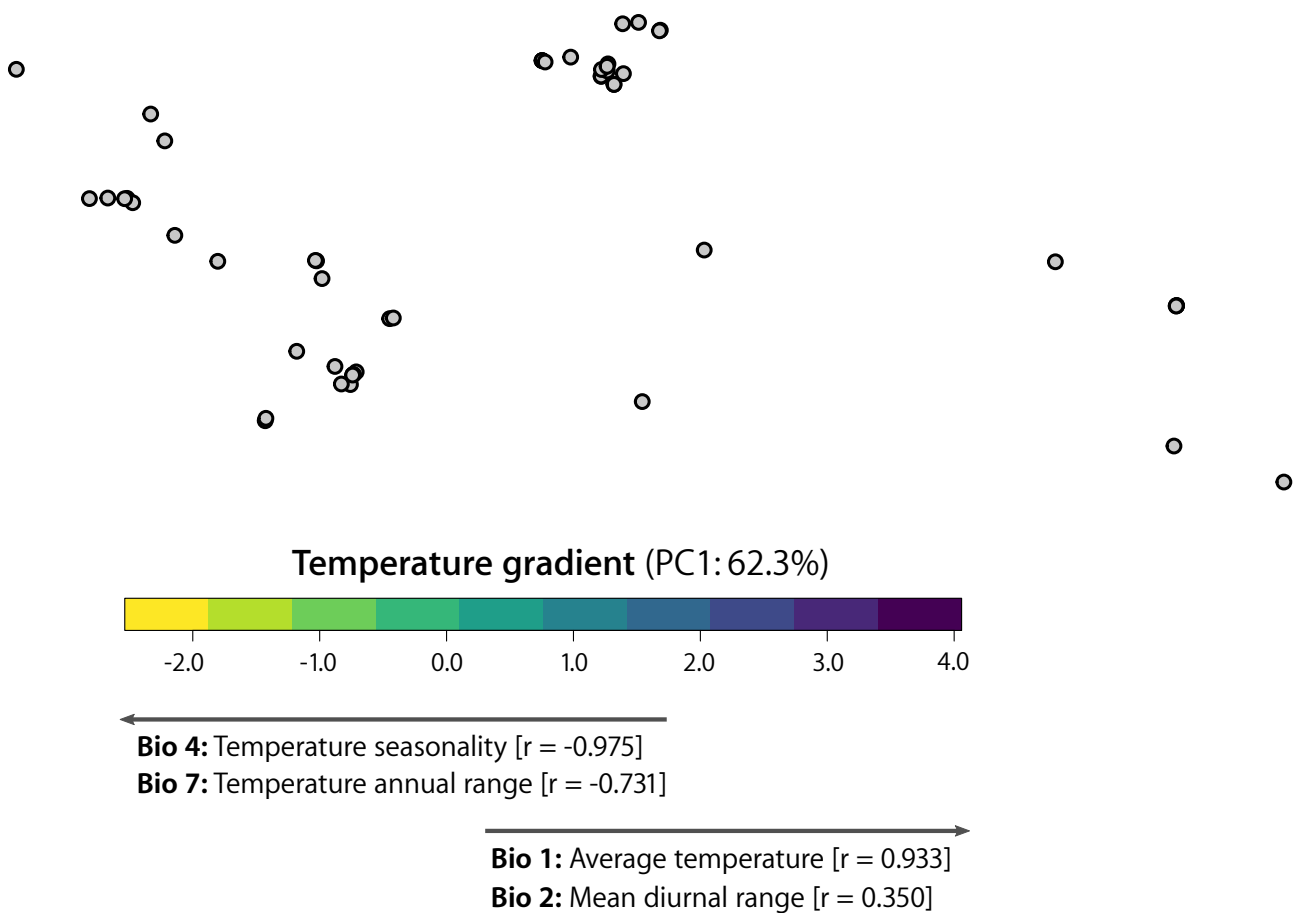
| | Richness | | Biomass | | Body size | |
|---|---|---|---|---|---|---|
| | *z* | P | *z* | P | *z* | P |
| **a) Total** | | | | | | |
| Temperature (experiment) | - | - | -2.81 | **0.005** | -2.68 | **0.007** |
| *Model comparison:* | | | | | | |
| AICc$_{full\ model}$ | 121.33 | | 79.67 | | 64.91 | |
| AICc$_{reduced\ model}$ | 116.81 | | 64.78 | | 59.67 | |
| **b) Predators** | | | | | | |
| PC1$_{precipitation}$ | -2.38 | **0.017** | - | - | - | - |
| Temperature (experiment) | - | - | -2.51 | **0.012** | - | **-** |
| Precipitation (experiment) | - | - | - | - | 3.29 | **0.001** |
| *Model comparison:* | | | | | | |
| AICc$_{full\ model}$ | 104.45 | | 76.53 | | 83.31 | |
| AICc$_{reduced\ model}$ | 93.15 | | 63.42 | | 66.38 | |
| **c) Herbivores** | | | | | | |

| | | | | | | |
|---|---|---|---|---|---|---|
| PC1$_{precipitation}$ | - | - | - | - | - | - |
| PC1$_{temperature}$ | - | - | - | - | - | - |
| Temperature (experiment) | -2.49 | **0.013** | - | - | - | - |
| Predator abundance | - | - | 2.30 | **0.021** | - | - |
| *Model comparison:* | | | | | | |
| AICc$_{full\ model}$ | 111.17 | | 68.57 | | 85.20 | |
| AICc$_{reduced\ model}$ | 103.21 | | 63.54 | | 70.03 | |

**a) Precipitation**

**Precipitation gradient** (PC1: 65.1%)

Color scale: 0.0 — 5.0 — 10.0 — 15.0

**Aridity:** Thornthwaite index [r = -0.859]
**Bio 15:** Precipitation seasonality [r = -0.684]

**Bio 14:** Precipitation of driest month [r = 0.917]
**Bio 12:** Annual precipitation [r = 0.745]

**b) Temperature**

**Temperature gradient** (PC1: 62.3%)

Color scale: -2.0 — -1.0 — 0.0 — 1.0 — 2.0 — 3.0 — 4.0

**Bio 4:** Temperature seasonality [r = -0.975]
**Bio 7:** Temperature annual range [r = -0.731]

**Bio 1:** Average temperature [r = 0.933]
**Bio 2:** Mean diurnal range [r = 0.350]

## a) Experimental design and effect size calculation

Control leaf

Rolled leaf

$X_c$

≥ 2 meters

Control

Treatment

Block

**Dependent variables**
→ Richness
→ Biomass
→ Body size

$X_e$

Hedges' d $= \dfrac{Xe - Xc}{SD_{pooled}}$

$-\infty$          $+\infty$

d

− effects of leaf rolls

+ effects of leaf rolls
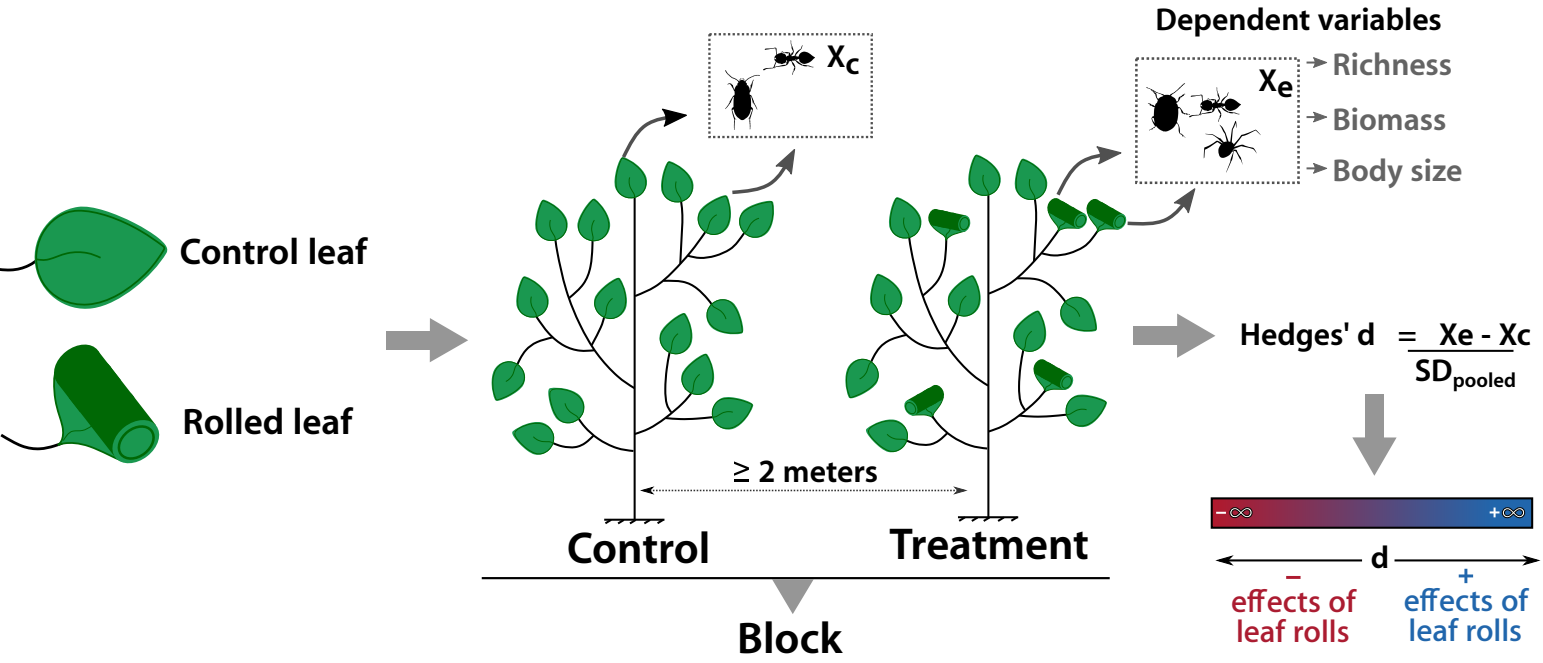
## b) Testing beneficial effect of leaf rolls (meta-analytical approach)

**Dependent (Hedges' d)**
**(Total, Predators or Herbivores)**

Moderators

**Global**

**Local**

Sites | $d_{richness}$ $d_{biomass}$ $d_{body\ size}$

∼

Latitude (lat)
Elavation (elev)

+

Sites | Temperature variables → PCA → $PCA_t$

Sites | Precipitation variables → PCA → $PCA_p$

+

Average temperature (atemp)
Average precipitation (aprec)
Average humidity (ahumi)
Herbivore abundance (herb)
Predator abundance (pred)
Leaf size (leaf)

**Model selection (testing the effects of moderators on each effect size)**

full model = rma(d ∼ lat + elev + PCAt + PCAp + tri + leaf + atemp + herb...)

⋮

reduced model = rma(d ∼ PCAp) → △ AIC = AICc(full) - AICc(reduced) ≥ 2

**i) Full model: selected variables were those with VIF < 2**

**ii) significant climate-effect size associations were used to build predictive maps (C)**
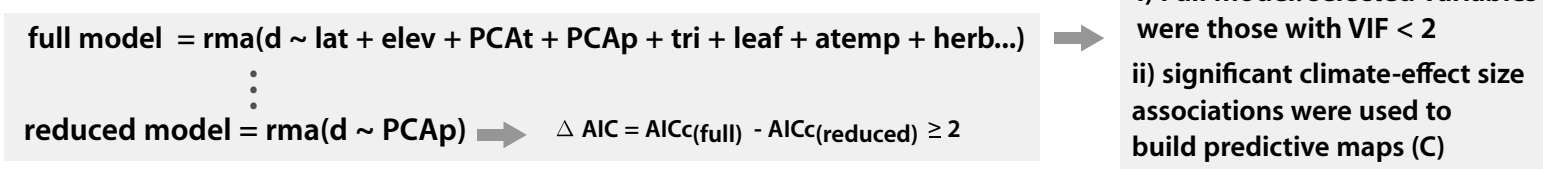
## c) Predicting spatial and temporal variations (predictive maps)

Current climate (c)

Future climate (f)

Same retained variables

Sites | Temperature variables → VIF → $TEMP_{uncor}$ → Model selection → $X_{temp(c)}$    $X_{temp(f)}$

Sites | Precipitation variables → VIF → $PREC_{uncor}$ → Model selection → $X_{prec(c)}$    $X_{temp(f)}$

**Predictive map** (example with temperature)

mod_ct = lm(d ∼$X_{temp(c)}$) → pred_ct = predict(mod_ct, "response")

mod_ft = lm(d ∼$X_{temp(f)}$) → pred_ft = predict(mod_ft, "response")

**Cross validation**

Sites | d → k fold (80%) → $d_{train}$ / $d_{validation}$

10 folds

mod_train(k) = lm($d_{train(k)}$ ∼$X_{temp(c)}$)

↓ Train

pred_k = predict(mod_train(k), "response")
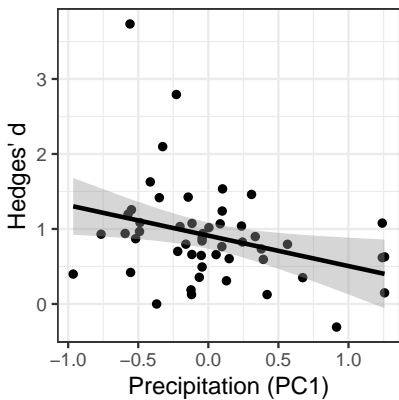
↓ Validation

predict(mod_train(k), newdata = $d_{validation}$)
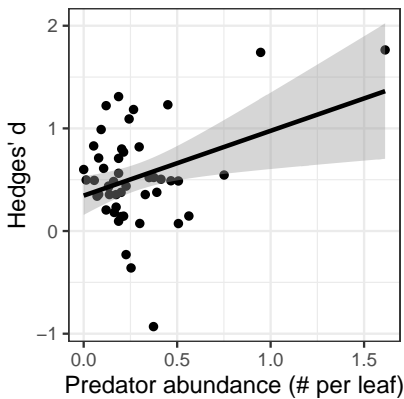
a) Biomass (All)

b) Body size (All)

a) Predator richness
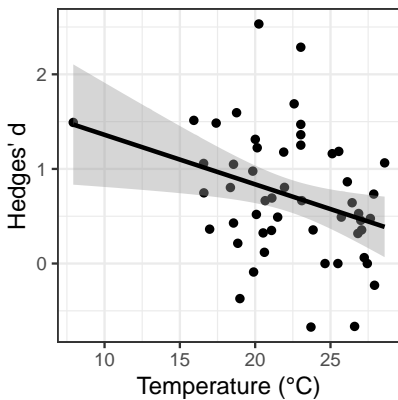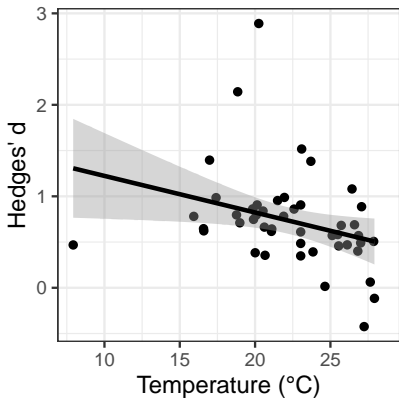
b) Predator biomass

c) Predator body size

d) Herbivore richness

e) Herbivore biomass