Current knowledge and research gaps in Cerrado seed ecology: from seed viability to ecological restoration

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Abstract: Although seed ecology underpins plant recruitment, conservation, and restoration, knowledge in this field in the Cerrado, the largest Neotropical savanna, remains fragmented across taxa, regions, environmental factors, and stages of the seed life cycle. Here we conducted a scoping review to map existing evidence, identify gaps, and synthesise ecological patterns in this megadiverse biome. We reviewed 357 studies published between 1973 and 2025, covering 644 species from 319 genera and 79 families, and characterised temporal, thematic, taxonomic, functional, methodological, and geographical research coverage. We also assembled a biome-wide dormancy profile for 1,473 species and descriptively reanalysed germination responses to light and temperature. Publication output increased markedly after the late 2000s, but research was concentrated on germination, controlled experiments, woody species, and central and southern Cerrado regions. More than half of the species were investigated within only one research topic, and laboratory–field integration was limited. Reported seed viability varied widely among families, while community soil seed banks were dominated by herbaceous species and appeared largely transient and seasonally replenished. Approximately two-thirds of species in the dormancy profile were classified as dormant, primarily with physiological or physical dormancy, although direct experimental evidence remained limited. Among the species and conditions evaluated, light generally favoured germination, and the highest germination under tested constant temperatures occurred most frequently at 25 or 30 °C. Heat shock was usually neutral or detrimental, evidence for smoke responses remained inconclusive, and responses to water availability varied with habitat, seed traits, provenance, and developmental

stage. Biotic interactions were seldom studied beyond seed predation, and applied research remained poorly integrated from seed collection and storage to field establishment. Progress requires coordinated, field-validated, trait-based research linking seed traits and environmental processes across populations, vegetation types, and regeneration stages.

Keywords: Ex situ conservation; fire-related cues; functional traits; seed dormancy; soil seed banks.

Introduction

The Cerrado is the largest Neotropical savanna, originally covering more than 2 million square kilometres, mostly in central Brazil, and occupying nearly a quarter of the country's land area (Borghetti et al., 2019). Its pronounced rainfall seasonality, recurrent fires, and heterogeneous soils create a mosaic of grasslands, savannas, and forests across distinct biogeographic regions (Lehmann et al., 2014; Françoso et al., 2020; Bustamante & Reis, 2026). Together, these features make the Cerrado the world's richest savanna, harbouring at least 13,000 plant species, nearly half of them endemic (The Brazil Flora Group, 2018). The biome is also of major socioecological importance because of the ecosystem services it provides, including carbon storage, water supply, and climate regulation (Lahsen, Bustamante, & Dalla-Nora, 2016).

Yet the Cerrado has undergone unprecedented transformation over the last decades, with around half of its original vegetation converted into croplands, pastures, and forestry plantations (Alencar et al., 2020). Concurrently, long-term climatic records show that the biome has become markedly hotter and drier, with monthly maximum temperatures increasing as much as 4 °C and relative humidity declining by approximately 15% between 1961 and 2019 (Hofmann et al., 2021). As a result, more than a thousand Cerrado plant species are currently under some level of threat (Strassburg et al., 2017). Together with its limited representation in protected areas, which cover less than 8% of the biome, these pressures have led the Cerrado to be recognised both as a global biodiversity hotspot (Myers et al., 2000) and as one of the world's most threatened biomes (Strassburg et al., 2017). Reversing this trend will require both the conservation of native species and the restoration of degraded areas. Indeed, ecological restoration in the Cerrado has recently been recognised as a global priority for restoring biodiversity and mitigating the effects of climate change (Strassburg et al., 2020).

In this context, understanding the processes that allow Cerrado plant species to persist, recover, and re-establish is urgently needed (Buisson et al., 2019). Seed ecology seeks to understand how seed traits and their interactions with biotic and abiotic factors influence seed fate, and the timing and success of recruitment (Fenner & Thompson, 2005; Gallagher, 2014). It therefore provides fundamental information on seed viability, persistence in the soil, dormancy, germination requirements, and interactions between seeds and other organisms (Long et al., 2015; Jiménez-Alfaro et al., 2016; Larson & Funk, 2016). This ecological knowledge is complemented by applied aspects of seed science, including seed collection, processing, storage, and propagation, which are essential for developing effective conservation and restoration strategies (Dalziell et al., 2022; Larson et al., 2023; Liyanage et al., 2023). Thus, integrating these ecological and applied perspectives is crucial for understanding seed regeneration in the Cerrado and translating that knowledge into conservation and restoration practice.

Despite this importance, a comprehensive and up-to-date synthesis of seed ecology across Cerrado species is still lacking. Recent reviews have addressed seed ecology in other Brazilian open ecosystems (Gonçalves et al., 2024; Ordóñez-Parra et al., 2025; Thomas et al., 2025), whereas reviews concerning the Cerrado remain either outdated (Zaidan & Carreira, 2008) or focused on particular families (Silveira, Fernandes, & Lemos-Filho, 2013; Paraguassu et al., 2026), vegetation types (L. V. Santos et al., 2025), or environmental cues (Daibes et al., 2022). Such fragmentation limits our ability to identify where evidence is concentrated, which regeneration processes remain understudied, and how existing evidence could inform restoration, for which insufficient seed and germination knowledge is a recognised constraint (Buisson et al., 2021).

Here, we conduct a scoping review to map research coverage, synthesise available evidence, and identify priorities for Cerrado seed ecology. First, we assess temporal, thematic, taxonomic, functional, methodological and geographical patterns in the literature. Second, we synthesise findings on seed viability, persistence, dormancy, germination, and biotic interactions, together with its applications to seed conservation, propagation, and ecological restoration. We complement this evidence map with a biome-wide dormancy profile and descriptive reanalyses of published light and temperature responses. Finally, we identify research priorities for developing a more representative, mechanistic, and applicable understanding of seed ecology in this megadiverse biome.

Materials & Methods

Literature survey

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: Cerrado AND (seed* OR germina* OR dormancy). The search, last updated on 10 February 2026, was restricted to publications up to 2025 and yielded 3,591 records. After de-duplication using the R package *revtools* (Westgate, 2019) and manual checking, 2,008 records remained.

Each record was independently screened by two randomly assigned reviewers for relevance to our research questions, with disagreements resolved by a third reviewer. We included published studies written in English, Portuguese or Spanish that addressed at least one of the following topics: (i) seed viability; (ii) dormancy; (iii) persistence and soil seed banks; (iv) germination; (v) interactions between seeds and other organisms; and (vi) applied aspects. Studies were required to have been conducted within the Cerrado boundaries defined by the

Instituto Brasileiro de Geografia e Estatística (IBGE) or in explicitly identified transition zones adjoining the biome. We excluded studies conducted elsewhere, even when they investigated Cerrado-occurring species, along with studies conducted in *campo rupestre* vegetation and those concerning major crops or species of forestry interest. *Campo rupestre* was excluded because of its current consideration as an azonal biome extending beyond the Cerrado (Miola, Ramos, & Silveira, 2021).

After screening, the final database comprised 337 papers. This database was supplemented with 20 additional papers identified from three literature reviews retrieved during the database search (Zaidan & Carreira, 2008; Silveira, Fernandes, & Lemos-Filho, 2013; Almeida et al., 2026). The full literature search and selection process is summarised in the PRISMA flowchart shown in Suppl. Material 1.

Data extraction was distributed among reviewers using a shared spreadsheet and pre-defined variables. We recorded publication language, species, coordinates, vegetation type, experimental setting (laboratory, greenhouse and/or field), growth form, and research topic, as described above. Studies could be assigned to multiple topics, and germination studies were additionally categorised by abiotic cue: light, temperature, water, fire-related cues, substrate or other factors. Vegetation types were classified following Ribeiro & Walter (1998), including *campo limpo* (open grassland), *campo sujo* (shrubby grassland), *campo úmido* (wet grassland), *cerrado sensu stricto* (wooded savanna), *cerradão* (closed-canopy woodland), *mata de galeria* (gallery forest), and other physiognomies. Growth form followed the original publication or retrieved from Flora e Funga do Brasil using the R package *florabr* (Trindade, 2024), provided the database listed only one growth form (i.e. herb, subshrub, shrub, tree, palm or vine). Finally,

nomenclature was standardised against Flora e Funga do Brasil (v. 393.428) using *florabr*, with synonyms consolidated under accepted names before species-level summaries.

To structure the thematic synthesis, we further organised the available evidence according to the processes and experimental approaches investigated within each research topic. For seed viability, we distinguished among assessment methods, including germination assays, tetrazolium testing, and embryo inspection. Studies on seed persistence and soil seed banks were classified into burial experiments assessing the persistence of individual species and community-level soil seed-bank studies. Germination studies were further classified according to the specific aspects of each abiotic factor investigated: light (availability and spectral quality), temperature (constant and alternating regimes), water (water deficit, flooding, and desiccation), fire-related cues (heat shocks and smoke), and substrate. Studies addressing additional germination factors were retained in the 'other' category. Biotic interactions were classified into seed predation, interactions with microorganisms, and allelopathy, whereas applied studies were grouped into seedling production, seed-based restoration, and ex situ conservation. Consistent with the evidence-mapping objectives of this scoping review, we did not conduct formal quality appraisal or risk-of-bias assessment or weight studies by methodological quality, and we only synthesised findings descriptively.

Dormancy profile

To complement our synthesis on seed dormancy, we built a biome-wide dormancy profile by matching the list of Cerrado seed plants from Flora e Funga do Brasil, retrieved using *florabr*, with two regional (Amaral-Garcia et al., 2026; D. N. Oliveira et al., 2026) and two global databases (Zhang et al., 2022; Rosbakh et al., 2023). Names from each database were

standardised as above and dormancy classes followed the classification by Baskin & Baskin (2021): non-dormant (ND), physiological (PD), morphological (MD), physical (PY), morphophysiological (MPD), or combinational (PD + PY) dormancy.

Species were assigned ND only when all available records indicated ND. Consistent records of the same dormant class retained that class. Where ND and a dormant class co-occurred, we assigned the dormant class, indicating the potential of that species of presenting this trait. Species with conflicting dormancy classes or no dormancy information were excluded. The final dataset contained dormancy classifications for 1,473 Cerrado species.

Germination responses to light and temperature

We further characterise species responses to light and temperature, the two most frequently studied germination cues identified in our review. For light responses, we extracted paired germination percentages under light (continuous or 12-h photoperiod) and continuous darkness and calculated the Light Response Index (LRI; Milberg et al., 2000): LRI = GL/(GD + GL), where GL and GD are the germination percentages under light and darkness, respectively. LRI ranges from 0 (germination only in darkness) to 1 (only in light), with 0.5 indicating equal germination under both conditions. Comparisons with zero germination in both treatments were excluded. We averaged LRI across temperature treatments within studies and across study-level values for species evaluated in multiple studies (five species), obtaining one estimate for each of 80 species (21 families; 62 genera). For descriptive classification, LRI $\leq$ 0.4 indicated light inhibition, 0.4 < LRI < 0.6 light indifference, and LRI $\geq$ 0.6 light stimulation.

For constant temperatures, we included studies testing at least four temperatures at 5 °C intervals and reporting germination percentage alongside a measure of germination timing or

speed and identified the tested temperature yielding the highest germination percentage. In case of ties, they were resolved by faster germination according to the reported timing, speed or rate (Labouriau, 1983). If tied treatments remained indistinguishable, all were retained. This yielded best-performing tested temperatures for 78 species (21 families; 63 genera).

For alternating temperatures, we compared germination percentage with the within-study control treatment, using the original studies' statistical comparisons. Responses were classified as positive or negative when significantly higher or lower than the control, respectively, and neutral only when a non-significant difference was explicitly reported. Responses were classified for 78 species (21 families; 63 genera), focusing on the four most frequently tested regimes: 30/20, 35/15, 35/20 and 35/25 °C.

Data analyses

We summarised annual publication counts and numbers and proportions of studies and species by research topic, experimental setting, plant family, growth form, vegetation type, geographical region and, within germination studies, abiotic cue. Knowledge depth was measured as the number of topics investigated per species and, for germination studies, the number of five focal abiotic cues evaluated per species (excluding 'other'). Because studies could contribute to more than one topic, abiotic cue, experimental setting, or vegetation type, these categories were non-mutually exclusive. All summaries and figures were produced in R (v. 4.5.1) (R Core Team, 2025).

Research Coverage & Knowledge Depth

Our scoping review recovered 357 studies published between 1973 and 2025, encompassing 644 species, 319 genera and 79 families. Although the earliest study dated from 1973, publication output increased markedly after the late 2000s, with more than half of all studies published between 2015 and 2025, indicating that current knowledge of Cerrado seed ecology is largely based on a relatively recent body of work (Fig. 1A). Most were published in English (68.3%), although Portuguese accounted for 31.4%, underscoring the importance of regional-language literature. Research was concentrated in controlled settings: 257 studies included laboratory experiments, compared with 83 involving fieldwork and 80 greenhouse experiments. Only 24 studies combined laboratory and field components, 16 combined greenhouse and field conditions, and two included all three settings. Overall, this distribution indicates that most knowledge of Cerrado seed ecology has been generated under (semi)controlled conditions, with limited integration between experimental and field-based evidence.

Research effort was unevenly distributed among topics. Germination dominated the literature (175 studies, 49.0%) and covered the largest number of species (349, 54.2%). Applied aspects were the second most studied topic (110 studies, 30.8%), followed by dormancy (61, 17.1%) and viability (48, 13.4%). Species representation, however, did not always mirror study frequency. Soil seed-bank studies accounted for only 7.8% of studies but encompassed 222 species (34.5%), whereas biotic interactions remained comparatively restricted in both number of studies (36, 10.1%) and species (65, 10.1%; Fig. 1B). Together, these patterns show that research has concentrated on germination, while other dimensions of Cerrado seed ecology remain less explored.

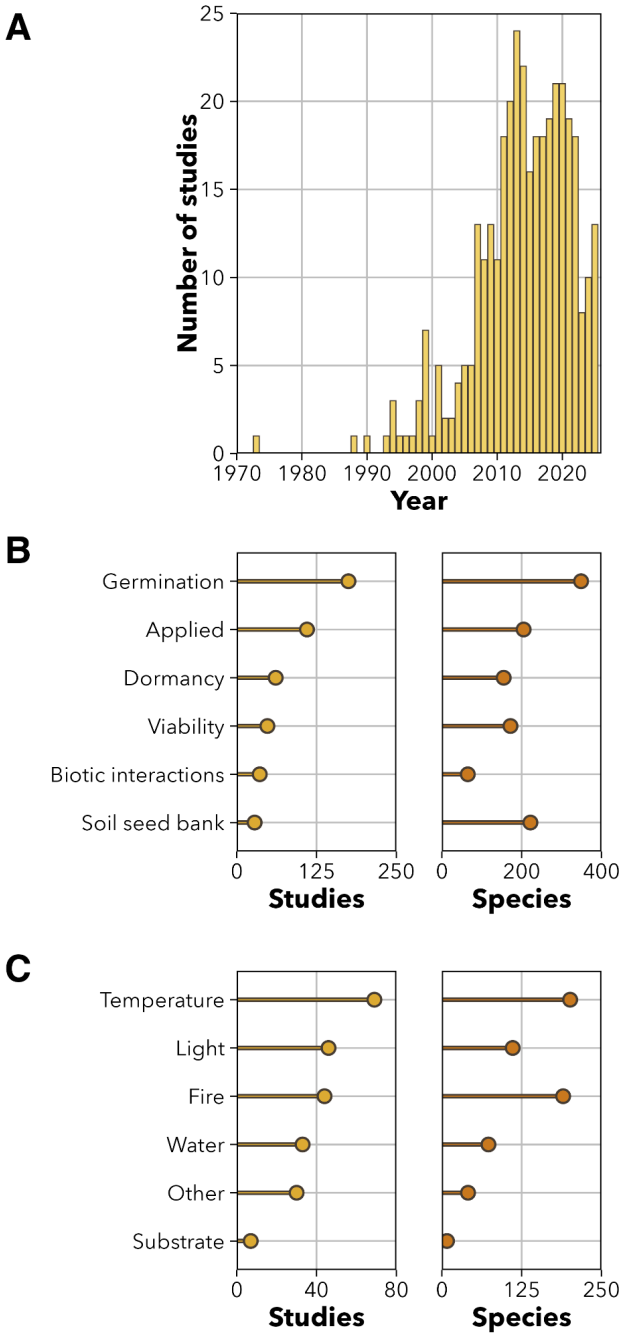


Fig. 1. Research effort, thematic distribution, and knowledge depth in Cerrado seed ecology. **A.** Number of studies published per year between 1973 and 2025. **B.** Number of studies (left) and species represented (right) across the six research topics considered in this review. **C.** Number of

studies (left) and species represented (right) across the abiotic factors investigated within germination studies.

Among germination studies, temperature was the most frequently investigated germination cue (69 studies, 201 species), followed by light (46 studies, 111 species) and fire-related cues (44 studies, 190 species). Despite similar study numbers, fire-related research encompassed substantially more species than light-related research. Water availability was investigated in 33 studies (73 species), other abiotic factors in 30 studies (41 species), and substrates in only seven studies (eight species; Fig. 1C).

Taxonomic representation was similarly uneven. Fabaceae (126 species), Poaceae (108) and Asteraceae (65) jointly accounted for 46.4% of recorded species (Table 1). Seven of the ten most studied species belonged to Fabaceae, including *Dimorphandra mollis* Benth. (30 studies), *Copaifera langsdorffii* Desf. (25), *Dipteryx alata* Vogel (24) and *Hymenaea stigonocarpa* Mart. ex Hayne (19; Fig. 2). Our dataset included 24 of the 30 hyperdominant Cerrado tree species (Fig. 2; Alvarez et al., 2025) and 11 of the 15 most abundant herbaceous species (M. C. Silva et al., 2022), although only one of these herbs, *Echinolaena inflexa* (Poir.) Chase (Poaceae), was among the ten most studied species.

Knowledge depth was similarly uneven across species: 343 species (53.3%) were investigated within only one research topic, 159 (24.7%) within two, and 142 (22.0%) within three or more; only three species were covered across all six topics. This pattern was mirrored within germination research. Among 338 species assessed for at least one of five focal abiotic germination cues, 183 (54.1%) were evaluated for only one cue, 85 (25.1%) for two and 70 (20.7%) for three or more. Only two species were investigated across all five cues.

Table 1. The ten most represented plant families in the Cerrado seed ecology dataset, showing the number and proportion of recorded species and studies in each family. Families are ranked following species number.

Family	Species, n (%)	Studies, n (%)
Fabaceae	126 (19.6)	132 (37.0)
Poaceae	108 (16.8)	43 (12.0)
Asteraceae	65 (10.1)	30 (8.4)
Melastomataceae	29 (4.5)	31 (8.7)
Cyperaceae	24 (3.7)	16 (4.5)
Bignoniaceae	23 (3.6)	30 (8.4)
Rubiaceae	22 (3.4)	33 (9.2)
Malvaceae	18 (2.8)	32 (9.0)
Lamiaceae	16 (2.5)	12 (3.4)
Arecaceae	12 (1.9)	25 (7.0)

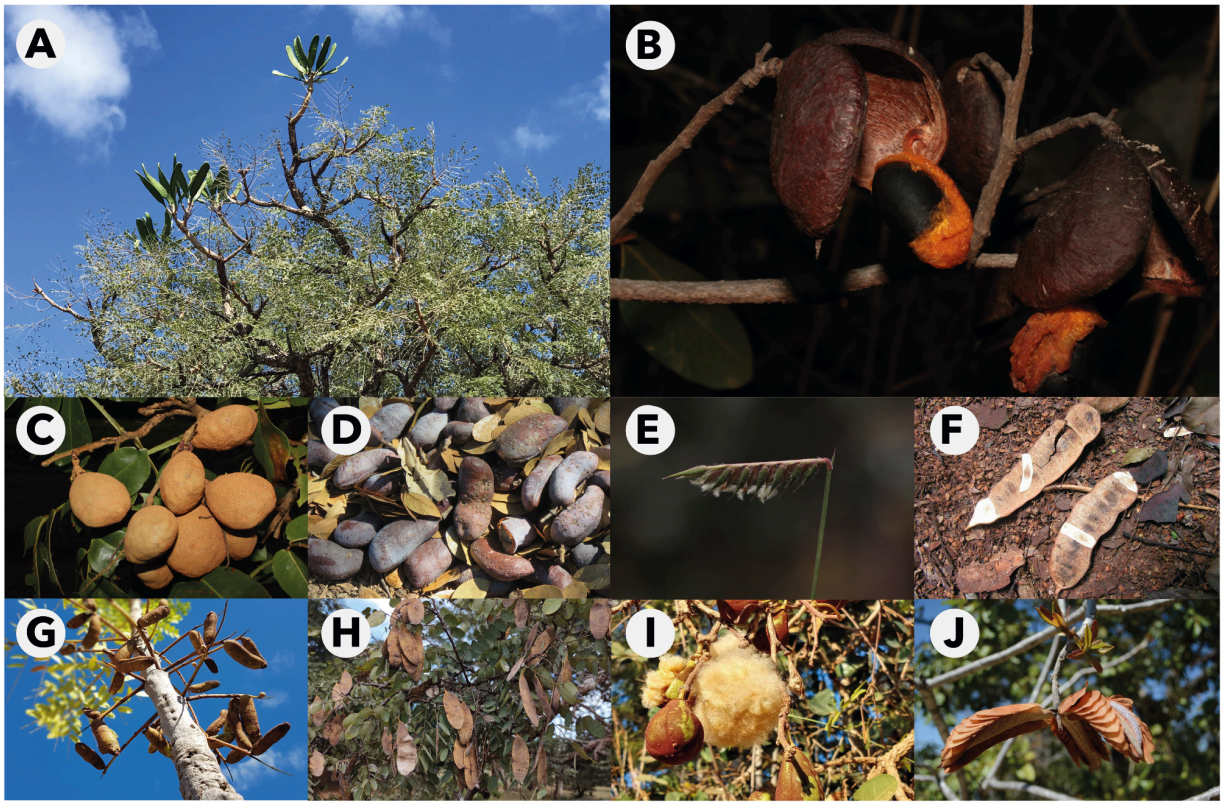


Fig. 2. Photographs of the ten most frequently studied species in the dataset, ranked by number of studies. **A.** *Dimorphandra mollis* (Fabaceae), photographed by Onildo João Marini Filho via iNaturalist (https://www.inaturalist.org/photos/35853785). **B.** *Copaifera langsdorffii* (Fabaceae), photographed by Luciano P. Queiroz. **C.** *Dipteryx alata* (Fabaceae), photographed by Luciano P. Queiroz. **D.** *Hymenaea stigonocarpa* (Fabaceae), photographed by Scott Hecker via Wikimedia Commons. **E.** *Echinolaena inflexa* (Poaceae), photographed by Pedro F. Cruz-Júnior. **F.** *Plathymenia reticulata* Benth. (Fabaceae), photographed by Tarciso Leão via Wikimedia Commons. **G.** *Stryphnodendron adstringens* (Mart.) Coville (Fabaceae), photographed by Mônica E. Carvalho via iNaturalist (https://www.inaturalist.org/photos/140033800). **H.** *Dalbergia miscolobium* Benth. (Fabaceae), photographed by Eric Fischer Remp via iNaturalist (https://www.inaturalist.org/photos/133322931). **I.** *Eriotheca pubescens* (Mart.) Schott & Endl.

(Malvaceae), photographed by Marluce Gomes Oliveira via iNaturalist (https://www.inaturalist.org/photos/565964572). **J.** *Kielmeyera coriacea* Mart. & Zucc. (Calophyllaceae), photographed by Lara Amaral-Garcia. All photographs sourced from iNaturalist are licensed under CC BY-NC 4.0, whereas those sourced from Wikimedia Commons are licensed under CC BY 2.0.

Growth forms were also unevenly represented across the literature. Herbs accounted for 42.1% of recorded species but appeared in only 21.0% of studies, whereas trees comprised 30.7% of species and occurred in 57.7% of studies. Shrubs and subshrubs were represented more proportionally, whereas palms accounted for only 1.6% of the recorded species but appeared in 5.9% of studies. This concentration of research effort on woody growth forms was also evident among the ten most studied species, of which only one was herbaceous and the remaining nine were trees (Fig. 2).

The geographic distribution of studies was markedly uneven across the Cerrado, with most research concentrated in the central and southern portions of the Cerrado, with fewer studies in the northern and southwestern regions (Fig. 3A). Vegetation type was reported in only 162 studies (45.4%), encompassing 461 species, of which 115 investigated natural vegetation types. *Cerrado sensu stricto* (47 studies, 237 species), *campo sujo* (25, 210) and *campo úmido* (15, 70) were the most frequently reported vegetation types (Fig. 3B–E). Degraded areas were represented in 48 studies (29.6%) and encompassed 217 species (47.1%), highlighting the prominence of human-modified habitats in Cerrado seed ecology research (Suppl. Material 2).

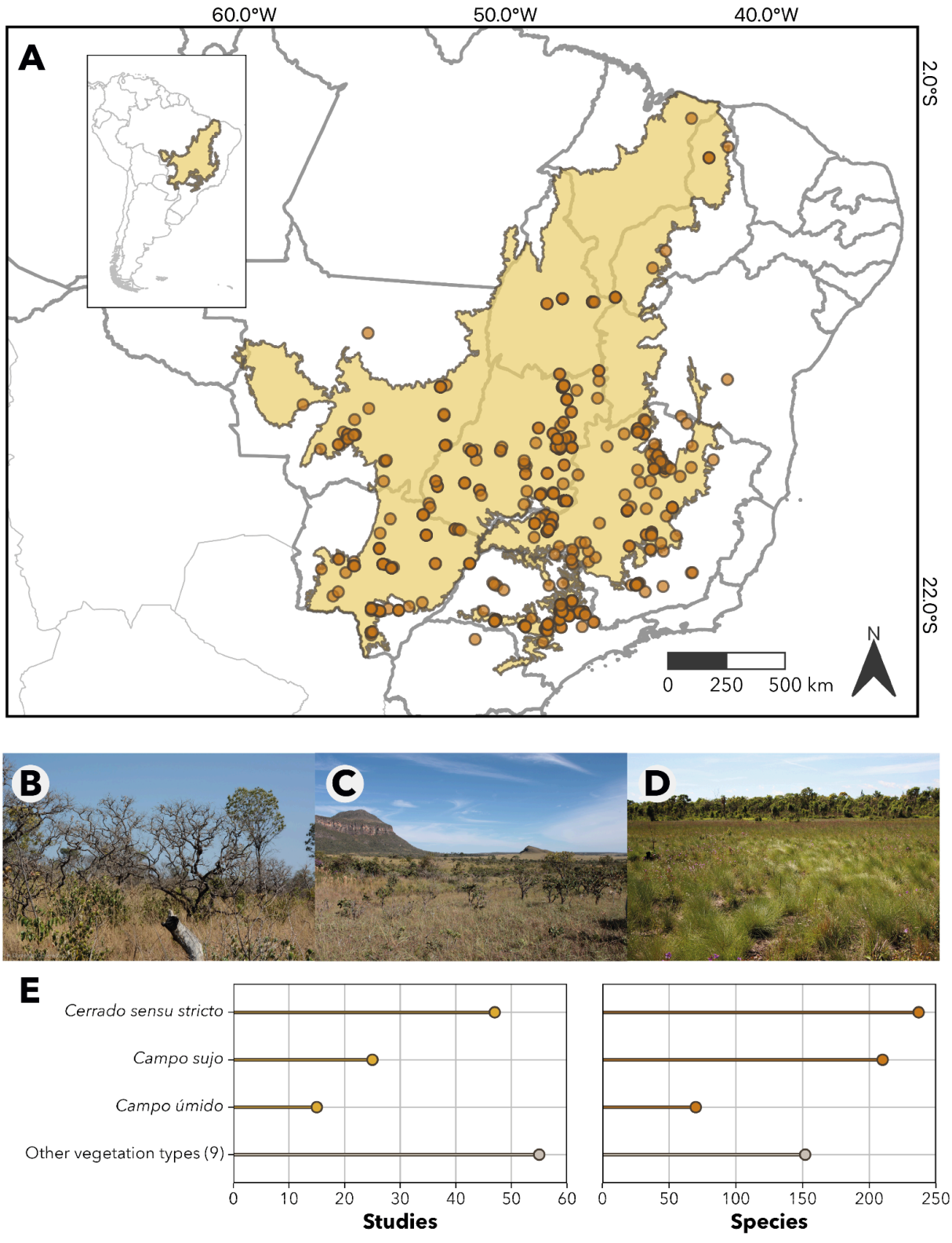

A
60.0°W
50.0°W
40.0°W
2.0°S
22.0°S
0
250
500 km
N
B
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D
E
Cerrado sensu stricto
Campo sujo
Campo úmido
Other vegetation types (9)
0
10
20
30
40
50
60
Studies
0
50
100
150
200
250
Species

Fig. 3. Geographic distribution of studies and representation of vegetation types in Cerrado seed ecology. **A.** Location of studies across the Cerrado domain. Points indicate study sites, and the inset shows the position of the Cerrado within South America. **B–D.** Representative images of major Cerrado vegetation types: **B.** *cerrado sensu stricto*, photographed by Lara Amaral-Garcia at Parque Nacional da Chapada dos Veadeiros (Goiás, Brazil); **C.** *campo sujo*, photographed by Carlos A. Ordóñez-Parra at Parque Nacional da Chapada dos Veadeiros (Goiás, Brazil); and **D.** *campo úmido,* photographed by Pedro F. Cruz-Júnior at Estação Ecológica de Santa Bárbara (São Paulo, Brazil). **E.** Number of studies (left) and species represented (right) across the main vegetation types sampled in the literature.

Taken together, the literature is recent and concentrated on germination, controlled experiments, woody taxa, and study sites in the central and southern portions of the Cerrado. Most species have been investigated within only one research topic or abiotic cue, while field integration and coverage across vegetation types remain limited. This uneven distribution of research effort, together with the limited integration of evidence across topics and experimental settings, constrains our ability to generalise findings across the biome and highlights priorities for broader taxonomic, geographical, and mechanistic research.

Seed Viability

Seed viability, defined as the capacity of a living seed to germinate under suitable conditions, sets an upper limit on potential germination and therefore influences recruitment, propagation, and ecological restoration (Borza, Westerman, & Liebman, 2007; Baskin & Baskin, 2014). Numerical estimates were available for 166 of the 172 species covered by viability

studies, with values spanning 0 to 100%. Evidence was concentrated in herbaceous species, which accounted for 62.7% of the viability values with growth-form information.

Mean viability was highest in Fabaceae and Velloziaceae, at 75.3% and 71.5%, respectively, with some species reaching 100% (Table 2). Nevertheless, 44.1% of records reported viability below 60%. Poaceae and Asteraceae were the best-represented families, with 71 records from 54 species and 20 records from 19 species, respectively. Both showed intermediate mean viability—58.1% in Poaceae and 61.0% in Asteraceae—but values ranged from almost zero to nearly 100%. Low viability was also frequent in Cyperaceae. The family-level variation observed here is consistent with evidence of phylogenetic structure in seed viability from other tropical open ecosystems (Ordóñez-Parra et al., 2025). Still, seed viability has been found to change across different vegetation types in the Cerrado, with *campos úmidos* exhibiting higher values than *campos limpos* (E. J. S. Silva et al., 2026).

Viability was assessed functionally through germination assays, biochemically through tetrazolium testing, and structurally through embryo inspection, often using more than one approach. Germination assays complemented by tetrazolium testing accounted for 56.9% of viability records, followed by tetrazolium testing alone (21.3%). Median estimates were 84% for tetrazolium tests, 79% for embryo inspection, and 70% for germination assays. Germination may underestimate viability when dormant seeds are not exposed to appropriate conditions, whereas tetrazolium testing detects living tissues independently of germination. Embryo inspection confirms embryo presence but not metabolic viability (Frischie et al., 2020). Estimates derived from these methods should therefore not be treated as interchangeable.

Table 2. Seed viability, expressed as the mean (minimum–maximum) of species-level mean values, for the ten plant families represented by at least five viability records. Each species contributed equally to its respective family mean.

Family	Records	Species	Seed viability, mean (min–max) (%)
Poaceae	71	54	58.1 (1.8–99)
Fabaceae	25	18	75.3 (13–100)
Asteraceae	20	19	61.0 (3.8–100)
Velloziaceae	11	10	71.5 (43–97)
Cyperaceae	9	9	53.6 (5–96)
Lamiaceae	9	7	59.3 (17–99)
Melastomataceae	6	6	44.3 (3.7–68)
Arecaceae	5	3	77.2 (31–95)
Bignoniaceae	5	5	70.9 (58–94)
Orchidaceae	5	4	70.2 (45.9–83.9)

These patterns require cautious interpretation because sampling was strongly uneven. Poaceae accounted for more than one-third of all records, 15 of the 33 families were represented by only one species, and only ten families had at least five records. Apparent family-level

differences may therefore partly reflect uneven coverage and should not be generalised to poorly represented lineages.

Seed Persistence & Soil Seed Banks

The soil seed bank comprises viable seeds remaining on or within the soil after dispersal. Seed banks are commonly classified as transient when seeds persist for less than one year and persistent when viability extends beyond this period (Thompson & Grime, 1979). The few burial experiments conducted in the Cerrado (10 studies, 19 species) show that some species can form persistent seed banks (e.g., Matheus et al., 2017; Rodrigues-Junior et al., 2018; Xavier et al., 2021). Nevertheless, transient seed banks may be more common at the community level, especially since perennial species that rely heavily on vegetative persistence through below-ground bud banks tend to dominate Cerrado vegetation (Pilon et al., 2021; Zupo et al., 2021). Moreover, community studies show pronounced changes in seed density, consistent with the strong seasonal dynamics of seed dispersal and germination of the biome (Salazar et al., 2011; Andrade & Miranda, 2014). Consequently, many Cerrado species may replenish the soil seed bank seasonally rather than accumulate long-lived seed reserves, potentially limiting the capacity of the seed bank to support regeneration following prolonged or severe disturbance.

Community seed banks are dominated by herbaceous species, particularly Poaceae, Asteraceae, Cyperaceae, Rubiaceae, and Melastomataceae, but generally contain lower diversity than standing vegetation (Pereira-Diniz & Ranal, 2006; Salazar et al., 2011; Andrade & Miranda, 2014). Seed density tended to peak in the dry season in grasslands and savannas, but in the rainy season in woodland formations, potentially reflecting differences in dispersal phenology and soil moisture. Most viable seeds occurred in the upper 5 cm of soil, with densities and viability

declining with depth (Sassaki et al., 1999; Pereira-Diniz & Ranal, 2006; R. R. P. Silva & Vieira, 2017).

Fire can influence seed banks directly through heat and smoke and indirectly by changing light, competition, and soil conditions (Andrade & Miranda, 2014; Dairel & Fidelis, 2024). Burned areas sometimes showed greater seedling emergence, particularly among eudicots, whereas monocot emergence tended to decline (Ikeda et al., 2008; Andrade & Miranda, 2014). Conversely, prolonged fire exclusion may instead increase woody species in the seed bank, potentially preceding encroachment in above-ground vegetation (Dairel & Fidelis, 2024).

Land-use change imposes additional pressures. Cultivated areas generally contained fewer seeds and native species, with tillage contributing to reduced richness (Ikeda et al., 2007, 2008; Machado et al., 2013; R. R. P. Silva & Vieira, 2017). Invasive African grasses, particularly *Melinis minutiflora* P.Beauv. and *Urochloa decumbens* (Stapf) R.D.Webster, can instead form dense and persistent seed banks. Their high propagule availability and distinct dispersal periods may help sustain their dominance across a wide range of environmental conditions (Dairel & Fidelis, 2020; Xavier et al., 2021).

Seed-bank composition may therefore indicate disturbance history and inform restoration planning, but available evidence remains concentrated in central and southern Cerrado regions and open vegetation types. Moreover, seedling-emergence assays may underestimate viable dormant seeds that fail to germinate under experimental conditions. Broader surveys combining seed extraction, viability tests, and burial experiments are needed to establish long-term persistence and the contribution of soil seed banks to regeneration.

Seed Dormancy

In seasonal environments such as the Cerrado, seed dormancy may play a key role in regulating germination timing (Zaidan & Carreira, 2008; Escobar, Silveira, & Morellato, 2018). Our dormancy profile, assembled from regional and global databases, included 1,473 Cerrado species, approximately two-thirds of which were classified as dormant. PD and PY were the most common classes, recorded for 584 and 257 species, respectively (Table 3). However, the studies recovered by our scoping review provided direct evidence for only 155 species, highlighting the limited experimental basis for characterising dormancy across the biome.

PD predominated in Poaceae (Kolb, Pilon, & Durigan, 2016; Ramos et al., 2017; Dairel & Fidelis, 2020), with alternating temperatures and dry storage alleviating it in native and invasive species (Aires, Sato, & Miranda, 2014; Musso et al., 2015; Gorgone-Barbosa et al., 2016). Notably, dormancy has shown to be more frequent among grasses from dry habitats that dispersed their seeds late in the rainy season, potentially preventing germination and seedling establishment during the subsequent dry season (Ramos et al., 2017). However, a recent review identified inconsistent classifications among Cerrado grasses, including species reported as both non-dormant and physiologically dormant and classifications unsupported by suitable experiments (Paraguassu et al., 2026). These inconsistencies highlight the need for more rigorous dormancy characterisation in Cerrado grasses.

PD was also reported for 47 Asteraceae, 40 Rubiaceae, and 21 Cyperaceae species in the dormancy profile. Yet few Cerrado studies directly examined dormancy in these families, and those recovered formed part of broader community-level investigations (Salazar et al., 2011; Escobar, Silveira, & Morellato, 2018; Fontenele & Miranda, 2022). This reveals a marked

discrepancy between the apparent prevalence of PD in available databases and the limited Cerrado-specific experimental evidence supporting these classifications.

PY was most prevalent in Fabaceae and occurred in three of the most frequently studied Cerrado species: *Dimorphandra mollis*, *Stryphnodendron adstringens*, and *Hymenaea stigonocarpa*. Although water-impermeable seed coats may protect seeds against fire-associated heat (Daibes et al., 2019), fire does not appear to be a major cue for releasing PY in Cerrado legumes, possibly because Cerrado surface fires generate relatively low soil temperatures (Pausas & Lamont 2022; see *Fire-related cues*). Temperature fluctuations alone also seem insufficient, whereas seasonal interactions between temperature and humidity may be more important (Matheus et al., 2017; Rodrigues-Junior et al., 2018; Daibes et al., 2021). PY was also prevalent in Malvaceae, despite limited direct experimental evidence (Escobar, Rubio De Casas, & Morellato, 2021).

Despite these general patterns, major gaps remain in our understanding of seed dormancy in the Cerrado. Available studies often provide insufficient evidence to determine dormancy status or class, even for widely investigated species such as *Dypterix alata* and *Copaifera langsdorffii* (Durigan et al., 1997; Mori, Piña-Rodrigues, & Freitas, 2012; W. V. S. Pereira et al., 2025). Moreover, most studies have evaluated laboratory treatments promoting germination rather than the cues releasing dormancy under natural conditions. Combining controlled experiments with seasonal field observations could clarify how environmental variation regulates dormancy release and germination phenology.

Table 3. Number and percentage of Cerrado-occurring species assigned to each seed dormancy class based on regional and global databases, ranked by decreasing number of species, with examples of representative plant families. Percentages were calculated relative to the 1,473 species with assignable classifications.

Dormancy class	Species (%)	Examples
Physiological dormancy (PD)	584 (39.6)	Poaceae, Asteraceae, Rubiaceae
Non-dormancy (ND)	497 (33.7)	Melastomataceae, Bromeliaceae, Bignoniaceae
Physical dormancy (PY)	257 (17.4)	Fabaceae, Malvaceae, Convolvulaceae
Morphophysiological dormancy (MPD)	104 (7.1)	Annonaceae, Arecaceae, Asteraceae
Combinational dormancy (PD + PY)	18 (1.2)	Fabaceae, Malvaceae
Morphological dormancy (MD)	13 (0.9)	Piperaceae, Amaryllidaceae, Arecaceae

Germination Responses to Abiotic Factors

Light

Among the 80 species analysed, Light Response Index (LRI) values were skewed towards 1, indicating predominantly light-stimulated germination (Fig. 4A). Nearly two-fifths had intermediate values (0.4 to 0.6), whereas only *Aristida riparia* Trin. and *Eriotheca pubescens* were classified as light-inhibited (LRI $\leq$ 0.4). Responses differed among families and growth forms: Melastomataceae and shrubs showed the strongest stimulation, Fabaceae and trees were predominantly light-indifferent, and Poaceae and herbs included both light-stimulated and light-indifferent species (Fig. 4B, C).

Despite widespread investigation of light availability, spectral quality was examined in only three studies involving 14 species. Their findings suggest that spectral responses vary substantially, even among ground-layer plants (Escobar & Cardoso, 2015; Pinheiro et al., 2022). Light quality may influence whether seeds detect canopy shade despite receiving some illumination, a response not captured by binary light–dark experiments. Changes in light quantity and spectral composition associated with different vegetation types and even woody encroachment could therefore alter regeneration opportunities, warranting further investigation (Pinheiro et al., 2022).

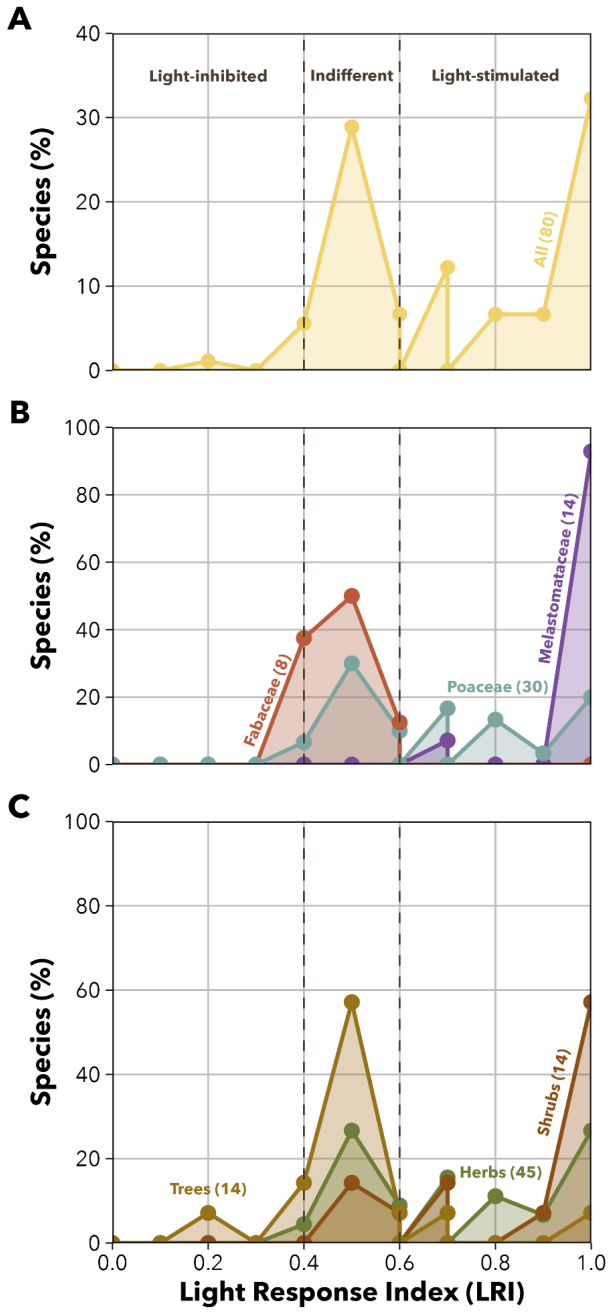


Fig. 4. Distribution of the Light Response Index (LRI) among Cerrado species. Relative-frequency distributions are shown for **A.** all species analysed, **B.** the three best-represented families in the LRI dataset—Poaceae, Melastomataceae and Fabaceae—and **C.** herbs, shrubs and trees. LRI values were grouped to the nearest 0.1 for visualisation, and points

represent the percentage of species assigned to each grouped value. Dashed vertical lines indicate the thresholds used to classify the original, ungrouped observations as light-inhibited (LRI ≤ 0.4), light-indifferent (0.4 < LRI < 0.6) or light-stimulated (LRI ≥ 0.6). Numbers in parentheses indicate the number of species represented in each distribution.

Temperature

Previous research has suggested that the optimum germination temperature of Cerrado species is around 30 °C (Brancalion, Novembre, & Rodrigues, 2010). In our analysis of 78 species, the highest germination under tested constant-temperature treatments occurred most often at 25 or 30 °C, encompassing nearly two-thirds of species (Fig. 5A). However, best-performing tested temperatures varied among families: 20 to 30 °C in Melastomataceae, predominantly 20 to 25 °C in Asteraceae, and 20 to 45 °C in Fabaceae, although most Fabaceae species peaked between 25 and 35 °C (Fig. 5B). More than half of herbaceous species reached their maximum at 30 °C, whereas shrubs and trees generally peaked at 25 to 30 °C (Fig. 5C).

Tropical species may germinate across broad thermal windows, but climate warming could increasingly expose seeds to temperatures near their upper limits (Sentinella et al., 2020). Thermal-time models can estimate germination temperature limits and heat requirements, but have rarely been applied to Cerrado species. In a study with 14 woody species, projections indicated comparatively greater vulnerability among species with non-dormant seeds and high thermal-time requirements, whereas widely distributed taxa were less vulnerable (Correa et al., 2021). Broader modelling across habitats and growth forms could improve our understanding of how temperature regulates germination in Cerrado species and our ability to predict how these responses may change under future climates.

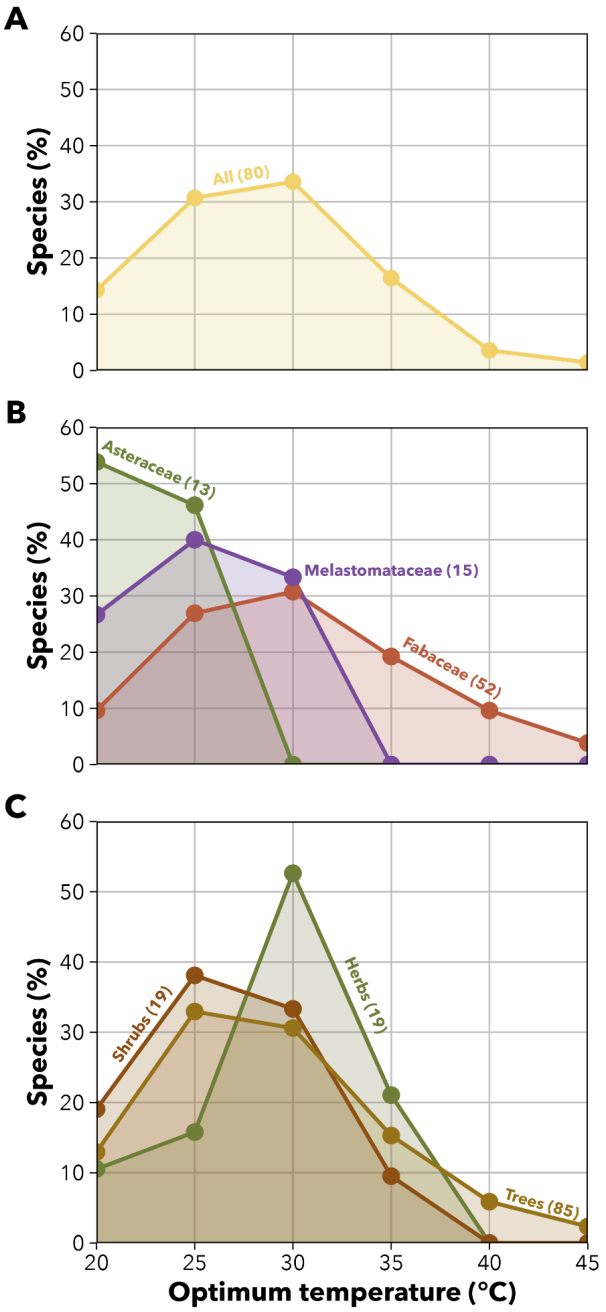


Fig. 5. Distribution of temperatures associated with maximum observed germination among the constant-temperature treatments evaluated for Cerrado species. Relative-frequency distributions are shown for **A.** all observations included in the analysis, **B.** the three best-represented families in the temperature dataset—Asteraceae, Melastomataceae and Fabaceae—and **C.** herbs, shrubs

and trees. Points represent the percentage of species whose highest germination occurred at each tested temperature. Connecting lines and shaded polygons are included to facilitate visual comparison across the discrete temperature treatments and do not imply estimates at intermediate temperatures. Numbers in parentheses indicate the sample size represented in each distribution.

Alternating temperatures may reflect daily fluctuations associated with soil depth and vegetation openness. Under the most frequently tested regime (30/20 °C), 36 of 58 species (62.0%) showed no statistically significant difference from within-study controls, while negative responses appeared more frequent with wider thermal amplitudes (Fig. 6). However, alternating temperatures can also alleviate physiological dormancy in grasses, so effects on dormancy release and subsequent germination performance should be distinguished (see *Seed Dormancy*).

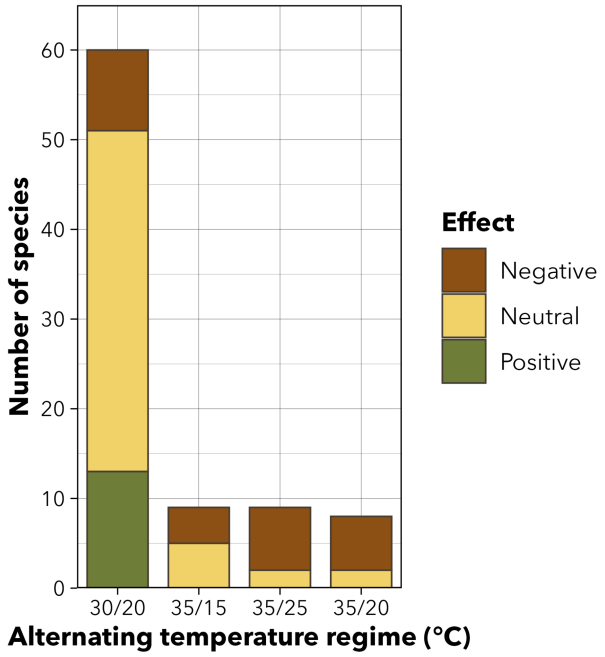


Fig. 6. Effects of alternating temperature regimes on the germination of Cerrado species. Stacked bars show the number of species exhibiting positive, neutral or negative germination responses

under the four most frequently evaluated alternating temperature regimes. Responses were classified by comparing germination under each alternating regime with the corresponding control treatment.

Fire-related cues

Fire-related cues are widely recognised as promoters of seed germination, particularly in Mediterranean-type vegetation (Pausas & Lamont, 2022). In the Cerrado, however, their role in regeneration from seed remains debated. Of 44 studies examining fire-related cues, 34 tested heat shocks (141 species), and half included only one or two species. The two broadest multispecies studies revealed remarkably similar patterns. Among 46 legumes from Cerrado savannas and seasonal forests, heat-shock effects were neutral in 64 to 93% of species, depending on the treatment, whereas positive responses occurred in fewer than 10% of species exposed to 100 °C for 3 min or 200 °C for 1 min (Daibes et al., 2019). Similarly, across 26 graminoid, forb, and shrub species from an open savanna community, neutral responses occurred in 42 to 88% of species, while positive effects were detected in no more than 15% (Zupo et al., 2021). In both studies, negative responses increased with treatment severity, particularly at 200 °C. Experimental heat shocks do not necessarily reproduce natural fire conditions: Cerrado fires spread rapidly and temperatures above 100 °C may persist at the soil surface for only 2 to 3 min and rarely exceed 100 °C at 1 cm depth (Zupo et al., 2022).

Thus, heat shocks do not appear to be a general dormancy-breaking or germination-promoting cue in the Cerrado. Responses, nevertheless, depend on seed traits. In legumes, survival under high temperatures was associated with seed mass and physical dormancy, whose water-impermeable seed coats may provide thermal protection (L. C. Ribeiro

et al., 2015; Daibes et al., 2019). The limited role of direct heat is also consistent with the importance of resprouting and post-fire flowering in open Cerrado vegetation (Fidelis & Zirondi, 2021; Pilon et al., 2021; Zirondi, Ooi, & Fidelis, 2021; Zupo et al., 2021). Consequently, regeneration may depend more strongly on post-fire conditions, including temperature fluctuations and cues derived from charred wood, ash and smoke.

Smoke-related cues can reach seeds through airborne smoke or smoke-derived compounds entering the soil (Nelson et al., 2012). Only eight laboratory studies, in which seeds were exposed to smoke-related treatments using fumigation (Sanchez et al., 2022), aqueous infusions of burned material (Fichino et al., 2016), or smoke extracts (Ramos et al., 2019; Motta et al., 2024). Some treatments increased germination percentage or speed, or seedling growth, particularly in Poaceae, Velloziaceae and Xyridaceae (Ramos et al., 2019; Zirondi et al., 2019; Motta et al., 2024). However, responses varied across treatment methods and concentrations and may depend on storage duration, temperature and water availability (Reinke, 2025; Cruz-Júnior et al., 2026; Zirondi et al., 2026), revealing potentially important interactions with environmental conditions that remain largely unexplored. Overall, fire-related cues appear to stimulate germination in only a limited subset of Cerrado species, whereas severe heat is often detrimental and the importance of smoke remains unresolved because of restricted taxonomic coverage and substantial methodological heterogeneity.

Water

Of the 33 studies addressing water availability, nearly all were conducted under laboratory or greenhouse conditions, and 75.8% involved woody species. Research on the effects of water on seed germination was evenly distributed: nine studies addressed water-deficit stress,

seven addressed flooding, and eight addressed seed desiccation. . Most of the studies about water-deficit stress used polyethylene glycol 6000 to simulate osmotic potentials between −0.2 and −1.6 MPa. Some woody species, particularly Fabaceae, maintained 30 to 80% germination at −0.4 MPa, with a subset exceeding 30% at −0.8 or −1.0 MPa (Perez, Fanti, & Casali, 2001). Among grasses, wetland species generally germinated more than dryland species at −0.8 MPa, although both groups declined sharply at −1.0 MPa (Souza et al., 2022). Post-stress recovery, however, remains poorly studied, limiting our understanding of whether seeds that fail to germinate during drought resume germination after rehydration.

Flooding similarly revealed habitat-dependent responses. Species from seasonally flooded environments, including gallery forests and *veredas*, generally tolerated waterlogging and submergence better than those from well-drained savannas (Porto, Nunes, & Ribeiro, 2018; J. W. F. Ribeiro, Gonçalo, & Kolb, 2021; J. W. F. Ribeiro, Luscenti, & Kolb, 2025). Seeds of *Mauritia flexuosa* L.f. (Arecaceae), for example, remained viable underwater for more than 180 days, forming a temporary seed bank from which germination occurred after water receded (Porto, Nunes, & Ribeiro, 2018). By contrast, scarified seeds of dryland Fabaceae lost viability after 15 days of submergence (J. W. F. Ribeiro, Gonçalo, & Kolb, 2021).

Desiccation tolerance seems to depend on phylogeny and habitat, as some Caryocaraceae and Fabaceae tolerated drying to a 5 to 10% seed moisture content, whereas certain species from humid environments were less tolerant. For example, *Hancornia speciosa* Gomes (Apocynaceae) lost viability when dried below 20% moisture content (Masetto & Scalon, 2014), whereas *Alibertia edulis* (Rich.) A.Rich. tolerated drying to 15% but not to 10% (Cremon et al., 2018). Nonetheless, the number of studied species is too limited to reach a definitive conclusion.

Tolerance also varied with provenance, drying rate, and germination stage (W. V. S. Pereira et al., 2017). Such variation might explain differences in persistence and regeneration niches.

Across abiotic factors, limited field validation and few studies testing cue interactions or recovery after stress constrain predictions of germination under natural seasonal conditions. Combining controlled experiments with seasonal field observations would help establish how these responses influence seed fate and subsequent recruitment.

Biotic Interactions

Interactions between seeds and other organisms were among the least studied dimensions of Cerrado seed ecology. Most studies addressed seed predation (26 studies), whereas interactions with microorganisms and allelopathy were examined in only six and four studies, respectively.

The main pre-dispersal seed predators in the Cerrado include insects (Hymenoptera, Lepidoptera and Coleoptera), birds, and rodents (Uchôa et al., 2012; Christianini, 2017; Sousa-Lopes et al., 2019). Within species, predation has been associated with density dependence, crop size, seed mass, and seed hardness, although these factors did not consistently predict losses across communities (Christianini, 2017). Pre-dispersal losses are often limited, whereas post-dispersal predation, particularly by ants, can represent a major recruitment bottleneck influenced by seed mass, species identity, and vegetation type (Ferreira, Bruna, & Vasconcelos, 2011; Costa, Vasconcelos, & Bruna, 2017), and may explain why some tree species occur at relatively low densities in Cerrado communities (Salazar et al., 2012).

Research on seed–microorganism interactions is recent, with most studies published since 2018. Cerrado seeds harbour diverse microbiota capable of facilitating or constraining regeneration (Magalhães et al., 2008; P. R. R. Santos et al., 2022). *Bacillus* bacteria can inhibit seed-decomposing fungi and promote germination under environmental stress (J. S. Santos et al., 2020; J. C. Oliveira et al., 2021). By contrast, endophytic fungi isolated from *Copaifera oblongifolia* Mart. ex Hayne leaves reduced the germination and establishment of conspecific seeds and seedlings (P. S. Silva et al., 2023).

Allelopathic effects remain similarly underexplored. Although Cerrado plant extracts have been tested on model species (Marchi et al., 2017), only four studies evaluated effects on species occurring in the biome. Extracts from native plants had no effect on other native woody species but reduced germination of the invasive grass *Megathyrsus maximus* (Jacq.) B.K.Simon & S.W.L.Jacobs (Hernández-Terrones et al., 2007; El Id, Braga, & Junior, 2020). In contrast, seeds or extracts of the invasive grasses *Urochloa decumbens* and *Arundo donax* L. reduced germination of both native and invasive species, suggesting that chemically mediated effects may contribute to their competitive advantage (Gorgone-Barbosa, Pivello, & Meirelles, 2008; Girotto et al., 2021).

Overall, current evidence is dominated by seed predation, while microbial, allelopathic, and multitrophic interactions remain poorly understood. Future studies should move beyond isolated laboratory assays and test how these interactions vary across vegetation types, seasons, and disturbance regimes, particularly during the transition from seed persistence to seedling establishment.

Applied Aspects

Applied seed research was the second most frequently studied topic (110 studies), with most (83.9%) publications appearing since 2010. Three prominent themes emerged: seedling production (40 studies, 53 species), seed-based restoration (18 studies, 160 species), and ex situ seed conservation (35 studies, 44 species).

Seedling production

Studies focused on tree propagation under greenhouse and in vitro conditions, whereas research on shrubs and herbs often examined in vitro protocols, particularly for orchids. Given the slow growth of many Cerrado plants under seasonal water and nutrient constraints, studies also tested ways to improve propagation. Water-retaining polymers partially substituted for continuous irrigation in *Anacardium humile* A.St.-Hil. (Anacardiaceae) (Soares et al., 2020), whereas mineral fertilisation had species-dependent effects (Massi, 2015; A. C. C. Oliveira, Forti, & Viani, 2022), and seed priming also accelerated or increased germination in some greenhouse experiments (Mota, Scalon, & Mussury, 2012; Scalon, Mota, & Mussury, 2013).

Seed sourcing and processing remain understudied despite their importance for propagation and restoration (Erickson & Halford, 2020; Frischie et al., 2020). Studies focused on trees and documented considerable variation within and among populations (Leão, Peixoto, & Morais Júnior, 2012; Dorneles, Ranal, & Santana, 2013; Moura et al., 2013; Filho et al., 2014), highlighting the need for careful source selection. Yet, comparable information is still missing for other growth forms, limiting source recommendations for diverse restoration assemblages.

Seed-based restoration

Direct seeding is increasingly used to restore grasslands and savannas and has successfully reintroduced native Cerrado species and increased vegetation cover during early restoration (R. R. P. Silva et al., 2015; Pellizzaro et al., 2017; Sampaio et al., 2019; Wiederhecker et al., 2024). However, only 18 studies addressed seed-based restoration: 12 monitored establishment after direct seeding, five evaluated seed-enhancement treatments, and one investigated sowing methods.

Restoration outcomes were typically evaluated using species richness, abundance, vegetation cover, survival and growth (Martins, Leite, & Haridasan, 2001; R. R. P. Silva et al., 2015; Sampaio et al., 2019; Passaretti, Pilon, & Durigan, 2020). Yet only three studies explicitly examined relationships between seed traits and field establishment, two reporting positive associations between seed mass and seedling density or survival (S. R. Pereira, Laura, & Souza, 2013; Passaretti, Pilon, & Durigan, 2020). None tested whether interspecific differences in germinability predicted field establishment, despite considerable variation among Cerrado taxa (Zaidan & Carreira, 2008; L. V. Santos et al., 2025). Addressing this gap could improve predictions of restoration outcomes based on the seed traits and germination performance of the species sown.

Seed-enhancement effects differed between controlled and field conditions. Hydropriming accelerated greenhouse germination but reduced field emergence (Laumann et al., 2023); scarification accelerated germination but had variable emergence effects and increased processing costs (S. R. Pereira, Laura, & Souza, 2013; Correia et al., 2022). Coating approaches produced mixed results as well: pelleting had no detectable effect on germination or seedling

development, whereas biodegradable multispecies agglomerates improved germination relative to untreated seeds (Montanhim et al., 2014; Lopes et al., 2025). Only one study investigated sowing techniques directly and found that seed burial and straw mulching had species-specific effects on emergence associated with seed shape (R. R. P. Silva & Vieira, 2017). While seed-enhancement techniques show promise for some Cerrado species, their ecological and economic benefits still need to be evaluated under field conditions.

We identified two further gaps in the germination literature relevant to ecological restoration. First, only three restoration studies included grasses, none of which explicitly quantified their germination or emergence (Martins, Leite, & Haridasan, 2001; Pellizzaro et al., 2017; Sampaio et al., 2019). This reflects the disproportionate emphasis on woody species in the restoration of tropical open ecosystems (Medeiros, Buisson, & Silveira, 2025), but might also be due to several Cerrado exhibiting low percentages and seed lots often contain high proportions of empty or non-viable seeds (see *Seed Viability*). Seed-enhancement techniques could potentially improve grass establishment and facilitate the restoration of open vegetation, but our survey recovered no studies directly testing this possibility.

Second, none of the 18 restoration studies assessed intraspecific germination variation. Population origin, seed fill, viability, dormancy and storage history may influence seed-lot performance, yet routine quality testing can be constrained by cost and logistics. Comparing seed quality across populations and storage periods could improve sowing decisions.

Ex situ seed conservation

Thirty-five studies covered 44 species from 32 genera and 14 families, with Poaceae being the best-represented family (18 species, 40.9%). Conventional storage was investigated in

21 studies, desiccation tolerance in ten, and cryopreservation in seven. Seed performance was generally assessed through germination, occasionally supplemented by timing or speed metrics. Storage outcomes varied: some species maintained germination, others declined, and some increased germination as dormancy was alleviated (A. K. M. Oliveira, Schleder, & Favero, 2006; Aires, Sato, & Miranda, 2014; Jeromini et al., 2015; Esteves et al., 2022; Bonamigo, Masetto, & Scalon, 2024; Pinto et al., 2025). Overall, responses depended on storage temperature, seed moisture content, container type, and duration, reinforcing the need for species-specific protocols.

Desiccation sensitivity limits conventional storage for some species, while cryopreservation may provide alternatives if seed moisture, cryoprotectants, freezing and thawing are optimised (Suzuki et al., 2018; Barbosa et al., 2019; Frugeri et al., 2023). However, most studies sampled only one population, and much of the apparent herbaceous coverage derived from one study with 18 Poaceae species (Aires, Sato, & Miranda, 2014). Other herbs, palms, and lianas were underrepresented, and only six studies examined storage beyond one year. Longer-term, population-replicated experiments are needed for germplasm banking.

Overall, applied seed research remains poorly integrated across collection, storage, propagation and field establishment. Linking provenance, seed quality, dormancy, storage behaviour and enhancement treatments to restoration outcomes could translate ecological knowledge into more effective conservation and restoration strategies.

Future Perspectives

Despite growing research on Cerrado seed ecology, evidence remains uneven across taxa, regions, environmental factors and regeneration stages. In particular, limited integration of seed

quality, dormancy, persistence, germination, and establishment constrains ecological inference and practical application. Accordingly, we propose five priorities for developing a more representative, mechanistic, and applicable understanding of seed ecology across the Cerrado.

1. Expand research across underrepresented taxa, regions, and vegetation types. Research effort is concentrated on a relatively small set of families, woody species, and in the central and southern portions of the biome. Moreover, several vegetation types remain poorly represented. Future sampling should therefore target these taxonomic, functional, geographical, and physiognomic gaps. Coordinated multispecies studies across contrasting vegetation types would help distinguish Cerrado-wide patterns from lineage-, region-, and habitat-specific responses.

2. Close the seed-regeneration loop. More than half of the species were studied within a single research topic, and only 24 studies combined laboratory and field components. Tracking identified populations and seed lots across successive early life-cycle stages, from seed production and dispersal to soil seed persistence, germination, emergence, and seedling establishment, could reveal where recruitment is most strongly constrained. Incorporating seed predation, microbial interactions, and seasonal seed-bank dynamics would help distinguish limitations imposed by seed supply, seed quality, environmental conditions, and seedling mortality.

3. Move from isolated cues to realistic environmental interactions. More than half of species assessed for germination cues were investigated under only one of the five focal factors, despite seeds experiencing a combination of changing light, temperature, moisture and fire-related conditions. Factorial experiments linked to seasonal field observations could identify

interactions controlling dormancy release and germination. Thermal-time and hydrothermal-time models, validated against field microclimates, could improve predictions under climate change. Once sufficiently comparable studies become available, meta-analyses could quantify the magnitude and consistency of germination responses.

4. Place intraspecific variation and seed provenance at the centre of seed ecology. Most ex situ conservation studies relied on single populations, and no seed-based restoration study explicitly assessed intraspecific variation in germination. Comparing seed lots among populations, maternal plants, collection years, and storage periods could establish how viability, dormancy, germination thresholds, and storage behaviour vary across climatic and edaphic gradients. Assessing whether these differences reflect local adaptation or phenotypic plasticity would strengthen ecological inference and guide seed sourcing for conservation, propagation, and restoration.

5. Translate seed ecological knowledge into conservation and restoration decisions. Few restoration studies have linked seed traits to establishment success, making it difficult to determine whether germinability, dormancy or enhancement treatments predict field performance. Integrated trials should link provenance, seed quality, storage behaviour, and germination requirements to emergence, survival, and cost-effectiveness, especially for native grasses and other underrepresented herbs. Long-term storage experiments and collaboration with germplasm banks, restoration practitioners, and community seed networks could turn species-specific findings into useful conservation and restoration protocols.

Conclusions

This scoping review reveals rapidly expanding but uneven knowledge of Cerrado seed ecology, concentrated in particular taxa, regions and research topics. Viability varied widely, while community soil seed banks were dominated by herbs and showed pronounced seasonal dynamics; evidence for long-term persistence remains limited. Database-derived classifications indicate that dormancy is widespread, particularly physiological and physical dormancy, but direct Cerrado-specific evidence is scarce and the cues regulating dormancy release remain unclear.

Germination responses varied across species, traits, and habitats. Light generally stimulated germination, especially in Melastomataceae and shrubs, whereas Fabaceae and trees were more often light-indifferent. Among the constant temperatures tested, germination most frequently peaked at 25 or 30 °C, although responses varied among taxa. Alternating temperatures had mixed effects, while heat shocks rarely enhanced germination and became increasingly detrimental under severe treatments. Smoke responses remain poorly resolved, and tolerance of water deficit, flooding and desiccation depended on habitat and seed characteristics.

Research on biotic interactions remains dominated by seed predation, with comparatively little evidence on microbial and allelopathic effects. Applied studies have advanced propagation, restoration and ex situ conservation, yet links between seed quality, germination and field establishment are rarely tested. Progress will require coordinated studies spanning populations, vegetation types and regeneration stages, combining controlled experiments with field observations. Such integration is essential for translating seed ecological knowledge into reliable conservation and restoration strategies across the Cerrado.

Data Availability

The data and code for the figures and analyses will be available on GitHub (https://github.com/caordonezparra/cerrado_germination_ecology) upon acceptance.

Declarations

Competing interests. The authors have no competing interests to declare that are relevant to the content of this article.

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Generative AI and AI-assisted technologies in the writing process. ChatGPT (GPT-5.5) was used for language editing of the text written by the authors, including grammar, clarity and readability; not to generate original scientific content, analyses or interpretations. The authors reviewed all edited text and remain fully responsible for the content of the manuscript.

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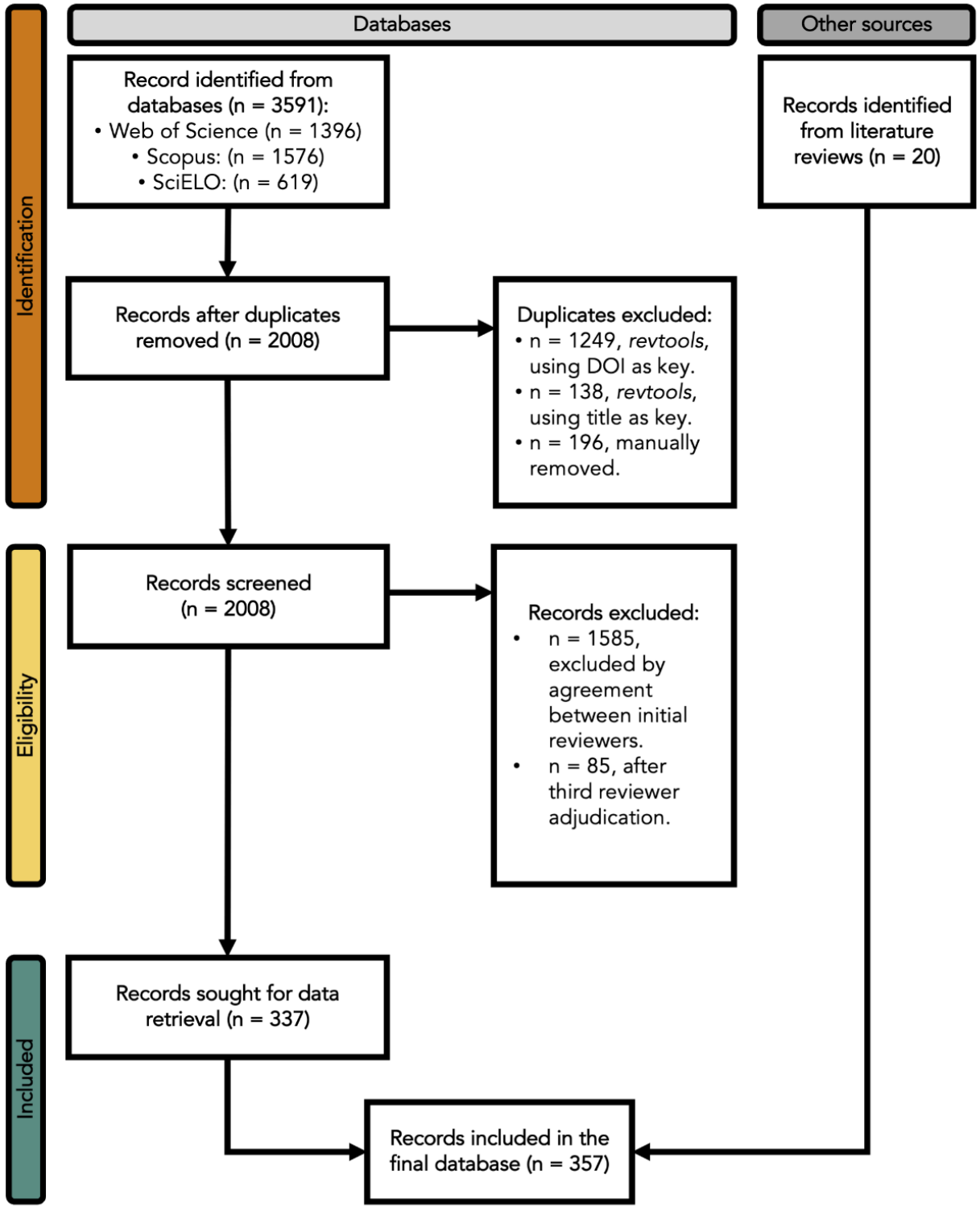
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Supplementary Material

Suppl. Material 1. PRISMA flowchart showing the literature search and screening process used to construct the study database. **Suppl. Material 2.** Representation of vegetation types in the Cerrado seed ecology dataset, showing the number and proportion of species and studies associated with each vegetation type. Percentages were calculated relative to the subset of studies that reported vegetation type and the species recorded within that subset.



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Vegetation type	Species, n (%)	Studies, n (%)
Natural physiognomies		
Cerrado sensu stricto (wooded savanna)	237 (51.4)	47 (29.0)
Campo sujo (shrubby grassland)	210 (45.6)	25 (15.4)
Campo úmido (wet grassland)	70 (15.2)	15 (9.3)
Cerradão (closed-canopy woodland)	46 (10.0)	13 (8.0)
Campo limpo (open grassland)	35 (7.6)	7 (4.3)
Mata de galeria (gallery forest)	28 (6.1)	10 (6.2)
Cerrado denso (dense wooded savanna)	23 (5.0)	2 (1.2)
Floresta estacional semidecidual (seasonal semideciduous forest)	16 (3.5)	5 (3.0)
Ecotone (transition zone)	12 (2.6)	10 (6.2)
Cerrado rupestre (rocky savanna)	5 (1.1)	5 (3.1)
Vereda (palm swamp)	5 (1.1)	9 (5.6)
Capões (forest patches)	3 (0.7)	1 (0.6)
Human-modified environment		
Degraded area	217 (47.1)	48 (29.6)