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**ROCK N' SEEDS: AN ECOLOGICAL SYNTHESIS OF SEED GERMINATION  
ECOLOGY IN BRAZILIAN ROCK OUTCROP VEGETATION**

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*I just made something unexpected  
Something sharp, something new  
It's not symmetrical or perfect  
But it's beautiful and it's mine  
What else can I do?*

What Else Can I Do? from *Encanto*



## ABSTRACT

The plant economic spectrum is a valuable body of knowledge to describe the main axis of plant structure and function. However, reproductive organs and tropical flora have seldom been included in global-scale analysis and databases, preventing further advances. In this dissertation, we focus on Brazilian rock outcrop vegetation, a promising study subject that can contribute significantly to advancing trait-based seed ecology. In the first chapter, I present *Rock n' Seeds* –a database of seed functional traits and germination experiments. The database builds on 103 references identified through a systematic literature search and compiles information on 16 functional traits for 383 taxa. Specifically, it contains information of two dispersal (seed dispersal syndrome and season), six production (seeds per fruit and the percentage of embryoless, non-viable, dormant, non-dormant and viable seeds), four morphological (seed mass, length, width, and thickness), two biophysical (seed water content and desiccation tolerance) and two germination (presence of primary dormancy and dormancy class) traits. *Rock n' Seeds* also provides the raw data for 48 germination experiments for a total of 10,187 records for 281 taxa. These experiments assessed the effect of a wide range of abiotic and biotic factors on germination and dormancy-breaking treatments. Notably, 8,255 of these records include daily germination counts, an input allowing its use for various ecological questions. In the second chapter, I use this database to provide a quantitative synthesis of the germination ecology of these ecosystems using meta-analytical and phylogenetically-controlled approaches. We calculated the phylogenetic signal of seven seed traits [dry seed mass (mg), seed water content (%), percentage of empty seeds (%), percentage of viable seeds (%), seed dispersal syndrome, seed dispersal season and the presence/absence of primary dormancy] and compared their variation among growth-forms, geographical distributions, and microhabitats. We also performed a meta-analysis of germination responses to light, temperature, and fire-related cues and compared effect sizes among the same abovementioned predictors and seed mass. Finally, we evaluated the relationship between dormancy and other traits controlling germination timing and risk-reducing strategies. All traits showed a strong phylogenetic signal. Most species produced small, non-dormant, light-demanding seeds whose optimal germination temperature was between 20-30°C. The effect of sub- and supraoptimal temperatures was modulated by growth form, with shrubs requiring and tolerating higher temperatures. Although shrubs had

significantly heavier seeds than herbs, seed mass did not modulate the effect of light or temperature on germination. However, it controlled responses to heat shocks, with bigger seeds showing higher tolerance. Moreover, dormant seeds tolerate heat better than non-dormant ones. We also found that smoke significantly reduced seed germination time. Unexpectedly, no consistent differences were found between species distributions or microhabitats, implying that community assembly at this level is not explained by the assessed seed traits or germination requirements. Still, species from xeric habitats evolved phenological strategies to synchronize germination with water availability. This research contributes to our understanding of the seed germination ecology of these diverse ecosystems and provides a starting point for further questions on the role of seed functional traits in their natural regeneration.

**Keywords:** *Campo de altitude*. *Campo rupestre*. *Canga*. Dispersal season. Dispersal syndrome. Inselberg. Meta-analysis. Phylogenetic comparative methods. Seed dormancy. Seed mass. Seed viability.

## RESUMO

O espectro econômico da planta é uma teoria valiosa para descrever o eixos principais da estrutura e função das plants. Entretanto, os órgãos reprodutivos e a flora tropical raramente foram incluídos nas análises e bancos de dados globais, impedindo novos avanços. Tendo isso em vista, o foco desta dissertação é a vegetação de afloramentos rochosos brasileiros, um objeto de estudo promissor que pode contribuir significativamente para o avanço da ecologia de sementes baseada em traços funcionais. No primeiro capítulo, apresento *Rock n' Seeds* - um banco de dados de traços funcionais de sementes e experimentos de germinação. O banco de dados se baseia em 103 referências identificadas através de uma revisão sistemática da literatura e compila informações sobre 16 traços funcionais para 383 taxa. Especificamente, o banco de dados contém informações de dois traços de dispersão (síndrome de dispersão de sementes e época), seis de produção (sementes por fruto e a porcentagem de sementes sem embrião, não viáveis, dormentes, não dormentes e viáveis), quatro morfológicos (massa de sementes, comprimento, largura e espessura), dois biofísicos (teor de água da semente e tolerância de dessecação) e dois germinativos (presença de dormência primária e classe de dormência). *Rock n' Seeds* também fornece os dados brutos para 48 experimentos de germinação para um total de 10.187 registros para 281 taxa. Estes experimentos avaliaram o efeito de uma ampla gama de fatores abióticos e bióticos sobre a germinação e vários tratamentos de quebra de dormência. Particularmente, 8.255 desses registros incluem contagens diárias de germinação, um input que permite seu uso para várias questões ecológicas. No segundo capítulo, utilizo este banco de dados para fornecer uma síntese quantitativa da ecologia da germinação destes ecossistemas utilizando abordagens meta-analíticas e filogenéticas. Calculamos o sinal filogenético de sete características de sementes [massa de semente seca (mg), teor de água da semente (%), porcentagem de sementes vazias (%), porcentagem de sementes viáveis (%), síndrome de dispersão de sementes, estação de dispersão de sementes e presença/ausência de dormência primária] e comparamos suas variações entre formas de crescimento, distribuições geográficas e microhabitats. Também realizamos uma meta-análise das respostas da germinação à luz, temperatura e sinais relacionados ao fogo e comparamos os tamanhos dos efeitos entre os mesmos preditores acima mencionados e a massa de sementes. Finalmente, avaliamos a relação entre a dormência e outros traços que controlam o tempo de germinação e as estratégias de redução de risco. Todos os traços mostraram um forte sinal filogenético. A maioria das espécies produz sementes pequenas, não dormentes e dependentes da luz, cuja temperatura ideal de

germinação está entre 20-30°C. O efeito das temperaturas sub e supra-ótimas foi modulado pela forma de crescimento, com arbustos exigindo e tolerando temperaturas mais altas. Embora os arbustos tivessem sementes significativamente mais pesadas do que as ervas, a massa das sementes não modulava o efeito da luz ou da temperatura sobre a germinação. Em vez disso, a massa controlou as respostas aos choques térmicos, com sementes maiores mostrando maior tolerância. Além disso, as sementes dormentes toleram melhor o calor do que as não dormentes. Também encontramos que a fumaça reduziu significativamente o tempo de germinação das sementes. Inesperadamente, não foram encontradas diferenças consistentes entre as distribuições das espécies ou seus microhabitats, o que implica que a montagem da comunidade neste nível não é explicada pelos traços das sementes ou pelos requerimentos de germinação avaliados. Ainda assim, as espécies de habitats xéricos desenvolveram estratégias fenológicas para sincronizar a germinação com a disponibilidade de água. Esta pesquisa contribui para nossa compreensão da ecologia da germinação de sementes destes ecossistemas diversos e fornece um ponto de partida para outras questões sobre o papel dos traços funcionais das sementes em sua regeneração natural.

**Palavras-chave:** *Campo de altitude. Campo rupestre. Canga. Época de dispersão. Dormência. Inselberg. Massa da semente. Meta-análise. Métodos filogenéticos comparativos. Síndrome de dispersão. Viabilidade da semente.*

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## INTRODUCTION

Ecologists have a long-standing tradition of understanding plants as an economic system, where plants use resources (e.g., water, carbon dioxide and mineral nutrients) to build organs (e.g., leaves, stems and roots) that allow them to harvest more resources. This relationship between organs and resources would be rather trivial if plant structures and shapes were not as diverse as the plant kingdom. Therefore, plant ecologists have been fascinated by the factors that shape how plants allocate resources between organs and their associated functions. Again, these factors can also be simplified into economic decisions, being determined by three elements: i) cost-benefit relationships, ii) allocation between functions, and iii) viability in the short- and long-term (Bloom *et al.* 1985). First, cost-benefit relationships dictate how much resources are gained per investment of a given set of resources; for example, how much more carbon dioxide would be fixated per investment in leaf area. Second, resources are not infinite, so once a resource has been used for a given function –such as building leaves– it cannot be used for another, for instance, reproduction. Finally, these resource-use decisions must be physiologically and biophysically viable: a plant could invest all its resources in an enormous leaf, but if a strong stem does not support this gigantic structure, it will fall off. Also, if such a structure appeared in a dry, warm environment, it would require a finely tuned physiological machinery to deal with water deficit and high temperatures. Otherwise, it has an extremely high probability of wilting.

These ideas led Peter B. Reich and his collaborators to hypothesize that only a reduced combination of plant traits could exist and that selective forces were restricting the combination of traits a given species could have (Reich *et al.* 1992, 1997; Reich 1993). A couple of decades later, these hypotheses paved the way for the theory of *the plant economic spectrum*, a body of knowledge that describes trait coordination and trade-offs within and among plant organs (Reich 2014; Díaz *et al.* 2016). This theory has successfully described the major axis of variation in different organs –namely, leaves (Wright *et al.* 2004), wood (Chave *et al.* 2009), roots (Roumet *et al.* 2016) and flowers (Roddy *et al.* 2021)– and how these integrate at the whole plant-level (Díaz *et al.* 2016). Despite its rampant success, the plant economic spectrum theory has two major drawbacks, which are the gaps I aim to tackle in this dissertation.

Despite its rampant success, the plant economic spectrum theory has two major drawbacks, which are the gaps I aim to tackle in this dissertation. The plant economic spectrum's first limitation is the absence of reproductive organ traits. Díaz *et al.* (2016) did

include seed traits in their seminal work, but they were only seed mass and production. These two traits have a long history in plant ecology since they have a negative relationship: the more seeds a given plant produces, the smaller they tend to be (Westoby *et al.* 2002). Still, no matter how central this trait could be, recent studies have highlighted the need to explore the functional role of additional traits, especially those that could provide more robust information about the mechanism behind natural regeneration (Jiménez-Alfaro *et al.* 2016; Larson and Funk 2016). For instance, seed traits have shown to be independent of different vegetative traits, implying that their inclusion in the plant economic spectrum theory might provide an additional axis of variation within the plant trait space (Grime *et al.* 1997; Pierce *et al.* 2014; Hoyle *et al.* 2015; Ladouceur *et al.* 2019). As a result, Saatkamp *et al.* (2019) outlined a research agenda for seed-trait functional ecology, which provided an exciting framework for subsequent research in the area. Most notably, they highlight two major steps that are required for further advances: i) the consolidation of a global seed-trait database and ii) the assessment of how different dimensions of the seed-trait space integrate.

This first step is inherently linked to the second drawback of the plant economic spectrum: the pervasive absence of trait data from tropical regions. In fact, TRY –the largest functional traits repository– only has data for ~1% of known plants from the tropics (Kattge *et al.* 2020). This same scenario occurs when we consider seed trait databases since most of them are restricted to species from temperate ecosystems (e.g., Harel, Holzappel, and Sternberg 2011; Rivière *et al.* 2018; Rosbakh, Baskin, and Baskin 2020; Fernández-Pascual 2021).

In this context, this dissertation aims to tackle these gaps: the lack of seed trait and germination data from the tropics and our little understanding of how seed and germination traits integrate within them and other aspects of plant life history. Since the tropics host such a diverse and unique flora, any ecosystem could arguably be a fascinating study subject. Still, we focused on the rock outcrop vegetation present in Brazil –specifically the vegetation types locally known as *campo rupestre*, *canga*, *campo de altitude* and inselbergs– which is widely known for its high diversity and endemism (Porembski *et al.* 2016; Campos *et al.* 2018). Moreover, since rock outcrops occur in different biomes across the country, working with these ecosystems provides us with the unique opportunity to deal with various evolutionary histories and environmental contexts (Porembski and Barthlott 2000; Hopper *et al.* 2021). Finally, rock outcrops can be found on all continents, and their vegetation tends to conserve similar structural and functional features (Barthlott and Porembski 2000), facilitating global-scale comparisons.

In the first chapter of this research, I present *Rock n' Seeds*—a database of seed functional traits and germination experiments from Brazilian rock outcrop vegetation. It builds on 103 references identified through a systematic literature search and compiles information on 16 functional traits for 383 taxa and 10,187 records for 281 taxa. Trait data include information on several of the major axis of the seed ecological spectrum. Regarding germination data, the database contains experiments that assessed the effect of a wide range of abiotic and biotic factors on germination and different dormancy-breaking treatments. In the second chapter, we use this database to provide a quantitative synthesis of the germination ecology of these ecosystems using meta-analytical and phylogenetically-controlled approaches. Since most of our data come from a particular vegetation type—the campo rupestre—a major emphasis is given to that ecosystem. We focused on three main issues: i) the ecological and phylogenetic variation of seed functional traits, ii) germination responses to abiotic factors and iii) the association between traits shaping germination timing; and compared these aspects between growth forms, species geographic distribution and microhabitats.

The first chapter has been published as a Data paper in *Ecology*, and the second is formatted to be submitted to *Annals of Botany*. For convenience, all cited literature is provided in a single section at the end of the document.





**CHAPTER I – ROCK N’ SEEDS: A DATABASE OF SEED  
FUNCTIONAL TRAITS AND GERMINATION EXPERIMENTS FROM  
BRAZILIAN ROCK OUTCROP VEGETATION**

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## **Rock n' Seeds: a database of seed functional traits and germination experiments from Brazilian rock outcrop vegetation**

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**Abstract:** Advancing functional ecology depends fundamentally on the availability of data on reproductive traits, including those from tropical plants, which have been historically underrepresented in global trait databases. While some valuable databases have been recently created, they are mainly restricted to temperate areas and vegetative traits such as leaf and wood traits. Here, we present Rock n' Seeds, a database of seed functional traits and germination experiments from the Brazilian rock outcrop vegetation, recognized as outstanding centers of diversity and endemism. Data were compiled through a systematic literature search, resulting in 103 publications from which seed functional traits were extracted. The database includes information for sixteen functional traits for 383 taxa from 148 genera, 50 families and 25 orders. These sixteen traits include two dispersal, six production, four morphological, two biophysical and two germination traits; the major axes of the seed ecological spectrum. The database also provides the raw data for 48 germination experiments for a total of 10,187 records for 281 taxa are also provided. Germination experiments in the database assessed the effect of a wide range of abiotic and biotic factors on germination and different dormancy-breaking treatments. Notably, 8,255 of these records include daily germination counts. This input will facilitate synthesizing germination data and using this database for a myriad of ecological questions. Given the variety of seed traits and the extensive germination information made available by this database, we expect it to be a valuable resource advancing comparative functional ecology and guiding seed-based restoration and biodiversity conservation in tropical megadiverse ecosystems.

**Key words/phrases:** *campo de altitude, campo rupestre, canga*, dispersal season, dispersal syndrome, inselberg, seed dormancy, seed mass, seed viability.

**Open Research Statement:** Data and metadata are available as Supporting Information and on Figshare ([10.6084/m9.figshare.19747495](https://doi.org/10.6084/m9.figshare.19747495)).

## Introduction

In the 1990s, Peter B. Reich and collaborators hypothesized that only a reduced combination of plant traits could be found across biomes and distantly related taxa as a consequence of selective forces constraining the collective set of traits a given species could have (Reich *et al.* 1992, 1997; Reich 1993). Since then, an ongoing, continuous effort by functional ecologists worldwide during the past decades has culminated in the consolidation of the plant economic spectrum theory, a body of knowledge aiming to describe trait coordination and trade-offs within organs –leaves (Wright *et al.* 2004), wood (Chave *et al.* 2009), roots (Roumet *et al.* 2016) and flowers (Roddy *et al.* 2021)– and the integration of traits among plant organs (Grime *et al.* 1997; Reich 2014; Díaz *et al.* 2016). While this theory has proven to be highly valuable in describing the main axes of variation in plant function and structure, two key factors have limited further advances. First, traits from reproductive organs have been generally overlooked, with only seed number and seed mass being included in these global studies (see Díaz *et al.* 2016). Second, global trait databases are strongly biased towards temperate species. For instance, the largest repository of plant functional traits, TRY (<https://www.try-db.org/>), only has data for less than 1% of the estimated species present in the tropics (Kattge *et al.* 2020).

The proper inclusion of seed functional traits in the plant economic spectrum is increasingly recognized as a major research avenue for advancing functional ecology. For instance, seed traits have shown to be decoupled from vegetative traits and provide an additional axis of variation within the plant trait space (Grime *et al.* 1997; Pierce *et al.* 2014; Hoyle *et al.* 2015; Ladouceur *et al.* 2019). Seed traits also modulate critical ecological processes, such as natural regeneration, community assembly, and landscape-scale dynamics (Poschlod *et al.* 2013; Jiménez-Alfaro *et al.* 2016; Larson and Funk 2016), and provide critical information for the development of restoration and conservation programs (Saatkamp *et al.* 2019; Pedrini and Dixon 2020).

Recently, Saatkamp *et al.* (2019) outlined a research agenda to advance the field of seed functional ecology, which includes 1) characterizing interspecific seed trait variation across biomes and lineages, 2) associating major axes to functions, processes, and ecological strategies; 3) and assessing its covariation with other plant organ traits. Still, a major barrier to achieving these goals is the lack of freely available, standardized databases of seed traits encompassing sufficient trait variation and biogeographic coverage. So far, only a few seed trait databases have been developed (e.g., Harel, Holzappel, and Sternberg 2011; Rivière *et al.*

2018; Rosbakh, Baskin, and Baskin 2020; Fernández-Pascual 2021), but their coverage is mainly restricted to species from temperate ecosystems. In fact, recent large-scale studies on seed functional ecology have highlighted this lack of seed trait data from tropical species (Arène *et al.* 2017; Gioria *et al.* 2020). Overall, the underrepresentation of tropical flora and seed traits results in pervasive ecological and evolutionary theory biases and prevents novel and broad generalizations.

Among the different vegetation types found in the tropics, those associated with rock outcrops stand as an appealing starting point for consolidating seed functional traits database. First of all, they host high species richness and endemism (Porembski *et al.* 2016; Campos *et al.* 2018). Moreover, rock outcrops are present all over the world, including different biomes and evolutionary histories (Porembski and Barthlott 2000; Hopper *et al.* 2021). Still, they conserve their structural and functional properties (Barthlott and Porembski 2000), facilitating ecological comparisons on a large scale. In the case of regeneration from seeds, seedlings from rock outcrop vegetation tend to establish directly on the rock surface or shallow, nutrient-poor soils. Hence, water- and nutrient-limitation, coupled with high substrate temperature, are thought to be harsh conditions faced by seeds in these ecosystems (Nunes *et al.* 2016; Schaefer *et al.* 2016).

Here, we present Rock n' Seeds, a database of seed functional traits and germination experiments from 383 taxa (including species and subspecies) from vegetation associated with different kinds of rock outcrops in Brazil. It compiles information on sixteen functional traits associated with the major dimensions of the seed ecological spectrum (Saatkamp *et al.* 2019), including dispersal, production, morphological, biophysical, and germination traits. Moreover, it provides 10,187 germination records for 281 taxa. Notably, 8,255 (81%) of these records correspond to the raw daily germination count records, an input unavailable in current seed traits databases that will allow for several approaches to be used for a complete exploration of the germination behavior of these species. By making these data available, we aim to advance the sharing of seed trait data and the understanding of multidimensional plant ecological strategies.

Rock outcrops can be found throughout Brazil, from Mount Roraima in the Amazon (~5°00'N) (Prance 1996) to the inselbergs of Rio Grande do Sul (~30°00'S) in the South (Safford and Martinelli 2000). Vegetation associated with these outcrops includes a wide variety of open, grassy-shrubby, fire-prone ecosystems that often represent centers of diversity and endemism (Porembski *et al.* 2016; Silveira *et al.* 2016; Giulietti *et al.* 2019). Some characteristics of rocky outcrop vegetation vary according to their main rock parent

material, prompting their classification into main vegetation types, including those locally known as *campo rupestre*, *canga*, *campo de altitude* and inselbergs (Martinelli 2007). The *campo rupestre* is found on quartzite, sandstone, and ironstone outcrops, between 900-2000 m above sea level (a.s.l) (Silveira *et al.* 2016). Its main distribution is the Espinhaço Range in eastern Brazil (Conceição *et al.* 2016), but smaller, isolated patches are found across all major Brazilian biomes (Miola *et al.* 2021). The *campo rupestre* that develops on ironstone outcrops is specifically addressed as *canga* and is mainly distributed in the Iron Quadrangle, a large ironstone outcrop area in the southern portion of the Espinhaço Range, and Serra dos Carajás in Eastern Amazon (Jacobi *et al.* 2007; Skiryycz *et al.* 2014). Still, several other *canga* sites can be found in southeastern, northeastern, northern and central-west Brazil (Miola *et al.* 2021). Overall, the *campo rupestre* covers 0.78% of the Brazilian terrestrial surface (66,447 km<sup>2</sup>) and hosts around 5,000 species, of which more than 40% are endemic (Silveira *et al.* 2016). The *campo de altitude* is an open grassland formation found above 1500 m a.s.l. on granite and gneissic outcrops within the Atlantic Forest biome (Vasconcelos 2011). The most prominent mountain ranges where this vegetation is found are the Serra da Mantiqueira, Serra do Caparaó, and Serra do Mar, all in southeastern Brazil (Safford 1999). Like *campo rupestre*, *campos de altitude* are also recognized for their high species richness and many endemic species (Safford 2007; Campos *et al.* 2018). Finally, inselbergs are isolated granitic outcrops that emerge abruptly from their surroundings. In Brazil, they are found throughout the country's eastern region –from the arid northeastern to the cool, subtropical southeastern (Safford and Martinelli 2000)– and are considered one of the global inselberg plant diversity hotspots (Porembski 2007).

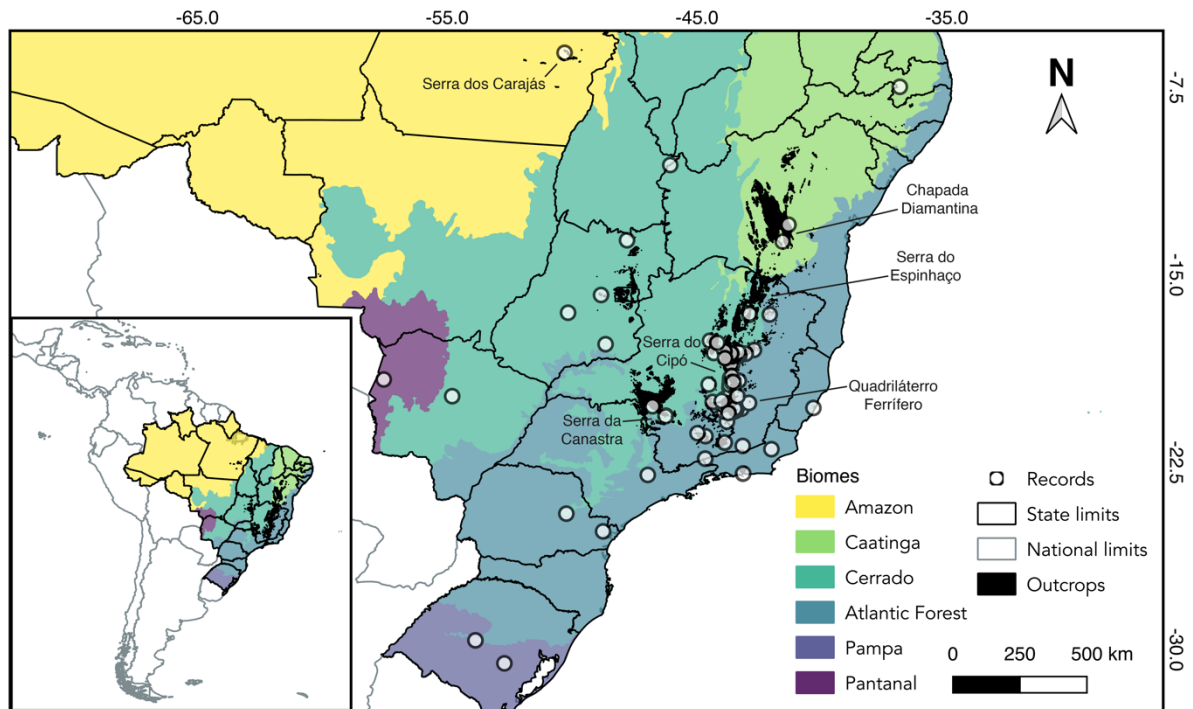
## **Metadata**

### **Class I. Data set descriptors**

#### **A. Data set identity**

**Title:** Rock n' Seeds: a dataset of seed functional traits and germination experiments in Brazilian rock outcrop vegetation





**Figure 1.** Distribution of seed and germination trait data records for rocky outcrop vegetation in Brazil (Geodatum: WGS84). Brazilian biomes shapefile retrieved from Instituto Brasileiro de Geografia e Estatística (IBGE, <https://www.ibge.gov.br/>). Outcrops boundaries are the combination of shapefiles for the *campo rupestre* in Silveira et al. (2016) and the ironstone outcrops of Serra dos Carajás provided by Fernando M. G. Santos. Mapping *campo de altitude* and inselbergs is not currently feasible at this scale due to knowledge gaps and the small size of individual inselbergs.

## B. Data set identification code

Suggested Data set Identity Code: rocknseeds

## C. Data set description

The present dataset includes information for 16 seed traits from 383 taxa in 148 genera, 50 families and 25 orders from Brazilian rock outcrop vegetation. Data was collected in several study sites across Brazil, including locations from all six Brazilian biomes, namely Atlantic Forest, Amazon, Caatinga, Cerrado, Pampa and Pantanal (Figure 1). The most represented families in the database are Melastomataceae (67 taxa), Fabaceae (38) and Velloziaceae (36), with ~37% of all reported species (Figure 2). The 16 seed traits include two dispersal, six production, four morphological, two biophysical and two germination traits. The traits with the highest number of records are the presence/absence of primary dormancy (499 records), dispersal syndrome (497) and dormancy class (353) (Figure 3). Additionally, Rock n' Seeds

compiles the primary data of 48 germination experiments for a total of 10,187 records. Experiments available in this database include tests that assessed the effect of different dormancy-breaking treatments (e.g., scarification and hormone application) and germination responses to various abiotic (e.g., temperature, photoperiod, and fire-related cues) and biotic (e.g., intraspecific variability, gut passage, and reproductive systems) factors.

### Principal investigators:

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- **Fernando A. O. Silveira.** Centro de Síntese Ecológica e Conservação, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil.



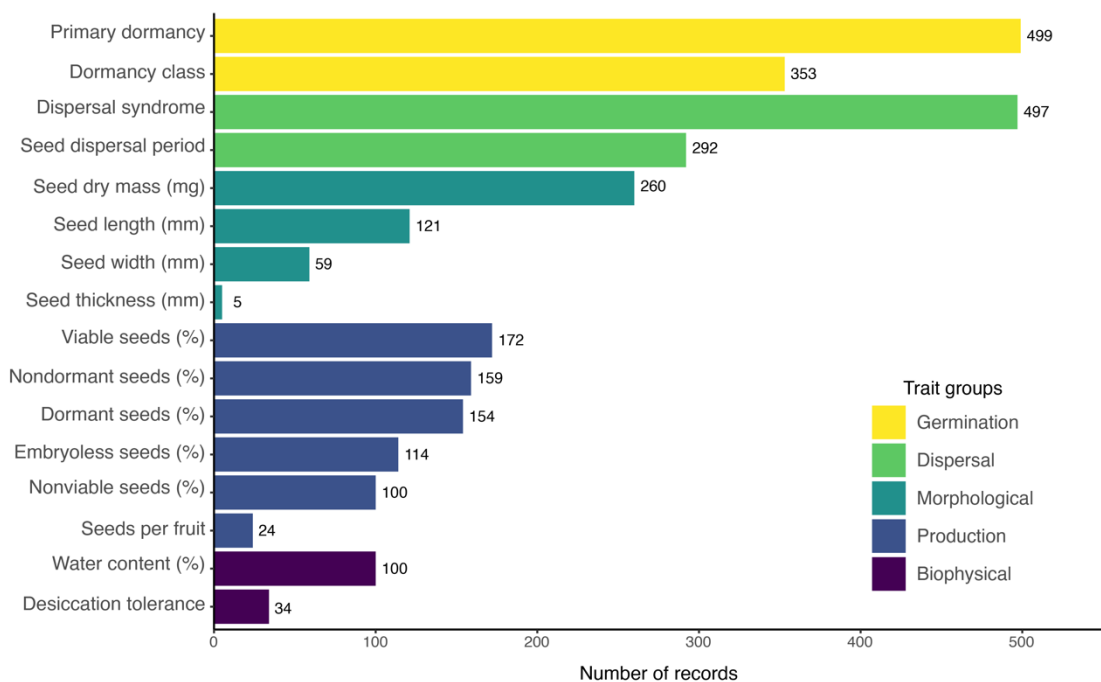
**Figure 2.** Top ten families in terms of number of species present in the Rock n' Seeds database and some representative species. The area of the squares represents the proportion of each species in each family in relation to the total number of species (381). The number below each name corresponds to the total number of species of each family present in the database. Melastomataceae: *Lavoisiera crassifolia* Mart. & Schrank ex DC.<sup>1</sup>. Fabaceae: *Mimosa macedoana* Burkart<sup>2</sup>. Velloziaceae: *Vellozia caruncularis* Mart. ex Seub.<sup>3</sup>. Asteraceae:

*Richterago arenaria* (Baker) Roque<sup>3</sup>. Bromeliaceae: *Dyckia consimilis* Mez<sup>4</sup>. Eriocaulaceae: *Actinocephalus bongardii* (A.St.-Hil.) Sano<sup>3</sup>, Verbenaceae: *Stachytarpheta radlkoferiana* Mansf<sup>5</sup>. Xyridaceae: *Xyris* sp.<sup>3</sup> Poaceae: *Echinolaena inflexa* (Poir.) Chase<sup>4</sup>, Cyperaceae: *Rhynchospora ciliolata* Boeckeler<sup>1</sup>. Photos by 1. Fernando A. O. Silveira, 2. Roberta L. C. Dayrell, 3. Carlos A. Ordóñez-Parra, 4. Marcílio Zanetti, 5. Fernando M. G. Santos. Figure made using RAWGraphs (Mauri *et al.* 2017).

## Abstract

Advancing functional ecology depends fundamentally on the availability of data on reproductive traits, including those from tropical plants, which have been historically underrepresented in global trait databases. While some valuable databases have been recently created, they are mainly restricted to temperate areas and vegetative traits such as leaf and wood traits. Here, we present Rock n' Seeds, a database of seed functional traits and germination experiments from the Brazilian rock outcrop vegetation, recognized as outstanding centers of diversity and endemism. Data were compiled through a systematic literature search, resulting in 103 publications from which seed functional traits were extracted. The database includes information for sixteen functional traits for 383 taxa from 148 genera, 50 families and 25 orders. These sixteen traits include two dispersal, six production, four morphological, two biophysical and two germination traits; the major axes of the seed ecological spectrum. The database also provides the raw data for 48 germination experiments for a total of 10,187 records for 281 taxa are also provided. Germination experiments in the database assessed the effect of a wide range of abiotic and biotic factors on germination and different dormancy-breaking treatments. Notably, 8,255 of these records include daily germination counts. This input will facilitate synthesizing germination data and using this database for a myriad of ecological questions. Given the variety of seed traits and the extensive germination information made available by this database, we expect it to be a valuable resource advancing comparative functional ecology and guiding seed-based restoration and biodiversity conservation in tropical megadiverse ecosystems.

**D. Keywords:** *campo de altitude*, *campo rupestre*, *canga*, dispersal season, dispersal syndrome, inselberg, seed dormancy, seed mass, seed viability.



**Figure 3.** Number of records for each of the sixteen seed functional traits registered in the Rock n’ Seeds database.

## Class II. Research origin descriptors

### A. Overall project description

**1. Identity:** Seed functional traits and germination experiments in the Brazilian rock outcrop vegetation.

**2. Originators:** The project “Rock n’ Seeds: a dataset of seed functional traits and germination experiments in Brazilian rock outcrop vegetation” is part of the Master Dissertation of Carlos A. Ordóñez-Parra at the Graduate Program of Plant Biology at Universidade Federal de Minas Gerais, Brazil.

**3. Period of study:** 1994-2021.

**4. Objectives:** To build a comprehensive database of seed functional traits and germination experiments from Brazilian rock outcrop vegetation that can be used in future studies of plant functional ecology.

**5. Abstract:** same as above.

**6. Sources of funding:** The research that originated these data and its compilation was supported by grants and scholarships from Cia Vale do Rio Doce, Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq); Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG), Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ), Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) (2019/09903-0, 2016/01563-7, 2015/06743-0, 2012/24240-8, 2013/50155-0, 2010/51307-0 and 2009/54208-6), Fundação Grupo Boticário, the Ministère Français des affaires étrangères et européennes [EGIDE 2009/657176K] and RTP CNRS-CEMAGREF “Ingénierie Ecologique”: SAVER.

## **B. Specific subproject description**

**1. Network establishment:** The Rock n’ Seeds network was established in June of 2020, led by Carlos A. Ordóñez-Parra and Fernando A. O. Silveira.

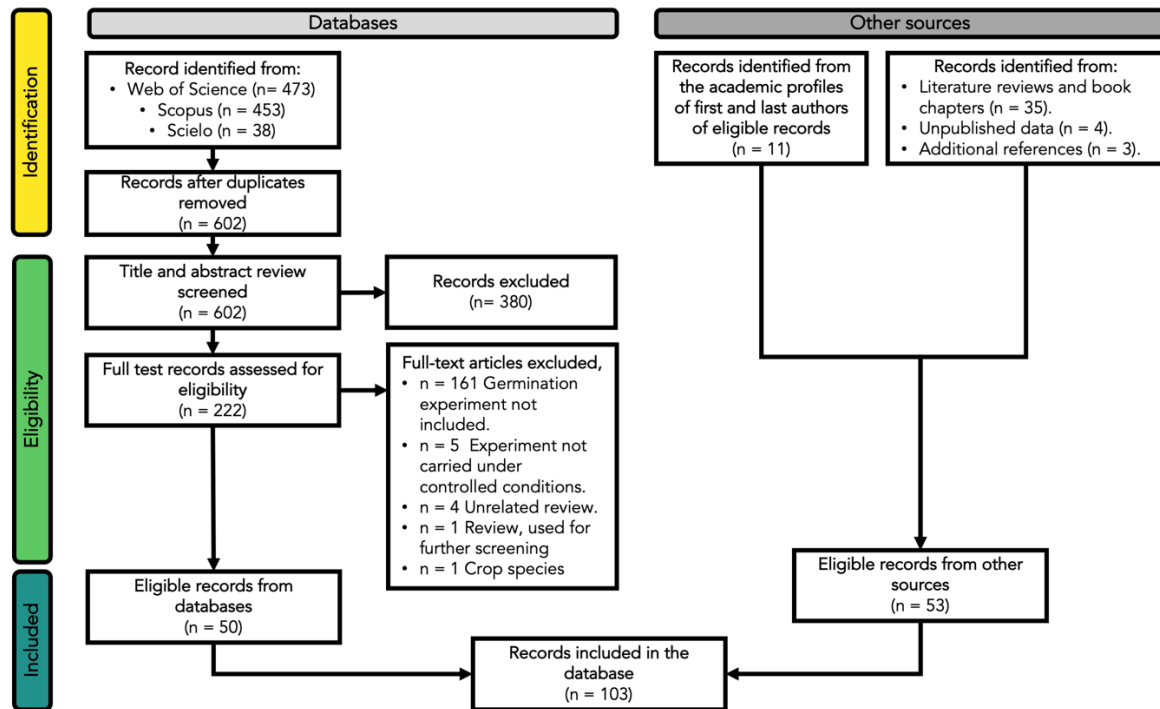
**2. Site description:** Data was collected in several study sites across Brazil (~7°30’ to 30°00’S) and represent different types of rock outcrop vegetation, including 1) *campo rupestre* developing in quartzitic and sandstone outcrops; 2) *canga* associated to ironstone outcrops; and 3) *campos de altitude*, and 4) inselbergs that occur on granite outcrops. Notably, this database has records from outcrops occurring in all six Brazilian biomes (Figure 1).

**3. Data sampling:** We searched for papers in the Web of Science, Scopus, and SciELO databases using the following terms and their combinations in the title, abstract, or keywords: (\*outcrop\* OR *canga*\* OR inselberg\* OR "campo rupestre" OR "rupestrian grassland\*" OR "campo de altitude" OR "tropical mountain\* grasslands") AND (seed\* OR germina\* OR \*dormancy OR "desiccation tolerance"). The last literature survey was conducted on January 24th 2022; but limited to publications up to December 2021. We considered published studies written in English, Spanish, or Portuguese that entailed germination experiments under controlled conditions with at least one species from a given rock outcrop vegetation. The Google Scholar or ResearchGate profiles of each retrieved paper's first and last authors were checked to look for further publications. Review papers (Garcia and Oliveira 2007; Nunes *et*

*al.* 2016; Garcia *et al.* 2020) and research that compiled seed functional traits databases from these ecosystems (Dayrell *et al.* 2017) were also screened for additional references. Three additional papers that were not recovered through methods (i.e., Oliveira *et al.* 2020, Andrade *et al.* 2021, Carmo *et al.* 2021) were then added. In the end, 99 studies met our inclusion criteria (Figure 4). Finally, raw data from germination experiments (i.e., daily germination counts) were solicited to the authors of each paper. Four unpublished datasets of germination experiments with ten species were provided during this process. With this addition, the total number of included studies increased to 103.

For each study, we registered information related to five aspects: i) plant species taxonomy, ii) study site location and characteristics, iii) species growth-form and geographic distribution, iv) seed functional traits, and v) germination data scored per day. Species names were updated according to Flora do Brasil, using the function *plantminer* from the R package *taxize* (Chamberlain *et al.* 2020), which searches for taxonomy data at Plantminer.com. The last nomenclature verification was carried out on April 8<sup>th</sup>, 2022. Orders and families were assigned following APG IV (The Angiosperm Phylogeny Group 2016). We also recorded the coordinates of each study site, its local name, and the main rock parent material of each outcrop (i.e., quartzite, ironstone, granite or sandstone). Species growth-form and distribution were determined according to information available in the paper or by searching species accepted name in Flora e Funga do Brasil (<http://floradobrasil.jbrj.gov.br/>, last access January 24<sup>th</sup>, 2022). In the case of species reported to have multiple growth-forms, preference was given to the original classification provided by the authors. Moreover, species reported as subshrubs were recorded as shrubs. Species' geographic distribution was classified into two categories depending on whether the species is exclusive to vegetation associated with rock outcrops (i.e., restricted) or not (i.e., widespread). Moreover, whenever available, we determined species microhabitat (xeric, mesic or both) based on information in the paper or by searching species accepted name in the speciesLink (<https://specieslink.net/>, last access January 24<sup>th</sup>, 2022) database and reviewing the information reported in the first 50 herbarium specimens available.

We recorded sixteen seed functional traits, including two dispersal (dispersal season and syndrome), six production (number of seeds per fruit and percentage of embryoless, non-viable, dormant, non-dormant, and viable seeds), four morphological (seed length, width, thickness and dry mass), two biophysical (seed water content and desiccation tolerance) and two germination traits (presence of primary dormancy and dormancy class). Seed dispersal season was assigned based on the seed collection date reported by the authors, which was



**Figure 4.** PRISMA flow diagram describing the systematic literature search approach employed for the construction of seed trait and germination experiment database (see *Data sampling*).

divided into four climatic seasons: early rainy season (ER) from October to December; late rainy season (LR) from January to March, early dry season (ED) from April to June, and late dry season (LD) from July to September (Dayrell *et al.* 2017). This trait was not recorded in studies that used different seed lots from different seasons or where species were reported to have continuous seed production throughout the year. Seed dispersal syndrome was established based on data reported in the paper, taxonomy specialists or previous studies (Jacobi and Carmo 2011; Kuhlmann 2016). Three categories were considered: zoochory, anemochory, and autochory.

The presence of primary dormancy was determined following the criteria established by Dayrell *et al.* (2017). Briefly, seeds were considered non-dormant (ND) if at least 70% of viable seeds germinated in about four weeks. In contrast, seeds were classified as dormant (D) if less than 30% of viable seeds germinated in about four weeks and pre-germination treatments increased or accelerated germination. Seeds were also considered dormant if germination occurred on a pretty narrow temperature range, a germination behavior associated with conditional dormancy (Baskin and Baskin 2014). Species with less than 10% of seed viability or a germination percentage inferior to 70% and no reference of seed viability were considered to provide a non-conclusive (NC) report of seed dormancy. When

reported by the author, the seed dormancy class (*sensu* Baskin and Baskin 2021) was recorded.

**4. Taxonomic data:** see *Data sampling*.

### **Class III. Data set status and accessibility**

#### **A. Status**

**Latest update:** July 6<sup>th</sup>, 2022.

**Latest archive date:** July 6<sup>th</sup>, 2022.

**Metadata status:** Last update, July 6<sup>th</sup>, 2022. Published version.

#### **B. Accessibility:**

**Storage location:** the data and metadata will be available as Supporting Information of the publication and on Figshare (Ordóñez-Parra et al. 2022).

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**Copyright restrictions:** None.

**Proprietary restrictions:** Please cite this paper when using the current data in publications and let us know how the data is used in the publications.

**Costs:** None.

### **Class IV. Data structural descriptors**



## A. Data set file

### Identity and size:

rocknseeds.zip (zipped CSV files), 144 KB.

Included in rocknseeds.zip:

- references.csv, 23 KB
- traits.csv, 128 KB
- germination.csv, 2,9 MB

**Format and storage mode:** All text files (.csv) are included in a compressed folder (.zip).

**Header information:** See column descriptions in Metadata worksheet.

**Alphanumeric attributes:** Mixed

**Data anomalies:** Missing information was classified as “NA”. This was also used for the Latitude and Longitude columns of the traits.csv file (see below) when papers did not provide any coordinates or references about the study site; or only provided extremely broad information on the collection site (e.g., the mountain range or municipality where the study was carried out). Additionally, some studies collected seeds from populations from different areas, but they did not provide enough information to track which populations were used to measure each trait. “NA” was also used in these cases.

## B. Variable information

**Table 1.** Variable names and descriptions for file references.csv.

Variables	Description
ID	Identification code, unique for each paper/data source.
First author	Full last name and the initials of the first and middle names of the first author. In the case of unpublished data, it corresponds the author that provided the dataset.
Year	Year of paper publication
Title	Title of the paper in its original language.
DOI	Digital Object Identifier link related to each paper. When a DOI was not

	available, a link or the full reference was provided.
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**Table 2.** Variable names and descriptions for file traits.csv.

<b>Variables</b>	<b>Description</b>
ID	Identification code, unique for each paper/data source.
Order	Taxonomic Order
Family	Taxonomic Family
Genus	Taxonomic genus, based on species accepted name.
Species_reported	Species scientific name as reported in the paper.
Authority_reported	Author of the species name reported in the paper.
Species_accepted	Accepted species name.
Authority_accepted	Author of the species accepted name.
Latitude	Latitude of the study site (in geographical coordinates; Geodatum: WGS84).
Longitude	Longitude of the study site (in geographical coordinates; Geodatum: WGS84).
Location	Local name of the study site.
Outcrop_Type	Outcrop type found in the study site, based on its rock material. Categorical variable. Levels: “Granite”, “Ironstone”, “Quartzite”, and “Sandstone”.
Growth_form	Plant growth-form. Categorical variable. Levels: “Herb”, “Liana”, “Shrub”, “Succulent”, and “Tree”.
Geographic_distribution	Category indicating whether species distribution is restricted to rock outcrop vegetation or not (see <i>Data sampling</i> ).
Microhabitat	Species microhabitat (see <i>Data sampling</i> ).
Dispersal_period	Species seed dispersal period (see <i>Data sampling</i> )
Dispersal_syndrome	Species seed dispersal syndrome (see <i>Data sampling</i> ).
Seed_number	Mean number of seeds per fruit.
Embryoless	Mean percentage of embryoless seeds in a seed lot.
Nonviable	Mean percentage of non-viable seeds in a seed lot.
Nondormant	Mean percentage of non-dormant seeds in a seed lot.
Dormant	Mean percentage of dormant seeds in a seed lot.
Viable	Mean percentage of viable (non-dormant + dormant) seeds in a seed lot.
Length	Mean seed length (in mm).
Width	Mean seed width (in mm).
Thickness	Mean seed thickness (in mm).
Dry_mass	Mean seed dry mass (in mg).
Water_content	Mean seed water content (%)
Dormancy	Presence/absence of primary dormancy (see <i>Data sampling</i> ).

Dormancy_class	Dormancy class <i>sensu</i> Baskin and Baskin (2021). Categorical variable. Levels: ND (non-dormant), PD (physiological dormancy), PD+PY (combinational dormancy) and PY (physical dormancy).
Desiccation_tolerance	Desiccation tolerance behavior.
Notes	Comments on taxonomy and trait estimations.

**Table 3.** Variable names and descriptions for file germination.csv.

Variables	Description
ID	Identification code, unique for each paper/data source.
Species_reported	Species scientific name as reported in the paper.
Species_accepted	Accepted species name.
Photoperiod	The light exposure period in hours, going from zero (i.e., experiments carried under dark conditions) to 24 (i.e., experiments under continuous light).
Temperature	Incubation temperature, in °C. Alternate temperature regimes are expressed so that day temperatures are followed by night temperatures (e.g., a regime with 25 °C during the day, and 15 °C during the night is expressed as 25/15).
HeatShock_Temperature	Heat shock temperature, in °C. “Control” indicates the treatment where seeds were not exposed to heat shocks prior to incubation.
HeatShock_Time	Heat shock exposure time, in minutes. “Control” indicates the treatment where seeds were not exposed to heat shocks prior to incubation.
Smoke	Treatments to emulate the effect of smoke. “Control” indicates seeds with no smoke treatment. “Charred wood” indicates seeds treated with aqueous suspension of charred wood. “Smoke water” indicates seeds treated with aqueous solution of burned leaves and stems.
Germination_Substrate	Treatments for experiments that tested the effect of different substrates in seed germination. “Control” indicates experiments carried on germination paper. Only recorded for experiments designed to test the effect of different substrates on germination.
Hypoxia	Treatments for experiments that tested the effect of hypoxia on seed germination. “Control” indicates treatments where seeds were not exposed to hypoxia.
Collection_Year	In experiments that compared the germination behavior of seeds collected in the same population but different years. Only recorded for experiments designed to test interannual differences on germination.
Reproductive_System	Controlled pollinations carried in experiments that assessed the reproductive system of a given species. “Control” indicates treatment where no manual pollination was carried (i.e., open pollination). CPC: Cross-pollination between close individuals. CPD: Cross-pollination between distant individuals. CPF: Cross-pollination with feeding pollen. CPP: Cross-pollination with pollination

	pollen. SP: Self-pollination (no pollen type specified). SPF: Self-pollination with feeding pollen. SPP: Self-pollination with pollination pollen.
Gut_Passage	Treatments for experiments that tested the effect of vertebrate gut passage on seed germination.
Fruit_Extract	Treatments for experiments that tested the effect of fruit extracts on seed germination. Numbers indicate the dilution proportion.
Individual	Number of the individuals tested in experiments that assessed the effect of intraspecific viability on seed germination.
Genotype	Genotype name, as used in the paper (see Feitosa et al. 2009).
Scarification	Scarification treatment, indicating acid concentration (in case of treatments with sulfuric acid) and exposure time (for acid and boiling water). “Control” indicates seeds that were not treated in any fashion.
Chemical_Compound	Chemical compounds used in hormone complementation (e.g., GA3, GA4 or cytokinin) and priming (e.g., KNO <sub>3</sub> ) treatments. “Control” indicates seeds that were not treated in any fashion.
Chemical_Concentration	Chemical compound concentration, in parts per million (ppm). “Control” indicates seeds that were not treated in any fashion.
Chemical_Exposure	Chemical exposure time, in hours. “Control” indicates seeds that were not treated in any fashion.
Burial_Time	Burial time, in months. “Control” indicates seeds that were not buried (i.e., unburied seeds).
Storage_Time	Storage time, in months. “Control” indicates seeds that were not stored (i.e., fresh seeds).
Storage_Temperature	Storage temperature, in °C. “Control” indicates treatments where seeds were not stored (i.e., fresh seeds).
Processing	Seed cleaning techniques. “Control” indicates seeds that were not subject to any cleaning technique.
Repetition	Replicate number.
D1-D60	Number of seeds germinated during each experiment day, from day one (D1) to 60 (D60).
GermSeeds	Number of germinated seeds.
nSeeds	Number of seeds used in each replicate.
Experiment_Length	Duration of the germination experiment, in days. “US” stands for experiments that did not set any duration beforehand but were terminated when germination stabilized.
Notes	Comments on germination experiment data.

## **Class V. Supplemental descriptors**

### **A. Data acquisition**

- 1. Data request history:** None.
- 2. Data set updates history:** None.
- 3. Data entry/verification procedures:** done by first author.

**B. History of data usage:** None.

### **Acknowledgments**

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**CHAPTER II – SEED GERMINATION ECOLOGY IN BRAZILIAN  
ROCK OUTCROP VEGETATION: A QUANTITATIVE SYNTHESIS**

Paper formatted for submission in *Annals of Botany*

## Seed germination ecology in Brazilian rock outcrop vegetation: a quantitative synthesis

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### ABSTRACT

#### *Background and Aims*

Rock outcrop vegetation is distributed worldwide and hosts a diverse, specialized flora that evolved under extremely harsh environmental conditions. However, the germination ecology of rocky outcrop vegetation has received little attention, especially regarding the association between seed germination traits, germination responses and adult plant traits. Here, we provide a quantitative review of the seed germination ecology of Brazilian rock outcrop vegetation through phylogenetically controlled meta-analyses.

#### *Methods*

Using a database with trait data for 383 taxa and 10,187 germination records for 281 taxa, we calculated the phylogenetic signal of seven seed traits and compared their variation among growth forms, geographical distributions, and microhabitats. We performed a meta-analysis of germination responses to 1) light, 2) constant and alternate temperatures, and 3) fire-related cues and compared effect sizes among the abovementioned predictors and seed mass. Finally, we evaluated the relationship between dormancy and other traits that putatively control germination timing and risk-reducing strategies.

### **Key Results**

All functional traits showed a strong phylogenetic signal. Most species from the *campo rupestre* required light to germinate and had optimal germination between 20-30°C. The effect of temperatures below and above this range was modulated by growth form, with shrubs requiring and tolerating higher temperatures. The effect of seed mass was only significant for heat shock, with bigger, dormant seeds showing higher heat tolerance. Heat shocks above 200 °C killed seeds, but smoke accelerated germination. Unexpectedly, no consistent differences were found between endemic and widespread species or species from different microhabitats. Instead, species from xeric habitats evolved phenological strategies to synchronize germination with water availability.

### **Conclusions**

Evolutionary history plays a major role in shaping the seed ecology of Brazilian rock outcrop vegetation. However, seed traits played a minor role in determining species' geographic distribution and ecological breadth. Therefore, vegetative traits and phenological traits are likely to explain such differences.

### **Keywords**

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

## **INTRODUCTION**

Rock outcrops are geological features where bedrock protrudes above the surface of the surrounding land due to the erosion of softer parts of the landscape (Fitzsimons and Michael 2017). They are present in all continents and biomes and, thus, content different evolutionary histories and constitute ideal platforms for globally distributed experiments (Porembski and Barthlott 2000; Hopper *et al.* 2021). Most notably, they provide a unique habitat that drastically differs from neighboring vegetation (Porembski 2007). As a result, they host a highly specialized biota characterized by high levels of species richness and endemism (Porembski *et al.* 2016; Campos *et al.* 2018).

Rock outcrops experience extreme surface temperatures and have shallow, extremely nutrient-poor soils; a combination that has led to the evolution of distinctive traits that enable plant species to establish and survive in such harsh environments (reviewed in Safford 1999;



Biedinger *et al.* 2000; Kluge and Brulfert 2000; Oliveira *et al.* 2016). These adaptations include vegetative desiccation tolerance (Porembski 2011), specialized root morphology (Poot *et al.* 2012; Teodoro *et al.* 2019; Abrahão *et al.* 2020), foliar water uptake (Boanares *et al.* 2018) and photosynthetic adjustments (Rios *et al.* 2022). Nevertheless, all these adaptations are related to the ecophysiology of adult plants and ignore the role of the regeneration niche, which has been shown to shape community assembly and species distribution (Grubb 1977; Donohue *et al.* 2010; Larson and Funk 2016; Rosbakh *et al.* 2022).

Here, we focus on Brazilian rock outcrop vegetation, which includes a wide variety of open, grassy-shrubby, fire-prone ecosystems that establish on various rock materials, mainly quartzite, ironstone and granite (Martinelli 2007). This vegetation is found throughout the country and is globally and locally recognized for its high diversity and endemism (Porembski *et al.* 2016; Silveira *et al.* 2016; Giulietti *et al.* 2019). Germination ecology in these ecosystems has been qualitatively reviewed (see Garcia and Oliveira 2007; Nunes *et al.* 2016; Garcia *et al.* 2020), providing promising insights into the mechanisms that shape germination and putting forward hypotheses about seed trait coordination and their potential influence on niche segregation. However, all available syntheses focus specifically on *campo rupestre* – a megadiverse montane vegetation found on quartzite, sandstone, and ironstone outcrops, mostly in southeastern Brazil (Silveira *et al.* 2016). Another limitation is a strong focus on the most emblematic families, which are not a random sample of the total megadiversity of rocky outcrop vegetation.

Here, we use meta-analytical and phylogenetically-controlled quantitative approaches to provide a comprehensive synthesis of the current knowledge about germination ecology in Brazilian rock outcrop vegetation. Specifically, we focused on three issues: i) the ecological and phylogenetic variation of seed functional traits, ii) germination responses to abiotic factors, and iii) the association between traits shaping germination timing. We compared these aspects between growth forms, species geographic distribution and microhabitats, looking for potential ecological strategies.

## MATERIALS AND METHODS

### Data sources

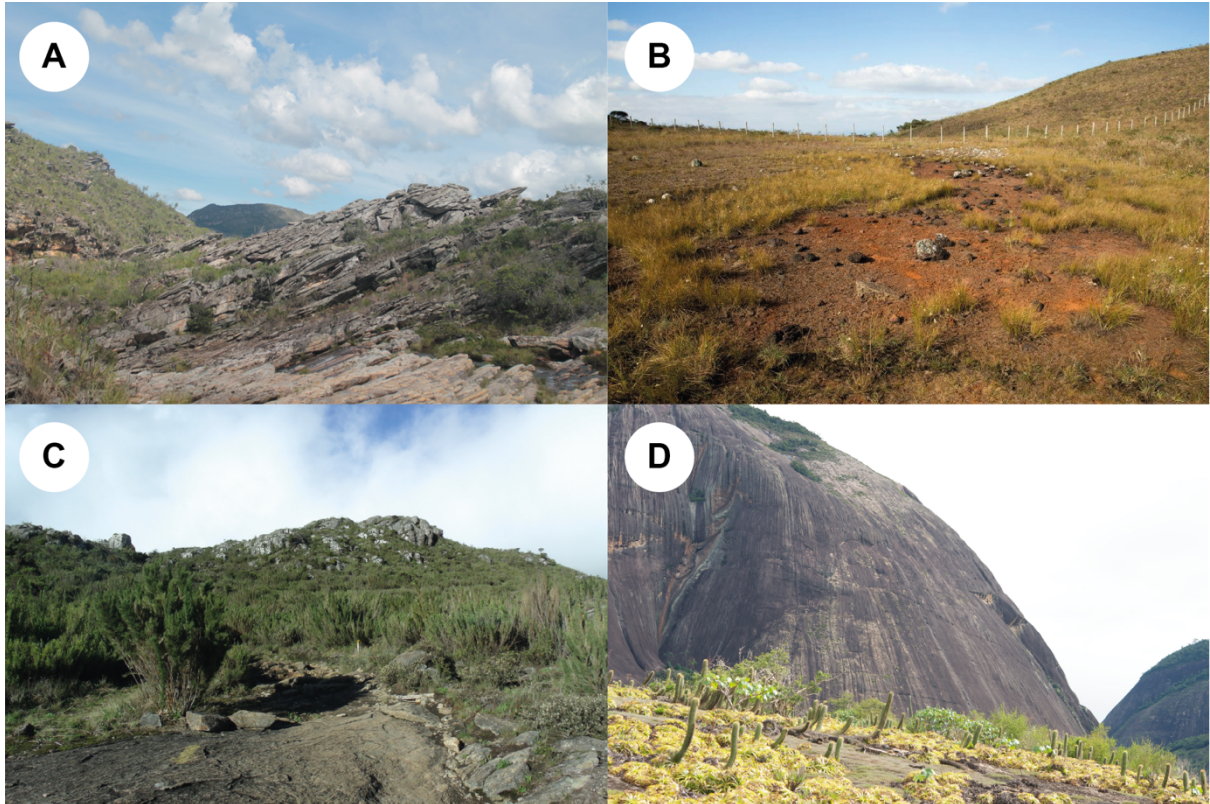
#### *Seed functional traits and germination experiments*

We retrieved traits and germination records from Rock n' Seeds (Ordóñez-Parra *et al.* 2022), a database of seed functional traits and germination experiments of species from Brazilian rock outcrop vegetation. This database builds on data available on 16 seed functional traits for 383 taxa and 10,187 germination records for 281 taxa from a wide variety of rock outcrop vegetation types, including *campo rupestre*, *canga*, *campo de altitude* and inselbergs (Figure 1). Here, we focused on seven functional traits –seed dry mass (mg), seed water content (%), percentage of empty seeds (%), percentage of viable seeds (%), seed dispersal syndrome, seed dispersal season and the presence/absence of primary dormancy– and experiments that assessed the effect of light availability, constant and alternate temperature regimes and fire-related cues (see Ordóñez-Parra *et al.* 2022, for details on trait data collection and germination experiments information).

Depending on the experimental factors assessed and measured variables, studies were classified into six non-mutually exclusive categories: (1) abiotic factors, (2) biotic factors, (3) seed dormancy, (4) viability, (5) longevity and (6) other (e.g., post-germination development, seed-based restoration experiments, and population ecology studies). Studies assessing the effect of abiotic factors were further subdivided into six categories –light, temperature, water availability, fire-related cues, substrate, and oxygen. Biotic factors studies were subdivided into intraspecific variability, reproductive systems and endozoochoric dispersal. Finally, seed longevity studies were divided into *ex situ* and *in situ* experiments.

#### *Phylogenetic tree*

Species names were checked and updated following The Leipzig Catalogue of Vascular Plants (LCVP) using the R package *lcvplants* (Freiberg *et al.* 2020). We only kept taxa identified to species level, and subspecies and varieties (18 cases) were upgraded to species-level. A phylogenetic tree for 370 species was generated using the package *V.PhyloMaker2* (Jin and Qian 2022), based on a tree from the GBOTB phylogeny for seed plants (Smith and Brown 2018) updated and standardized following Freiberg *et al.* (2020). Taxa absent from the



**Figure 1.** Main vegetation types associated to 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. 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).

backbone 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). Since these species belong to the Eupatorieae (Asteraceae), where relationships between genera within the tribe are yet to be resolved (Rivera *et al.* 2016), they were added to the base of the clade formed by the other species from the tribe as polytomies.

Most infrageneric relationships in the phylogeny remained unresolved, appearing as polytomies of several species from the same genus. Still, this result is aligned with recent studies showing that infrageneric relationships in highly diverse genera of the families in our database –such as Melastomataceae and Velloziaceae– have low support (Alcantara *et al.* 2018; Guimarães *et al.* 2019). Nevertheless, phylogenetic metrics estimated from phylogenetic trees resolved up to the genus level have shown to be highly correlated with

those derived from fully resolved trees, suggesting that these polytomies will have little effect on the phylogenetic structure of seed traits and germination responses (Qian and Jin 2021).

### **Statistical analysis**

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 Figshare upon acceptance (see Open Data).

### ***Variation and phylogenetic signal of seed functional traits***

To test for the phylogenetic signal in the quantitative traits (dry mass, water content, percentage of viable seeds and percentage of empty seeds), we calculated Pagel's  $\lambda$  (Pagel 1999) using the `phylosig` function from the package *phytools* (Revell 2012).  $\lambda$  ranges 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). The tests were carried out using log-transformed seed mass values and logit-transformed water content, and percentage of embryoless and viable seed values. For the qualitative traits (seed dormancy, seed dispersal syndrome and seed dispersal syndrome), the phylogenetic signal was tested following the approach implemented in Pavoine et al. (2010). This methodology decomposes the trait diversity among the nodes of the phylogenetic tree and assesses whether trait diversity is skewed towards the tree's root or tips. This test was carried out using the `rtestdeciv` function from the *adiv* package using 9,999 permutations (Pavoine 2020). Seed dormancy and dispersal season were treated as multichoice variables since 11 species had records of both dormant and non-dormant seeds, and 18 species had reports for more than one dispersal season.

To test the differences in quantitative traits between predictors (growth-forms, microhabitat, and geographic distributions), we used phylogenetic generalized least square (PGLS) models as implemented in the package *caper* (Orme et al. 2018). Likewise, differences in qualitative traits between predictors were assessed using a phylogenetic logistic regression (Ives and Garland 2010) as implemented in the *phylolm* package (Ho and Ané 2014). Since dispersal season and syndrome had more than two possible states, individual models were run to assess the probability of each trait state. Species with records for more than one distribution or microhabitat were classified as "Widespread" and "Mesic/Xeric", respectively. Additionally, 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).

Preliminary tests showed that the interaction between our qualitative predictors did not significantly affect any of the tested variables. As a result, our final models did not include these interactions. In both quantitative and qualitative traits analysis, trees (26 species), succulents (nine) and lianas (six) were excluded due to their low sample size. Therefore, growth-form comparisons were made between herbs and shrubs.

#### *Meta-analysis of germination responses to abiotic factors in the campo rupestre.*

We used the standardized mean difference (Hedges 1981) to estimate the effect of light, constant and alternate temperatures, and fire-related cues on germination, using the `escalc` function from the package *metafor* (Viechtbauer 2010). This metric –known as Hedges  $d$ – provides a measure of the proportional change in relation to control groups for each response variable and includes a correction by sample size and variance (Rosenberg *et al.* 2013). Experiments under total dark conditions were used as controls to test the effect of light. Results from different temperatures were pooled in a single effect for each species in each study. Given light's general positive effect on germination (see below), only experiments carried out under light conditions were used to assess the effect of temperatures and fire-related cues on germination. We used 25°C as a control for constant and alternate temperatures, considering its recognition as the optimal temperature for most species in this ecosystem. Finally, we used untreated seeds (i.e., seeds not exposed to heat shocks or smoke) as controls for fire-related cues.

We assessed the effect of these four abiotic factors on seed germination percentage and median germination time ( $t_{50}$ ). Germination percentage values were taken from the raw germination data deposited in Rock n' Seeds and were complemented with data from the experiments recovered from the systematic literature survey whose germination data was not deposited in the database. To be included in our meta-analysis, papers should present the mean germination percentage and its standard deviation in either tables or figures or provide enough information to calculate it. Data presented in the figures were extracted using ImageJ (Schneider *et al.* 2012). To avoid confounding effects, we only included observations where either the control or treatment had  $\geq 10\%$  germination. The  $t_{50}$  (Coolbear *et al.* 1984 as modified by Farooq *et al.* 2005) was calculated for the experiments deposited in our database 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 only calculated  $t_{50}$  for

observations where the control and treatment conditions had  $\geq 10\%$  germination. Moreover, considering the effect of light and constant and alternate temperatures as germination cues (see Thompson and Ooi 2010), we assessed these factors only in non-dormant seeds or in seeds where dormancy has been alleviated. Species with non-conclusive records regarding seed dormancy were also excluded. While alternate temperatures are known to break physical dormancy (Baskin and Baskin 2014), we did not have such an experimental setting in our dataset. In contrast, since fire-related cues are known to shape seed dormancy states (Baskin and Baskin 2014), we did include dormant species.

We assessed the global effect of each abiotic factor 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 as distinct populations using the `add.taxa.phylo` function from *daae* (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 global effect of each abiotic factor, we tested the moderating effect of growth forms, distributions, microhabitats, seed mass and dormancy (only for fire-related cues). Since seed mass exhibited a significant, strong phylogenetic signal (see below), missing seed values were inputted using average values for the genera from Rock n' Seeds (Ordóñez-Parra *et al.* 2022) or the Seed Information Database (<https://data.kew.org/sid/>). Ninety-five percent confidence intervals around the effect size were calculated and were considered significant if the bootstrap 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).

#### *Correlation between traits shaping germination timing and risk-reducing strategies.*

To test the association between traits controlling germination timing, we assessed the relationship between dormancy, dispersal syndrome and season, and seed mass through a phylogenetic logistic regression, as described above. Seed mass was included in the model, given its central role in the seed ecological spectrum (Saatkamp *et al.* 2019) and its reported relationship with seed dormancy and dispersal (Chen *et al.* 2020). Considering the differences in seed traits we found between growth-forms and microhabitats (see below), models were run with the whole dataset and with each growth-form and mesic and xeric habitats separately. As in the previous analysis, species with multiple dormancy states or growth

forms were considered separate populations, and missing seed mass values were filled using genera mean values.

## RESULTS

### *Seed germination ecology in Brazilian rock outcrop vegetation: how much do we know?*

Most studies (58.2%) assessed the effect of abiotic factors on germination, followed by studies on seed dormancy (27.2%) and biotic (24.3%) factors. Contrastingly, seed viability (13.6%) and longevity (11.7%) studies were relatively scarce (Figure 2a). The most studied abiotic factors were temperature and light, but other abiotic factors such as water, substrate and oxygen availability have been poorly studied in these ecosystems.

Regarding species and topics coverage, 40.9% of species have only been studied for at least one of the five major topics, and no species had studies across all major topics. Most notably, 63.4% of species with studies on the effect of biotic factors only had studies in this category (Figure 2b). Additionally, 10.4% of the species had studies on four of the topics. A similar pattern appears when considering the species addressed in studies about the effect of abiotic factors, with 47.2% only having studies for both light and temperature. Only two species had studies in four of the six abiotic factors, and no species had studies in either five or all six (Figure 2c).

### *Variation and phylogenetic signal of seed functional traits*

All six seed functional traits assessed exhibited a significant phylogenetic signal (Table 1, Figure 3). For the quantitative traits, the phylogenetic signal was found to be moderate to strong ( $\lambda$  between 0.57-0.90). Seed mass exhibited a variation of six orders of magnitude, with values ranging from 0.00035 (*Microlicia fulva*, Melastomataceae) to 175.15 mg (*Dioclea apurensis*, Fabaceae) (median: 0.245 mg). Among the most represented families in the database (see Figure 3), Fabaceae seeds were the heaviest (11.57 mg), whereas Melastomataceae (0.007 mg), Xyridaceae (0.016 mg) and Eriocaulaceae (0.044 mg) produced the lighter ones. Shrubs ( $t = 2.19$ ,  $p = 0.0398$ ) and species from mesic/xeric microhabitats ( $t = 2.01$ ,  $p = 0.04$ ) produced heavier seeds than herbs and species from mesic microhabitats, respectively (Table 2).

Seed water content was relatively less variable than the other quantitative seed functional traits, with values ranging from 3.9% (*Paepalanthus fasciculoides*, Eriocaulaceae) to 28.3% (*Dyckia ursina*, Bromeliaceae) (median: 11.7%). Cyperaceae (7.7%), Asteraceae

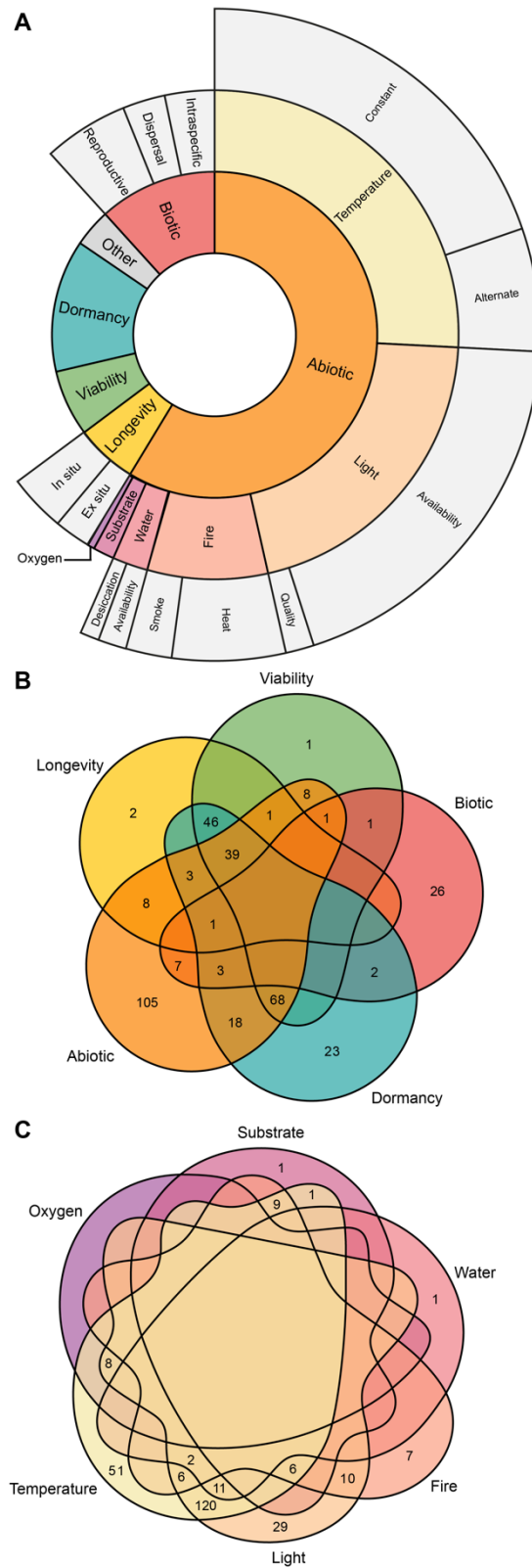
(9.2%) and Fabaceae (9.4%) had the seeds with the lowest water content, while Melastomataceae (12.2%), Bromeliaceae (13.6%) and Velloziaceae (14.2%) showed the highest values. No significant differences were found between any predictors.

The percentage of embryoless and viable seeds varied greatly among species. On the one hand, the percentage of embryoless seeds ranged from species producing lots with no embryoless seeds to several producing more than 95%, such as *Paspalum cangarum* (Poaceae, 96%), *Tibouchina edmundoi* (Melastomataceae, 98%) and *Axonopus laxiflorus* (Poaceae, 99.2%) (median: 10.6%). Poaceae and Asteraceae were the families that produced the seed lots with more embryoless seeds (82% and 66%, respectively), while Eriocaulaceae (0.9%), Xyridaceae (1.5%) and Fabaceae (4%) produced the seed lots with less embryoless seeds. Shrubs tended to produce more embryoless seeds than herbs, but these differences were only marginal ( $t = 1.93$ ,  $p = 0.06$ ). A similar trend was found for the percentage of viable seeds, with species producing no viable seeds (*Echinoalena inflexa*, Poaceae) to species producing lots with only viable seeds (e.g., *Hippeastrum morelianum*, *Vriesea bituminosa*, *Davilla grandiflora*, *Trimezia juncifolia*). Eriocaulaceae (89%), Xyridaceae (87.7%) and Velloziaceae (86%) produced the seed lots with a higher percentage of viable seeds, while species in Poaceae (11.5%) produced the seed lots with the lowest viability. No significant effect of any of the predictors was found.

Regarding seed dormancy, 64% produced non-dormant seeds, while 36% produced dormant seeds. Notably, eleven species had records of producing both dormant and non-dormant seeds. The phylogenetic logistic models indicated that species from xeric environments had higher probabilities of producing dormant seeds ( $z = 2.52$ ,  $p = 0.01$ ). The probability of producing dormant seeds did not vary significantly among other predictors (Table 2).

In terms of dispersal syndromes, autochory was the most common one (58.9% of species), followed by anemochory (26.2%) and zoochory (14.9%). Dispersal syndromes were equally distributed across categories, with none of our predictors significantly affecting the probability of possessing any of the three dispersal syndromes (Table 2).





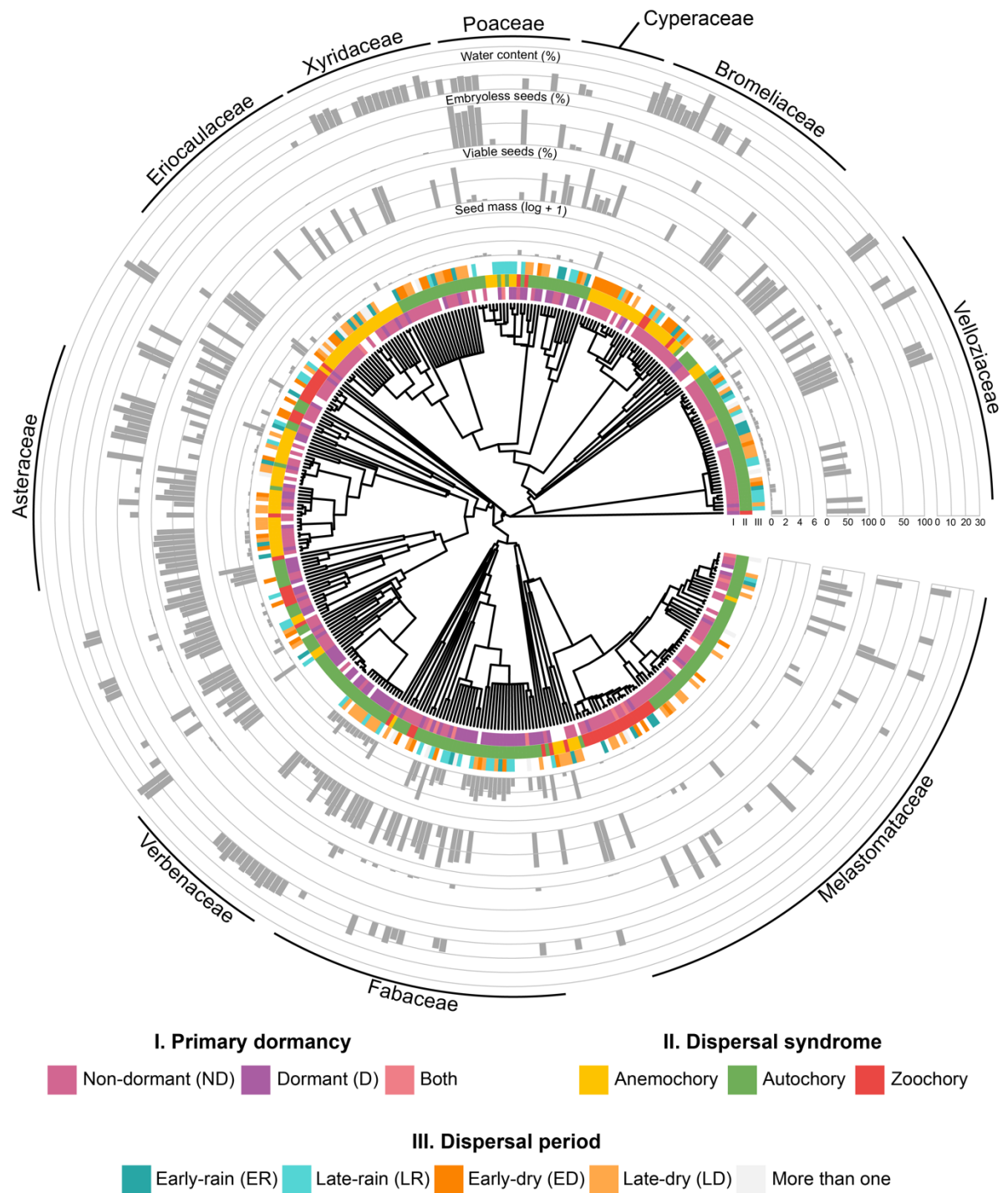
**Figure 2.** State of the art of the germination ecology of Brazilian rock outcrop vegetation. A. Percentage of studies for each germination ecology topic. B. Number of species studied each major topic and their combinations. C. Number of species studied for each abiotic factor and their combination. Figure made using RAWGraphs (Mauri *et al.* 2017) and the venn R package (Dusa 2022).

**Table 1.** Results of phylogenetic signal test. P-value 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 period	< 0.001	

Finally, most species dispersed their seeds during the dry season, either in the late-dry season (38.5%) or early-dry season (26.5%). In contrast, dispersal during the rainy season was relatively less frequent, especially during the early-rainy, when only 17.9% of species dispersed their seeds. Shrubs had a higher probability of dispersing seeds during the late-dry season ( $z = 3.43$ ,  $p < 0.001$ ), whereas dispersal during the late rainy season was more likely in herbs ( $z = -2.01$ ,  $p = 0.04$ ). In addition, species from mesic/xeric microhabitats ( $z = 2.03$ ,  $p = 0.04$ ) and those restricted from xeric microhabitats ( $z = 2.15$ ,  $p = 0.03$ ) had a higher probability of dispersing seeds during the late-rain season. The probability of dispersal during the early-dry or the early-rainy season did not vary significantly between predictors (Table 2).

In summary, shrubs tended to produce heavier seeds and had a higher probability of dispersal during the late-dry season. In contrast, herbs produced relatively smaller seeds dispersed during the late-rainy season. Species from mesic/ xeric microhabitats tended to produce heavier seeds dispersed during the late-rainy season than those from exclusively mesic microhabitats. Similarly, species restricted to xeric environments had a higher probability of producing dormant seeds and late-rainy dispersal than those from mesic environments. No differences between species restricted to outcrop vegetation and widespread ones were found for any trait.



**Figure 3.** Phylogeny of studied species with available information on seed functional traits. The ten families with the more 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).

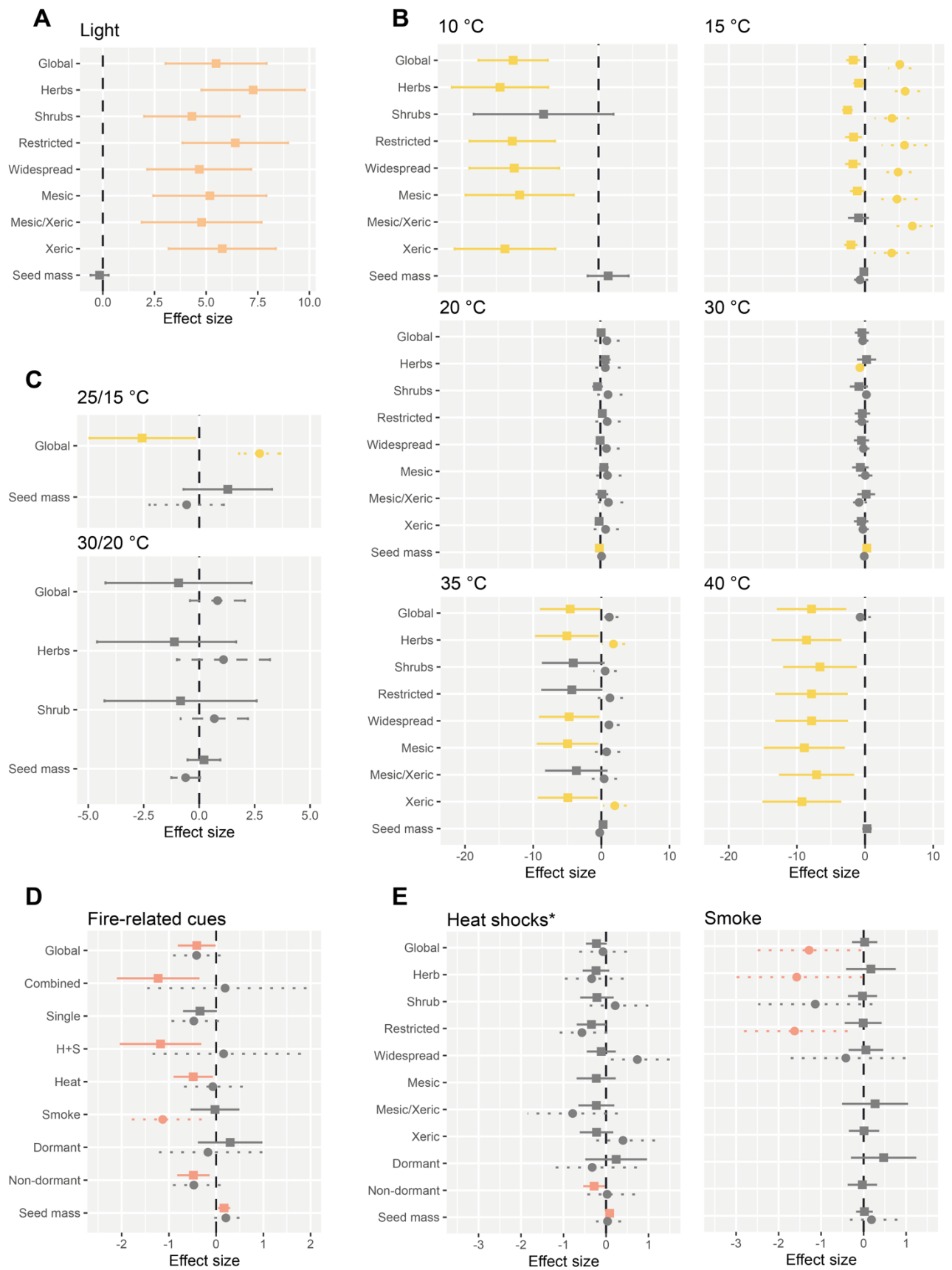
**Table 2.** Differences in seed functional traits between growth-forms (herbs vs. shrubs), and species distribution (Restricted vs. Widespread) and microhabitat (Mesic vs. Mesic/Xeric vs. Xeric). Bold values indicate significant results ( $p < 0.05$ ).

	Growth-form:		Distribution:		Microhabitat:		Microhabitat:	
	Shrub		Widespread		Mesic/Xeric		Xeric	
Quantitative traits	t	p.value	t	p.value	t	p.value	t	p.value
Seed mass	<b>2.1872</b>	<b>0.0298</b>	-0.5986	0.5501	<b>2.0141</b>	<b>0.0453</b>	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	<b>2.5218</b>	<b>0.0117</b>
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	<b>3.4323</b>	<b>0.0006</b>	-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	<b>-2.0137</b>	<b>0.0440</b>	-0.1826	0.8551	<b>2.0319</b>	<b>0.0422</b>	<b>2.1507</b>	<b>0.0315</b>

### *Meta-analyses of germination responses in the campo rupestre*

Overall, light had a significant, positive effect on germination percentage ( $z = 4.39$ ,  $p < 0.0001$ ) regardless of growth form, distribution, or microhabitat (Figure 4). The effect was significantly higher in herbs and restricted species when compared to shrubs ( $X^2 = 6.04$ ,  $p = 0.01$ ) and widespread ones ( $X^2 = 9.33$ ,  $p = 0.002$ ), respectively. No significant differences were found between microhabitats. Seed mass was found to be unrelated to effects of light on germination ( $z = -0.71$ ,  $p = 0.48$ ).

Germination responses to constant temperatures of 20 and 30 °C did not differ from the control treatment, regardless of growth form, distribution, or microhabitat. Temperatures below this range significantly reduced germination percentage and increased germination time. Contrastingly, temperatures above this range significantly decreased germination percentage but had no significant effect on germination time (Figure 4). Growth-form was found to moderate germination responses to temperature. On the one hand, the germination percentage was relatively more reduced at 15°C in shrubs ( $X^2 = 8.35$ ,  $p = 0.004$ ).



**Figure 4.** Germination responses to abiotic factors in the *campo rupestre*. A. Light availability (Control: total darkness). B. Constant temperatures (Control: 25 °C). C. Alternate temperature (Control: 25 °C). D.

Fire-related cues (Control: Untreated seeds). E. Heat shocks and smoke (Control: Untreated seeds). Dots indicate the standardized mean effect size for each environmental factor, and whiskers the 95 % CI of the effect size. Squares and continuous lines indicate the effect on germination percentage, while circles and dashed lines indicate the effect on median germination time. Colored estimates indicate significant effects (i.e., where confidence intervals do not overlap zero). \*This analysis excludes heat shock treatments of 200 °C by one minute.

On the other hand, germination in herbs was significantly accelerated at 30°C ( $z = -2.23$ ,  $p = 0.03$ ) but was decreased ( $z = -2.12$ ,  $p = 0.03$ ) and delayed ( $z = 2.03$ ,  $p = 0.04$ ) at 35°C, while it was unaffected in shrubs. Seed mass moderated germination responses at 20 and 30°C, with heavier seeds having lower germination percentage at the former ( $z = -2.20$ ,  $p = 0.03$ ), but higher under the latter ( $z = 2.90$ ,  $p = 0.003$ ). No consistent differences were found between microhabitats or distributions. Similar results were found when analyzing the effect of alternate temperatures, with 25/15°C regimes showing a significant, negative effect on germination percentage ( $z = -2.13$ ,  $p = 0.03$ ) and a positive effect on median germination time ( $z = 5.78$ ,  $p < 0.001$ ). Conversely, 30/20°C had no significant effect on germination percentage ( $z = -0.66$ ,  $p = 0.51$ ) or time ( $z = 1.31$ ,  $p = 0.19$ ). Seed mass did not moderate the effect of any of the assessed temperature regimes on germination percentage or time.

Finally, fire-related cues had a significant, negative effect on germination percentage ( $z = -2.01$ ,  $p = 0.04$ ) and time ( $z = -2.68$ ,  $p = 0.007$ ). This effect was moderated by the treatment applied, with heat shocks –alone or in combination with smoke–significantly reducing germination percentage but not affecting germination time. Seed mass moderated the overall effect of fire-related on germination percentage ( $z = 2.54$ ,  $p = 0.01$ ), but not on germination time ( $p = 0.16$ ). Instead, primary dormancy significantly shaped the responses to fire-related cues, with the germination percentage of ND species being negatively affected ( $z = -2.75$ ,  $p = 0.006$ ). Contrastingly, smoke did not significantly affect germination percentage, but it significantly reduced germination time ( $z = -2.05$ ,  $p = 0.04$ ). This effect of smoke was not moderated by seed mass or dormancy. When comparing heat shock treatments, it appeared that only exposures of 200 °C for 1 minute had a significant negative effect on germination ( $z = -5.56$ ,  $p < 0.001$ ). Further analysis without this treatment showed that heat had no significant effect on germination, regardless of growth form, distributions or microhabitat. Still, the germination percentage of ND species remained significantly affected by heat ( $z = -2.16$ ,  $p = 0.03$ ) and this effect was still moderated by seed mass ( $z = 2.05$ ,  $p = 0.04$ ).

### ***Correlation between traits shaping germination timing and risk-reducing strategies.***

When analyzing all species together, species dispersed via autochory ( $z = 2.04$ ,  $p = 0.04$ ) and zoochory ( $z = 2.48$ ,  $p = 0.01$ ) had higher probabilities of producing dormant seeds compared to anemochorous species. A similar pattern was found for species restricted to xeric microhabitats, although differences between autochorous and anemochorous species were only marginal ( $z = 1.88$ ,  $p = 0.06$ ). Contrastingly, there were no differences in the probability of dormancy across dispersal syndromes in herbs. Instead, the probability of seed dormancy increased in herbs whose seeds are dispersed either at late-dry ( $z = 2.32$ ,  $p = 0.02$ ) or early-rainy season ( $z = 2.15$ ,  $p = 0.03$ ). No significant differences were found when analyzing species from mesic environments alone. Likewise, no significant effect of seed mass was found (Table 3).

## **DISCUSSION**

### ***Seeds functional traits are phylogenetically conserved in Brazilian rock outcrop vegetation***

All seven functional traits assessed here exhibited a significant phylogenetic signal. The role of phylogenetic relatedness in shaping functional traits is widely reported for seed traits globally, including seed mass (Moles *et al.* 2005) and dormancy (Willis *et al.* 2014). Nevertheless, only part of our results agrees with studies carried at Brazilian rock outcrop vegetation and other Neotropical savannas. While both our and local studies agree that seed mass, dispersal syndrome, seed dormancy, and the percentage of embryoless and viable seeds have a significant, strong phylogenetic signal (Dayrell *et al.* 2017; Zanetti *et al.* 2020); contrasting results were found for seed water content and seed dispersal season. First, Zanetti *et al.* (2020) did not find a significant phylogenetic signal for seed water content in their study of 48 species from the *cangas* of Carajás, a result likely explained by their relatively smaller dataset. Second, we found a significant phylogenetic signal for dispersal season, while dispersal season (Escobar *et al.* 2021) and other phenophases (Zanetti *et al.* 2020; CS Oliveira *et al.* 2021) have shown to lack such signal. Potentially, this could result from a strong evolutionary pressure toward germination timing in Brazilian rock outcrop vegetation, where water is more scarce than in other savannas (CS Oliveira *et al.* 2021).

Seed mass and seed dispersal season differed significantly between herbs and shrubs, with shrubs tending to produce larger seeds and having higher probabilities of dispersing during the late-dry season, and herbs dispersing smaller lighter seeds with higher probabilities

**Table 3.** Differences in dormancy probability according to dispersal syndrome (compared to anemochory), dispersal season (compared to early-dry) and seed mass, for different growth forms and microhabitats. Bold values indicate significant results ( $p < 0.05$ ).

	Dispersal syndrome: Autochory		Dispersal syndrome: Zoochory		Dispersal period: Early-rain		Dispersal period: Late-dry		Dispersal period: Late-rain		Seed mass	
	z	p.value	z	p.value	z	p.value	z	p.value	z	p.value	z	p.value
All species	<b>2.0358</b>	<b>0.0418</b>	<b>2.4756</b>	<b>0.0133</b>	-0.9507	0.3418	0.1157	0.9079	-0.1849	0.8533	0.1594	0.87338
Herbs	0.0227	0.9819	0.0153	0.9878	<b>2.1543</b>	<b>0.0312</b>	<b>2.3157</b>	<b>0.0206</b>	1.5074	0.1317	0.3303	0.7411
Shrubs	0.9025	0.3668	1.2258	0.2203	-0.8225	0.4108	-1.6594	0.0970	0.2109	0.8329	0.1937	0.8464
Mesic	0.5878	0.5567	0.0326	0.9740	-0.1397	0.8889	0.1311	0.8957	0.2258	0.8214	- 0.3614	0.7178
Xeric	1.8822	0.0598	<b>2.0852</b>	<b>0.0370</b>	-1.4913	0.1359	0.0879	0.9300	-0.1545	0.8772	0.3983	0.6904



of dispersal during the late-rain season. This difference in seed mass agrees with results supporting a tight coordination between seed mass and other life history traits – such as plant size, lifespan, time to first reproduction and seedling survival (Westoby *et al.* 2002; Moles *et al.* 2005). On the other hand, differences in seed dispersal season suggest differences in phenological strategies to deal with precipitation seasonality (see below).

### ***Campo rupestre species depend on light for germination***

Our first meta-analysis showed that light positively affects seed germination across all ecological groups, supporting previous assessments about the germination ecology in the *campo rupestre* (Garcia and Oliveira 2007; Nunes *et al.* 2016; Garcia *et al.* 2020). Intriguingly, endemic species had a significantly stronger response to light, suggesting this kind of response is particularly prevalent in rock outcrop vegetation. This response was also stronger in herbs, which could be associated with their lower seed mass, as predicted by the well-established trade-off between germination responses to light and seed mass (Milberg *et al.* 2000). However, our results do not support such a trade-off. A possible explanation for this lack of support is 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, also known as photoinhibition of germination, 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 behavior has only been reported for one species in our study system (*Lippia filifolia*, Pimenta *et al.* 2007). Another explanation is the small variation in seed sizes in our data, with most species being light-seeded (86% records, < 1 mg) from lineages known to have positively photoblastic seeds, such as Melastomataceae, Xyridaceae and Velloziaceae (Nunes *et al.* 2016; Garcia *et al.* 2020). Large-seeded species, mainly from Fabaceae, have shown to be light-indifferent (Nunes *et al.* 2016), so additional studies in other species with relatively large seeds are needed to test the prevalence of the seed mass-light responses trade-off in rock outcrop vegetation.

Small-seeded species, such as those from Brazilian rock outcrop vegetation, are expected to have narrowly defined microsite requirements for successful establishment due to their limited internal resources (Pearson *et al.* 2003). Therefore, additional aspects of the light climate are expected to shape their germination (Pons 2000). For example, spectral quality (measured as R:FR ratio) provides information about overhead foliage and litter on the soil

surface, with high R:FR indicating no vegetation cover and, thus, high irradiance (Baskin and Baskin 2014). Still, in our study system, the effect of different R:FR ratios has only been assessed for a few 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. Responses to R:FR have been positively (Pearson *et al.* 2003) and negatively (Jankowska-Blaszczuk and Daws 2007) associated with seed mass. 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 behavior 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 the soil (Garcia *et al.* 2020), one could hypothesize that the relationship between seed mass and R:FR requirement in our species is similar to that reported by Jankowska-Blaszczuk and Daws (2007). However, these authors comment that such germination behavior implies that small-seeded species would germinate in high-risky environments where soils dry rapidly. Under this assumption –and in environments where the establishment is highly restricted by water limitation, such as the *campo rupestre* (Nunes *et al.* 2016)– 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. Further studies about the effect of light spectral quality and water availability on germination are needed to understand germination timing in these ecosystems better.

Another abiotic factor that moderates responses to light is the temperature regime under which germination occurs (Pons 2000). In our species, temperature-dependent germination responses to light have only been described in some Velloziaceae species in which germination in the darkness only occurs under high (30-40°C) temperatures (Garcia and Diniz 2003; Soares da Mota and Garcia 2013; Bicalho *et al.* 2018). This behavior is explained by the ABA catabolism induced at high temperatures (Vieira *et al.* 2017), but 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***

Our second meta-analysis indicated that the optimal germination temperature of species from the *campo rupestre* ranges between 20-30°C, supporting previous studies (Nunes

*et al.* 2016; Garcia *et al.* 2020). Temperatures below this range significantly reduced germination percentage and delayed germination. This reduction could arguably be seen as 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 species require higher temperatures to germinate. Once again, this contrast 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 °C, both temperatures where no significant differences between herbs and shrubs were found. Also, the small variation in seed size and the limited use of hydrothermal time models in our study system (but see Duarte *et al.* 2018; Oliveira *et al.* 2021) limit our capacity to test this hypothesis formally. On the other hand, temperatures above 30°C significantly decreased and delayed germination percentage, while shrubs remained unaffected, implying that shrub seeds tolerate germinating at higher temperatures.

Our third meta-analysis shows that alternate temperature regimes have either a negative or no effect on the germination of *campo rupestre* species. The negative effect on germination percentage and the positive effect on germination time at 25/15°C regime is probably due to part of these temperatures being below the optimal range. As with germination responses to light, the lack of a significant effect of 30/20°C and an association between response to alternate temperatures and seed mass could be attributed to the absence of relatively larger seeds in our dataset, which are the ones expected to benefit from alternate temperature regimes (Pearson *et al.* 2003). Nevertheless, in the *campo rupestre*, the germination percentage of the relatively larger *Stachytarpheta* seeds does increase when exposed to alternate temperature regimes (Barreto *et al.* 2016). Moreover, Andrade *et al.* (2021) indicate that species from *campo de altitude* germinate better at alternate temperature regimes, suggesting that this cue could be relatively more important in this vegetation. 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.

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

Our fourth and final meta-analysis showed that exposing seeds to 200 °C significantly reduced germination percentage. Otherwise, heat shocks did not significantly affect

germination percentage or time. This result supports experimental studies suggesting high heat tolerance in seeds from Neotropical savannas (Daibes *et al.* 2022). The effect of heat shocks on germination percentage was moderated by seed mass and seed dormancy, with lighter, non-dormant seeds being more sensitive to heat shocks. These results are aligned with those described for Cerrado species (Ramos *et al.* 2016; Daibes *et al.* 2019), suggesting a positive correlation between seed mass and heat tolerance. Contrastingly, dormant species remained unaffected by heat shocks. The absence of a positive effect on germination of dormant species is expected, considering that fire-released germination is expected only in areas with moderately frequent crown fires –such as Mediterranean ecosystems– but not in areas with surface fires such as 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 also promote heat tolerance. For example, Ramos *et al.* (2016) pointed out that the acquisition of seed dormancy occurs in parallel with the accumulation of heat shock proteins, which are known to protect tissues against desiccation and heat damage (Burke and O’Mahony 2001). Also, seeds with physical dormancy have water-impermeable coats that can offer physical protection against environmental hazards (Tweddle *et al.* 2003).

While smoke did not significantly affect germination percentage, it consistently reduced seed 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 (Thompson and Ooi 2010; Mackenzie *et al.* 2021). The ecological relevance of smoke-stimulated germination in the *campo rupestre* is convincingly explained by Fernandes *et al.* (2021), who argue that accelerated germination by smoke-derived compounds is advantageous for species resprouting and shedding seeds after a fire –a usual phenological syndrome in our study system (Figueira *et al.* 2016)– since it allows seeds to take advantage of the post-fire environment. They further suggest that smoke-stimulated germination might be an alternative to fire-stimulated emergence from the seed bank. While this hypothesis is largely supported by our last meta-analysis (i.e., no positive effect of heat on germination percentage or time and a negative effect on germination time), the effect of smoke has only been tested on a handful of species, all from *campo rupestre*. Consequently, further studies are needed to test the relative importance of this mechanism and whether these patterns can be generalized to other rock outcrop vegetation.

***Seed traits do not explain large-scale species distribution, but phenological shifts may play a role in local adaptation***

We did not find significant differences in the seed functional traits or the germination requirements between restricted and widespread species, as expected by the regeneration niche hypothesis (Grubb 1977). These results suggest that seed functional traits assessed here do not explain species distribution at a large scale. The main differences between rock outcrop vegetation and the surrounding lowlands are mostly related to nutrient and water availability, higher irradiance, and drastic daily temperature variation (Oliveira *et al.* 2016). Seed mass, although widely associated with nutrient availability for the plant during its early life, has a highly time-restricted effect that is unlikely to affect the plant life in the long term (Simpson *et al.* 2021). Instead, different studies have described the different morphological and physiological adaptations that allow these plants to cope with the stressful conditions of rock outcrops (Oliveira *et al.* 2015; Brum *et al.* 2017; Abrahão *et al.* 2019). As a result, community assembly at this scale is most probably unrelated to the germination niche (Donohue *et al.* 2010) but rather is shaped by vegetative traits.

Contrastingly, we did find significant differences between species at the local scale, namely between mesic and xeric microhabitats. Still, these differences were related to seed dispersal phenology rather than seed germination requirements. This result contrasts with previous studies that found significant differences in the germination niche of *campo rupestre* species according to their microhabitat (Oliveira and Garcia 2011; Ranieri *et al.* 2012; Silveira, Negreiros, *et al.* 2012; Marques *et al.* 2014; Giorni *et al.* 2018). Nevertheless, these studies were conducted with fewer species, suggesting that these differences probably appear between species of the same family, but they dilute at larger scales at which species do not coexist.

Most species were found to disperse their seeds during the late- or the early-dry season, and the probability of these periods did not change significantly between microhabitats. Therefore, dispersal during the dry season is the prevalent strategy in Brazilian rock outcrop vegetation. However, we found that species from xeric habitats had more 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. Late-rainy season dispersal presumably evolved to ensure dispersal during the part of the year when water is more readably available (Garcia *et al.* 2020). The prevalence of seed dormancy in xeric

microhabitats in our study agrees with the results of Silveira *et al.* (2012), who showed that dormancy evolved multiple independent times in Melastomataceae from *campo rupestre*, mostly in association with a transition to xeric habitats. One could argue that dormancy is an alternative strategy to dispersal during the rainy season in this ecosystem (Ramos *et al.* 2017; Escobar *et al.* 2018). Still, the probability of producing dormant seeds was not found to be associated with dispersal season but dispersal syndrome, with autochorous and zoochorous species having more probabilities of producing dormant seeds. The link between dispersal syndrome and dormancy agrees with local and global studies (Chen *et al.* 2020; Escobar *et al.* 2021) and suggests a compensation between risk-reducing strategies in time and space. Interestingly, the opposite relationship was found in herbs where dormancy was shaped by dispersal season –with dormant seeds dispersing more likely during the late-dry or the early-rain season– but not by dispersal syndrome. These differences between herbs and shrubs align with recent global studies that suggest that the adaptive value of seed dormancy depends on growth form (Zhang *et al.* 2022).

In the Brazilian Cerrado, shifts in dispersal phenology might be a more common adaptive adjustment than gains or losses of seed dormancy (Escobar *et al.* 2021). However, seed dormancy was relatively rare in our dataset, with only 36% of species producing dormant seeds. In fact, the *campo rupestre* is the vegetation type with the highest ND/D ratio worldwide (Dayrell *et al.* 2017), suggesting that seed dormancy is not the main driver of seedling establishment in rock outcrop vegetation. Additional strategies to control germination timing include germination requirements and the acquisition of secondary dormancy. Escobar *et al.* (2021) show that a mismatch between temperature germination requirements and environmental temperature at the moment of dispersal provides an alternative strategy to prevent germination in the absence of dormancy –for example, seeds dispersed during the dry season have evolved to germinate on the relatively higher temperatures of the rainy season. Further studies comparing the germination requirements of species dispersed during different seasons are needed to test whether a similar mechanism operates in Brazilian rock outcrop vegetation.

On the other hand, secondary dormancy has been reported in various Eriocaulaceae (Garcia *et al.* 2014; Duarte and Garcia 2015; Barreto *et al.* 2020) and Xyridaceae (Garcia *et al.* 2012; Oliveira *et al.* 2017; Oliveira and Garcia 2019) from *campo rupestre*. 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). Physiological experiments with species from both families indicate that secondary dormancy acquisition is the result of variations in GA metabolism after dispersal rather than phytohormone content before dispersal or ABA synthesis (Garcia *et al.* 2012; Barreto *et al.* 2020). Garcia *et al.* (2020) suggest that this mechanism avoids germination during the late-rain season when seedlings would only have a restricted growing season before the water becomes unavailable during the dry season.

### ***Implications for seed banking and seed-based restoration***

Rock outcrop vegetation worldwide is increasingly exposed to various threats of different magnitudes and scales (Porembski *et al.* 2016; Fitzsimons and Michael 2017). In Brazil, the most notable threats include plant overharvesting, uncontrolled tourism and large-scale opencast mining operations (Fernandes 2016; Porembski *et al.* 2016). Such is the pressure on these ecosystems that the *campo rupestre* has experienced one of the most extreme land use changes among all Brazilian ecosystems (Fernandes *et al.* 2018). Additionally, since most of these ecosystems occur on top of mountain systems and are composed of edaphic specialists, they are particularly vulnerable to the effects of ongoing climate change (Scarano *et al.* 2016). Consequently, conservation and restoration programs are urgently needed to prevent and revert biodiversity loss in these ecosystems, and seeds play central roles in these enterprises (Mattana *et al.* 2022). Below, we discuss the implications of our results for seed-based conservation and restoration strategies for rocky outcrop vegetation.

On the one hand, seed banking is recognized as 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). This strategy is limited to desiccation-tolerant seeds (i.e., those that tolerate a reduction in seed water content up to ~5%, Roberts 1973). Thus, assessing the seed desiccation-tolerance of a given species is a mandatory step in determining whether seeds can be stored in seed banks (Pritchard *et al.* 2004). While conventional screening methods can be time-consuming and resource-demanding, easy-to-measure traits have been shown to represent reliable proxies of seed desiccation tolerance. For example, dry seed mass has been widely associated with this trait, with lighter seeds having a higher probability of tolerating desiccation (Wyse and Dickie 2018). In fact, dry seed mass—coupled with moisture content— is a suitable surrogate for

desiccation tolerance in species with little information about their storage behavior (Lan *et al.* 2014). Under this model, known as the thousand seed weight-moisture content model (TSW-MC), seeds with both TSW < 500g and moisture content < 30% can be considered desiccation tolerant. Trait data for 87 species in our dataset suggest that most species from Brazilian rock outcrop vegetation have a high potential for storage in *ex-situ* seed banks, as in similar vegetation in Western Africa (Godefroid *et al.* 2020). However, model-based predictions should always be validated with experimental results given mixed support from empirical data (Lan *et al.* 2014; Mattana *et al.* 2020). Despite data scarcity for Brazilian rock outcrop vegetation, current evidence supports the notion that their species produce desiccation-tolerant seeds, amenable to being stored under *ex situ* conditions (Tarré *et al.* 2007; Andrade *et al.* 2021).

On the other hand, seed-based restoration is increasingly recognized as the most cost-effective way to restore degraded areas (Merritt and Dixon 2011). However, several functional traits from Brazilian rock outcrop vegetation indicate that applying these techniques might be challenging (see Dayrell *et al.* 2016). For example, direct seeding has proven effective for Neotropical savanna restoration (Pellizzaro *et al.* 2017; Sampaio *et al.* 2019), but it has yielded mixed results in *cangas* (Figueiredo *et al.* 2021a; b). While direct seeding 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). The establishment success in this experiment increased with the addition of plant litter, which led the authors to suggest that incorporating organic matter should facilitate seedling establishment. Nevertheless, in their subsequent study, incorporating a 1 cm layer of local substrate hampered establishment rates, particularly in small-seed species (Figueiredo *et al.* 2021a). The authors suggest that this relatively thin substrate layer was enough to reduce light availability to seeds, reducing germination. These results align with our first meta-analysis showing light's strong, positive effect on germination percentage across all ecological groups.

Another potential limitation for direct seeding is the prevalence of species that produce a considerable number of 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 projects involving these species must employ additional techniques to improve seed quality (Frischie *et al.* 2020). For instance, X-ray imaging and seed blowers have effectively increased the seed lot quality in Asteraceae species from *campo rupestre* (Feitosa



*et al.* 2009; Melo *et al.* 2009). Therefore, ecological restoration projects should benefit from incorporating seed processing methods before sowing. Restoration practitioners must also consider that the *ex-situ* stored seeds of several species from these ecosystems lose viability quite rapidly after collecting, implying they ought to be used as soon as possible (Zanetti *et al.* 2020). Despite all the beforementioned 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, it could be argued that topsoil transfer is a more useful 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, studies from the *campo rupestre* have shown impoverished soil seed banks (Medina and Fernandes 2007; Le Stradic *et al.* 2018; Luz *et al.* 2018). As a result, topsoil transfer (5 cm) has shown little use for ecological restoration (Le Stradic *et al.* 2018). However, transferring deeper topsoil samples in degraded *cangas* has shown more promising results. Restored areas recover a considerable percentage of floristic and functional composition after four years of topsoil transfer (30 cm; Onésimo *et al.* 2021). Likewise, transferring 20-40 cm depth samples reintroduces several characteristic species and recovers >50% of vegetation cover (Rezende *et al.* 2021). It should be noted, however, that this technique in these ecosystems 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). Therefore, topsoil translocation should be done with caution to avoid undesired results.

## **Conclusion**

Seed germination ecology in Brazilian rock outcrop vegetation has been mostly focused on *campo rupestre* and the effect of abiotic factors on germination, mainly light availability and constant temperatures. Most species have studies on a few factors, hindering the integration of different aspects of the seed life cycle. However, all seed traits evaluated here –which represent the major dimension of the seed ecological spectrum (Saatkamp *et*

al. 2019)– are phylogenetically conserved, implying that many aspects of the seed ecology on this vegetation are explained by phylogeny. Germination in this ecosystem was positively influenced by light, while most species had optimal germination between 20-30 °C. Temperatures below and above this range had different effects according to growth form, with shrubs requiring higher temperatures to germinate but tolerating higher temperatures. Seed mass did not modulate responses to light or temperatures. Instead, it moderates responses to heat shocks, with bigger seeds better resisting heat. Seed dormancy also moderates heat tolerance, with dormant species being more heat tolerant. On the other hand, smoke was found to accelerate germination. Surprisingly, seed traits did not explain species distribution on a large-scale and germination requirements were not enough to explain microhabitat differences. However, xeric habitats promote phenological strategies such as dormancy and late-rain dispersal, ensuring germination where water is readably available. Further studies with species outside *campo rupestre* are essential to test whether the patterns described in this research can be generalized to other rock outcrop vegetation. Additionally, further studies about the effect of water availability and differences between dispersal seasons will likely increase our understanding of germination timing in *campo rupestre*.

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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 Figshare upon acceptance.



**FINAL CONSIDERATIONS**

This dissertation aimed to increase the availability of seed functional trait data and provide a quantitative synthesis of the germination ecology of Brazilian rock outcrop vegetation. For that purpose, we conducted a systematic literature search and compiled a database of 16 functional traits and more than 10 thousand germination records. This database was then used to conduct a quantitative synthesis using a meta-analytical and phylogenetically-controlled approach. These methods not only allowed us to provide a thorough review of the germination ecology of Brazilian rock outcrop vegetation but also to formally test hypotheses arising by previous researchers and outline knowledge gaps in the area. As a result, our research permits us to establish some general trends:

- The seven functional traits evaluated here had a strong phylogenetic signal, implying that evolutionary history plays a major role in the germination ecology of Brazilian rock outcrop vegetation. Moreover, this result highlights the need to continue using phylogenetic-comparative methods to analyze patterns at the community level.
- Species from *campo rupestre* had a strong tendency to produce small, non-dormant, light-demanding and heat tolerant seeds, implying that these features could be major drivers of natural regeneration in rock outcrop vegetation.
- Seed mass only moderated responses to heat, a result that contrast long-standing trade-offs reported at the global scale. This result might derive from the little variability in seed mass, so further studies with large-seeded to are required.
- Seed germination requirements and seed traits were insufficient to explain differences between species distributions and microhabitats, suggesting that vegetative traits have a relatively more important role in community assembly. However, our current knowledge about Brazilian rock outcrop vegetation's germination ecology is biased by light and temperature responses. Further studies should explore the functional role of other abiotic factors.
- Growth form was found to moderate responses to temperature and how dormancy interacts with traits that shape germination timing. Therefore, future studies in this vegetation should assess the integration of seed traits with other life-history traits to understand better the relevance of seed traits in the plant life cycle.
- Finally, differences in seed dispersal phenology and dormancy between microhabitats suggested different strategies to synchronize germination with the season where water

was readily available. Future studies looking for adaptations to specific microhabitats should increase our understanding of the functional role of these strategies and the mechanisms that allow them.

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