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

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Running Title: Seed ecology in Brazilian rock outcrop vegetation

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. The germination ecology in such ecosystems has received little attention, especially regarding the association between seed traits, germination responses and adult plants ecology. Here, we provide a quantitative and meta-analytical 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, geographical distributions, and microhabitats. We also conducted a meta-analysis 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 optimal 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 tolerating heat better. Heat shocks above

200°C killed seeds, but smoke accelerated germination. No consistent differences in germination responses were found between restricted and widespread species or microhabitats. Still, species from xeric habitats evolved phenological strategies to synchronise germination with higher soil water availability.

Conclusions

Evolutionary history 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 microhabitats, 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 extremely nutrient-poor 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 attention, however, has been given to the ecophysiology of adult plants, overlooking the potential role of regeneration traits and regeneration niche, two aspects that are expected to drive species distribution and community assembly (Grubb 1977; Donohue *et al.* 2010; Larson and Funk 2016). Up to date, only a few qualitative reviews of germination ecology in these ecosystems have been conducted (Wyatt 1997; Biedinger *et al.* 2000).

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). The *campo rupestre* that develops on ironstone outcrops receives the name *canga* (Jacobi *et al.* 2007; Skirycz *et al.* 2014). The *campo de altitude* is found on granite and gneissic outcrops within the Atlantic Forest (Vasconcelos 2011), whereas inselbergs are isolated, dome-shaped granitic outcrops present across the country (Safford and Martinelli 2000). All these open, grassy-shrubby, fire-prone vegetations 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 vegetations 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 among some of its most emblematic families (i.e., 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 by pointing out that 1) seed traits shape germination responses to abiotic factors and 2) that contrasting microhabitat preferences and geographical ranges derive from distinct germination requirements, as assumed under the regeneration niche hypothesis and the seed ecological spectrum framework (Grubb 1977; Saatkamp *et al.* 2019). Nevertheless, they have only been assessed with a handful of species from a single family or could not be formally tested without large-scale databases made available only recently (Ordóñez-Parra *et al.* 2023). Furthermore, these qualitative reviews do not explicitly address the potential role of shared evolutionary history in species seed ecology. Studies carried out both at the local and global scale have highlighted that several key seed traits are highly conserved across the phylogeny, 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). As a result, a proper assessment of the ecological hypotheses raised by these reviews must incorporate this phylogenetic component.

In this research, we test these two long-standing hypotheses using a phylogenetically-controlled approach with the ultimate goal of providing an integrative synthesis of seed functional ecology in Brazilian rock outcrop vegetation. First, we assessed whether seed functional traits associated with different dimensions of the seed ecological spectrum are phylogenetically conserved 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. These 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 the before mentioned ecological groups and tested if such responses were moderated by seed mass –a central trait that is considered to control various aspects of germination (Saatkamp *et al.* 2019). Finally, given that seed traits data provide critical information for biodiversity conservation and ecological restoration (Mattana *et al.* 2022) and rock outcrop vegetation is increasingly exposed to several threats –both in Brazil and worldwide (Fernandes 2016; Porembski *et al.* 2016; Fitzsimons and Michael 2017)– we discuss how the available information on seed traits and germination responses support and inform conservation and restoration programs. Since 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 the investment in regeneration via seeds and seeds main functions (Grubb 1977;

Saatkamp *et al.* 2019) [i.e., seed dry mass (mg), seed water content (%), percentage of embryoless seeds (%), percentage of viable seeds (%), seed dispersal syndrome (anemochoroy, autochory and zoochory), seed dispersal season (early-dry, late-dry, early-rain and late-rain) and primary dormancy (dormant and non-dormant)]; and 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 information on species growth form, microhabitat ('xeric' when substrate experiences pronounced seasonal drought, or otherwise 'mesic'), and geographic distribution ('restricted' to rock outcrop vegetation, and otherwise 'widespread') of each species (see Ordóñez-Parra *et al.* 2023 for a full description of data collection).

Phylogenetic tree

We reconstructed the phylogenetic tree of the study 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 impair 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 $\lambda = 0$ indicating that related taxa are not more similar than expected by chance (i.e., no phylogenetic signal) and $\lambda = 1$ implying that a given trait evolves under a Brownian motion model (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 further explored this phylogenetic signal by calculating Moran's I 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, and percentage of embryoless and viable seed values, to reduce the skewness of the data. For species with more than one record, we carried out the analyses using the mean 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 seed 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 seed 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 classified 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 were always 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 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 effects of light, constant and temperatures, and fire-related cues on germination only for *campo rupestre* 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. We used the standardised mean difference Hedge's g (Hedges 1981) using the escalc function from the package *metafor* (Viechtbauer 2010). This metric measures the standardized change in a given response variable in treatment groups compared to control groups and includes a correction by sample size and variance (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 25ºC as a control for constant and alternate temperatures since 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 shocks or smoke) as controls for fire-related cues.

We assessed the effect 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* database and were complemented with data from thirteen experiments recovered 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). 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 deposited in the database *Rock n' Seeds* that include 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, since fire-related cues are known to shape seed dormancy states (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 assessed the overall effect of each abiotic factor (i.e. light, temperature and fire) on germination percentage and time 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-forms, distribution, microhabitats, seed mass and dormancy, but the last one only for fire-related cues. Because seed mass exhibited a significant, strong phylogenetic signal (see below), the missing seed mass values for some 54 species were inputted using average values for the genera from *Rock n' Seeds* database (Ordóñez-Parra *et al.* 2023) and the Seed Information Database (https://data.kew.org/sid/). Ninety-five percent confidence intervals around the effect sizes were calculated. 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, 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 correlation for the seed mass ($I = -0.39$, $p < 0.001$, Table S1).

Seed mass values ranged from 0.00035 to 175.15 mg (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 was less variable than seed mass, with values ranging from 3.9% to 28.3% (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 species 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) to species producing > 95% of empty seeds (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%) produced few embryoless seeds (Figure 2). Likewise, some species produce large amounts of unviable seeds while others produce mainly viable seeds (i.e., almost 100% of viable seeds). Eriocaulaceae (Median: 89%), Xyridaceae (87.7%) and Velloziaceae (86%) produced the highest proportion of viable seeds, while Poaceae species (11.5%) produced 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 seeds, whereas 36% produced dormant seeds (Figure 2). The most common dormancy class was physical dormancy (PY), being present in 37 Fabaceae, three Convolvulaceae and one Malvaceae species. Physiological dormancy (PD) was the second common dormancy class and Verbenaceae (nine species), Cyperaceae (six species) and Melastomataceae (five species) were the families with the highest number of species presenting it. Eleven species were reported to produce either mostly dormant or non-dormant seeds. We found moderate evidence that species from xeric environments had higher probabilities of producing dormant seeds ($z = 2.52$, $p = 0.012$).

Autochory was the most common dispersal syndrome (58.9% of species), which was present in families such as 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 predictors tested (Table 3). Most species dispersed seeds during the dry season, either in the late-dry season (38.5%) or early-dry season (26.5%), while only 25.6% and 17.9% dispersed in the late- and early-rainy season, respectively. 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-rain season than species from mesic microhabitats. There was no evidence that the

probability of dispersal during the early-dry or the early-rainy season varied between predictors (Table 3).

In summary, shrubs tended to produce heavier seeds and had a high probability of dispersal during the late-dry season. In contrast, herbs produced relatively smaller seeds that had high probabilities of being dispersed during the late-rainy season. Species from mesic/xeric microhabitats tended to produce heavy seeds and be dispersed during the late-rainy season compared to those from exclusively mesic microhabitats. Similarly, species restricted to xeric environments had a higher probability of producing dormant seeds and presenting 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 a positive overall 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 effect 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 temperatures below 20 ºC (10 and 15 °C) reduced germination percentage (10 ºC: $g = -12.53$, CI = -17.62 to -7.45, $z = -4.83$, $p < 0.0001$; 15ºC: $g = -1.75$, CI = -2.78 to -0.72, $z = -3.32$, $p <$

0.001) and increased germination time (15ºC: 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; 40ºC: g = -7.85, CI = -12.94 to -2.75, z = -3.02, p = 0.002) but no evidence that they affected germination time (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 15ºC (X^2 = 8.35, p = 0.004, Figure 5). Additionally, there was moderate evidence that germination in herbs was accelerated at 30ºC (z = -2.23, p = 0.03) but decreased (z = -2.12, p = 0.03) and delayed (z = 2.03, p = 0.04) at 35ºC. No evidence of an effect of these temperatures was found 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.

Similar results were found when evaluating the effects of alternate temperatures, with the data showing 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), but very strong evidence that they increased germination time (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 time (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) and time (g = -0.41, CI = -0.92 to 0.10, z = -2.68, p = 0.007). 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 ($z = 2.54$, $p = 0.01$), 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 200 ºC, 1 minute 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).

DISCUSSION

Seeds functional traits are phylogenetically conserved in Brazilian rock outcrop vegetation

We found that all the seed functional traits we assessed had a significant and moderate-to-strong phylogenetic signal, suggesting that phylogenetic relatedness plays a pivotal role in shaping seed traits in rock outcrop vegetation as globally reported for seed mass (Moles *et al.* 2005) and dormancy (Willis *et al.* 2014). Such phylogenetic signal could

be traced back up to the Family level, implying that several aspects of a species germination ecology can be inferred from other members of the family. However, our results partially contrast with local studies in other Brazilian open 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. Still, the authors tested and measured the phylogenetic signal of this trait using Bloomberg's K, an index known to be highly sensitive to sample sizes and incomplete phylogenetic background, and that provides divergent results to Pagel's λ (Münkemüller *et al.* 2012). Second, we found a significant phylogenetic signal for seed dispersal season, while seed dispersal season in the Cerrado (Escobar *et al.* 2021) and other phenophases in the *campo rupestre* (Zanetti *et al.* 2020; CS 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 (CS Oliveira *et al.* 2021).

Seed mass and seed dispersal season differed between herbs and shrubs, with shrubs tending to produce relatively larger seeds and having higher probabilities of dispersing during the late-dry season, whereas herbs produced lighter seeds with higher probabilities of dispersal 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 Brazilian rock outcrop vegetation. On the other hand, differences in seed dispersal season suggest differences in phenological strategies to cope with precipitation seasonality (see below).

Seed traits do not explain large-scale species distribution, but seed dispersal phenology may shape microhabitat differences

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). Despite that, we did not find differences in seed functional traits or germination requirements between restricted and widespread species, suggesting that the assessed seed traits do not explain large-scale species distribution, as predicted by the regeneration niche hypothesis, which suggests that differences in regeneration traits contribute to species ecological breadth and niche segregation (Grubb 1977). 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.* 2016) or by other seed and germination traits not included here.

Species from mesic and xeric microhabitats did differ in some of the traits we assessed, but these differences were related to seed dispersal phenology rather than seed germination requirements. This finding agrees with previous research showing little correspondence between seed traits and species ecological preferences (Fernández-Pascual *et al.* 2022) but contrasts with local-scale studies showing small-scale differences in the germination niche of *campo rupestre* species from distinct microhabitats (Oliveira and Garcia 2011; Ranieri *et al.* 2012; Silveira, Negreiros, *et al.* 2012; Marques *et al.* 2014; Giorni *et al.* 2018). All these local studies were conducted with fewer species from a single family, suggesting that these differences might dilute at larger scales when several different taxa are considered. While our results do not support the idea that germination responses to the abiotic factors explain distributions at the microhabitat level in the *campo rupestre*, a more detailed analysis within each family could be useful to test the relative importance of germination requirements for microhabitat differentiation across different scales.

Regardless of microhabitat, most species dispersed their seeds during the late- or the early-dry season. Therefore, dispersal during the dry season is the prevalent strategy in Brazilian rock outcrop vegetation. 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 synchronize germination with higher water availability (Silveira, Ribeiro, *et al.* 2012; Garcia *et al.* 2020). Yet, only 36% of species in our dataset produce dormant seeds, and *campo rupestre* is the vegetation type with the highest ND/D ratio worldwide (Dayrell *et al.* 2017), implying that seed dormancy is not the main driver of seedling establishment in rock outcrop vegetation. Additional strategies to control germination timing might include germination requirements and the acquisition of secondary dormancy. A mismatch between temperature germination requirements and environmental conditions at the moment of dispersal might provides 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. On the other hand, secondary dormancy has been reported in various Eriocaulaceae and Xyridaceae species from *campo rupestre* (see Garcia *et al.* 2020). All these species disperse their non-dormant seeds between the early-dry and the early-rain season, which become increasingly dormant as the rainy season advances, and humidity and temperature rise. 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 to our finding of them having lower seed mass compared to shrubs, as predicted by the well-established trade-off between light requirements and seed mass (Milberg *et al.* 2000). Under such trade-off, lighter seeds are expected have stronger light requirements, given the little amount of internal reserves to support seedling development. Still, our meta-analysis did not find evidence to support such a trade-off in Brazilian rock outcrop vegetation. A possible explanation for this lack of support is the high uniformity in germination responses to light in our species which either responded positively to light (i.e., positive photoblastic) or were light-indifferent (non-photoblastic) (Nunes *et al.* 2016; Garcia *et al.* 2020). Negative photoblastism is prevalent in dark and large-seeded herbaceous species from non-tropical latitudes (Carta *et al.* 2017); thus, it is not expected in Brazilian rock outcrop vegetation. For instance, this germination behaviour has only been reported for one species in our study system (*Lippia filifolia,* Pimenta *et al.* 2007). Another possible explanation is the small variation in seed size in our data, with most species producing small (86% records, < 1 mg) seeds and from lineages known to have positively photoblastic seeds, such as Melastomataceae, Xyridaceae and Velloziaceae (Nunes *et al.* 2016; Garcia *et al.* 2020; Ordóñez-Parra *et al.* 2022). Large-seeded species from *campo rupestre*, mainly from Fabaceae, have shown to be light-indifferent (Nunes *et al.* 2016), so additional studies with other large-seeded species are needed to test the prevalence of the seed mass-light responses trade-off in rock outcrop vegetation.

Small-seeded species from our study are expected to have narrowly defined microsite requirements for successful establishment due to their limited internal resources (Pearson *et al.* 2003). Therefore, futher aspects of the light environment, such as light spectral quality and

the interaction between light and temperature, and are expected to control their germination (Pons 2014). Spectral quality —measured as the ratio between red (R) and far-red (FR) light; i.e., R:FR— provides information about overhead foliage and litter on the soil surface, with high R:FR indicating no cover and, thus, high irradiance (Baskin and Baskin 2014). Still, in our study system, the effect of different R:FR has only been assessed for a handful Bromeliaceae (Pereira *et al.* 2009; Hmeljevski *et al.* 2014) and Velloziaceae species (Vieira *et al.* 2018), preventing us from providing robust inferences about the functional relevance of light quality as a germination cue in Brazilian rock outcrop vegetation. Globally, responses to R:FR have been both positively and negatively associated with seed mass (Tiansawat and Dalling 2013). Jankowska-Blaszczuk and Daws (2007) suggest that tiny seeds should restrict germination to high R:FR conditions to ensure high irradiance and that for such behaviour to be successful, seeds must be able to persist for extended periods in the soil. Considering that the small-seed species from Brazilian rock outcrop vegetation have been shown to persist for several years in soil seed banks (see Garcia *et al.* 2020), a positive relationship between seed mass and R:FR requirement would be expected. However, Jankowska-Blaszcuk and Daws (2007) comment that such germination behaviour implies that small-seeded species would germinate in high-risky environments where soils dry rapidly. In this case, one should expect that small-seeded species limit their germination to safer sites, such as those with low R:FR and likely higher soil moisture. Consequently, a positive relationship between seed mass and R:FR requirements (Pearson *et al.* 2003) could be adaptive in rock outcrop vegetation, a hypothesis that is yet to be tested. On the other hand, temperature-dependent germination responses to light have only been described in some Velloziaceae species in which germination in the darkness only occurs under high (30-40ºC) temperatures. Still, its functional or evolutionary relevance, if any, is yet to be described (Garcia *et al.* 2020).

Herbs and shrubs respond differently to low and high temperatures

We found that the optimal temperature for *campo rupestre* species germination ranges between 20-30ºC, supporting previous studies (Nunes *et al.* 2016; Garcia *et al.* 2020). Temperatures below this range significantly reduced germination percentage and delayed germination. This reduction is an arguably a mechanism to avoid germination during the dry season when temperatures decrease and water is not readily available for seedling establishment (Garcia *et al.* 2020). The negative effect of low temperatures was stronger in shrubs, suggesting that these require higher temperatures to germinate. Once again, differences between growth forms could arise from differences in seed size, with the relatively larger seeds of shrubs having higher base temperatures for germination (Arène *et al.* 2017). Still, our data only support a positive moderating effect of seed mass on germination responses to 20 and 30 ºC, both temperatures where no significant differences between herbs and shrubs were found. Also, the small variation in seed size mentioned earlier and the limited availability of data from hydrothermal time models our study system (but see Duarte *et al.* 2018; Oliveira *et al.* 2021) limit our capacity to test this hypothesis. On the other hand, temperatures above 30ºC decreased and delayed germination in herbs, while shrubs remained unaffected, implying that shrub seeds tolerate germinating at higher temperatures. Accordingly, we should expect increased shrub abundance in microsites that experience higher temperatures.

Alternate temperature regimes have either a negative or null effect on the germination in *campo rupestre*. The reduction of germination percentage and the increase of germination time at 25/15ºC regime is probably due to part of these temperatures being below the optimal range. Similarly to germination responses to light, the lack of a significant effect of 30/20ºC 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). Recent 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 with species with large seeds and from other Brazilian rock outcrop vegetation 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, but milder heat shocks (≤ 100 ºC) did not affect germination percentage or time, agreeing with previous evidence of high heat tolerance in seeds from Neotropical savanna species (Daibes *et al.* 2022). This effect was moderated by seed mass and seed dormancy, with lighter, non-dormant seeds being less tolerant to heat shocks. These results are aligned with those described for Cerrado species (Ramos *et al.* 2016; Daibes *et al.* 2019). Contrastingly, dormant 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). On the other hand, the lack of negative effects on germination in dormant species implies that traits associated with seed dormancy promote heat tolerance. For instance, dormancy acquisition occurs in parallel with the accumulation of heat shock proteins or the consolidation of water-impermeable coats, which can offer protection against environmental hazards, including heat (Tweddle *et al.* 2003; Ramos *et al.* 2016).

Smoke did not affect germination percentage but consistently reduced germination time. This result agrees with the role of smoke-derived compounds as germination stimulants of non-dormant seeds or those where dormancy has been alleviated (Mackenzie *et al.* 2021). Smoke-stimulated germination in the *campo rupestre* is thought to be ecologically relevant as

it promotes the germination of species resprouting and shedding seeds after a fire (Fernandes *et al.* 2021) –a usual phenological syndrome in our study system (Figueira *et al.* 2016)– allowing recently-dispersed seeds to exploit the post-fire environment where competition is relaxe (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 promising, low-cost *ex situ* conservation strategy with a high potential for efficiently conserving considerable amounts of plant material and its associated genetic diversity (Hay and Probert 2013). Easy-to-measure traits can be a reliable proxy for assessing whether the seeds of a given species are desiccation tolerant and, thus, suitable for seed banking. Dry seed mass is tightly linked with this trait, with lighter seeds having more probabilities of producing desiccation tolerant (Wyse and Dickie 2018). For instance, seeds with both a thousand seed wight < 500g and a moisture content < 30% are assumed to be tolerate desiccation (Lan *et al.* 2014). Trait data for 87 species in our dataset suggest that there is a high potential for storage in *ex-situ* seed banks, as shown by empirical studies in Brazilian rock outcrop vegetation (Tarré *et al.* 2007; Andrade *et al.* 2021) and similar ecosystems in Western Africa (Godefroid *et al.* 2013, 2020).

On the other hand, seed-based restoration is increasingly recognized as a highly cost-effective restoration strategy (Merritt and Dixon 2011), yet many of the seed traits assessed in this research indicate that it may be challenging to apply in Brazilian rock outcrop vegetation (Dayrell *et al.* 2016). For example, direct seeding has yielded mixed results in *cangas*: while it led to a high seedling density during the initial months, species showed high mortality and slow growth after the first year of seeding (Figueiredo *et al.* 2021b), even after the

incorporation of organic matter, which hampered seedling establishment, especially for species with small, light-dependent seeds species (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 in our study, we expect that its relatively easy to identify taxa that require additional processing before broadcasting, such as Poaceae and Asteraceae. Seed-based restoration projects involving these species must employ additional processing techniques to improve seed quality (e.g., Feitosa *et al.* 2009; Melo *et al.* 2009). Restoration practitioners must also consider that the *ex-situ* stored seeds of several species from these ecosystems lose viability quite rapidly after collection, implying they ought to be used as soon as possible (Zanetti *et al.* 2020). Despite all these limitations, direct seeding has an underused potential to help reintroduce species in a cheaper way than seedling planting (Figueiredo *et al.* 2021b).

Alternative seed-based restoration techniques for rock outcrop vegetation include hay transfer and topsoil translocation. Unfortunately, hay transfer is not a useful means to restore degraded areas of *campo rupestre* due to the high amount of non-viable seeds produced by most plants (Le Stradic *et al.* 2014). In contrast, topsoil transfer is a more promising technique to restore rock outcrop vegetation considering that species produce small, light-demanding, and long-lived seeds, suggesting a large potential for persistence in soil (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). Moreover, studies in the *campo rupestre* have shown impoverished soil seed banks (Medina and Fernandes 2007; Le Stradic *et al.* 2018; Luz *et al.* 2018), hence topsoil transfer (5 cm) has shown little use for ecological restoration (Le Stradic *et al.* 2018). However, transferring deeper topsoil samples in degraded *cangas* showed more promising results with restored areas

recovering a considerable percentage of floristic and functional composition (Onésimo *et al.* 2021; Rezende *et al.* 2021). However, this technique has two major limitations. First, areas where topsoil is removed show little recovery after extraction (Le Stradic *et al.* 2018); thus, topsoil extraction is recommended exclusively for sites targeted for mining operations. Second, soil samples –especially thicker ones– might contain a considerable amount of exotic and non-target species (Le Stradic *et al.* 2018; Rezende *et al.* 2021).

Conclusion

Seed germination ecology in Brazilian rock outcrop vegetation is shaped by species evolutionary history, but we were also able to find differences between ecological groups. Unexpectedly, seed traits did not explain large-scale species distribution, neither germination requirements explained microhabitat preferences, providing low support to the regeneration niche hypothesis (Grubb 1977). As a result, large-scale community assembly might be better explained by vegetative traits or other seed germinaton traits not explored here. Still, species from xeric habitats evolved specific risk-reducing strategies exemplified by seed dormancy and late-rain dispersal, ensuring germination is synchronized 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. Temperatures below and above this range had different effects according to growth form, with shrubs requiring higher temperatures than herbs. Therefore, we should expect shrubs to colonize microsites that experience higher soil temperatures better, with likely changes in vegetation physiognomy. Larger, dormant seeds showed higher heat tolerance, but seed mass did not affect germination responses to light or temperatures. Smoke accelerated germination, providing opportunities for establishment under conditions of relaxed competition in post-fire environments.

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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.

	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**

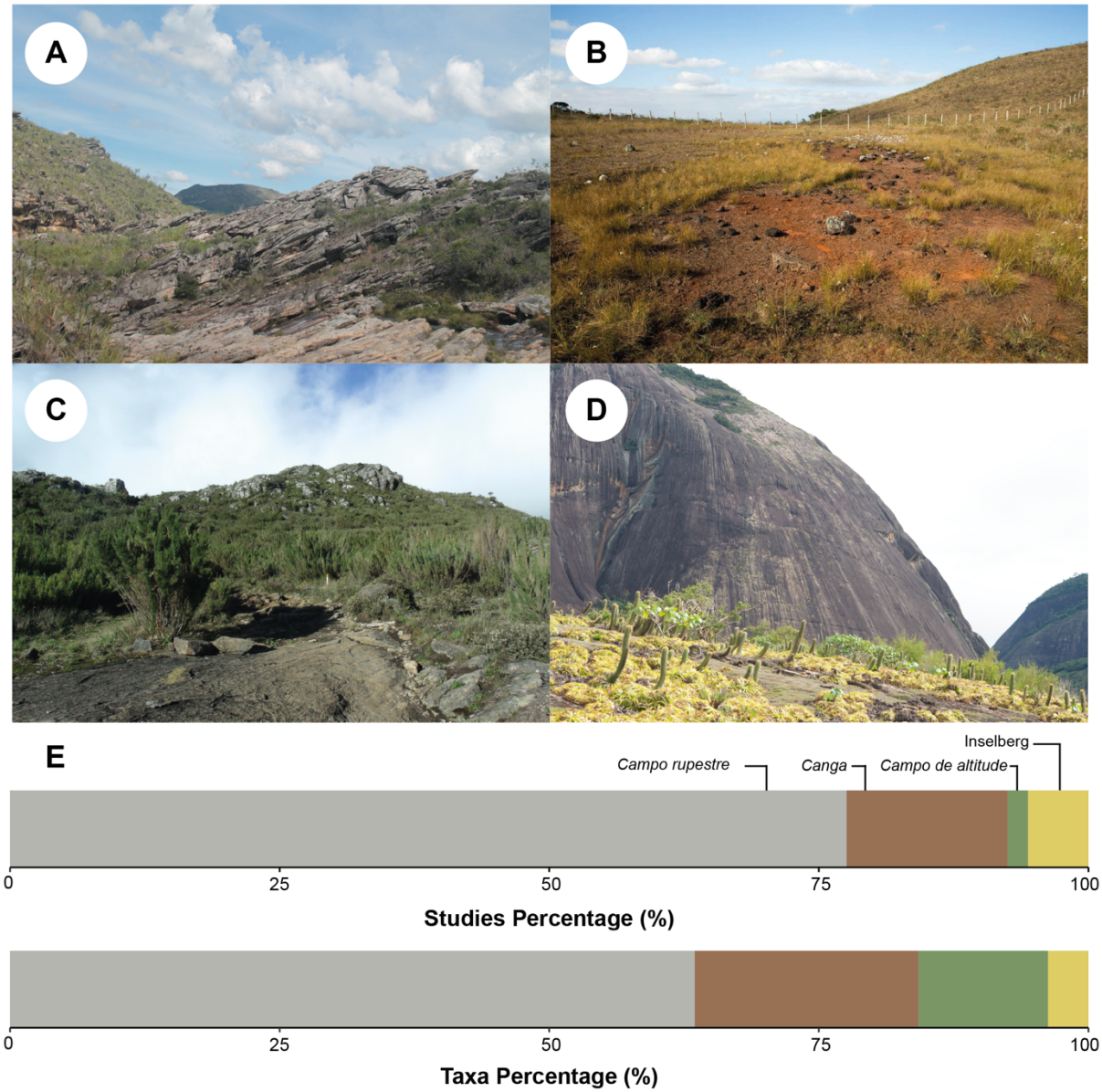

Figure 1. Main vegetation types associated with rock outcrops in Brazil. A. *Campo rupestre* at Serra do Cipó. B. *Canga* at Parque Estadual da Serra do Rola Moça. C. *Campo de altitude* at Parque Nacional do Caparaó. D. Inselberg at Teófilo Otoni municipality. E. Percentage of studies and taxa evaluated 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).

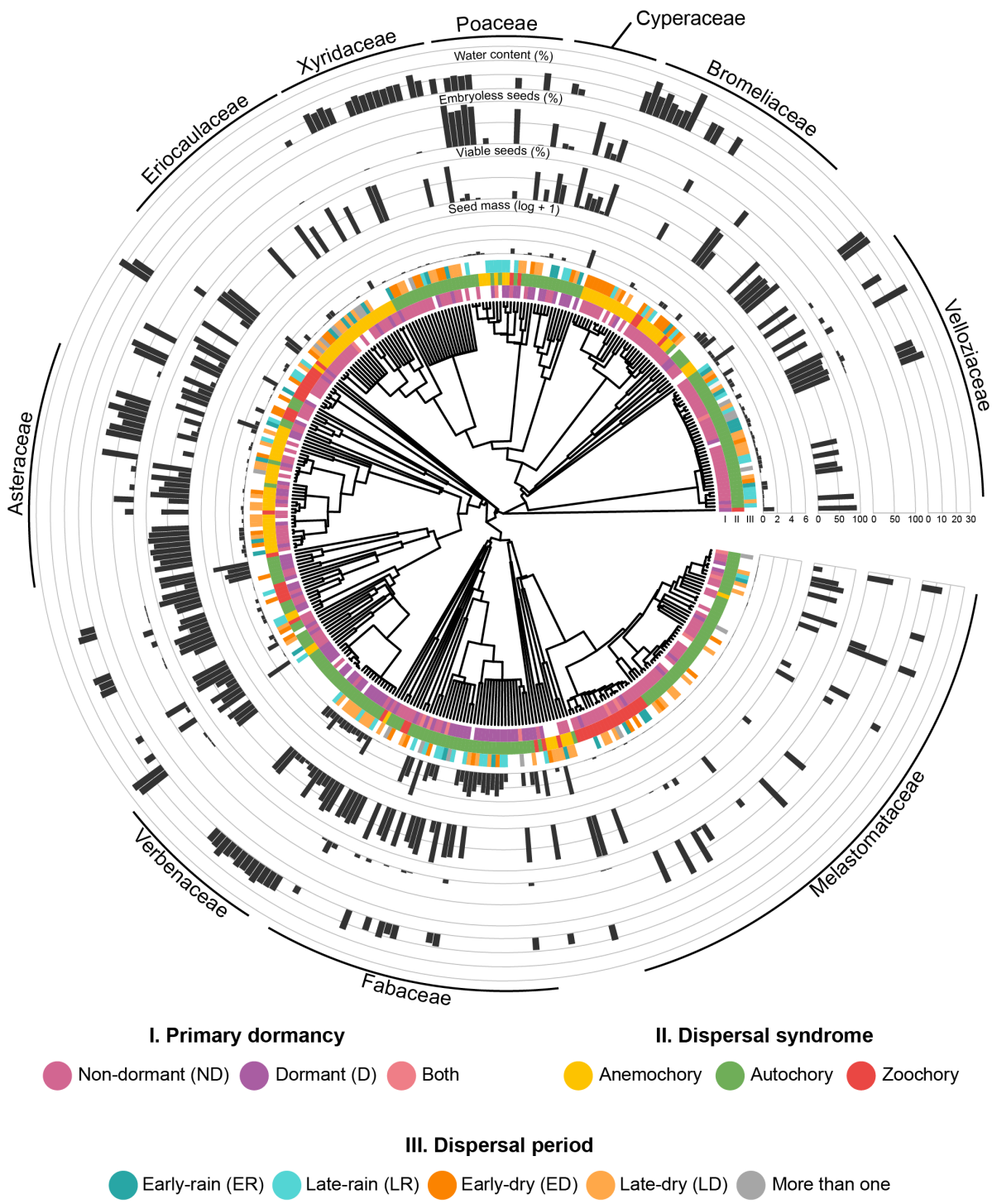

Figure 2. Phylogeny of studied species with available information on seed functional traits. The ten families with the largest number of species in the dataset are labelled. Figure elaborated with the R packages ggtree (Yu *et al.* 2017), ggtreeExtra (Xu *et al.* 2021) and ggnewscale (Campitelli 2022).

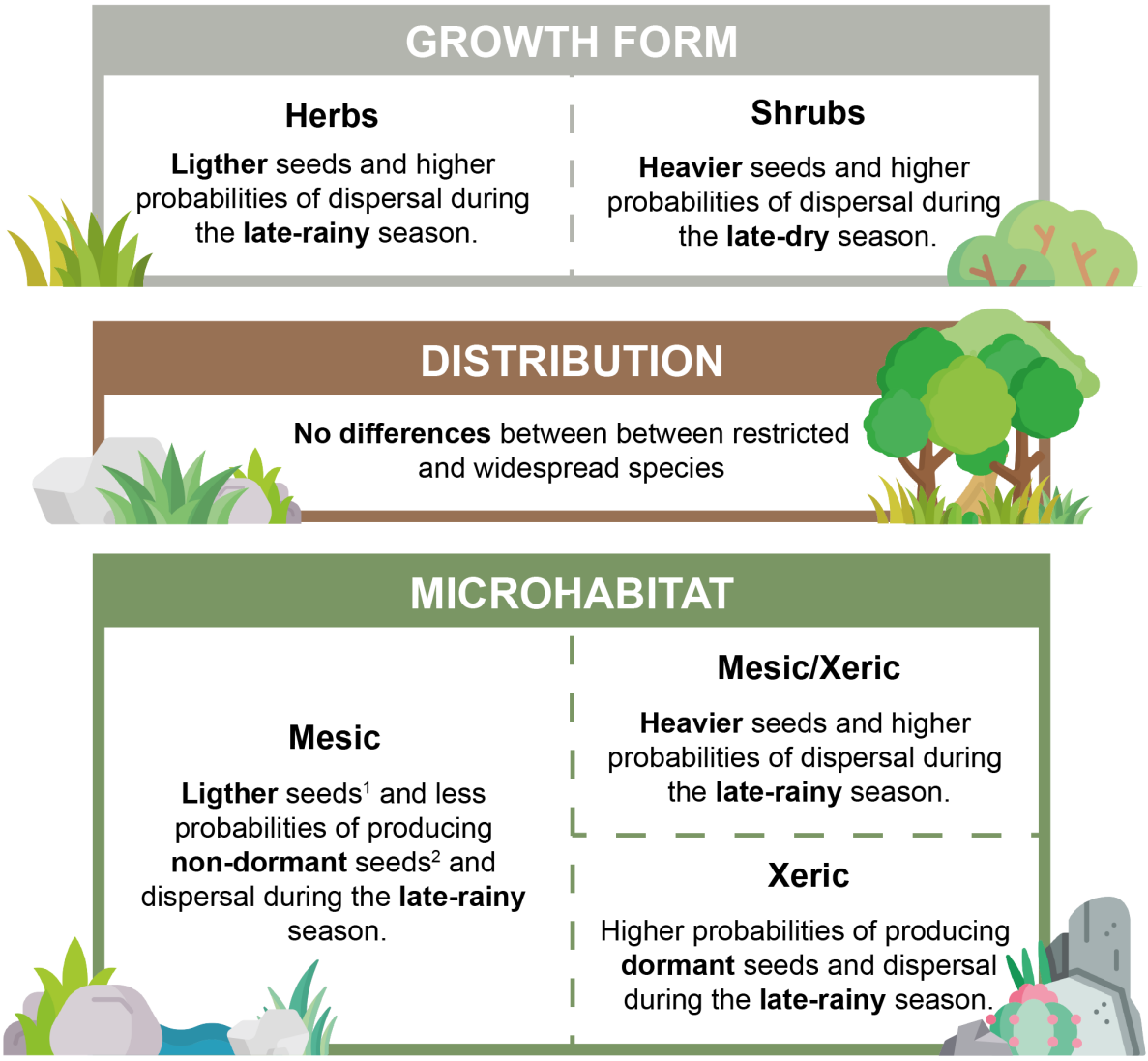

Figure 3. Seed trait differences among growth forms and species distribution and microhabitat, based on statistical results from Table 2. Notes: 1. In relation with species form Mesic/Xeric microhabitats. 2. When compared to species from xeric microhabitats. This figure was made using icons from Flaticon.com

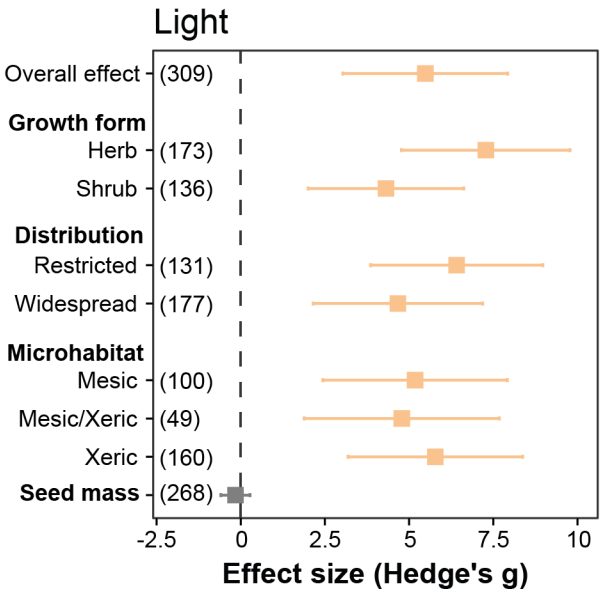

Figure 4. Effect of light availability on germination percentage in *campo rupestre* species (Control: total darkness). Squares indicate the standardised mean effect size for each moderator (growth form, distribution and microhabitat) and whiskers the 95 % confidence interval of the effect size. Coloured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

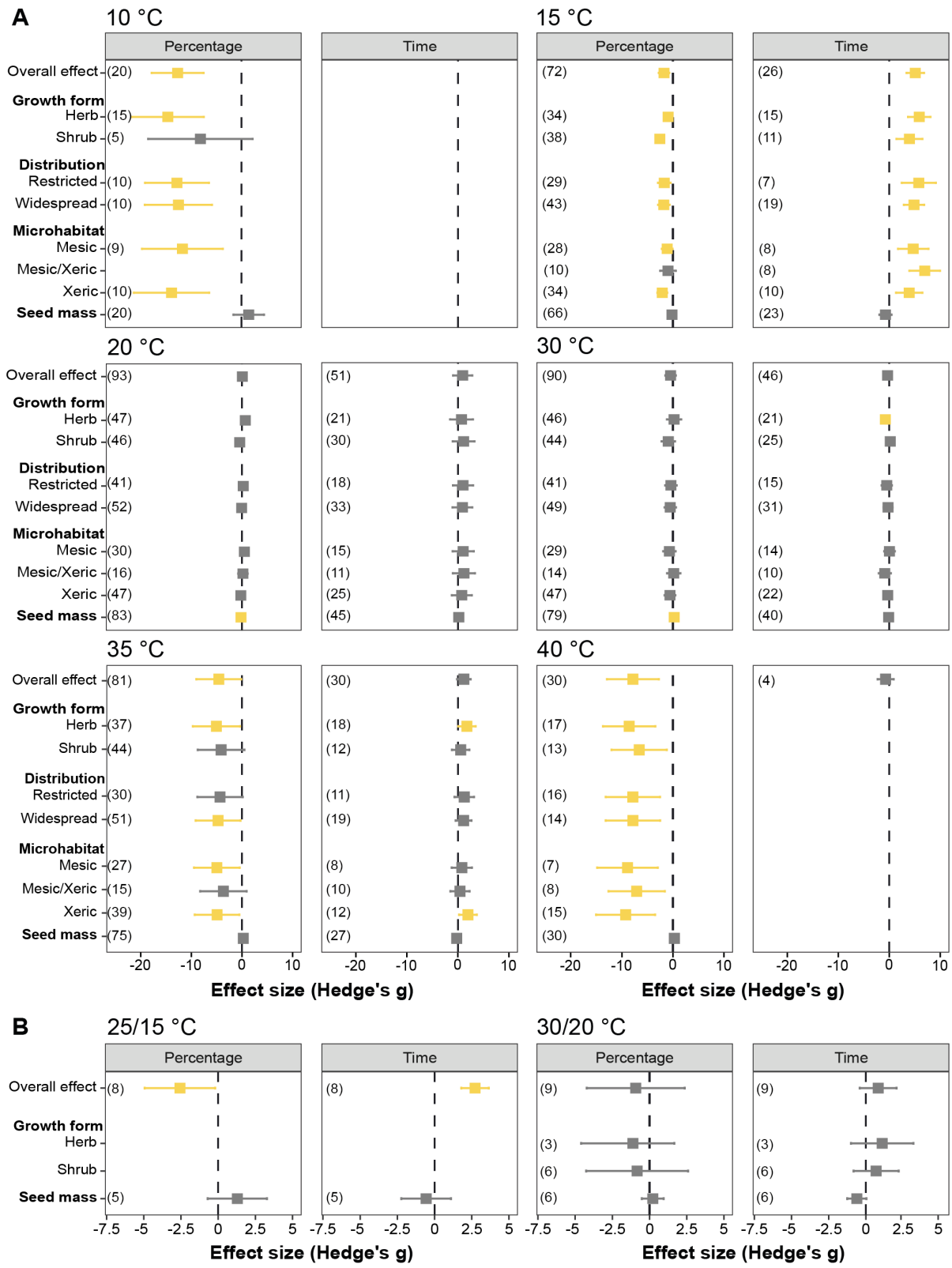

Figure 5. Germination responses to (A) constant and (B) alternate temperatures in *campo rupestre* species (Control: 25 ºC). Squares indicate the standardised mean effect size for each moderator (growth form, distribution and microhabitat) and whiskers the 95 % confidence interval of the effect size.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

estimates indicate significant effects (i.e., where confidence intervals do not overlap zero). Numbers in parenthesis indicate the number of observations.

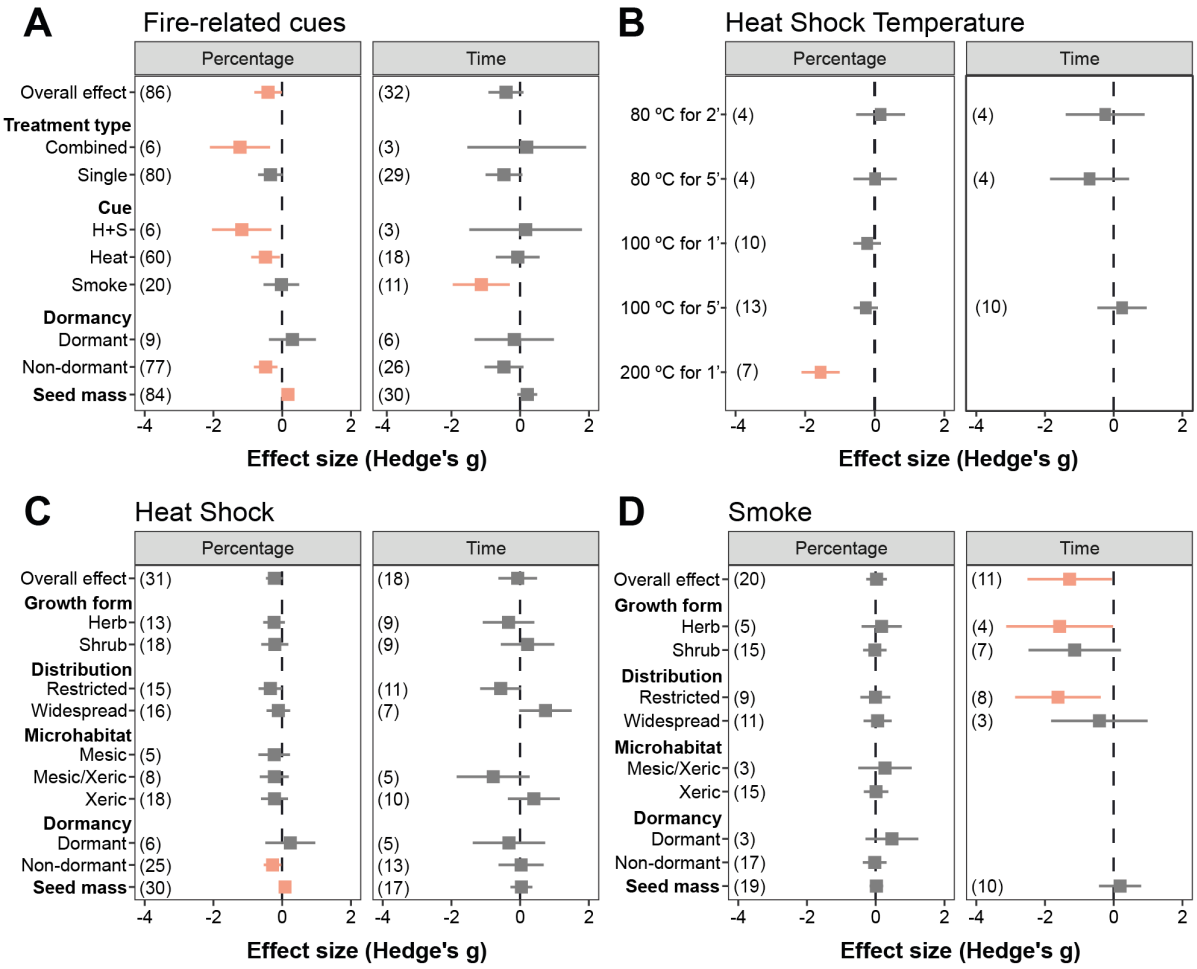

Figure 6. Germination responses to fire-related cues in *campo rupestre* species (Control: untreated seeds). (A) Overall effects. (B) Heat shocks temperatures. (C) Heat shocks without the 200 ºC for one minute. (D) Smoke. Squares indicate the standardised mean effect size for each moderator (growth form, 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

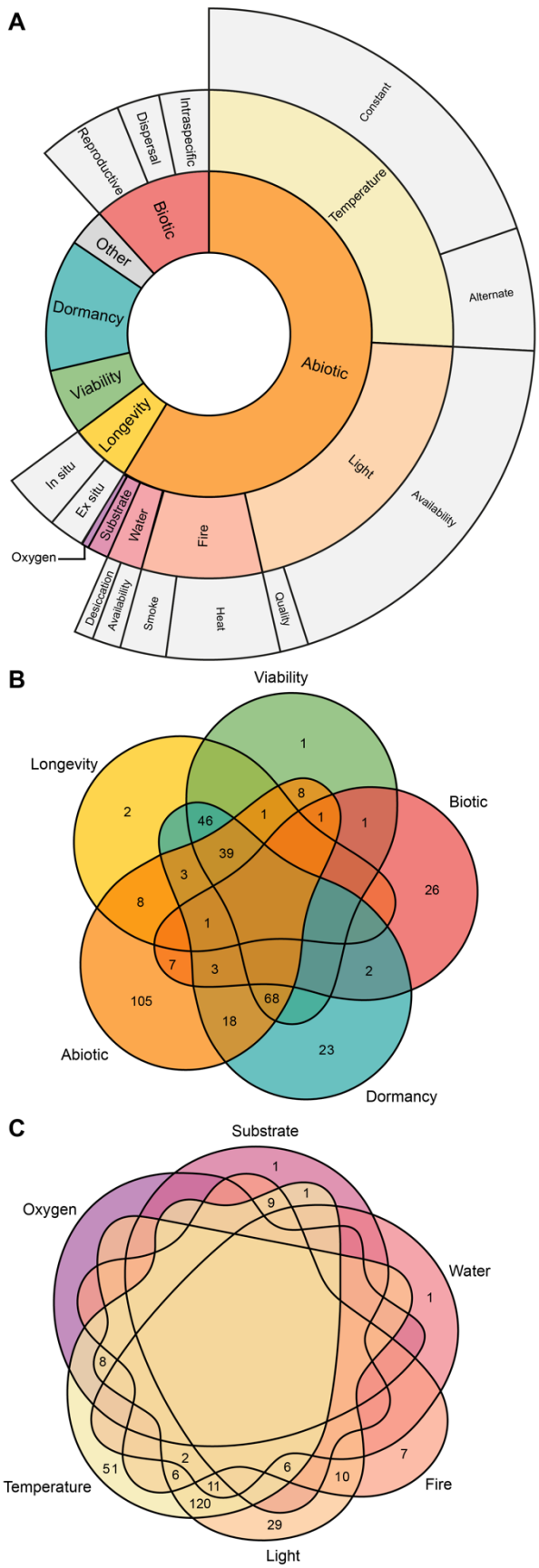
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Figure S1. State of the art of the germination ecology of Brazilian rock outcrop vegetation. A. Percentage of studies for each germination ecology topic. B. Number of species studied each major topic and their combinations. C. Number of species studied for each abiotic factor and their combination. Figure made using RAWGraphs (Mauri *et al.* 2017) and the venn R package (Dusa 2022).