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Seed functional ecology in Brazilian rock outcrop vegetation: an integrative synthesis

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ABSTRACT

Background and Aims

Rock outcrop vegetation is distributed worldwide and hosts a diverse, specialised, and unique flora that evolved under extremely harsh environmental conditions. Unfortunately, seed ecology in such ecosystems has received little attention, especially regarding the association between seed traits, germination responses and adult plant ecology. Here, we provide a quantitative and phylogenetically-informed review of the seed functional ecology of Brazilian rocky outcrop vegetation, focusing on four vegetation types: *campo rupestre*, *canga*, *campo de altitude* and inselbergs.

Methods

Using a database with functional trait data for 383 taxa and 10,187 germination records for 281 taxa, we calculated the phylogenetic signal of seven seed traits and tested whether they varied among growth forms, geographic distributions, and microhabitats. We also conducted meta-analyses to understand the effects of light, temperature, and fire-related cues on the germination of *campo rupestre* species and how the beforementioned ecological groups and seed mass affect such responses.

Key Results

All traits showed a strong phylogenetic signal. *Campo rupestre* species responded positively to light and had their maximum germination between 20-30ºC. The effect of temperatures below and above this range was modulated by growth form, with shrubs requiring and tolerating higher temperatures to germinate. We only found evidence of a moderating effect of seed mass for responses to heat shocks, with larger, dormant seeds better tolerating heat.

Seeds exposed to heat shocks above 200° C lost viability, whereas smoke accelerated germination. No consistent differences in germination responses were found between restricted or widespread species or microhabitats. However, species from xeric habitats evolved phenological strategies to synchronise germination during periods of higher soil water availability.

Conclusions

Phylogenetic relatedness plays a major role in the seed ecology of Brazilian rock outcrop vegetation. However, seed traits and germination responses did not explain species' geographic distribution and microhabitat differentiation, suggesting other traits are more likely to explain such differences.

Keywords

Campo rupestre; *campo de altitude*; *canga*; germination requirements; inselberg; regeneration niche; seed dispersal; seed dormancy; seed mass; seed viability.

INTRODUCTION

Rock outcrops are outstanding geological features where the bedrock protrudes above the land's surface due to the erosion of softer parts of the landscape (Fitzsimons and Michael 2017). They offer a unique habitat that drastically contrasts with the neighbouring vegetation (Porembski 2007). Notably, they experience severe surface temperatures and have shallow, poorly-developed soils with low water retention capacity, a combination of abiotic factors that has driven the evolution of distinctive traits that allow plants to establish and survive in such harsh environments (Kluge and Brulfert 2000; Escudero *et al.* 2015; Oliveira *et al.* 2016). Most studies, however, have focused on the ecophysiology of adult plants, and only a couple of reviews on germination ecology have been produced to date. (Wyatt 1997; Biedinger *et al.* 2000). As a result, the potential role of regeneration traits (Donohue *et al.* 2010; Larson and Funk 2016) and niche (Grubb 1977) in driving species distribution and community assembly in this ecosystem has been largely overlooked.

In Brazil, there are four main vegetation types associated with rock outcrops: *campo rupestre*, *canga*, *campo de altitude* and inselbergs (Martinelli 2007). *Campo rupestre* occurs on quartzite, sandstone, and ironstone outcrops throughout the country, but it is most common at the high elevations of the Espinhaço Range in eastern Brazil (Miola *et al.* 2021). This vegetation is characterised by sandy and rocky grasslands dominated by grasses, sedges and forbs (mostly Xyridaceae and Eriocaulaceae) with isolated patches of shrubs (mainly Melastomataceae, Fabaceae, Asteraceae, Myrtaceae, Vochysiaceae and Clusiaceae) and desiccation-tolerant and epilithic species establishing directly in the rock (Silveira *et al.* 2016). The *campo rupestre* that develops on ironstone outcrops receives the name *canga* (Jacobi *et al.* 2007). The *campo de altitude* is found on granite and gneissic outcrops within the Atlantic Forest, and consists of a mosaic of shrubs (mostly Asteraceae, Melastomataceae,

and Myrtaceae) and small patches of dwarf forests amidst a matrix of grasses (Safford 1999). In contrast, inselbergs are isolated, dome-shaped granitic outcrops present across the country. In such geological formations, the mat-like vegetation – dominated mostly by Bromeliaceae, Cactaceae, Orchidaceae, Velloziaceae and shrubs from several families – is notably patchy, occurring only in depressions in the rock surface that accumulate soil (Safford and Martinelli 2000). All these open, grassy-shrubby, fire-prone and highly heterogeneous vegetation types are centres of species richness, phylogenetic diversity and endemism (Porembski 2007; Silveira *et al.* 2016; Campos *et al.* 2018).

The germination ecology of Brazilian rock outcrop vegetation has been previously reviewed (Garcia and Oliveira 2007; Nunes *et al.* 2016; Garcia *et al.* 2020), but these syntheses were restricted to the *campo rupestre* and focused on the differences in germination responses in a few emblematic families (e.g., Asteraceae, Bromeliaceae, Cactaceae, Eriocaulaceae, Melastomataceae, Velloziaceae and Xyridaceae). Still, these syntheses put forward promising hypotheses about the role of seed and germination traits in the ecological dynamics of these plant communities. First, they point out that seed traits, primarly seed mass, are expected to shape germination responses to abiotic factors. For example, Nunes *et al.* (2016) suggested that *campo rupestre* species with lighter seeds were more dependent on light for germination than larger ones, as expected under the well-known trade-off between light requirements and seed mass (Milberg *et al.* 2000), an association that remains to be formally tested for this ecosystem. Second, these reviews have suggested that contrasting microhabitat preferences and geographical ranges derive from distinct germination requirements, as assumed under the regeneration niche hypothesis (Grubb 1977; Saatkamp *et al.* 2019). For instance, species from xeric microhabitats in the *campo rupestre* have been shown to be able to germinate at higher temperatures than those from mesic environments (Oliveira and Garcia 2011), and generalist species have shown wider germination niches than those restricted to a

single substrate (Marques *et al.* 2014). Species with the widest distribution range have also been shown to have a broader germination temperature range (Ranieri et al. 2012). However, similar studies have failed to find such a significant association between microhabitat preferences or geographic distributions in the *campo rupestre* (Oliveira and Garcia 2011; Silveira *et al.* 2012b; Giorni *et al.* 2018). Moreover, these studies have been limited to a small number of species within single families, making it impossible to draw broad conclusions for the entire rock outcrop community. A new opportunity to address these questions at the community level has emerged owing to a comprehensive database recently published (Ordóñez-Parra *et al.* 2023).

Another limitation of these previous reviews is that they did not explicitly address the potential role of shared evolutionary history in seed ecology. Local and global scale studies have highlighted that several seed traits are phylogenetically clustered, including seed mass (Moles *et al.* 2005; Zanetti *et al.* 2020), dormancy (Willis *et al.* 2014; Dayrell *et al.* 2017) and germination requirements (Arène *et al.* 2017), potentially due to a combination of adaptive evolution and phylogenetic conservatism (Vandelook *et al.* 2012; Carta *et al.* 2022). As a result, a proper assessment of the ecological hypotheses regarding seed ecology must incorporate the phylogenetic component.

In this research, we addressed the two previously described long-standing hypotheses using a phylogenetically informed approach, with the aim of providing an integrative synthesis of the seed functional ecology of Brazilian rock outcrop vegetation. First, we assessed whether seed functional traits associated with different dimensions of the seed ecological spectrum exhibit a significant phylogenetic signal and evaluated whether they differed between growth forms, species geographic distribution and microhabitats. We then assessed the effect of light, temperature, and fire-related cues on the germination of plant species in these communities through meta-analyses. The evaluated abiotic factors are

established germination cues in these ecosystems and are the most studied cues in Brazilian rock outcrop vegetation, allowing us to provide more robust conclusions about their effects on germination (Figure S1). We then contrasted germination responses between growth forms, species geographic distribution and microhabitats and tested if such responses were moderated by seed mass –a central trait associated with multiple seed functions (Saatkamp *et al.* 2019). Finally, given that seed traits data provide critical information for biodiversity conservation and ecological restoration (Dalziell *et al.* 2022; Larson *et al.* 2023) and rock outcrop vegetation is increasingly exposed to several threats locally and globally (Porembski *et al.* 2016; Fitzsimons and Michael 2017; Fernandes *et al.* 2018), we discuss how the available information on seed traits and germination responses may support and inform conservation and restoration programs. Because rock outcrops occur in all continents and biomes, and their associated vegetation is quite similar in structure and function (Barthlott and Porembski 2000), we hope this study provides a solid starting point towards a global synthesis of the germination ecology of rock outcrop vegetation.

MATERIALS AND METHODS

Data sources

Seed functional traits and germination experiments

We retrieved seed trait and germination records from *Rock n' Seeds* (Ordóñez-Parra *et al.* 2023), a database of seed functional traits and germination experiments of plant species from Brazilian rock outcrop vegetation (Figure 1). We focused on seven functional traits associated with regeneration from seeds and seed major functions (Grubb 1977; Saatkamp *et al.* 2019): seed dry mass (mg), seed water content (%), percentage of embryoless seeds (%), percentage

of viable seeds (%), seed dispersal syndrome (anemochory, autochory and zoochory), seed dispersal season (early-dry, late-dry, early-rain and late-rain) and primary dormancy (dormant and non-dormant). We also retrieved information from experiments assessing the effects of light availability, constant and alternate temperatures, and fire-related cues (i.e., heat shocks and smoke). Beyond seed and germination traits, the database also provides species-level data on growth form, microhabitat ('xeric' when substrate experiences pronounced seasonal drought, or otherwise 'mesic'), and geographic distribution ('restricted' to rock outcrop vegetation, and 'widespread' if found in other vegetation types in addition to rock outcrops) (see Ordóñez-Parra *et al.* 2023 for a full description of database construction).

Phylogenetic tree

We reconstructed the phylogenetic tree of the studied species using the package *V.PhyloMaker2* (Jin and Qian 2022). First, species names were checked and updated following The Leipzig Catalogue of Vascular Plants using the R package *lcvplants* (Freiberg *et al.* 2020). We kept taxa identified at the species level, and all subspecies and varieties (18 cases) were upgraded to the species level. A phylogenetic tree for the resulting 370 species was generated, based on the GBOTB phylogeny (Smith and Brown 2018) updated and standardised following Freiberg *et al*. (2020). Taxa absent from this phylogeny were bound to their designated relatives using the bind.relative function of *V.PhyloMaker2* based on different sources (Almeda *et al.* 2016; Rivera *et al.* 2016). Species with no known relatives in the phylogeny (*Austrocritonia velutina*, *Cavalcantia glomerata, Cavalcantia percymosa* and *Parapiqueria cavalcantei*) were added using the at.node function from the *ape* package (Paradis and Schliep 2019). All these species belong to the Eupatorieae (Asteraceae), a tribe where infrageneric relationships are yet to be resolved (Rivera *et al.* 2016). Therefore, they were added to the base of the tribe as polytomies.

Most infrageneric relationships in the phylogeny remained unresolved, appearing as polytomies, partially because the relationships within some genera of the highly diverse families in our database have low support (Alcantara *et al.* 2018; Guimarães *et al.* 2019). Nevertheless, phylogenetic metrics estimated from trees resolved to the genus-level have shown to be highly correlated with those derived from fully-resolved trees, suggesting that these polytomies do not weaken the results (Qian and Jin 2021).

Statistical analyses

All analyses were made using R v. 4.2.0 (R Core Team 2022), and the code prepared will be provided as Supplementary Material and uploaded to GitHub upon acceptance (see Open Data). Results are presented using a gradual language of evidence, which allows communicating scientific findings in a more nuanced way (Muff *et al.* 2022).

Variation and phylogenetic signal of seed functional traits

To test for the phylogenetic signal in the quantitative seed traits (i.e., dry mass, water content, percentage of viable and embryoless seeds), we calculated Pagel's λ (Pagel 1999) using the phylosig function from the package *phytools* (Revell 2012). λ values range from zero to one, with λ = 0 indicating that there is no phylogenetic signal, thus related taxa are not more similar than expected by chance; and λ = 1 implying a strong phylogenetic signal, so the traits of related taxa are more similar than expected by chance (Pagel 1999). Pagel's λ was selected among the available phylogenetic signal indices given its robustness in measuring phylogenetic signals based on incompletely resolved phylogenies (Molina-Venegas and Rodríguez 2017). We also calculated Moran's I coefficient to assess the phylogenetic autocorrelation of traits at the Genus, Family and Order levels using the correlogram.formula function from *ape* (Paradis and Schliep 2019). Values of Moran's I range from -1 to 1, with I

= 0 indicating that species resemble each other as expected by Brownian motion model. Values above and below zero imply that related species are more or less similar than expected by such model, respectively (Moran 1950; Gittleman and Kot 1990). All these tests were carried out using log-transformed seed mass values and logit-transformed water content, percentage of embryoless and viable seed values to reduce the skewness of the data. For species with more than one record (25 species), we carried out the analyses using the average species value.

For the qualitative seed traits (i.e., seed dormancy, seed dispersal syndrome and seed dispersal season), the phylogenetic signal was tested by implementing the rtestdeciv function from the *adiv* package using 9,999 permutations (Pavoine 2020). This method decomposes trait diversity among the nodes of the phylogenetic tree and assesses whether it is skewed towards the tree's root or tips, with significant root skewness implying the presence of a significant phylogenetic signal. Seed dormancy and dispersal season were treated as multichoice variables as 11 species had records of both dormant and non-dormant seeds, and 18 species reported more than one dispersal season.

To test for differences in quantitative traits between ecological groups (growth form, microhabitat, and geographic distribution), we used phylogenetic generalised least square models as implemented in the package *caper* (Orme *et al.* 2018). Likewise, variation in qualitative traits were assessed using a phylogenetic logistic regression (Ives and Garland 2010) implemented in the *phylolm* package (Ho and Ané 2014). Because the dispersal season and syndrome had more than two possible states, individual models were run to assess the probability of each season and syndrome. Species with records for more than one distribution records were classified as "widespread" and species with occurrence in both microhabitats were coded as "mesic/xeric". For this analysis, species with records from more than one combination of qualitative traits were included as different populations, using the

add.taxa.phylo function from the *daee* package (Debastiani 2021) and keeping the tree ultrametric.

Preliminary tests showed that the interaction between our qualitative predictors did not significantly affect any of the tested variables. Moreover, the model that included such interactions were outperformed by simple additive models based on Akaike Information Criteria (see code provided). As a result, our final models did not include these interactions. Growth form comparisons were made between herbs and shrubs only, due to the low sample size of trees (26 species), succulents (nine species) and lianas (six species).

Meta-analyses of germination responses to abiotic factors

We estimated the overall effects of light, constant and alternate temperatures, and fire-related cues on germination through a meta-analysis. This analysis was restricted to *campo rupestre* and *canga* species, given the lack of data from *campo de altitude* and the small sample size of independent observations for inselbergs (two studies, three species) for these abiotic factors. Our effect size metric was the standardised mean difference Hedge's g (Hedges 1981) (Equation 1), which was calculated using the escalc function from the package *metafor* (Viechtbauer 2010). This metric measures the standardised change in a given response variable in treatment groups compared to control groups and includes a correction for sample size (Rosenberg *et al.* 2013). Experiments under total darkness were used as controls to test the effects of light, with results from different temperatures being pooled into a single effect for each plant species in each study. Given the overall positive effect of light on germination (see below), only experiments carried out under light conditions were used to assess the effects of different temperatures and fire-related cues on seed germination. We used 25 ºC as a control for constant and alternate temperatures because it is considered the optimal temperature for most species in this ecosystem (Garcia and Oliveira 2007; Nunes *et al.* 2016;

Garcia *et al.* 2020). Finally, we used untreated seeds (i.e., seeds not exposed to either heat shock or smoke) as controls for fire-related cues.

$$g = \frac{\bar{Y}_1 - \bar{Y}_2}{\sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2}{n_1 + n_2 - 2}}} J,$$

$$\text{where } J = 1 - \frac{3}{4(n_1 + n_2 - 2) - 1}$$

Equation 1. Formula for the calculation of Hedge's g, where $\bar{Y}$ is the observed mean, n is the sample size and s^2 is the variance. Subscripts 1 and 2 denote values pertaining to the treatment and control groups, respectively.

We assessed the effects of these abiotic factors on seed germination percentage and median germination time (t_{50}). Mean germination percentage values were taken from the raw germination data deposited in *Rock n' Seeds* and supplemented with additional data from 13 experiments that were retrieved from the database literature survey whose raw data was not already available. To be included in our meta-analysis, the latter studies should present the mean germination percentage and its standard deviation (or any other statistical measure that could be converted into standard deviation units) in either the text, tables, figures or supplementary materials or provide enough information for calculations. Data presented in figures were extracted using ImageJ (Schneider *et al.* 2012). This supplementation allowed us to add germination data for 36 species from six families, including four emblematic ones from *campo rupestre* –Bromeliaceae, Eriocaulaceae, Velloziaceae and Xyridaceae (Silveira *et al.* 2016)– that were underrepresented in the original dataset.

To avoid confounding effects from treatments with extremely low germination, we only included observations where either the control or treatment had ≥10% germination. The

t_{50} (Coolbear *et al.* 1984 as modified by Farooq *et al.* 2005) was calculated for the experiments that included raw daily germination data using the *germinationmetrics* package (Aravind *et al.* 2022). To reduce the effect of low germinability in our analysis, we calculated t_{50} for observations where both the control and treatment conditions had ≥10% germination. Moreover, we assessed the effect of light, constant and alternate temperatures as germination cues in non-dormant seeds or in seeds where dormancy has been alleviated. Alternate temperatures are known to break physical dormancy (Baskin and Baskin 2014), but none of the studies in the dataset have tested this. In contrast, because fire-related cues are known to break seed dormancy of some species in fire-prone ecosystems (Baskin and Baskin 2014), we included dormant species in the meta-analysis of fire-related cues. Species with non-conclusive records regarding seed dormancy were excluded.

We evaluated the overall effect of each abiotic factor (i.e. light, temperature and fire) on germination percentage and t_{50} by implementing mixed effect models using the rma.mv function of *metafor* (Viechtbauer 2010), with effect sizes as response variables and observations, study and species phylogeny as random variables. Species appearing in more than one study were included in the phylogeny as distinct populations using the add.taxa.phylo function from *daee* (Debastiani 2021) with a branch length of zero (Lajeunesse *et al.* 2013). A covariance matrix for each species set was built using the vcv function from *ape* (Paradis and Schliep 2019).

After assessing the overall effect of each abiotic factor, we tested the moderating effects of growth form, distribution, microhabitats, seed mass and dormancy on seed germination percentage and time. The effects of seed dormancy were tested only for fire-related cues. Because seed mass exhibited a significant, strong phylogenetic signal (see below), the missing seed mass values for 54 species were inputted using average values for the genera from *Rock n' Seeds* (Ordóñez-Parra *et al.* 2023) and the Seed Information Database

(https://ser-sid.org/). Ninety-five percent confidence intervals around the effect sizes were calculated and effect size was considered significant if the confidence intervals did not overlap zero (Hedges *et al.* 1999). Comparisons within predictors were carried out using the function linearHypothesis from the *car* package (Fox and Weisberg 2019).

RESULTS

Variation and phylogenetic signal of seed functional traits

We found very strong evidence that all seed traits exhibited a significant phylogenetic signal (Table 1, $p < 0.001$). For all quantitative traits (i.e., seed mass, water content and the percentage of embryoless and viable seeds), the phylogenetic signal was moderate to strong (λ between 0.57-0.90), with closely related taxa strongly resembling each other at both the Genus and Family level (Table S1). At the Order level, we only found (very strong) evidence of a negative phylogenetic autocorrelation for the seed mass (I = -0.39, $p < 0.001$, Table S1).

Seed mass values ranged from 0.00035 (*Microlicia serpyllifolia*, Melastomataceae) to 175.15 mg (*Dioclea apurensis*, Fabaceae) (Median: 0.245 mg). Among the most well-represented families in the database, Fabaceae exhibited the heaviest seeds (Median: 11.57 mg), whereas Melastomataceae (0.007 mg), Xyridaceae (0.016 mg) and Eriocaulaceae (0.044 mg) exhibited the lighter ones (Figure 2). There was moderate evidence that shrubs (t = 2.19, p = 0.030) and species occurring at both mesic and xeric microhabitats (t = 2.01, p = 0.045) produced heavier seeds than herbs and species from mesic microhabitats, respectively (Table 2).

Seed water content values ranged from 3.9% (*Paepalanthus fasciculoides*, Eriocaulaceae) to 28.3% (*Dyckia ursina*, Bromeliaceae) (Median: 11.7%). Cyperaceae (7.7%), Asteraceae (9.2%) and Fabaceae (9.4%) had the seeds with the lowest water content,

whereas Melastomataceae (12.2%), Bromeliaceae (13.6%) and Velloziaceae (14.2%) showed the highest values (Figure 2). There was no evidence that seed water content varied between growth forms, microhabitats or geographic distribution (Table 2).

The percentage of embryoless and viable seeds varied greatly among species. On the one hand, the percentage of embryoless seeds ranged from 0% [i.e., species producing only filled seeds, such as *Mimosa dasilvae* (Fabaceae), *Xyris brachysepala* (Xyridaceae) and *Paepalanthus fasciculoides* (Eriocaulaceae)] to species producing 99.2% of empty seeds (*Axonopus laxiflorus*, Poaceae) (Median: 10.6%). Poaceae and Asteraceae produced the highest proportion of embryoless seeds (Median: 82% and 66%, respectively), while Eriocaulaceae (0.9%), Xyridaceae (1.5%) and Fabaceae (4.0%) produced few embryoless seeds (Figure 2). Likewise, some species exhibited large amounts of non-viable seeds [e.g., 0% in *Echinolaena inflexa*, Poaceae] while others exhibited mainly viable seeds [e.g., *Vriesea bituminosa* (Bromeliaceae)]. The highest proportion of viable seeds was found in Eriocaulaceae (Median: 89%), Xyridaceae (87.7%) and Velloziaceae (86%), while Poaceae species (11.5%) exhibited the seeds with the lowest viability (Figure 2). We found no evidence that the percentage of embryoless and viable seeds varied between growth forms, microhabitats nor species distributions (Table 2).

Sixty-four percent of species produced non-dormant (ND) seeds, whereas 36% produced dormant (D) seeds (Figure 2). The most common dormancy class was physical dormancy (PY), being primarily present in 37 Fabaceae (37 species), but also in three Convolvulaceae and one Malvaceae species. Physiological dormancy (PD), the second most common dormancy class, was found mostly in Verbenaceae (nine species), Cyperaceae (six species) and Melastomataceae (five species). Eleven species produced either D or ND seeds. We found moderate evidence that species from xeric environments had higher probabilities of producing D seeds ($z = 2.52$, $p = 0.012$).

Autochory was the most common dispersal syndrome (58.9% of species), as exemplified by Melastomataceae (49 species), Fabaceae (38) and Velloziaceae (36). This dispersal syndrome was followed by anemochory (26.2%) –exhibited by Asteraceae (29 species), Eriocaulaceae (24) and Bromeliaceae (24)– and zoochory (14.9%, e.g., Melastomataceae). There was no evidence that the probability of dispersal syndrome was driven by any of the evaluated predictors (Table 3).

Most species dispersed seeds during the dry season, either in the late-dry season (38.5%) or early-dry season (26.5%), and around 45% of the plants dispersed seeds during the rainy season. There was strong evidence that shrubs had a higher probability of dispersing seeds during the late-dry season ($z = 3.43$, $p < 0.001$), and moderate evidence that dispersal during the late-rainy season was more likely in herbs ($z = -2.01$, $p = 0.044$). Additionally, the data exhibited moderate evidence that species from mesic/xeric microhabitats ($z = 2.03$, $p = 0.042$) and those restricted to xeric microhabitats ($z = 2.15$, $p = 0.031$) had a higher probability of dispersing seeds during the late-rainy. season than species from mesic microhabitats. There was no evidence that the probability of dispersal during the early-dry or the early-rainy season was explained by the evaluated predictors (Table 3).

In summary, shrubs tended to produce heavier seeds and to have higher probabilities of dispersal during the late-dry season. In contrast, herbs produced relatively smaller seeds with higher probabilities of dispersal during the late-rainy season. Species from mesic/xeric microhabitats tended to produce heavier seeds and during the late-rainy season compared to those from exclusively mesic microhabitats. Moreover, species restricted to xeric environments had higher probabilities of producing D seeds during late-rainy dispersal than those from mesic environments (Figure 3). Finally, there was no evidence that species restricted to outcrop vegetation and widespread ones differed in any seed trait.

Meta-analyses of germination responses

There was very strong evidence that light had an overall positive and strong effect on germination percentage (g = 5.48, CI = 3.03 to 7.93, z = 4.39, $p < 0.001$) regardless of growth form, distribution, or microhabitat (Figure 4). The effect was higher in herbs and restricted species when compared to shrubs ($\chi^2 = 6.04$, p = 0.014) and widespread species ($X^2 = 9.33$, p = 0.002), respectively. There was no evidence of differences in germination responses to light between microhabitats, or that seed mass moderated the effects of light on germination percentage (z = -0.71, p = 0.48).

Regarding the effect of constant temperatures on germination, there was no evidence that 20 and 30 ºC differed from the control treatment (25 ºC), regardless of growth form, distribution, or microhabitat (Figure 5A). Still, the data showed very strong evidence that incubation in temperatures below 20 ºC (10 and 15 °C) reduced germination percentage (10 ºC: g = -12.53, CI = -17.62 to -7.45, z = -4.83, $p < 0.0001$; 15 ºC: g = -1.75, CI = -2.78 to -0.72, z = -3.32, $p < 0.001$) and increased t_{50} (15 ºC: g = 5.09, CI = 3.37 to 6.81, z = 5.80, $p < 0.0001$). Moreover, there was moderate-to-strong evidence that temperatures above 30 ºC (35 and 40 °C) decreased germination percentage (35 ºC: g = -4.57, CI = -9.00 to -0.14, z = -2.02, p = 0.04), but no evidence that they affected t_{50} (Figure 5A). Growth form moderated germination responses to temperature, with our data showing very strong evidence that shrubs exhibited the most pronounced decreases in germination percentage at 15 ºC ($X^2 = 8.35$, p = 0.004, Figure 5). Additionally, there was moderate evidence that germination in herbs was accelerated at 30 ºC (z = -2.23, p = 0.03) but decreased (z = -2.12, p = 0.03) and delayed (z = 2.03, p = 0.04) at 35 ºC. No evidence of an effect of these temperatures was found on the germination of shrubs. Seed mass modulated germination responses at 20 and 30 ºC, with moderate evidence that relatively heavier seeds had low germination at 20 ºC (z = -2.20, p =

0.03), but strong evidence that they had higher germination percentage at 30 °C (z = 2.90, p = 0.003). No consistent differences were found between microhabitats or distributions.

When evaluating the effects of alternate temperatures, the data showed moderate evidence that 25/15 ºC regimes reduced germination percentage (g = -2.58, CI = -4.94 to -0.20, z = -2.13, p = 0.03) and very strong evidence that they increased t_{50} (g = 2.72, CI = 1.80 to 3.65, z = 5.78, p < 0.001). Conversely, there was no evidence that 30/20 ºC affected germination percentage (g = -0.93, CI = -4.22 to 2.36, z = -0.66, p = 0.51) or t_{50} (g = 0.83, CI = -0.42 to 2.06, z = 1.31, p = 0.19). Moreover, there was no evidence that seed mass modulated the effect of alternate temperatures on germination percentage or time (Figure 5B).

Finally, we found moderate evidence that fire-related cues reduced germination percentage (g = -0.41, CI = -0.81 to -0.01, z = -2.01, p = 0.04) but no evidence that it affected t_{50} (g = -0.41, CI = -0.92 to 0.10, z = -2.68, p = 0.11). This effect varied according to the treatment applied, with heat shocks –alone or in combination with smoke– reducing germination percentage but not germination time. The data showed moderate evidence that the germination percentage of relatively heavier seeds increased after exposed to fire-related cues (z = 2.54, p = 0.01), while no evidence of an effect on germination time was found (z = 1.41, p = 0.16). Moreover, there was strong evidence that primary dormancy significantly shaped the responses to fire-related cues, with an overall decrease in germination percentage in ND species (z= -2.75, p = 0.006, Fig 6A). When comparing heat shock treatments, there was only evidence of a negative effect on germination percentage by 1-min 200 ºC heat shocks (z = -5.56, p < 0.001, Figure 6B). Further analysis excluding this treatment showed no evidence that heat shocks affected germination, regardless of growth form, distribution or microhabitat (Figure 6C). Still, there was moderate evidence that ND (z = -2.16, p = 0.03) and relatively lighter seeds were more sensitive to heat (z = 2.05, p = 0.04). The data showed no evidence that smoke affected germination percentage, but moderate evidence that it

accelerated germination (g = -1.28, CI = -2.51 to -0.06, z = -2.05, p = 0.04). However, the available data only provided evidence for such an effect in herbs (g = -1.57, CI = -3.13 to -0.02, z = -1.9860, p = 0.047) and restricted species (g = -1.62, CI = -2.87 to -0.38, z = -2.55, p = 0.01). There was no evidence that smoke's effect was modulated neither by seed mass nor by dormancy (Figure 6D).

Overall, phylogeny played a major role in moderating the effects of light and temperatures above 30 º C on germination percentage. In contrast, the effect of phylogeny in responses to constant temperatures ≤ 25 ºC, alternated temperature and fire-related cues was minimal (Table S2). Likewise, phylogeny played a minor role in shaping the effects of abiotic factors on t_{50} (Table S3).

DISCUSSION

In this research, we carried out an integrative and phylogenetically-informed synthesis of seed functional ecology in Brazilian rock outcrop vegetation, with the aim of testing two long-standing hypotheses: that seed traits shape germination responses to abiotic factors and that contrasting microhabitat preferences and geographical ranges are the result of distinct germination requirements. Our results provide a detailed account of variation in seed trait and germination responses in these ecosystems. All seed traits exhibited a significant phylogenetic signal, underscoring the importance of phylogenetic relatedness for seed ecology in rock outcrop vegetation. For instance, such a signal could be traced back up to the Family level, implying that several aspects of a species seed ecology might be inferred from information about other members of the Family. Our meta-analyses indicated that seed germination in *campo rupestre* is i) positively affected by light; ii) reduced and slowed down at constant temperatures below 20 ºC and above 30 ºC; iii) little to not affected by alternated temperatures; iv) unaffected by heat shocks ≤ 100 ºC; and v) accelerated under smoke

exposure. From these germination responses, only the effects of light and constant temperatures above 30 ºC were shaped by phylogeny, reiterating the role of phylogenetic relatedness for the comprehension of seed germination in these ecosystems

Seed mass shaped heat tolerance but not germination responses to light and temperature

Regarding our first hypothesis, where germination responses were expected to be controlled by seed functional traits, we only found enough evidence for a relationship between seed mass and heat tolerance, with heavier seeds tolerating heat better than lighter ones. This positive association between seed mass and heat tolerance agrees with previous studies in the Cerrado (Ribeiro *et al.* 2015; Daibes *et al.* 2019) and could be explained by the fact that the surface-to-volume ratio decreases with increasing seed mass, so larger, heavier seeds have better insulation against higher temperatures that can be detrimental to seed tissues (Ruprecht *et al.* 2015).

Surprisingly, we found no evidence to support the association between seed mass and responses to light in the *campo rupestre*. Possible explanations for the lack of support for the well-known trade-off between light responses and seed mass include the high uniformity in germination responses to light in *campo rupestre* species –which are either light-stimulated or insensitive to light (Nunes *et al.* 2016; Garcia *et al.* 2020)– and the small variation in seed size in our data (86% records, < 1 mg). Moreover, light indifference in the *campo rupestre* has been reported in families with notably different seed sizes, including Bromeliaceae, Verbenaceae and Fabaceae (Nunes *et al.* 2016).

In addition to the small variation in seed size, the lack of support for an association between seed size and temperature responses in a phylogenetically controlled analysis may be due to the strong phylogenetic signal of temperature requirements at the global scale (Arène *et al.* 2017). Therefore, differences in germination responses to temperature are probably better

explained by phylogeny rather than by seed mass, an observation supported by the role of phylogeny in our meta-analyses of the effects of temperature on germination percentage. Similarly, the lack of a significant effect of 30/20 ºC and an association between response to alternate temperatures and seed mass could be attributed to the fact that most *campo rupestre* species produce small, lighter seeds, which are not expected to benefit from alternate temperature regimes (Pearson *et al.* 2003).

Seeds functional traits are phylogenetically clustered in Brazilian rock outcrop vegetation

Our results indicating that all seed traits had a significant and moderate-to-strong phylogenetic signal is consistent with global studies showing phylogenetic clustering for other seed traits, such as seed mass (Moles *et al.* 2005) and dormancy (Willis *et al.* 2014). However, our results partially contrast with local studies in similar ecosystems. First, Zanetti *et al.* (2020) did not find a phylogenetic signal for seed water content in their study of 48 species from the *cangas* of Carajás (Eastern Brazilian Amazon). This discrepancy between this and our study might arise from differences in sample size and geographic extent or from the distinct phylogenetic structure of each rock outcrop vegetation type (Massante *et al.* 2023). Second, we found a significant phylogenetic signal for seed dispersal season, while seed dispersal season in the Cerrado (Escobar *et al.* 2021) and other phenological events in the *campo rupestre* (Zanetti *et al.* 2020; Oliveira *et al.* 2021) have not shown such signal. As a result, seed dispersal season is the only phenophase that has shown a significant phylogenetic signal in the Brazilian rock outcrop vegetation, potentially as a result of an intense evolutionary pressure towards germination timing in these ecosystems, where water is even more scarce than in the Cerrado (Oliveira *et al.* 2021).

Seed mass and seed dispersal season differed between herbs and shrubs, with shrubs tending to produce relatively larger seeds during the late-dry season and herbs producing

lighter seeds during the late-rain season. Differences in seed mass between herbs and shrubs have been attributed to the distinct strategies employed by such growth forms: while shrubs invest in fewer, larger seeds that cope better with environmental hazards, herbs invest in numerous, lighter seeds to increase their establishment opportunities (Westoby *et al.* 2002; Moles *et al.* 2005). This relationship is also supported by the global spectrum of plant form and function (Díaz *et al.* 2016), suggesting that this global pattern also stands for rock outcrop vegetation in Brazil. On the other hand, differences in seed dispersal season suggest differences in phenological strategies to cope with precipitation seasonality (see below).

Seed traits and germination responses do not explain large-scale species distribution, but seed dispersal phenology may contribute to microhabitat segregation

Rock outcrops and the surrounding vegetation differ in several aspects that should impact germination, such as nutrient and water availability, irradiance, and daily temperature fluctuations (Oliveira *et al.* 2016). Still, we did not find enough evidence of differences in seed traits or germination requirements between restricted and widespread species, suggesting that the assessed seed traits do not explain large-scale species distribution. Therefore, community assembly at this scale is probably shaped by vegetative traits that allow these plants to cope with the stressful conditions of rock outcrops (Oliveira *et al.* 2015) or by other seed and germination traits not included here. In contrast, species from mesic and xeric microhabitats were found to differ in terms of dispersal phenology rather than germination responses, agreeing with studies showing little correspondence between seed traits and species ecological preferences, both in ours (Oliveira and Garcia 2011; Silveira *et al.* 2012b; Giorni *et al.* 2018) and other ecosystems (Fernández-Pascual *et al.* 2021; Fernández-Pascual *et al.* 2022). As a result, our second hypothesis –where distinct germination requirements

were expected to explain contrasting microhabitat preferences and geographical ranges– was not supported.

Regardless of microhabitat, most species dispersed their seeds during the late- or the early-dry season. However, we found that species from xeric habitats had higher probabilities of producing dormant seeds and dispersing their seeds during the late-rain season –two strategies that presumably arise due to evolutionary pressures towards strategies to synchronise germination with higher water availability (Silveira *et al.* 2012a; Garcia *et al.* 2020). Yet, only 36% of our species produce dormant seeds, and *campo rupestre* is known to have the highest ND to D species ratio globally (Dayrell *et al.* 2017), implying that seed dormancy might not be the main driver of seedling establishment in our study system. Additional strategies for controlling germination timing include germination requirements and the acquisition of secondary dormancy. A mismatch between temperature germination requirements and environmental conditions at the moment of dispersal might provide an alternative strategy to prevent germination in the absence of dormancy (Escobar *et al.* 2021) – for example, seeds dispersed during the dry season have evolved to germinate under relatively higher temperatures of the rainy season. Secondly, secondary dormancy, as reported in a few Eriocaulaceae and Xyridaceae species from *campo rupestre* (see Garcia *et al.* 2020), can help fine-tune seedling establishment with optimum conditions. All these species disperse their non-dormant seeds between the early-dry and the early-rain season and become increasingly dormant as the rainy season advances. When the dry season starts, dormancy is progressively alleviated by reduced temperatures and low water availability (Duarte and Garcia 2015).

Campo rupestre *species depend on light for germination*

Our meta-analysis showed that light positively affects seed germination across all ecological groups, supporting previous assessments about its importance in *campo rupestre*

germination ecology. Interestingly, restricted species had a stronger response to light than widespread species, suggesting this kind of response may be particularly prevalent in this ecosystem. We also found that germination responses to light were stronger in herbs, which could be associated with our finding of them having lower seed mass compared to shrubs. Still, as mentioned before, we did not find evidence to support such a trade-off.

Small-seeded species from our study are expected to have narrowly defined microsite requirements due to their limited internal resources, so further aspects of the light environment, such as spectral quality and the interaction between light and temperature, are expected to control their germination (Pearson *et al.* 2003; Pons 2014). Still, studies assessing such aspects in our study system are scarce and have only involved very few species (Pereira *et al.* 2009; Hmeljevski *et al.* 2014; Vieira *et al.* 2018; Garcia *et al.* 2020), preventing robust inferences about the functional relevance of these germination cues.

Herbs and shrubs respond differently to low and high temperatures

We found that the germination of *campo rupestre* species was maximised between 20-30 ºC, supporting previous qualitative reviews (Nunes *et al.* 2016; Garcia *et al.* 2020). Decreases in germination percentage below this range could be a putative mechanism to avoid germination during the dry season when temperatures decrease and soil water potential do not support seedling establishment (Garcia *et al.* 2020). As this effect was not controlled by phylogeny, it could be expected to be a generalised response in the *campo rupestre*. The negative effect of low temperatures was stronger in shrubs, suggesting that these require higher temperatures to germinate, possibly due to differences in seed size (Arène *et al.* 2017). Still, our data support a positive effect of seed mass on germination responses only between 20-30 ºC, a range where there was no evidence of differences between herbs and shrubs. On the other hand, temperatures above 30 ºC decreased and delayed germination in herbs, while

shrubs remained unaffected, implying that shrub seeds tolerate germinating at higher temperatures and thus, are able to dominate microsites experiencing higher soil temperatures.

Alternate temperature regimes had either a negative or null effect on the germination. The reduction of germination percentage and the increase of germination time at 25/15ºC regime is probably due to part of these temperatures being suboptimal. Conversely, studies in the *campo de altitude* have shown that several species benefit from alternate temperature regimes, suggesting this cue could be more important in this vegetation (Andrade et al. 2021). Therefore, additional studies are required to elucidate the functional relevance of alternate temperatures and whether this varies between vegetation types.

Heat kills small, non-dormant seeds, but smoke accelerates germination

Seeds exposed to 200 ºC had their germination percentage reduced, while milder heat shocks (≤ 100 ºC) did not affect germination percentage or time, supporting studies showing heat tolerance in Neotropical savanna (Daibes *et al.* 2022). In addition to seed mass, responses to heat shocks were also moderated by seed dormancy, with ND seeds being relatively less tolerant to heat shocks, as previously described for Cerrado species (Ramos *et al.* 2016; Daibes *et al.* 2019). D species were mostly unaffected by heat shocks, supporting the notion that fire-mediated dormancy alleviation is not expected in rocky areas or savannas (Pausas and Lamont 2022). The lack of negative effects on D species implies that traits associated with seed dormancy promote heat tolerance, such as the accumulation of heat shock proteins or the presence of hard and water-impermeable coats (Tweddle *et al.* 2003; Ramos *et al.* 2016).

Smoke did not affect germination percentage but consistently shortened germination time, aligning the role of smoke-derived compounds in stimulating non-dormant seeds or those where dormancy has been alleviated (Mackenzie *et al.* 2021). Smoke-stimulated

germination in the *campo rupestre* is thought to promote the germination of species resprouting and shedding seeds after fire (Fernandes *et al.* 2021) –a usual phenological syndrome in this vegetation (Figueira *et al.* 2016)– allowing recently-dispersed seeds to exploit the post-fire environment where competition is relaxed (Le Stradic *et al.* 2015; Fernandes *et al.* 2021). While our meta-analysis largely supports this hypothesis, the effect of smoke has only been tested on a handful of species, and further studies are needed to rigorously test it.

Implications for seed banking and seed-based restoration

Seed banking is a cost-effective strategy for efficiently conserving genetic diversity in plants (Hay and Probert 2013). Easy-to-measure traits, such as dry seed mass and moisture content, can be a useful proxy for assessing whether seeds of a given species are desiccation tolerant and, thus, suitable for seed banking. For instance, seeds with both an average thousand seed weight < 500g and a moisture content < 30% are assumed to tolerate desiccation (Lan *et al.* 2014). Trait data for 87 species stored in our dataset suggest a high potential for *ex-situ* seed banking, as also shown by empirical studies in rock outcrop vegetation in Brazil (Tarré *et al.* 2007; Andrade *et al.* 2021) and Western Africa (Godefroid *et al.* 2013, 2020).

Seed-based restoration, in turn, is increasingly recognised as a highly cost-effective restoration strategy, yet many of the seed traits assessed here indicate that implementing it in Brazilian rock outcrop vegetation may be challenging (Dayrell *et al.* 2016). For example, direct seeding has yielded mixed results in *cangas*: high seedling density during the initial months but high mortality and slow growth after the first year of seeding (Figueiredo *et al.* 2021b), even with added organic matter (Figueiredo *et al.* 2021a). One potential limitation for direct seeding is the prevalence of species that produce many embryoless and non-viable

seeds (Figueiredo *et al.* 2021b). Since these traits showed a strong phylogenetic signal, it should be relatively easy to identify taxa that require additional processing before broadcasting, such as Poaceae and Asteraceae. Restoration practitioners must also consider that *ex-situ* stored seeds from several species from these ecosystems lose viability quite rapidly after collection, implying they require prompt use (Zanetti *et al.* 2020). Despite all these limitations, direct seeding has an underused potential to help reintroduce species in a cheaper way than planting seedlings (Figueiredo *et al.* 2021b).

Alternative seed-based restoration techniques for rock outcrop vegetation include hay transfer and topsoil translocation. However, empirical studies have shown that hay transfer is not a useful technique for the *campo rupestre* due to the high amount of non-viable seeds (Le Stradic *et al.* 2014). In contrast, topsoil transfer could be a more promising technique to restore rock outcrop vegetation considering that species have traits that indicate long-term soil persistence, such as small, light-demanding, and long-lived seeds (Long *et al.* 2015). Still, topsoil translocation has proven useful for restoration purposes in some (Burke 2008), but not all vegetation associated with rock outcrops (Le Stradic *et al.* 2016).

Conclusion

Seed germination ecology in rock outcrop vegetation in Brazil is shaped by species' evolutionary history but also by ecological context. Seed traits did not explain large-scale species distribution, nor did germination requirements explain microhabitat preferences. As a result, large-scale community assembly might be better explained by vegetative traits or other seed germination traits not explored here. At smaller scales, species from xeric habitats evolved specific risk-reducing strategies exemplified by seed dormancy and late-rain dispersal, ensuring germination is synchronised with optimum conditions for seedling establishment.

Germination in *campo rupestre* was positively influenced by light and most species had optimal germination between 20-30 ºC, were unaffected by heat shocks ≤ 100 ºC and germinated faster under smoke exposure. Given the differences in seed traits and germination responses between growth forms found in our study, our results have potential implications for rock outcrop vegetation dynamics. First, increasing soil temperatures may result in shifts in physiognomy because seeds of shrubs performed better at higher temperatures compared to herbs. Second, changes in fire regimes may favour species with larger, dormant seeds that show higher heat tolerance and species that germinate faster under smoke treatments post-fire environments. The consequences of changes in species and functional composition need to be examined in detail to support better assessments of the potential effects of climate change drivers in megadiverse rock outcrop vegetation.

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OPEN DATA

The R code for the analysis and creation of the figures will be provided as Supplementary Material and uploaded to GitHub upon acceptance.

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Table 1. Results of phylogenetic signal test for seed traits in Brazilian rocky outcrop vegetation. P.values for quantitative traits comes from the likelihood ratio test performed by phylosig function, while for qualitative traits it corresponds to the root-to-tip skewness test performed by the rtestdecdiv function.

Quantitative traits	Lambda	p.value
Seed mass	0.90	< 0.001
Water content	0.72	< 0.001
Percentage of embryoless seeds	0.75	< 0.001
Percentage of viable seeds	0.57	< 0.001

Qualitative traits	p.value
Primary dormancy	< 0.001
Dispersal syndrome	< 0.001
Dispersal season	< 0.001

Table 2. Differences in seed functional traits between growth forms (herbs vs. shrubs), and species distribution (restricted vs. widespread) and microhabitat (mesic vs. mesic/xeric vs. xeric) in Brazilian rocky outcrop vegetation. Bold values indicate p.values < 0.05. t and z correspond to the values obtained in the t- and z-tests that are part of the implementation of phylogenetic least square models and phylogenetic logistic regressions, respectively.

	Growth form: Shrub		Distribution: Widespread		Microhabitat: Mesic/Xeric		Microhabitat: Xeric	
Quantitative traits	t	p.value	t	p.value	t	p.value	t	p.value
Seed mass	**2.1872**	**0.0298**	-0.5986	0.5501	**2.0141**	**0.0453**	1.6115	0.1086
Water content	0.2789	0.7811	-0.0770	0.9388	0.6075	0.5453	0.7834	0.4358
Embryoless seeds	1.9274	0.0572	-0.2368	0.8134	0.9752	0.3322	1.2967	0.1982
Viable seeds	-1.0221	0.3085	0.2381	0.8122	-0.3040	0.7616	0.7006	0.4847
Qualitative traits	z	p.value	z	p.value	z	p.value	z	p.value
Dormancy	1.4125	0.1578	1.5052	0.1323	1.5266	0.1268	**2.5218**	**0.0117**
Anemochory	-1.2154	0.2242	1.3943	0.1632	1.0047	0.3150	1.1497	0.2503
Autochory	0.0387	0.9691	-0.0710	0.9434	-0.0792	0.9368	-0.0998	0.9205
Zoochory	0.3290	0.7422	0.0048	0.9962	0.6844	0.4937	-0.0040	0.9968
Early-Dry	-0.9086	0.3636	-0.1266	0.8993	-1.0427	0.2971	0.4504	0.6524
Late-Dry	**3.4323**	**0.0006**	-0.7443	0.4567	0.7421	0.4580	-1.3673	0.1713
Early-Rain	0.1036	0.9175	-0.7541	0.4508	-0.4839	0.6284	0.0445	0.9645
Late-Rain	**-2.0137**	**0.0440**	-0.1826	0.8551	**2.0319**	**0.0422**	**2.1507**	**0.0315**

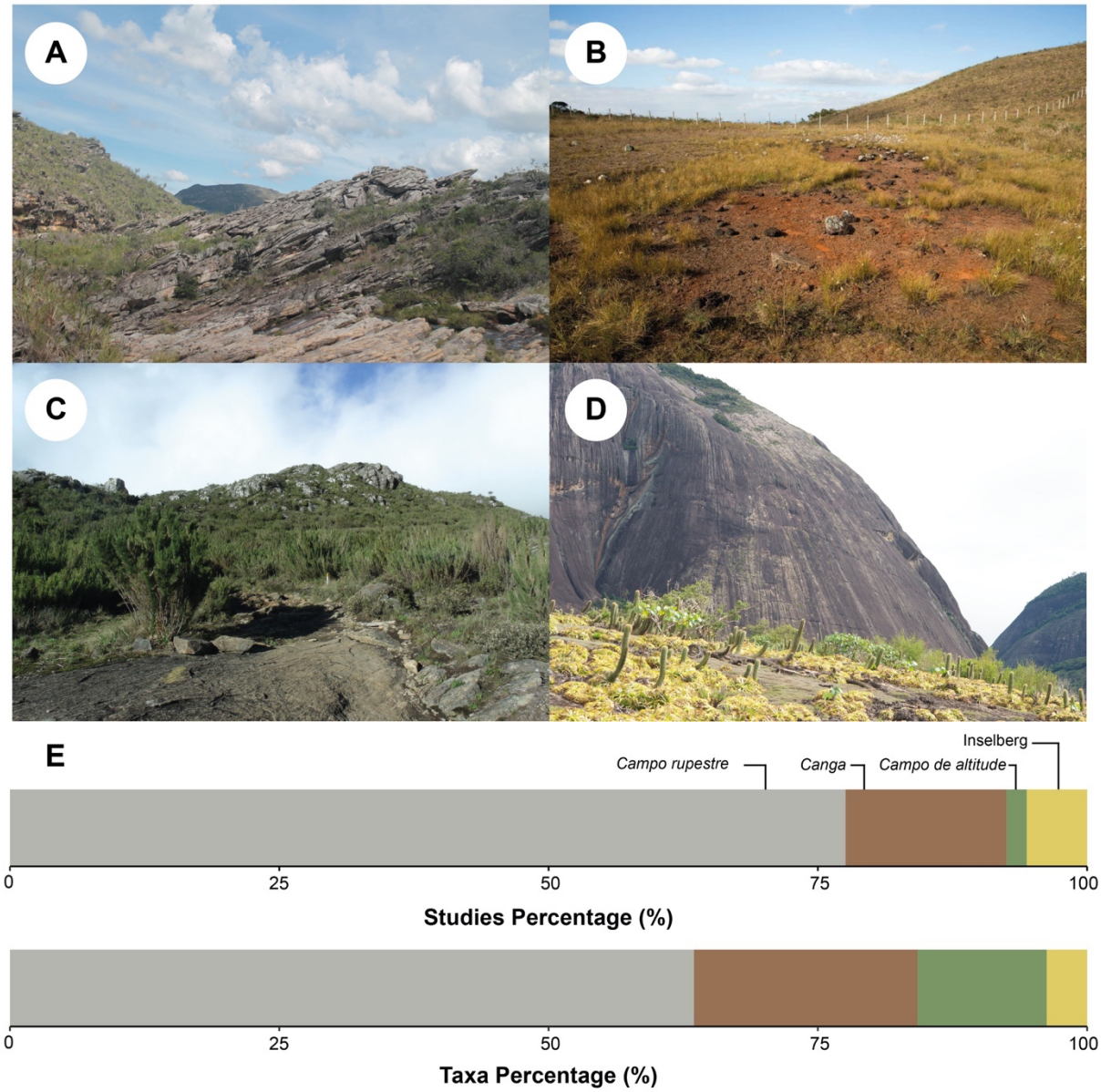

Figure 1. Main vegetation types associated with rock outcrops in Brazil. A. *Campo rupestre* at Serra do Cipó. B. *Canga* at Parque Estadual da Serra do Rola Moça. C. *Campo de altitude* at Parque Nacional do Caparaó. D. Inselberg at Teófilo Otoni municipality. E. Percentage of studies and taxa evaluated on each vegetation type. All locations are in the State of Minas Gerais. Photos by Carlos A. Ordóñez-Parra (A), Roberta L. C. Dayrell (B), Daniela Calaça (C) and Fernando A. O. Silveira (D).

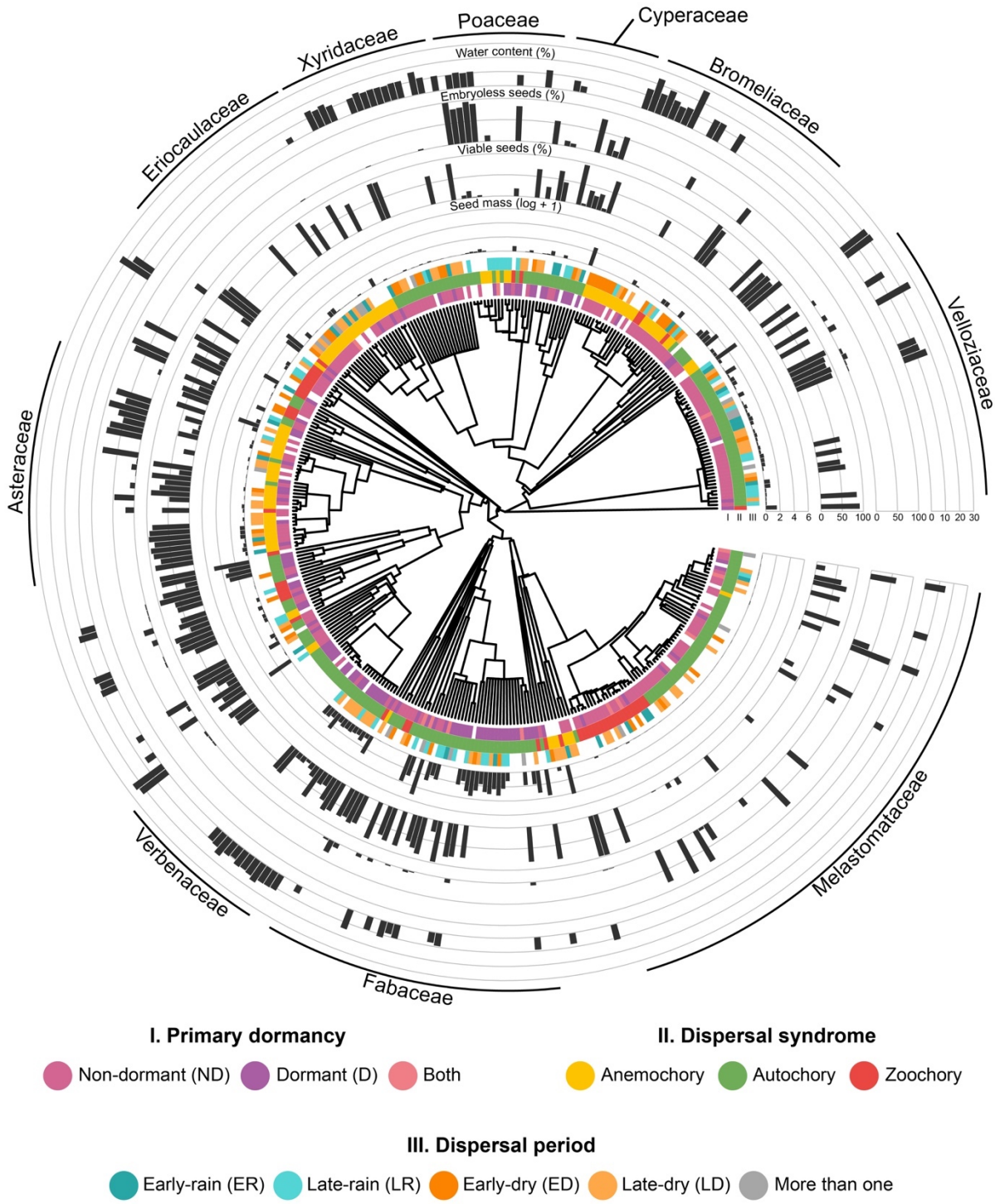

Figure 2. Phylogeny of studied species with available information on seed functional traits. The ten families with the largest number of species in the dataset are labelled. Figure elaborated with the R packages ggtree (Yu *et al.* 2017), ggtreeExtra (Xu *et al.* 2021) and ggnewscale (Campitelli 2022).

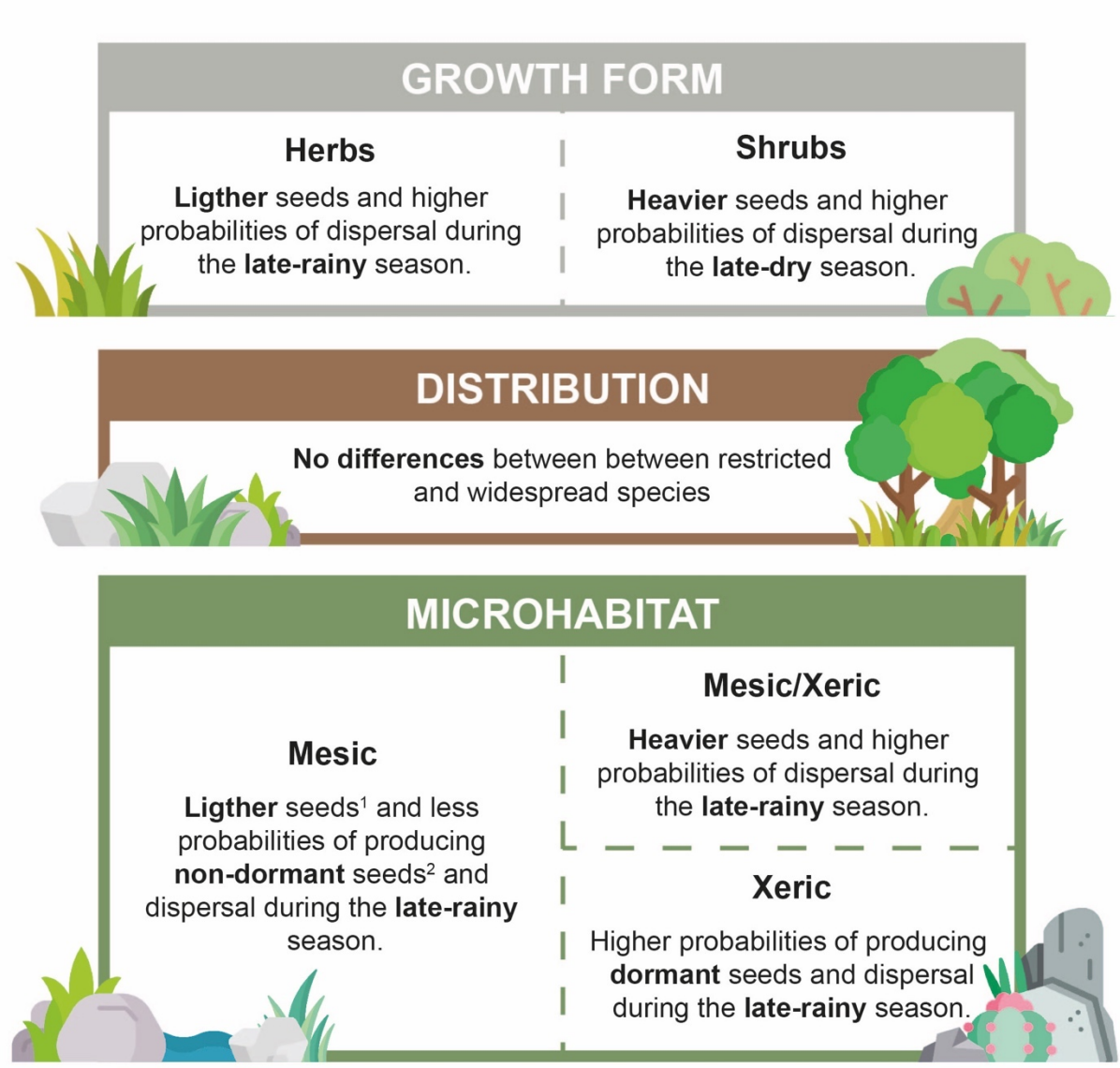

Figure 3. Seed trait differences among growth forms and species distribution and microhabitat, based on statistical results from Table 2. Notes: 1. In relation to species form Mesic/Xeric microhabitats. 2. When compared to species from xeric microhabitats. This figure was made using icons from Flaticon.com.

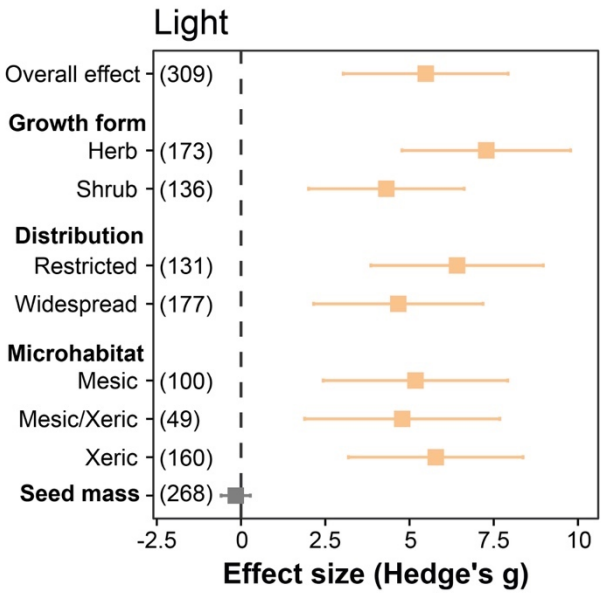

Figure 4. Effect of light availability on germination percentage in *campo rupestre* species (Control: total darkness). Squares indicate the standardised mean effect size for each moderator (growth form, distribution and microhabitat) and whiskers the 95 % confidence interval of the effect size. Coloured estimates indicate significant effects (i.e., where confidence intervals do not overlap zero). Numbers in parentheses indicate the number of observations.

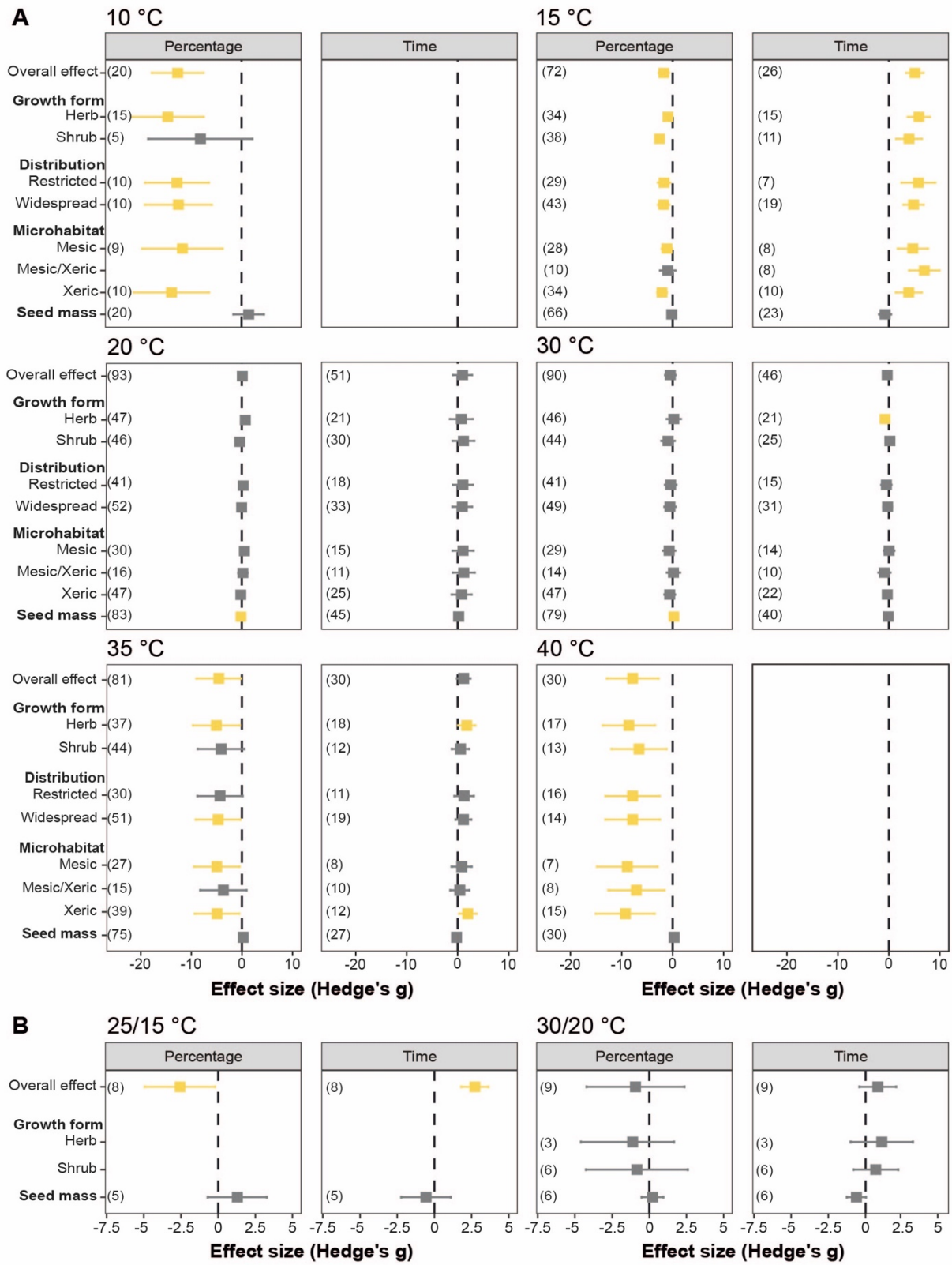

Figure 5. Germination responses to (A) constant and (B) alternate temperatures in *campo rupestre* species (Control: 25 ºC). Squares indicate the standardised mean effect size for each moderator (growth form, distribution and microhabitat) and whiskers the 95 % confidence

interval of the effect size. Coloured estimates indicate significant effects (i.e., where confidence intervals do not overlap zero). Numbers in parentheses indicate the number of observations. The empty panel for germination time at 10 and 40 ºC refers to a lack of data.

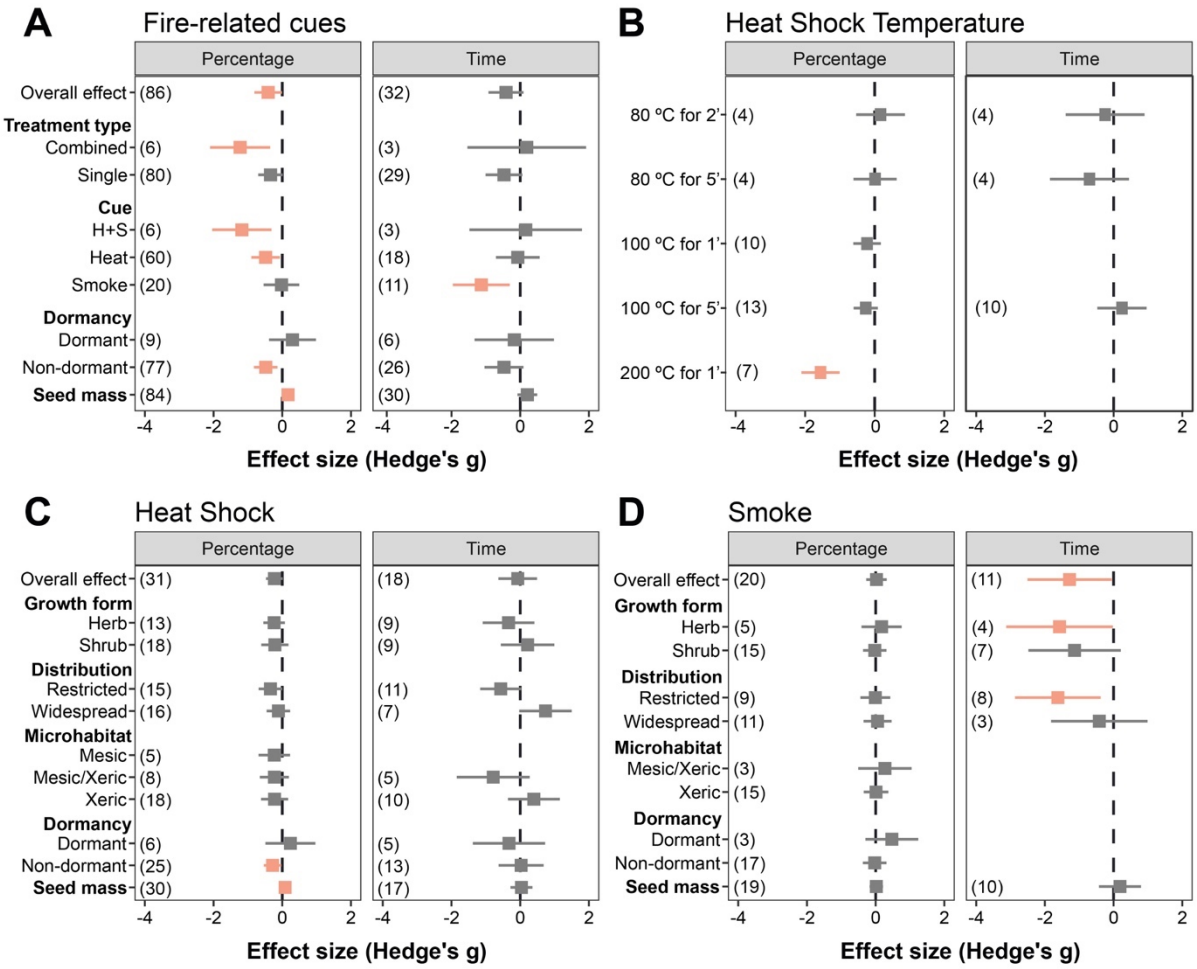

Figure 6. Germination responses to fire-related cues in *campo rupestre* species (Control: untreated seeds). (A) Overall effects. (B) Heat shocks temperatures. (C) Heat shocks without the 200 ºC for one minute. (D) Smoke. Squares indicate the standardised mean effect size for each moderator (growth form, distribution and microhabitat) and whiskers the 95 % confidence interval of the effect size. Coloured estimates indicate significant effects (i.e., where confidence intervals do not overlap zero). Numbers in parentheses indicate the number of observations.

Table S1. Moran's I value for the quantitative seed traits across different taxonomic levels. Bold values indicate values significantly different from zero.

Seed trait	Genus		Family		Order	
	I	p.value	I	p.value	I	p.value
Seed mass	**0.7035**	**< 0.001**	**0.6545**	**< 0.001**	**-0.3912**	**< 0.001**
Water content	**0.4456**	**< 0.001**	**0.2368**	**0.0287**	-0.0623	0.4592
Percentage of embryoless seeds	**0.6269**	**< 0.001**	**0.4324**	**< 0.001**	-0.0668	0.5038
Percentage of viable seeds	**0.4808**	**< 0.001**	**0.2176**	**< 0.001**	-0.0998	0.1337

1 **Table S2.** Summary of the random effects (σ ± 95% CI) of the mixed effect models on the effects of abiotic
2 factors on germination percentage. *Upper boundary of CI not found due to convergence problems derived from
3 high heterogeneity and small sample size.

Abiotic factor	Random effects		
	Observation	Study	Phylogeny
Light			
Overall	1.45 (0.59-2.35)	3.47 (2.14-5.56)	2.51 (0.59-4.57)
Growth form	1.49 (0.71-2.38)	3.48 (2.15-5.46)	1.80 (0.00-3.74)
Distribution	1.19 (0.29-2.05)	3.28 (2.01-5.24)	2.67 (1.16-4.65)
Microhabitat	1.49 (0.60-2.41)	3.26 (1.87-5.33)	2.75 (0.84-5.08)
Seed mass	5.16 (0.00-10.93)	4.26 (0.00-26.03)	11.92 (0.00-24.13)
10 ºC			
Overall	7.72 (2.9-12.75)	3.76 (0.00-16.38)	0.00 (0.00->3.16)*
Growth form	6.82 (1.14-NA)*	5.84 (0.00-17.19)	0.00 (0.00->3.16)*
Distribution	7.74 (0.00-12.79)	3.69 (0.00-16.39)	0.00 (0.00->3.16)*
Microhabitat	7.88 (2.23-13.37)	4.41 (0.00-20.08)	0.00 (0.00->3.16)*
Seed mass	5.16 (0.00-10.93)	4.26 (0.00-26.03)	11.92 (0.00-24.13)
15 ºC			
Overall	2.04 (1.50-2.75)	0.58 (0.00-1.92)	0.91 (0.00-2.97)
Growth form	2.12 (1.61-2.78)	0.00 (0.00-1.4)	0.00 (0.00-1.58)
Distribution	2.04 (1.49-2.75)	0.55 (0.00-1.92)	0.92 (0.00-2.97)
Microhabitat	2.05 (1.53-2.75)	0.82 (0.00-1.96)	0.00 (0.00-2.48)
Seed mass	1.84 (1.32-2.51)	0.52 (0.00-2.02)	2.00 (0.52-3.64)
20 ºC			
Overall	1.75 (0.93-2.22)	0.00 (0.00-2.06)	0.00 (0.00-2.58)
Growth form	1.65 (1.01-2.16)	0.00 (0.00-1.90)	0.52 (0.00-2.15)
Distribution	1.74 (0.90-2.22)	0.00 (0.00-2.10)	0.00 (0.00-2.66)
Microhabitat	1.73 (1.14-2.20)	0.00 (0.00-1.52)	1.73 (1.14-2.20)
Seed mass	0.00 (0.00-1.52)	0.00 (0.00-1.94)	1.68 (1.22-2.23)
30 ºC			
Overall	1.31 (0.57-1.79)	0.62 (0.00-2.02)	1.19 (0.00-3.85)
Growth form	1.27 (0.57-1.74)	0.10 (0.00-1.83)	1.50 (0.10-3.84)
Distribution	1.31 (0.54-1.79)	0.59 (0.00-2.00)	1.22 (0.00-3.97)
Microhabitat	1.28 (0.25-1.78)	0.56 (0.00-1.97)	1.16 (0.00-4.10)
Seed mass	1.63 (0.55-2.20)	0.00 (0.00-1.6)	0.72 (0.00-4.46)
35 ºC			
Overall	1.92 (1.09-3.04)	1.97 (0.00-5.00)	5.65 (1.83-8.91)
Growth form	1.93 (1.10-3.05)	2.03 (0.22-5.08)	5.52 (1.66-8.80)
Distribution	1.94 (1.10-3.05)	1.98 (0.00-4.98)	5.59 (1.84-8.85)
Microhabitat	1.96 (1.09-3.09)	1.95 (0.07-5.07)	5.47 (1.27-8.79)
Seed mass	1.94 (1.11-3.00)	1.62 (0.00-4.40)	5.96 (3.23-9.15)
40 ºC			
Overall	3.36 (1.42-5.66)	5.59 (2.61-12.39)	2.15 (0.00-6.04)
Growth form	3.39 (1.54-5.68)	5.34 (2.50-11.69)	2.14 (0.00-5.81)
Distribution	3.36 (1.42-5.66)	5.60 (2.61-12.39)	2.15 (0.00-6.04)
Microhabitat	2.95 (0.00-5.48)	5.44 (2.71-11.85)	2.80 (0.00-7.36)
Seed mass	3.83 (1.91-5.94)	8.93 (2.35-17.96)	0.00 (0.00-3.16)
25/15 ºC			
Overall	3.21 (1.83-6.09)	0.00 (0.00->3.1623)	0.00 (0.00->3.16)*

Seed mass	3.96 (0.00-9.22)	0.00 (0.00-0.00)	0.00 (0.00->3.16)*
30/20 ºC			
Overall	0.00 (0.00-0.97)	3.18 (1.47-8.32)	0.00 (0.00-1.7)
Growth form	0.00 (0.00-0.92)	3.31 (1.51-8.66)	0.00 (0.00-1.63)
Seed mass	0.00 (0.00-1.12)	2.58 (0.00-12.13)	0.00 (0.00->1.73)*
Fire-related cues			
Overall	0.67 (0.38-1.00)	0.09 (0.00-0.58)	0.31 (0.00-0.86)
Treatment type	0.66 (0.36-0.98)	0.13 (0.00-0.57)	0.25 (0.00-0.80)
Treatment	0.62 (0.32-0.93)	0.05 (0.00-0.54)	0.31 (0.00-0.82)
Dormancy	0.65 (0.36-0.97)	0.18 (0.00-0.73)	0.17 (0.00-0.69)
Seed mass	0.64 (0.35-0.96)	0.3 (0.00-0.85)	0.22 (0.00-0.75)
Heat shock			
Overall	0.64 (0.35-0.96)	0.00 (0.00-0.39)	0.00 (0.00-0.46)
Heat			
Overall	0.00 (0.00-0.42)	0.00 (0.00-0.40)	0.00 (0.00-0.55)
Growth form	0.00 (0.00-0.41)	0.00 (0.00-0.34)	0.00 (0.00-0.46)
Distribution	0.00 (0.00-0.41)	0.00 (0.00-0.41)	0.00 (0.00-0.55)
Microhabitat	0.61 (0.21-1.01)	0.00 (0.00-0.34)	0.00 (0.00-0.39)
Dormancy	0.00 (0.00-0.39)	0.00 (0.00-0.37)	0.00 (0.00-0.41)
Seed mass	0.66 (0.30-1.06)	0.0 (0.00-0.36)	0.00 (0.00-0.41)
Smoke			
Overall	0.18 (0.00-0.74)	0.00 (0.00-0.53)	0.00 (0.00-0.78)
Growth form	0.16 (0.00-0.73)	0.00 (0.00-0.51)	0.00 (0.00-0.74)
Distribution	0.18 (0.00-0.74)	0.00 (0.00-0.57)	0.00 (0.00-0.84)
Microhabitat	0.25 (0.00-0.81)	0.00 (0.00-0.60)	0.00 (0.00-0.92)
Dormancy	0.19 (0.00-0.77)	0.00 (0.00-0.76)	0.00 (0.00-0.91)
Seed mass	0.00 (0.00-0.66)	0.26 (<0.09-1.05)	0.00 (0.00-0.65)

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Table S3. Summary of the random effects (σ ± 95% CI) of the mixed effect models on the effects of abiotic factors on median germination time (t_{50}). *Upper boundary of CI not found due to convergence problems derived from high heterogeneity and small sample size.

Abiotic factor	Random effects		
	Observation	Study	Phylogeny
15 ºC			
Overall	4.13 (2.93-5.92)	0.00 (0.00-2.84)	0.00 (0.00->3.16)*
Growth form	3.98 (2.80-5.75)	0.00 (0.00-2.64)	0.00 (0.00-2.89)
Distribution	4.11 (2.91-5.89)	0.00 (0.00-2.95)	0.00 (0.00->3.16)*
Microhabitat	3.92 (2.76-5.64)	0.00 (0.00-3.00)	0.00 (0.00-3.00)
Seed mass	4.12 (0.00-6.45)	0.00 (0.00->3.16)	4.56 (1.71-20.24)
20 ºC			
Overall	1.28 (0.61-2.01)	0.00 (0.00-2.06)	2.22 (0.79-3.8)
Growth form	1.30 (0.60-2.01)	0.00 (0.00-2.07)	2.14 (0.80-3.80)
Distribution	1.29 (0.60-2.01)	0.00 (0.00-2.16)	2.20 (0.77-3.79)
Microhabitat	1.12 (0.59-1.97)	0.99 (0.00-1.98)	1.84 (0.81-3.80)
Seed mass	0.00 (0.37-1.88)	0.00 (0.00-2.79)	0.00 (0.30-3.52)
30 ºC			
Overall	1.26 (0.83-1.79)	0.00 (0.00-1.01)	0.82 (0.00-1.85)
Growth form	1.38 (0.86-1.89)	0.00 (0.00-0.9)	0.00 (0.00-1.72)
Distribution	1.27 (0.84-1.81)	0.00 (0.00-1.00)	0.74 (0.00-1.82)
Microhabitat	1.29 (0.84-1.84)	0.00 (0.00-0.92)	0.65 (0.00-1.75)
Seed mass	1.37 (0.87-2.01)	0.00 (0.00-1.08)	0.92 (0.00-2.18)
35 ºC			
Overall	2.20 (1.46-3.31)	1.30 (0.00-3.30)	0.00 (0.00-2.53)
Growth form	2.17 (1.44-3.27)	1.25 (0.00-3.16)	0.00 (0.00-2.25)
Distribution	2.19 (1.46-3.31)	1.33 (0.00-3.53)	0.00 (0.00-2.72)
Microhabitat	2.11 (1.40-3.18)	1.35 (0.00-3.26)	0.00 (0.00-3.13)
Seed mass	1.85 (1.14-2.79)	0.00 (0.00-2.59)	0.99 (0.00-2.76)
25/15 ºC			
Overall	0.00 (0.00-2.29)	0.00 (0.00-2.01)	0.63 (0.00-2.09)
Seed mass	1.83 (0.00-8.21)	0.00 (0.00-0.00)	2.61 (0.00-15.88)
30/20 ºC			
Overall	1.70 (0.58-3.25)	0.00 (0.00->3.16)	0.00 (0.00-2.78)
Growth form	1.69 (0.51-3.23)	0.00 (0.00->3.16)	0.00 (0.00-2.78)
Seed mass	1.12 (0.34-2.62)	0.00 (0.00-2.34)	0.00 (0.00->3.16)*
Fire-related cues			
Overall	1.27 (0.82-1.87)	0.00 (0.00-0.81)	0.00 (0.00-1.07)
Treatment type	1.27 (0.83-1.86)	0.00 (0.00-0.87)	0.00 (0.00-1.12)
Treatment	1.18 (0.75-1.74)	0.00 (0.00-0.93)	0.00 (0.00-1.56)
Dormancy	1.26 (0.82-1.86)	0.00 (0.00-0.80)	0.00 (0.00-1.14)
Seed mass	1.36 (0.89-2.00)	0.00 (0.00-0.95)	0.00 (0.00-1.44)
Heat shock			
Overall	0.92 (0.42-1.58)	0.00 (0.00-1.24)	0.00 (0.00-0.91)

Heat			
Overall	0.99 (0.48-1.68)	0.00 (0.00-0.87)	0.00 (0.00-0.93)
Growth form	0.93 (0.40-1.62)	0.00 (0.00-0.83)	0.00 (0.00-0.80)
Distribution	0.73 (0.04-1.36)	0.00 (0.00-1.10)	0.00 (0.00-0.99)
Microhabitat	0.97 (0.39-1.76)	0.00 (0.00-0.96)	0.00 (0.00-1.03)
Dormancy	0.97 (0.46-1.66)	0.00 (0.00-0.85)	0.00 (0.00-0.88)
Seed mass	1.04 (0.52-1.78)	0.00 (0.00-0.95)	0.00 (0.00-1.04)
Smoke			
Overall	0.83 (0.00-1.91)	0.73 (0.00-3.78)	0.00 (0.00-2.04)
Growth form	0.77 (0.00-1.84)	0.78 (0.00-3.92)	0.00 (0.00-1.91)
Distribution	0.52 (0.00-1.48)	0.75 (0.00-3.63)	0.00 (0.00-1.54)
Seed mass	0.95 (0.00-2.33)	1.31 (0.00-6.71)	0.00 (0.00->3.16)*

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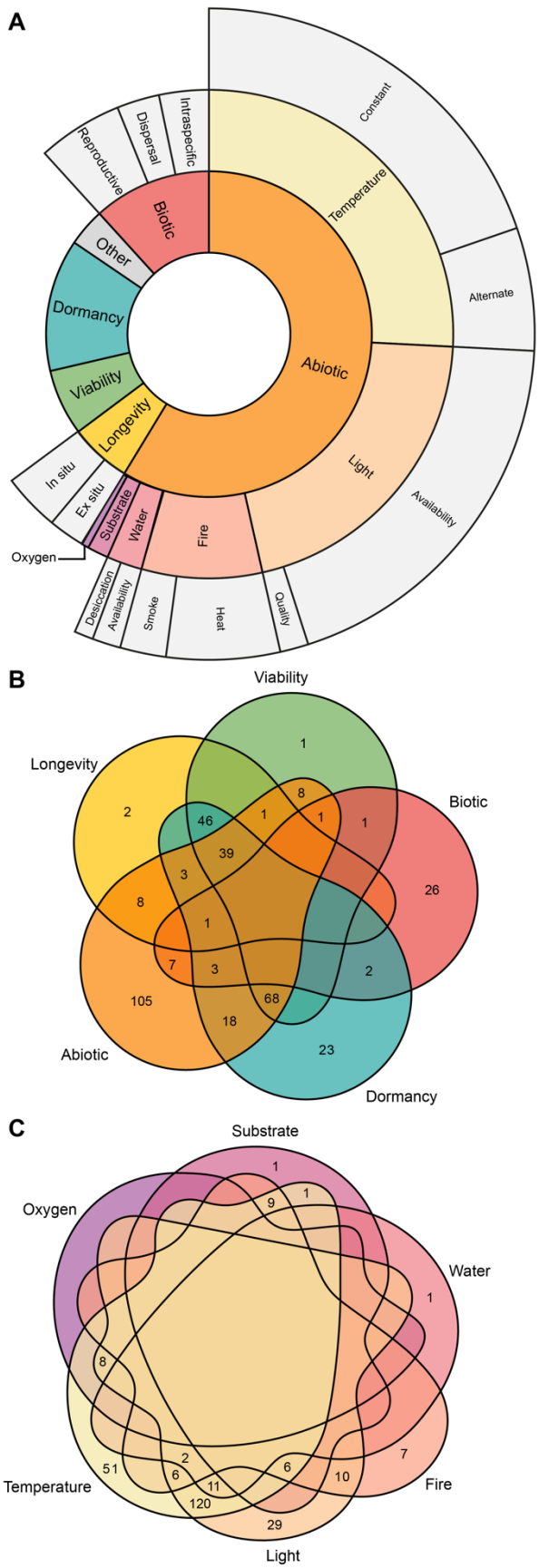
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Alternate
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Quality
Heat
Smoke
Availability
Desiccation
Oxygen
Ex situ
In situ
Intraspecific
Dispersal
Reproductive
Temperature
Light
Fire
Water
Substrate
Abiotic
Biotic
Other
Dormancy
Viability
Longevity
B
Viability
Longevity
Biotic
Abiotic
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39
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26
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Figure S1. State of the art of the germination ecology of Brazilian rock outcrop vegetation. A. Percentage of studies for each germination ecology topic. B. Number of species studied each major topic and their combinations. C. Number of species studied for each abiotic factor and their combination. Figure made using RAWGraphs (Mauri *et al.* 2017) and the venn R package (Dusa 2022).