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EDITED BY

Jasper A. Slingsby,
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South Africa

REVIEWED BY

Stefan Siebert,
North-West University,
South Africa
César Marín,
Santo Tomás University,
Chile

*CORRESPONDENCE

Mateus C. Silva
ms1190@exeter.ac.uk

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Toward diverse seed sourcing to upscale ecological restoration in the Brazilian *Cerrado*

Mateus C. Silva ^{1*}, Peter Moonlight ², Rafael S. Oliveira ³,
R. Toby Pennington ^{1,2} and Lucy Rowland ¹

¹Department of Geography, College of Life and Environmental Sciences, University of Exeter, Exeter, United Kingdom, ²Tropical Diversity Section, Royal Botanic Garden Edinburgh, Edinburgh, United Kingdom, ³Department of Plant Biology, Institute of Biology, University of Campinas, Campinas, Brazil

Seed markets are vital to scaling up ecosystem restoration in the Brazilian *Cerrado*, home of the world's most species-rich grasslands and savannas. We compiled lists of species traded by four major *Cerrado* seed supply systems to investigate the representativeness of the species currently available for seed-based restoration. We also identified whether dominant ground-layer species are being sourced for seed production. Seeds from 263 *Cerrado* species can be purchased for restoration, of which 68% are trees, particularly legumes (24%). 63% of the traded species were found in only one seed supply system. The five most dominant graminoids of the *Cerrado* ground layer were available for sale, but two additional species uncommon in old-growth areas represented 44% of the sales of a key seed trader in Central Brazil. The expansion of *Cerrado* seed supply systems should be supported to further increase the number of species on the market. Sourcing seeds from a diversity of herbaceous species is central to facilitating the restoration of species-rich grasslands and savannas in the *Cerrado*. Recovering the diversity and functioning of old-growth open ecosystems through seeds will depend on increasing the supply and demand for species typical of *Cerrado*'s ground layer.

KEYWORDS

ecosystem restoration, restoration planning, community-based seed production, old-growth savannas, tropical grassy biomes, open ecosystems

Introduction

Ecological restoration is central to tackling biodiversity loss and securing ecosystem services across the globe (Suding, 2011). Seeds provide a prominent avenue for recovering vegetation composition and functioning after degradation (Pedrini and Dixon, 2020). Seeds of native species can be sustainably collected from wild populations (Pedrini et al., 2020) and used to establish target species in restoration projects, easing dispersal limitations that may constrain natural regeneration (Shaw et al., 2020). Importantly, seed sowing can be more cost-effective than other restoration methods such as planting seedlings (Palma

and Laurance, 2015; Raupp et al., 2020). Upscaling restoration efforts may depend on the number and identity of species available on the seed market, as well as the seed provenance, quality, and quantity (León-Lobos et al., 2020; Nef et al., 2021). A market that sources seeds from a diverse set of species spread across numerous locations can allow practitioners to choose a range of locally adapted species and genotypes for restoration projects (Erickson and Halford, 2020). Furthermore, seed markets should ideally cover a comprehensive variety of life forms and evolutionary lineages to foster the restoration of functionally and phylogenetically diverse ecosystems (Fremout et al., 2022). Finally, when the goal is to restore the ecosystem to resemble surrounding old-growth vegetation, it is essential to source seeds of species typical of old-growth areas.

Ecological restoration is of particular importance in Brazil. Brazil is home to almost 34,000 flowering plant species (Reflora, 2020). Yet, land-use changes have led to a loss of about one-third of Brazil's native vegetation (Mapbiomas, 2021), putting this diversity under threat. Up to 19 million hectares of private land are required by law to be restored in Brazil, with deadlines varying by State (Guidotti et al., 2017). Additionally, Brazil's government has committed to restoring 12 million hectares by 2030 (MMA, 2017). Seed supply systems for native species have emerged as a key strategy to achieve these national restoration targets (Urzedo et al., 2022). These systems consist mainly of cooperatives, including indigenous populations, which harvest, store, process, and sell the seeds. Seed markets provide income to local communities, supporting their livelihoods and the sustainable use of their lands (Schmidt et al., 2019). Brazil's seed market will need to increase its seed sourcing capacity 6- to 30-times to achieve the 12 million hectare goal (Urzedo et al., 2020). Therefore, it is fundamentally important to design strategies to expand Brazilian seed supply systems before the end of this decade (2030).

The Brazilian *Cerrado* is a global biodiversity hotspot dominated by open ecosystems (i.e., grasslands and savannas; Myers et al., 2000). About 17–31% of Brazil's restoration projects are expected to take place in the *Cerrado*. However, relative to the Atlantic Forest, another Brazilian biodiversity hotspot, restoration in the *Cerrado* is still in its infancy in terms of restored area and methodologies (see Pinto et al., 2014; Crouzeilles et al., 2019). Targeted and strategic expansion of restoration infrastructure is essential to meet *Cerrado* restoration ambitions (Strassburg et al., 2017), which range from two to 6 million hectares (Guidotti et al., 2017; MMA, 2017). Three factors will be key to this expansion. First, more than 12,000 plant species are found in the *Cerrado* (Zappi et al., 2015), and their distribution is often regionalized (Bridgewater et al., 2004; Françoso et al., 2020), so seed sourcing needs to take place throughout the *Cerrado* to represent this remarkable plant diversity. Second, savannas and grasslands cover about 70% of the *Cerrado* region (Mapbiomas, 2021), with herbaceous plants being the dominant life form. Supplying a diversity of herbaceous species will, consequently, be essential to restoring species-rich open ecosystems (Buisson et al., 2021). Third, it is unclear whether the dominant species characteristic of

old-growth grasslands and savannas are available on the seed market, especially from the ground layer (i.e., vegetation strata composed of graminoids, forbs, and shrubs).

We aimed to assess how well the current seed market represents the diversity of the Brazilian *Cerrado* flora. We used this information to evaluate what the limits of the seed market may be and how this growing market can be expanded strategically. We focused on the four seed supply systems representing the main seed traders for restoration in the *Cerrado* (Caminhos da Semente, 2020): *Rede de Sementes do Xingu* (RSX), *Rede de Sementes do Cerrado* (RSC), *VerdeNovo* (VN), and *Restauradores da RDS Nascentes Geraizeiras* (RDS). We gathered data on the approximate location of seed collection and species on sale per system. This data was contrasted with estimates of species richness at the *Cerrado* scale. Additionally, we gathered ground layer vegetation survey data from the literature to identify its dominant species. We compared the species dominance rank with the 2017–2019 sales record of the RSC, the oldest and largest seed supplier of *Cerrado* species exclusively. We addressed the following questions.

1. How similar is the flora traded by different seed supply systems?
2. How are life forms and plant families represented in the systems?
3. Are dominant ground-layer species from old-growth open ecosystems available on the seed market?

Materials and methods

Seed harvesting sites

We mapped the centroid of the municipalities where the seed supply systems are active (Supplementary Table 1). The municipalities were obtained from the RSX website (6° *Boletim*, p. 2)¹ and by directly contacting personnel from the RSC, VN, and RDS supply systems. We calculated the centroid of each municipality polygon using the function “st_centroid” from the package “sf” (Pebesma, 2018) on R version 4.1.2 (R Core Team, 2021). We displayed the municipality centroids alongside the *Cerrado* floristic regionalization map proposed by Françoso et al. (2020). The map depicts areas sharing a similar set of woody species, termed here as “biogeographical districts.”

Species richness

We accessed the species list of each seed supply system by directly contacting them (VN and RDS) or through their websites

1 <https://www.sementesdoxingu.org.br/biblioteca>

(RSX and RSC; [Supplementary Table 2](#)). The lists consisted of the species on sale for the first half of 2021. We used the R package “flora” ([Carvalho, 2020](#)) to standardize species’ accepted names and check their endemism and threatening status according to the Brazilian Flora 2020 checklist (version 393.291). We filtered the species that occur in the *Cerrado* region (263 of 305 species) as the RSX system is in the transitional zone between the *Cerrado* and Amazon. Additionally, we checked whether the species turnover between the systems might be a result of their distance. For that, we used the function “st_distance” from the R package “sf” to calculate the minimum geographical distance between each pair of systems ([Karney, 2013](#)). We also investigated whether the species richness of a given system might be a function of its age. The year of creation of each seed supply system was confirmed on their websites (RSX: <https://www.sementesdoxingu.org.br/>, RSC: <https://www.rsc.org.br/>, VN: <https://consultoriaverdenovo.weebly.com/>) and by contacting their staff (RDS).

Life forms and families

Species were grouped both by life form (tree, palm, liana, shrub, subshrub, forb, and graminoid) and botanical family, according to the Brazilian Flora 2020 checklist, which follows the APG IV ([Flora do Brasil, 2020](#)). Brazilian Flora 2020 checklist life form classification is based on the notes from herbarium collections. We considered graminoid all the herbaceous species belonging to the Poaceae (grasses), Cyperaceae (sedges), and Juncaceae (rushes) families. All the non-graminoid herbaceous species were assigned to the forb life form. We used the Brazilian Flora 2020 online platform² to access the number of species per life form and family over the whole *Cerrado* region. We standardized the number of species per life form and family by the total number of species available on the seed supply systems and recorded in the *Cerrado*. The standardized (std.) species richness varied from 0 to 1. We then determined a metric of representativeness by calculating the difference between the std. species richness over the *Cerrado* region and the std. species richness within the seed supply systems for each life form and botanical family. We repeated the analysis within each seed supply system to verify whether the representation biases toward life forms or families were widespread among the systems.

Ground-layer dominant species

We searched for “Cerrado” and “Herbáceo” (“herbaceous” in Portuguese), in the Brazilian National Thesis and Dissertations repository (217 publications). We also searched for “Cerrado” and “Herbaceous” on the Web of Science (166 publications). We selected all the publications that included ground layer life

forms (i.e., graminoid, forb, and shrub) and displayed a table with either plant cover or density at the species level (39 publications). We only considered data from old-growth ecosystems. We analyzed different study sites separately when the publication made that distinction. In the case of time series, we selected the data from the most recent time interval. When two or more publications used the same data set, we retained the latest publication to include the most updated and revised data. Since our focus was on open ecosystems, we removed data from the ground layer of closed-canopy ecosystems (e.g., gallery forests, woody encroached savannas; four study sites). We ended up with 66 study sites from 25 publications ([Supplementary Table 3](#)). We standardized the species name and removed all tree and liana species based on the [Flora do Brasil \(2020\)](#). We calculated the abundance index of each species in each study site by dividing their cover or density value by the total value across all species for the whole site. The abundance index varies from 0 to 1, with an index of 1 representing a monodominant species and 0 if the species was absent from the study site. We, thus, averaged the abundance indices at the species level. We calculated the relative frequency by dividing the number of study sites where a given species was found by the total number of sites. Finally, we calculated the importance value index (IVI) by averaging the abundance index and relative frequency ([Munhoz and Araújo, 2011](#)). IVIs closer to 1 mean species that occur in several sites and are abundant wherever they occur and hence are dominant. IVI was chosen to flag dominant species as it balances local abundance and regional commonness. We emphasize that IVI may not capture the importance of some species, such as ecosystem engineering or others with strong legacy effects. However, IVI is still useful to pinpoint species most characteristic of reference ecosystems, which is the goal of this study.

Rede de Sementes do Cerrado sales record

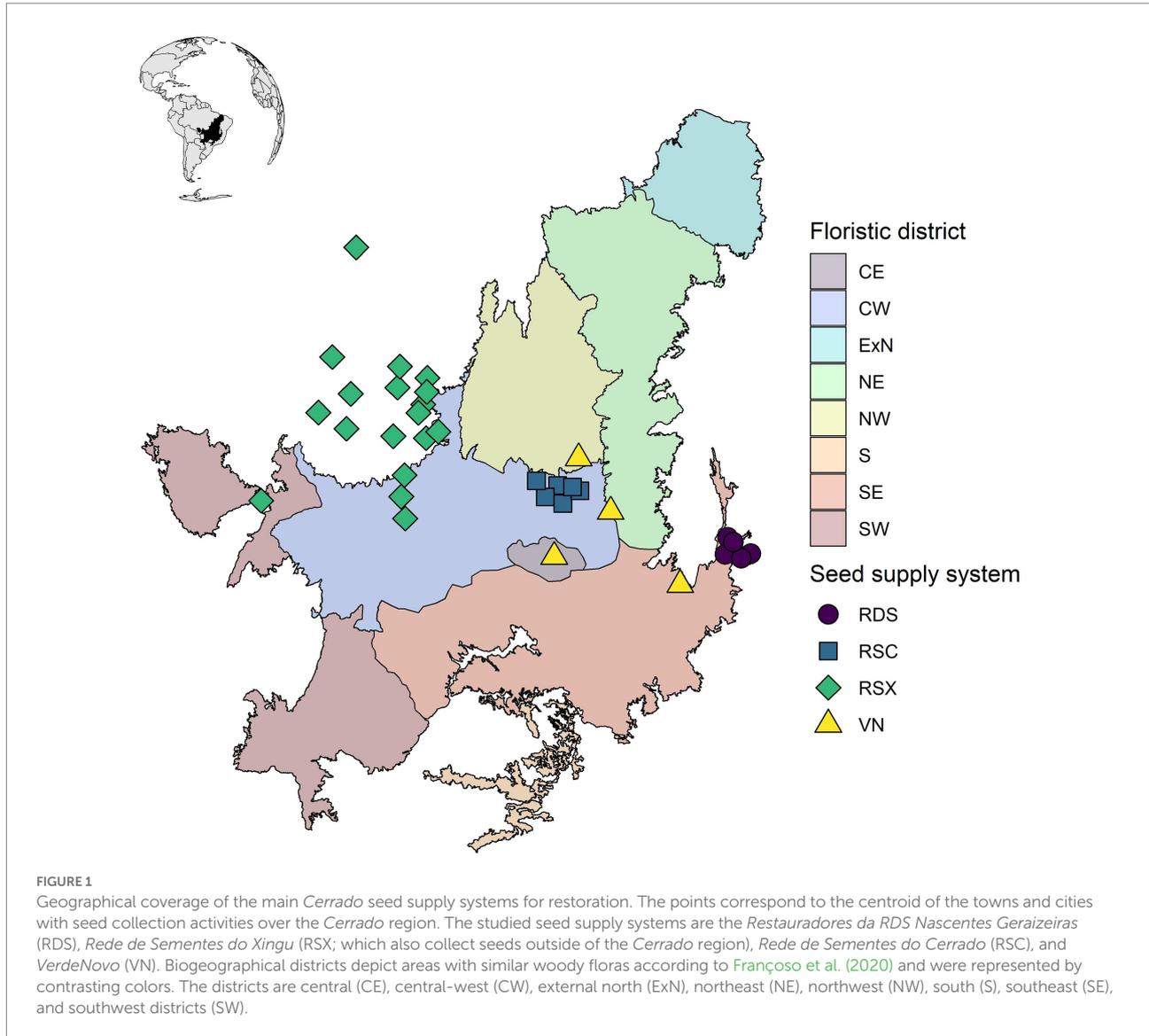
We obtained the total mass of seeds traded by the RSC in the period from 2017 to 2019 by directly contacting their personnel. Only ground-layer species were kept following the procedure mentioned in “Ground-layer dominant species.”

Results

Geographic distribution of seed sourcing

The seed supply systems are located approximately from 9°S to 16°S ([Figure 1](#)). RSX was the biggest seed supply system in terms of the number of municipalities (18), followed by RSC (6), RDS (5), and VN (4). The current extension of the four seed supply systems provided a good representation of the *Cerrado* central-west biogeographical district (6 RSC sites, 5 RSX sites) and the north of the southwest district (4 RDS sites, 1 VN site).

² <http://floradobrasil.jbrj.gov.br/>



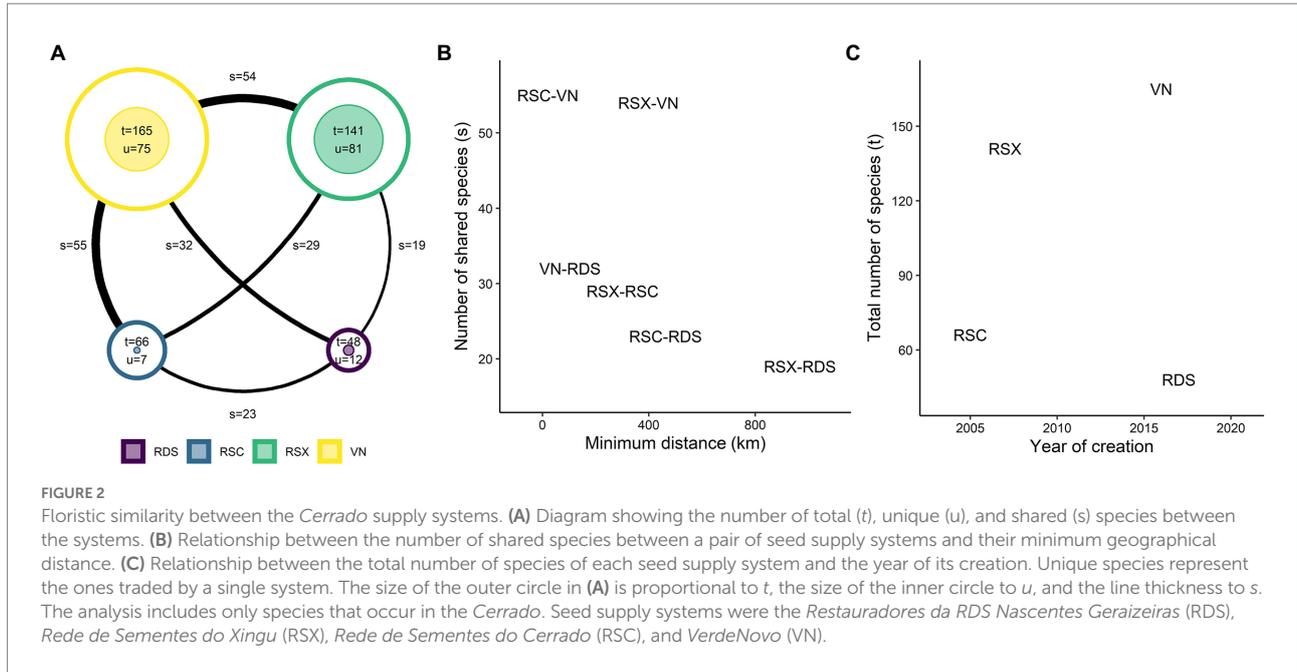
Floristic relationships

A total of 263 species were made available for restoration by the seed supply systems (Figure 2A). 12% of the traded species were endemic to the Cerrado (33 species). Regarding the conservation status of the traded species, one species was classified as endangered, five as vulnerable, four as near threatened, 40 as least concern, one as data deficient, and 212 were not evaluated. Only 13 out of 263 species (~4%) were sourced by all four systems. 167 species were found only in one system (i.e., unique species), representing around 63% of all traded species. The percentage of unique species per system ranged from 57 to 10% in the RSX and RSC systems, respectively. The VN system offered the greatest number of *Cerrado* species (165), followed by RSX (141), RSC (66), and RDS (48) systems. The number of shared species achieved its maximum (55) between the geographically closest

systems (RSC and VN) and minimum (19) between the systems farthest apart (RSX and RDS; Figure 2B). RSC was the oldest system (2005), followed by RSX (2007), VN (2016), and RDS (2017). The VN and RDS traded the highest and lowest *Cerrado* species richness, respectively, even though they were created in a similar period, 2016 and 2017, respectively (Figure 2C).

Representativeness of life forms and families

Trees were the best-represented life form in the seed supply systems, while forbs were the worst according to the Brazilian Flora 2020 checklist (Figure 3A). 68% of all traded species were trees, though only 14% of the *Cerrado* flora belonged to this life form (1,761 species). In contrast, 32% of *Cerrado* flowering plants



were forbs (3,948 species), but they represented just 3% of all traded species. Fabaceae (legumes) was the best represented of the 60 traded families (Figure 3B). Legumes accounted for 9% of the total *Cerrado* flora and 24% of the traded seed flora. No orchid species were traded, yet the Orchidaceae represented 5% of the *Cerrado* flowering plants. These patterns remained qualitatively similar when each seed supply system was analyzed separately (Figures 3C,D). All four systems had a good representation of trees and legumes and a lack of representation of forbs and orchids.

Dominant ground-layer species on the market

The seed supply systems traded 7 out of the 15 ground-layer species with the greatest Importance Value Index (IVI) among 66 *Cerrado* savanna sites (Figures 4A,B; Supplementary Table 4). The top five species in terms of IVI—*Trachypogon spicatus* (IVI of 0.29), *Echinolaena inflexa* (0.28), *Lagenocarpus rigidus* (0.26), *Rhynchospora globosa* (0.25), and *Axonopus brasiliensis* (0.23)—had commercialized seeds. *Paspalum lineare* and *Tristachya leiostachya* were not traded and occupied the sixth and seventh positions in the IVI rank, respectively. RSC sold 11.63 tons of seeds from ground-layer species between 2017 and 2019, 55% of the total seed they sell. Two species, the shrub *Lepidaploa aurea* and the grass *Andropogon fastigiatus*, accounted for 44% of the RSC sales in terms of weight. *L. aurea* had an IVI of 0.008 (796th position in the IVI rank) and occurred in *c.* 1.4% of the studied sites. *A. fastigiatus* was absent from all the 66 sites used to calculate the species IVI. After *L. aurea* and *A. fastigiatus*, *Schizachyrium sanguineum*, *Aristida riparia*, and *Aristida setifolia* were the top-selling species, representing 9, 8.3, and 7% of the seeds sales

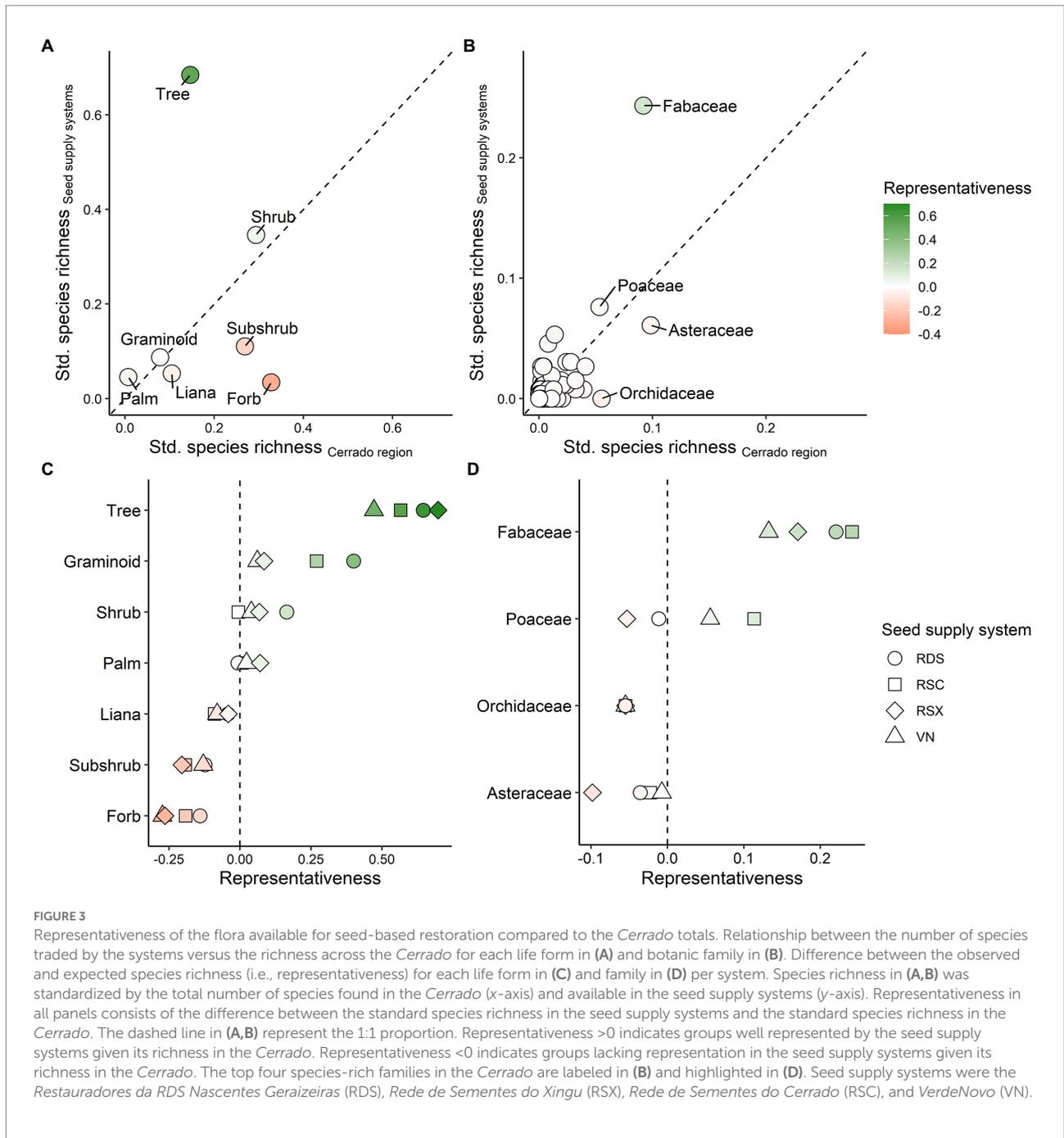
and occupying the 78th, 492nd, and 339th IVI rank positions, respectively (Figure 4C; Supplementary Table 5).

Discussion

We assessed the current locations of the major *Cerrado* seed supply systems and their species portfolio. We found that these systems have expanded remarkably across the *Cerrado*'s central zone in less than 20 years, making up to 260 species available for ecological restoration. Trees, especially legumes, were well represented among seed traders, but relatively fewer forb species were available. Dominant ground-layer species were accessible on the seed market, but the seed sales of the RSC system, a key *Cerrado* seed supplier, were concentrated in two species rarely found in old-growth open ecosystems, the shrub *Lepidaploa aurea* and grass *Andropogon fastigiatus*.

Cerrado's major seed suppliers have unique and complementary species portfolios

Each seed supply system traded a distinctive set of species, suggesting they are not interchangeable, as found in other seed supply systems across the world (Atkinson et al., 2021; Bosshard et al., 2021). Consequently, expanding the existing systems or creating new ones will probably increase the number of species available for seed-based restoration in the *Cerrado*. The seed supply systems were located in distinct biogeographical districts, which explains their floristic dissimilarity (Ratter et al., 1996; Bridgewater et al., 2004; Amaral et al., 2017; Françoso et al.,

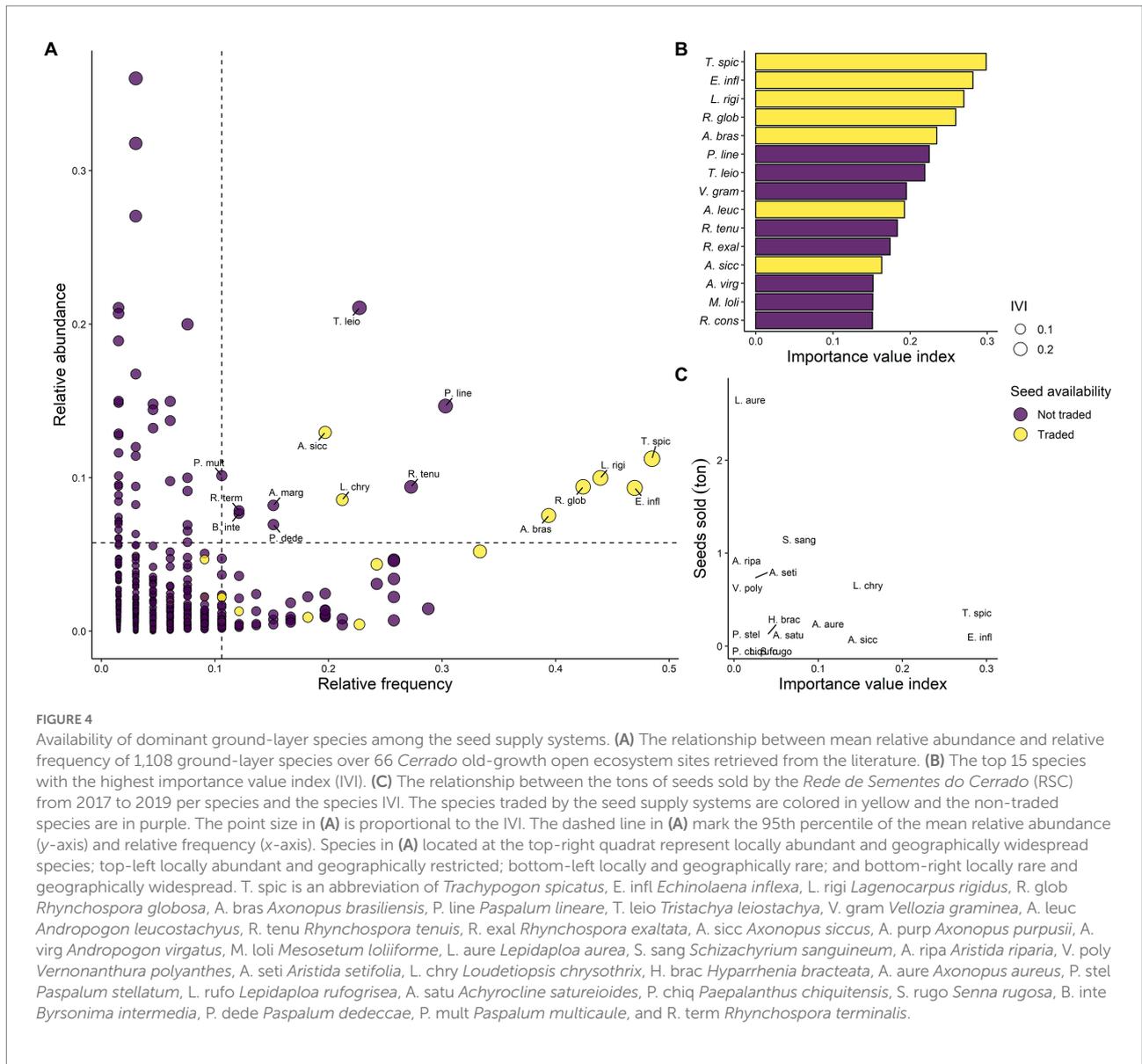


2020). The number of shared species decreased as the geographical distance increased, suggesting the broader the distribution of seed harvesting sites, the richer the flora available on seed markets for restoration. Additionally, there was no clear relationship between the year the seed supply systems were founded and their species richness. VN was created just ~7 years ago (2016) and already sells up to 160 species, suggesting the seed supply systems are flexible, innovative, and can expand their species portfolio over a few years (Schmidt et al., 2019). These findings reinforce that expanding the geographical coverage of the seed supply systems can be key to diversifying the seed

market and this diversification can potentially take place until the end of this decade (2030).

Trees are overrepresented and forbs are underrepresented in the seed market

Trees are the best-represented life form in the seed supply systems evaluated here. The diversity of legume tree species on sale is one of the factors underpinning tree dominance in the seed markets for restoration. The overrepresentation of trees and



legumes was found in all four seed supply systems. This finding suggests that currently the seed market is equipped to source plant material for the restoration of closed-canopy ecosystems (e.g., gallery forests) and the woody layer of savannas in the *Cerrado*. Yet, sourcing tree seeds is not the priority to restore the open ecosystems that cover up to 70% of the *Cerrado* region. Tree species often regenerate naturally in degraded lands within three decades in *Cerrado* savannas (Giles et al., 2021; Silva et al., 2021). Suggesting that assisted natural regeneration could be a prominent method to recover tree species. Forbs and graminoids, on the other hand, have a lower regeneration potential compared to trees (Cava et al., 2018; Overbeck et al., 2022), and they might be the life forms most reliant on active restoration, such as direct seeding.

Seeds from forbs were under-sourced given the richness of this life form in the *Cerrado*. Three causes may underly this pattern found in all the seed supply systems. First, open

ecosystems are often undervalued compared to their closed-canopy counterparts (Parr et al., 2014; Silveira et al., 2022). By extension, forbs are likely to be overlooked in restoration science and practice, relative to trees. Second, harvesting seeds from forb species can be more laborious than trees. Forb seeds are often smaller than tree seeds, so collectors need to spend more time harvesting multiple populations of forbs to collect the same amount of seeds found in a single tree. Third, some species-rich forb lineages, such as Orchidaceae and Asteraceae, are composed mainly of micro-endemic narrow-ranged species (Neto and Forzza, 2013; Campos et al., 2019), which may be absent or rare in the harvesting sites. Yet, forbs should not be neglected when designing restoration interventions in open ecosystems. Forbs in families such as Eriocaulaceae, Xyridaceae, and Velloziaceae can amplify vegetation resilience to fires and drought (de Oliveira Joaquim et al., 2018; Pilon et al., 2021), support pollinator

populations (Rabeling et al., 2019), and accelerate soil formation (Teodoro et al., 2019). Including forbs and not only graminoids in the seed mixes can, therefore, maximize the recovery of multiple ecosystem functions in *Cerrado* grasslands and savannas.

Dominant ground-layer species are available for sale but have low consumer demand

The species portfolio of the seed supply systems already includes plants that can dominate the ground layer of open ecosystems in the *Cerrado*. Previous studies have reported high ground cover by the grasses *T. spicatus* and *E. inflexa* in old-growth grasslands and savannas (de Souza et al., 2021; Nogueira et al., 2022; Teixeira et al., 2022). However, despite their ecological value, these species were not the most popular species for restoration, as evidenced by the RSC sales record. *E. inflexa* seeds cost c. USD 103 per kg, almost ten times more than the RSC top-selling species (*L. aurea* and *A. fastigiatus*), which may explain the low demand for *E. inflexa* seeds. *E. inflexa* spreads through rhizomes, which can facilitate its establishment through transplant techniques (Pilon et al., 2019). *T. spicatus* had a similar price to *L. aurea* and *A. fastigiatus*, so the price is unlikely to be the cause of its low demand. Instead, the low establishment rates of *T. spicatus* may underlie its low sale rank. Up to 80% of *T. spicatus* seeds can be empty (i.e., embryoless; Zanetti et al., 2020), clarifying its low germination and emergence rates in field conditions (Pellizzaro et al., 2017). Poor seeds and strong dormancy are common in *Cerrado* grasses (Le Stradic et al., 2015; Fontenele et al., 2020). It is, therefore, fundamental to improve seed quality control and enhancement techniques to establish key ground-layer species when direct seeding is chosen as the main restoration method (Buisson et al., 2021).

The biennial shrub *L. aurea* and the annual grass *A. fastigiatus* accounted for almost half of the seeds from ground-layer species sold by RSC from 2017 to 2019. The high demand for *L. aurea* and *A. fastigiatus* is probably related to their ability to cover the ground during the first 2 years after direct seeding (Pellizzaro et al., 2017; Coutinho et al., 2019; Sampaio et al., 2019), coupled with a relatively low price for their seed. These species can play an important role in immediately controlling soil erosion due to their fast ground cover. However, *L. aurea* and *A. fastigiatus* are rare in *Cerrado* open ecosystems, suggesting that these species might possess life history strategies that diverge from ones in old-growth areas. For instance, *A. fastigiatus* and *L. aurea* have an annual and biennial life cycle, respectively (Motta, 2017; Wolfsdorf et al., 2021), thus relying on seeds as the persistence strategy. Annual and biennial “seeder” species are often rare in *Cerrado* grasslands and savannas, where the perennial life cycle coupled with below-ground resprouting is the dominant strategy (Pilon et al., 2021). The abundant aboveground biomass produced by short-lived species, such as *L. aurea* and *A. fastigiatus*, can lead to high fuel loads, exposing the

vegetation to intense fires early in the restoration process when “resprouter” species are not sufficiently abundant to confer ecosystem resilience to fire (Giles et al., 2022). Therefore, continuing to improve the availability and quality of seeds from species characteristic of old-growth sites, alongside continuing to develop techniques to successfully incorporate these species in the early stages of restoration, could increase the likelihood of restoring open ecosystems to a state similar to that of old-growth areas.

Concluding remarks and future perspectives

Our findings suggest that: (1) Brazilian *Cerrado* seed supply systems are irreplaceable and complement each other in the species they trade; (2) increasing the number of forb species on sale could lead to a more even representation of the flora available for open ecosystem restoration in the *Cerrado*; and (3) amplifying the demand for species typical of old-growth areas remains a challenge to effectively restore the ground layer of *Cerrado* grasslands and savannas. We acknowledge that, first, the present insights are based on a momentary picture of the four seed supply systems. However, a snapshot of the current state of the seed market for restoration is a vital step toward its development. Second, we stress that low-IVI species can also be targets in restoration projects, especially when they increase the desired ecosystem function or facilitate the establishment of other species. Third, our IVI rank does not diminish the need of surveying local reference ecosystems as species with low IVI at the scale of the entire *Cerrado* might be abundant in the region where restoration will take place. We advocate for: (1) more public and private support for creating new or expanding existing seed supply systems over the *Cerrado* region; (2) a better understanding of the motivations underlying species selection for seed-based restoration; (3) more awareness about the importance of sourcing and using a diverse set of herbaceous plants in open-ecosystem restoration; and (4) clear guidelines on which species should dominate in the seed mixes, potentially *T. spicatus*, *E. inflexa*, *L. rigidus*, *R. globosa*, or *A. brasiliensis* when the goal is restoring old-growth grasslands and savannas and/or boosting the multifunctionality of grassy ecosystems. We hope these suggestions provide a roadmap toward a strategic advancement of the seed markets for the restoration of *Cerrado*'s open ecosystems, especially during the UN Decade on Ecosystem Restoration (2021–2030).

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

MS, RP, LR, and PM conceived the research. MS gathered and analyzed the data and drafted the manuscript. MS, PM, RO, RP, and LR edited and gave input to the final version of the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

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