# Facilitating Large-Scale Restoration of Brazilian Savannas

Submitted by Mateus Cardoso Silva, to the University of Exeter for the degree
of Doctor of Philosophy in Physical Geography, May 2024

I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

(Signature) Mateus Cardoso Silva

## Abstract

Restoring degraded ecosystems has emerged as a solution to tackling global biodiversity loss and climate change. However, scaling ecosystem restoration depends on matching species to site conditions today and in the future. I aimed to fill this knowledge gap for the Brazilian *Cerrado*, a global biodiversity hotspot characterized by a mosaic of tropical savannas and forests. I assessed the diversity of plant species available for seed-based restoration by compiling species lists of four major seed suppliers to evaluate how well they cover the *Cerrado* flora. I found that each supplier trades a unique set of species, but herbaceous species are underrepresented relative to trees, and that ruderal species dominate seed sales rather than species typical of old-growth vegetation. I also assessed the future distribution of the *Cerrado* flora under climate change by fitting Species Distribution Models (SDMs) for up to 7,400 *Cerrado* angiosperm species. I found that montane species will lose range while lowland species will expand their range towards high-elevation sites, resulting in net species loss in the lowlands and species turnover in the mountains. Finally, I combined the two previous studies to develop a tool for designing climate-smart seed mixes for restoration. The user sets the focal species, restoration site, and level of climate optimisation, then the tool takes advantage of SDMs to make species-specific suggestions for the best areas to collect seeds from natural populations and the proportion of seeds to be obtained from different active seed vendors. I conclude that diversifying seed supply, aligned with climate-informed species and seed origin selection, will be critical to scaling up restoration in the *Cerrado*.

## Acknowledgements

Once I was told “a PhD is a marathon, not a sprint”. Looking back a few steps from the finishing line now, I realise Peter Moonlight’s piece of wisdom couldn’t be more accurate. Running a marathon takes one to be prepared and perseverant, but it’s only possible with the support of a sea of people who help us to make it to the end. I would like to dedicate the first thanks to my very first supporters, my mum Vanda, dad Toninho and brother Rafael. I feel lucky to have a family who believed I could get anywhere I’d put my mind on, *as minhas conquistas são suas também*. Back to the marathon, I have no words to express my gratitude and admiration to my coaches, Toby Pennington and Lucy Rowland. You have taught me that mentoring is about creating an environment where students are seen and listened to and free to think, try, learn, and grow. Thank you Peter, my co-supervisor, not only for giving me the perfect quote for opening this, but for helping me get back on track when I was running into a stone wall. I’d like to thank Chris Kettle and Stephen Sitch, who kindly joined in as examiners, I appreciate you taking the time to read through the ideas squeezed in this document.

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## Abbreviations

**LULCC:** Land Use and Land Cover Change.

**GHG:** Greenhouse gas.

**SER:** International Society for Ecological Restoration.

**PLANAVEG:** Brazil National Native Vegetation Recovery Plan.

**RSC:** "*Rede de Sementes do Cerrado*".

**ACP:** "*Associação Cerrado de Pé*.

**RSX:** "*Rede de Sementes do Xingu*".

**VN:** "*VerdeNovo Semetes*".

**RDS:** "*Rede de Sementes da Reserva do Desenvolvimento Sustentável Nascentes Geraizeiras*".

**EMBRAPA:** Brazilian Agricultural Research Corporation.

**COSST:** Climate Oriented Seed Sourcing Tool.

**IVI:** Importance Value Index.

**SDM:** Species Distribution Model.

**MaxEnt:** Maximum Entropy.

**SSP:** Shared Socioeconomic Pathway.

**GBIF:** Global Biodiversity Information Facility.

**GCM:** Global Circulation Model.

**VIF:** Variance Inflation Factor.

**CBI:** Continuous Boyce Index.

**S-SDM:** Stacked Species Distribution Model.

*“Nossa meta é plantar sementes na quantidade de estrelas no céu”*

(Our goal is to plant as many seeds as the stars in the sky)

**Claudomiro Cortes**

Courtesy of Bia Carvalho

# Chapter 1

Courtesy of Tim Hill

# Chapter 1 – General introduction

## 1.1. Global context

Earth is home to more than 377,749 vascular plant species (WFO, 2024), which are the foundation of terrestrial ecosystems. Nature provides innumerable contributions to people, including the regulation of environmental processes (e.g., carbon and water cycles, soil, pollinators) and the provision of material (e.g., food, fibre, genetic resources) and other immaterial goods (e.g., natural heritage) (IPBES, 2019). Yet, plant populations, species, and ecosystems are declining globally, a phenomenon known as biodiversity loss. Six out of the nine boundaries defining the planetary safe space for humanity have been crossed, and biodiversity loss is the most prominent of the six (Richardson *et al.*, 2023). The main global driver of biodiversity loss is habitat loss and fragmentation due to land use and land cover change (LULCC) (WWF, 2022). LULCC ramped up since the beginning of the 20th century due to advances in agricultural technology. Half of the Earth's habitable land is now used for growing livestock and crops (Ellis *et al.*, 2010). LULCC does not exert an isolated effect on biodiversity and ecosystem services but rather interacts with other threats such as species overexploitation, biological invasions, pollution, and climate change.

Habitat loss and fragmentation intensify climate change, adding more pressure to the world's ecosystems and their contributions to people. Earth's surface temperature is 1.1 °C warmer at present (2011–2020) relative to the pre-industrial period (1820–1900) (IPCC, 2023). The frequency and intensity of climatic events such as droughts, fires, heatwaves, and floods are changing across the planet as a direct result of global warming. Extreme climatic events can push organisms outside their physiological limits, contributing to biodiversity loss through mass mortality events, local extinctions, and biome shifts. Anthropogenic greenhouse gas (GHG) emissions are the primary cause of modern global warming. Carbon dioxide ($CO_2$) emissions come primarily from burning fossil fuels, though LULCC represents a significant $CO_2$ source, accounting for 12% of total anthropogenic carbon emissions in 2022 (Friedlingstein *et al.*, 2023). LULCC emissions originate from the release of carbon stored in the living biomass and soils mainly after deforestation and fire events. Between 20–40% of global land is degraded to some extent due to the compound effects of LULCC and climate change (UNCCD, 2022).

Ecosystem restoration emerged as a nature-based solution to reverse land degradation and tackle biodiversity loss and climate change (UNEP, 2021). The United Nations declared 2021–2030 as the Decade on Ecosystem Restoration, defining ecosystem restoration as “the process of halting and reversing degradation, resulting in improved ecosystem services and recovered biodiversity” (UNEP, 2021). Biodiversity trends from LULCC could become positive by 2050 if exceptional efforts were made to restore degraded land, increase protected area coverage, and transition to a more sustainable agricultural production, trade, and human diet (Leclère *et al.*, 2020; WWF, 2022). Empirical data support these conclusions as meta-analyses reveal an overall positive effect of restoration interventions on biodiversity metrics across taxa compared to the degraded state ranging from 15% to 84% biodiversity gain (Benayas *et al.*, 2009; Crouzeilles *et al.*, 2016; Atkinson *et al.*, 2022). Ecosystem restoration also contributes to mitigating climate change through carbon capture and storage in vegetation and soils (Bustamante *et al.*, 2019; Strassburg *et al.*, 2020; Littleton *et al.*, 2021). However, high failure rates among restoration projects challenge their capacity to provide habitat for endangered species and sequester and store carbon (Brudvig *et al.*, 2021; Svejcar, Davies and Ritchie, 2023).

Increased biodiversity is not only an outcome of ecosystem restoration but also a condition for its success. Re-establishing species (e.g., by seeding or planting) is often essential to trigger or accelerate the regeneration process (i.e., active restoration) (Li *et al.*, 2018; Philipson *et al.*, 2020). In such cases, the initial set of species used for restoring an area can be a critical driver of the recovery trajectory (Coutinho *et al.*, 2019; Weidlich *et al.*, 2021; Manhães *et al.*, 2022). For instance, species selection must match the site’s abiotic conditions, such as climate, soils, and hydrology, otherwise, species will die over time resulting in restoration failure (Temperton *et al.*, 2004; Funk *et al.*, 2023). The role of environmental filtering (i.e., abiotic conditions mediating community assembly) in shaping restoration trajectory is even more critical where land degradation has introduced novel conditions, such as compacted or eutrophicated soils (Funk, 2021). Furthermore, biotic interactions also play a key role in driving the restoration process. For example, invasive exotic species can compete and exclude target native species in areas under restoration (Kuebbing and Nuñez, 2016; Kaul and Wilsey, 2021). Selecting species with a competitive advantage over invasives is, then, crucial to maximizing the long-term success of restoration projects (Funk *et al.*, 2008; Hess, Mesléard and Buisson, 2019). Predicting the effect of abiotic and biotic filtering on the assemblage trajectory is challenging due to species-specific responses to the environment and competitors (Brudvig *et al.*, 2017). Therefore, investing in initial diversity can be key to ensuring that at least a subset of species will persist over time and that a species-rich assemblage will ultimately be restored (Halassy *et al.*, 2023; Mazzochini *et al.*, 2023).

Climate fit also plays a central role in restoration's long-term trajectory alongside initial biodiversity. Failing to account for climate change can cause target plant species to die over the course of months to years to decades after the restoration intervention (Zabin *et al.*, 2022). Three mechanisms underlie the resilience of a community to climatic events (de Bello *et al.*, 2021). First, mass-ratio effects when the traits of dominant species shape ecosystem responses to a stressor (Finegan *et al.*, 2015; Smith *et al.*, 2020). Second, complementarity effects when a diverse set of species explore the resources differently, increasing the resistance of the ecosystem against a stressor (Morin *et al.*, 2011; Teste *et al.*, 2014). Third, insurance/redundancy effects when a diverse set of species is likely to contain at least a few species capable of recovering from a stressor while others perish (Yachi and Loreau, 1999; Mori, Furukawa and Sasaki, 2013). At the species level, genetic variation increases the chance that some individuals within a population will persist under climate change and the evolutionary flexibility of the species to adapt to future climates (Kremer *et al.*, 2012; Aitken and Whitlock, 2013). Irrespective of the scale or mechanism, the diversity of species and genes is critical to climate-proof ecosystem restoration (Nef *et al.*, 2021). In summary, restoring degraded lands can mitigate LULCC impacts on biodiversity and GHG emissions if biodiversity and climate adaptation are considered early on in the restoration planning phase.

## 1.2. Strategies and challenges

The International Society for Ecological Restoration (SER) conceptualized ecosystem restoration as a continuum of interventions (Gann *et al.*, 2019) (Figure 1.1). At one end, the “reduced impacts” category encompasses conservation actions to avoid further degradation, such as halting LULCC. Degradation can be so severe that basic ecosystem functions such as primary productivity and soil integrity have been virtually lost, which is the case of former mining or polluted sites. In these cases, “remediation” can decelerate degradation (e.g., removing pollutants) and “rehabilitation” can help to recover ecosystem functions (e.g., controlling soil erosion with revegetation) (Brancalion and Holl, 2016). At the opposite end of the continuum is “ecological restoration[1]”, which aims to recover biodiversity and ecosystem function to the levels of an undegraded reference site. Ecological restoration methodologies fall within a spectrum from passive to active approaches (Atkinson and Bonser, 2020). Passive restoration involves enabling natural regeneration by ceasing anthropogenic disturbances (e.g., logging, pollution) or reintroducing natural disturbances (e.g., fires, wildlife). On the other hand, active restoration aims to assist regeneration by modifying the abiotic conditions (e.g., soil preparation), controlling invasive species, and re-establishing plants as seeds or seedlings, for example. The regeneration potential is a key ecosystem property that will shape whether passive *vs*. active restoration is more appropriate.

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[1] Throughout the thesis, I use “ecosystem restoration” and “ecological restoration” as synonyms since ecological restoration represents most of the ecosystem restoration efforts in the *Cerrado*.

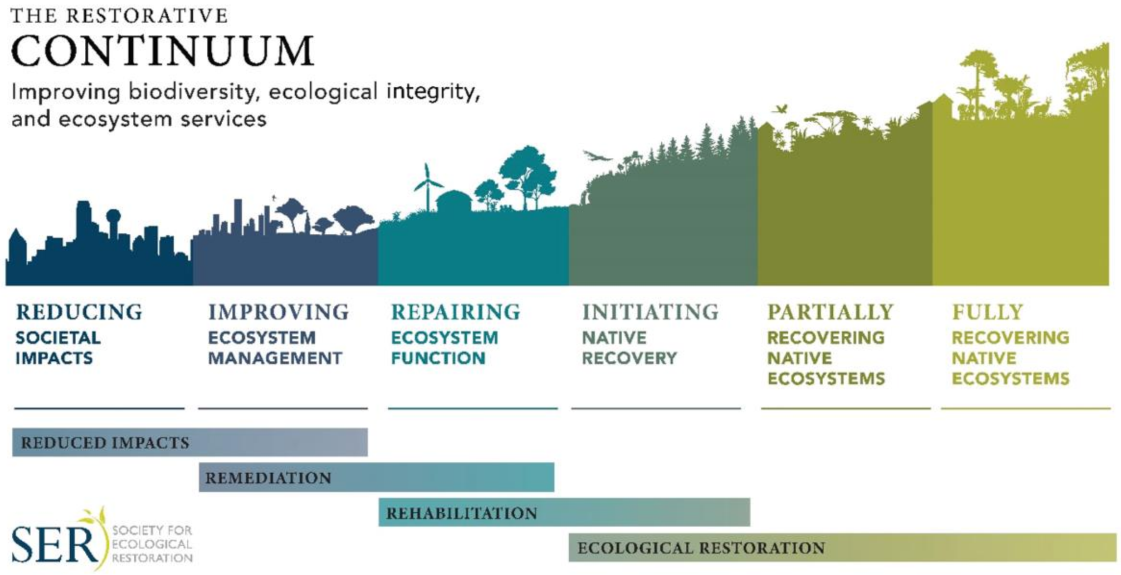

**Figure 1.1.** The spectrum of ecosystem restoration interventions from avoiding degradation to fully restoring habitats and ecosystem functions lost due to degradation. Adapted from Gann *et al.* (2019).

The regeneration potential of an ecosystem will depend upon the reproductive strategy of the constituent species, the landscape configuration, and competitive interactions. Seeds are the basis of sexual reproduction in flowering plants, and they sometimes can stay dormant until germination conditions are appropriate. Seeds can accumulate in the soil creating a “seed bank”, which is the cornerstone of natural regeneration in some ecosystems (Paula *et al.*, 2023). In disturbance-prone ecosystems, such as Mediterranean-climate shrublands and savannas, resprouting (asexual reproduction) can play a bigger role than seed germination (i.e., that results from sexual reproduction) (Pilon *et al.*, 2021; Simpson *et al.*, 2021). In this case, regeneration potential depends also on the “bud bank”, often in developed bud-bearing belowground organs, in addition to the seed bank (Pausas *et al.*, 2018; Ott, Klimešová and Hartnett, 2019; Bombo, Siebert and Fidelis, 2022). Seed and bud banks can be depleted after degradation limiting the regeneration potential, which can be the case for many agricultural systems (Ferraro *et al.*, 2021) or mining sites (Le Stradic, Fernandes and Buisson, 2018). Neighbouring vegetation remnants can work as sources of propagules (e.g., seed rain) helping to regenerate seed banks, but the lack of vegetation cover in human-modified landscapes can further hinder this process in degraded sites (Holl, 1999;

Santos *et al.*, 2020; Vindica *et al.*, 2020). Finally, even if seed banks can be restored, invasive exotic species can suppress seed germination and seedling development of native species (Damasceno *et al.*, 2018; Langmaier and Lapin, 2020), adding another barrier to the spontaneous regeneration of native species.

Seedling planting and seed sowing are the main active revegetation strategies where natural regeneration is unlikely to occur. Seedlings can be grown in nurseries and planted on the site, a common practice in forest restoration (Silva *et al.*, 2017; Vidal *et al.*, 2020). Alternatively, seeds can be sown directly at the site, a common practice in grassland restoration (Shaw *et al.*, 2020). In Brazil, across forest and savanna ecosystems, seedling planting costs on average US$ 2,328 per hectare while seeding costs US$ 1,754 ha$^{-1}$ (a 24% reduction) (Brancalion *et al.*, 2019). Another study in Brazilian forests and savannas showed that seeding was, on average, 2.5 times cheaper than seedling planting to establish around a thousand trees per hectare considering >50 species (Raupp *et al.*, 2020). The fact that many seeds are easier to store and transport and cheaper to produce than nursery-grown seedlings has stimulated the use of seed-based restoration across the globe (De Vitis *et al.*, 2017; Atkinson *et al.*, 2021; Bosshard *et al.*, 2021; Gibson-Roy *et al.*, 2021; Silva *et al.*, 2022; Giacomini *et al.*, 2023). The seed supply chain is therefore the pillar of seed-based restoration programmes and consists of multiple links (Pedrini and Dixon, 2020) (Figure 1.2). First, appropriate species and seed sources for the site must be identified (Erickson and Halford, 2020). Second, seeds can be either collected from natural populations or produced in seed farms (Pedrini, Gibson-Roy, *et al.*, 2020). Third, seeds need to be purified when they are embedded in fruits, tested for viability, and stored (De Vitis *et al.*, 2020; Frischie *et al.*, 2020). An additional step is easing seed dormancy or increasing germination, growth, or survival rates by enhancement (e.g., priming/hydration in pure water, coating with polymers/clay) (Kildisheva *et al.*, 2020; Pedrini, Balestrazzi, *et al.*, 2020). Finally, seeds need to be available for delivery to the site after site preparation (e.g., soil decompaction, invasive species control) (Shaw *et al.*, 2020).

**Figure 1.2.** The seed supply chain for ecosystem restoration. The chain is divided into two parts: restoration activities representing restoration planning, execution, and monitoring; and the chain itself that captures many steps from seed collection in the beginning to enhancement in the end. Adapted from Cross, Pedrini and Dixon (2020).

Identifying the best species to include in seed mixes depends on three factors. First, it is essential to set clear restoration targets and select species that will deliver such outcomes (Hobbs, 2007; Gann *et al.*, 2019). In agroforestry systems, for example, the goal is often to restore soil health while producing food and generating income (Santos, Crouzeilles and Sansevero, 2019; Jansen *et al.*, 2020). In such cases, practitioners may target species that will provide ecosystem services, such as regulating microclimate and soil organic matter, and/or goods, such as forage, fruits, or timber (Fremout *et al.*, 2022; Kindt *et al.*, 2023). Alternatively, ecological restoration often aims to recover plant assemblages that resemble the vegetation lost or damaged by degradation (White and Walker, 1997; Toma *et al.*, 2023). In these cases, practitioners can use species lists from reference sites to plan the restoration project (Menezes *et al.*, 2022). Second, the target species should not only be able to meet the restoration objectives but also to form viable populations on the site. Environmental filtering emerges as a key concept to ensure the selected species can germinate, grow, and reproduce under the abiotic and biotic conditions of the restoration site (Funk *et al.*, 2023). However, as climate changes, practitioners must also consider selecting species capable of withstanding both contemporary and future environmental filters (Butterfield *et al.*, 2017; Fremout *et al.*, 2020). Finally, after shortlisting a set of species fit for purpose, practitioners need to consider how to get enough seeds of such species, which often requires buying from seed vendors for large-scale projects (Barga *et al.*, 2020).

Designing seed mixes involves not only selecting appropriate species but also seed sources, i.e., the location where seeds are harvested. Natural selection and genetic drift structure a population's genetic composition over geographical space. Consequently, seed geographic origin affects the genetic composition of the plant species population re-established through restoration (Breed *et al.*, 2019). Maladaptation occurs when the fitness of a population is decreased due to the absence of adaptive genes, posing a risk to the sustainability of restoration projects (Gellie *et al.*, 2016). Moreover, climate change exacerbates the risk of maladaptation since viable populations will need to contain genes adaptive to current and future conditions (Aitken and Whitlock, 2013). Several seed provenance strategies (i.e., provenancing) have been proposed to minimize the chance of maladaptation across timescales (Figure 1.3). Local provenancing encourages the use of the seed source closest to the restoration site, assuming that local adaptation is prevalent (McKay *et al.*, 2005). However, sourcing the seeds from a single population might lead to seed mixes with low genetic variation which can result in inbreeding depression and low adaptive potential (Hufford and Mazer, 2003; Frankham *et al.*, 2011; Kremer *et al.*, 2012). As a solution, the admixture and composite strategies were adopted to encourage the use of seeds from multiple populations in uniform proportions (admixture) (Broadhurst *et al.*, 2008) or proportional to the proximity to the restoration site (composite) (Breed *et al.*, 2013). Predictive provenancing brought a climate adaptation dimension by prioritizing seed sources with the potential to carry genes adaptive to future climates at the restoration site (Havens *et al.*, 2015). A critical limitation is that climatic forecasts are uncertain, which motivated the development of climate-adjusted provenancing, a combination of the composite and predictive approaches (Prober *et al.*, 2015).

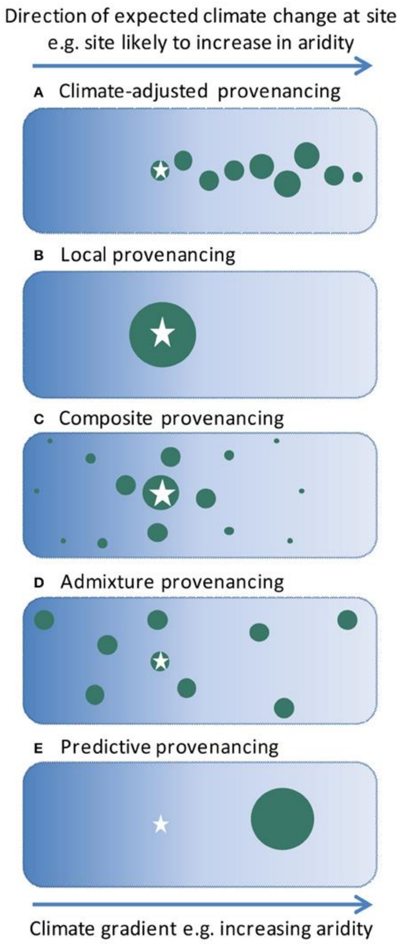

**Figure 1.3.** Graphical representation of seed provenance strategies for ecosystem restoration. The star indicates the site to be restored, the circles the hypothetical populations from which seeds can be sourced, and the arrow the expected change in the climate of the restoration site. The size of the circle is proportional to the amount of seeds sourced from that population. (**a**) Climate-adjusted provenancing consists of collecting seeds from multiple populations both close to the restoration site (near the star) and theoretically adapted to future climate (alongside the arrow). (**b**) Local provenancing consists of sourcing seeds from the population closest to the restoration site. (**c**) Composite provenancing consists of sourcing seeds from multiple populations proportionally to their distance to the restoration site. (**d**) Admixture provenancing consists of sourcing seeds from multiple populations uniformly. (**e**) Predictive provenancing consists of sourcing seeds from the population theoretically best adapted to the future climate. Adapted from Prober *et al.* (2015).

### 1.3. Brazil's *Cerrado*

The Brazilian *Cerrado* is a global biodiversity hotspot (Myers *et al.*, 2000) distributed mostly in Brazil, covering 23.3% of Brazil's land area, though it extends into Paraguay and Bolivia (Velazco *et al.*, 2023). The *Cerrado* is critical for Brazil's water security as it hosts the headwaters of nine out of the 12 most important watersheds in the country. Savannas (*cerrado sensu stricto*) are the *Cerrado*'s main vegetation type, covering 57% of it before 21st century LULCC (Rodrigues *et al.*, 2022). However, the landscape is characterized by complex mosaics of these savannas co-occurring with seasonally dry forests (*mata seca*), gallery forests (*mata de galeria*), encroached savannas (*cerradão*), rock outcrops (*campo rupestre*), well-drained grasslands (*campo sujo*/*limpo*), palm swamps (*veredas*), and finally, seasonally floodable grasslands (*campo limpo*) (Ribeiro and Walter, 1998) (Figure 1.4). Fire and soil properties (e.g., phosphorus concentration and water table depth) jointly drive the coexistence of the *Cerrado* vegetation types (Dantas, Batalha and Pausas, 2013; Abrahão *et al.*, 2019; Mattos *et al.*, 2023). 12,050 angiosperm species are native to the Brazilian *Cerrado* (42% endemism), a diversity level higher than the Brazilian Amazon (11,955 species) (Reflora, 2020). Montane taxa drive *Cerrado* endemism levels, which are exceptionally high in the *campos rupestres* rock outcrops, 'sky islands' generally > 900 m.a.s.l. (Silveira *et al.*, 2016). The *campos rupestres* have a disjunct spatial distribution and soil nutrients, texture, and moisture vary over a scale of a few metres. Geographical isolation and edaphic heterogeneity potentially explain endemism in the campos rupestres and *Cerrado* more broadly (Alcantara, Ree and Mello-Silva, 2018; Rapini *et al.*, 2021).

Half of *Cerrado*'s native vegetation (52.1%) has been converted to alternative land-uses threatening its unique flora. Pastures account for the majority of the land conversion (52%), followed by croplands (26%), pasture-cropland mosaics (19%), and tree plantations (3%) (MapBiomas, 2023) (Figure 1.5). *Cerrado* LULCC became extensive from the 1970s onwards after Brasília became Brazil's capital in 1960. Pasture area increased by 1.5 times and cropland 6.5 times from 1985 to 2022 (MapBiomas, 2023). LULCC started from the southern part of the *Cerrado* (states of São Paulo, Mato Grosso do Sul, and Goiás) and moved northwards in the 1990s. The region known as MATOPIBA (states of Maranhão, Tocantins, Piauí, and Bahia) is currently one of Brazil’s main agricultural frontiers (Zalles *et al.*, 2019). Under a business-as-usual scenario, LULCC can expose 1,140 *Cerrado* plant species to extinction risk by 2050 (Strassburg *et al.*, 2017). Moreover, LULCC-driven habitat fragmentation limits fire spread (Rosan *et al.*, 2022), which can disrupt the life cycle of the *Cerrado*’s fire-dependent taxa. In such human-modified landscapes, criminal or accidental ignition can change fire timing towards anthropogenically driven mid-dry season fires, rather than lightning-ignited natural fires in the late-dry season (Klink *et al.*, 2020). Fires can become destructive to native vegetation after years of fuel accumulation due to fire suppression (Fidelis *et al.*, 2018; Durigan, 2020; Schmidt and Eloy, 2020) and biological invasions, e.g., flammable African forage grasses (Rossi *et al.*, 2014; Gorgone-Barbosa *et al.*, 2015). LULCC threaten not only *Cerrado*’s flora and fire regime but also groundwater recharge and rainfall recycling rates (Hunke *et al.*, 2015; Rodrigues *et al.*, 2022), making ecosystem restoration a priority to protect biodiversity and ecosystem services.

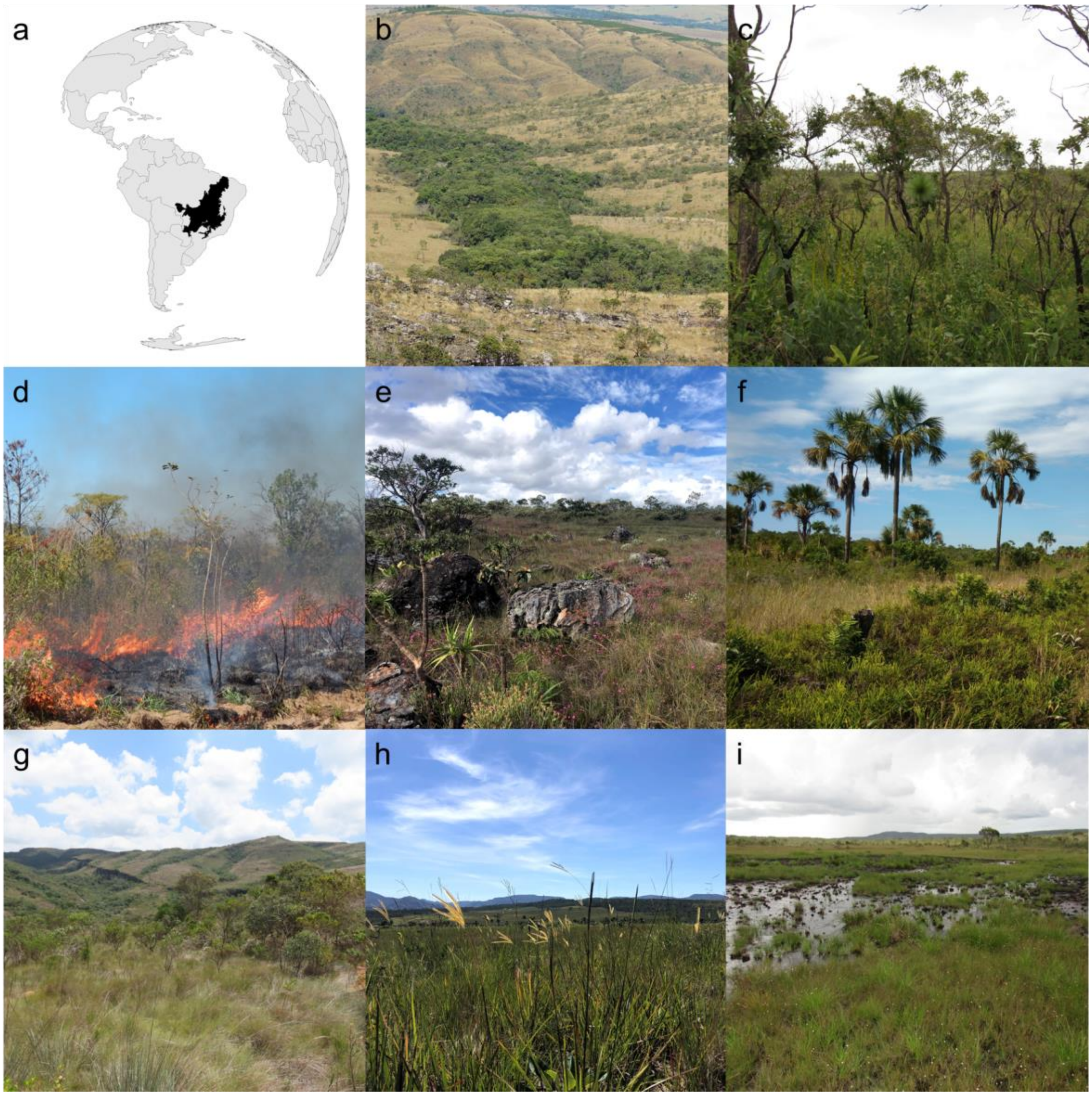

**Figure 1.4.** The location and vegetation of the Brazilian *Cerrado*. (**a**) *Cerrado* extent according to the IBGE (2019) classification. Names in parentheses in **b**–**i** refer to Ribeiro and Walters' (1998) vegetation classification. (**b**) Mosaic of savannas and rock outcrops on the hilltop and gallery forests in the valley. (**c**) Typical savanna (*cerrado sensu stricto*). (**d**) Natural fire in a typical savanna. (**e**) Rock outcrop grassland (*campo rupestre*). (**f**) Wet savanna dominated by *Mauritia flexuosa* L.f. (Arecaceae) (*vereda*). (**g**) Grassland landscape (*campo limpo*). (**h**) Grassland dominated by *Axonopus aureus* P.Beauv. (Poaceae) (*campo limpo*). (**i**) Wet grassland (*campo úmido*). Pictures courtesy of Eduardo van den Berg (a), Bruna Campos (d, g), Fernanda Barros (e, h), Luísa Lobo (c, i), and João Alcantara (f).

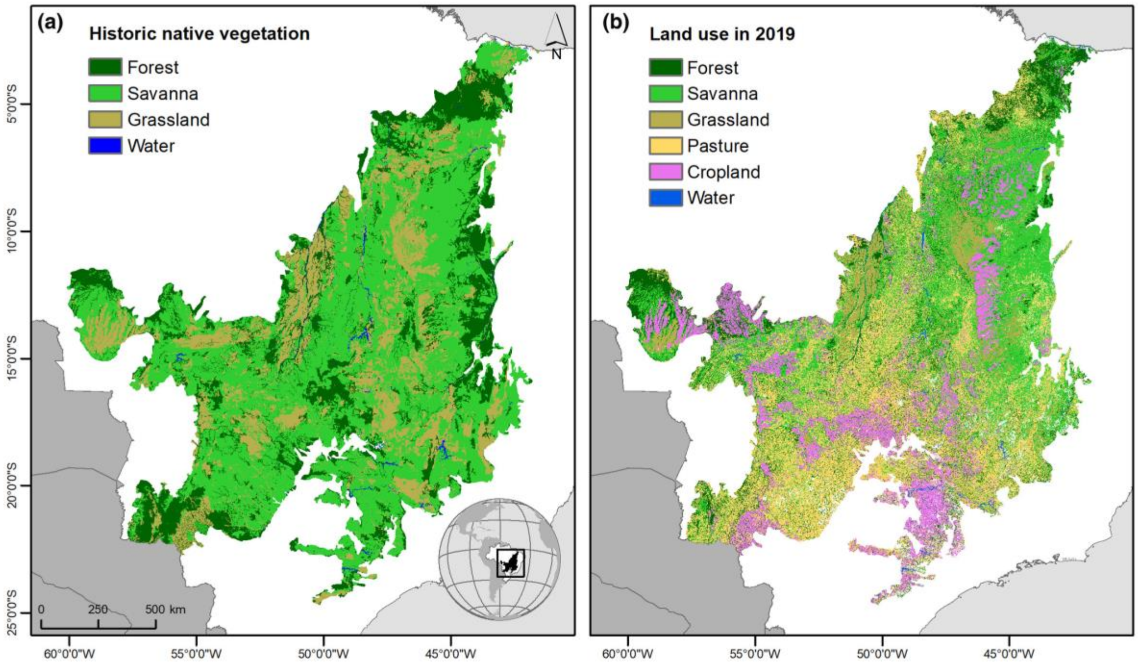

**Figure 1.5.** Land-use and land-cover in the Brazilian *Cerrado* in 2019 compared to a historical reconstruction (i.e., before large-scale human occupation). Adapted from Rodrigues *et al.* (2022).

Ecosystem restoration remains neglected in the Brazilian *Cerrado* despite the *Cerrado*'s size, importance for biodiversity, and key role in the water cycle. Of 291 restoration studies compiled from 1945 to 2018 in Brazil, only 16% of them focused on the *Cerrado* savanna, while 78% of them focused on the Amazon and Atlantic rainforests (Guerra *et al.*, 2020). Similarly, 85% of the job creation in the restoration sector in 2019 in Brazil was linked to the Atlantic rainforest exclusively (Brancalion *et al.*, 2022). International funding to avoid LULCC is disproportionally allocated to Amazon and Atlantic Rainforests, with the *Cerrado* savanna remaining far more neglected (Qin *et al.*, 2023). Brazil's restoration ambitions were set in the National Native Vegetation Recovery Plan (PLANAVEG) (MMA, 2017). PLANAVEG's target for the *Cerrado* is 2.1 million hectares whereas Amazonia's is 4,8 million hectares. In the context of remaining undegraded vegetation, a 2.2 times higher target for Amazonia, which has 81% of native vegetation intact, illustrates the neglect of the *Cerrado*, which has only 47%. Globally, open ecosystems, including most of *Cerrado* vegetation, are overlooked in the international media and scientific literature relative to forested ecosystems, a phenomenon named “Biome Awareness Disparity” (Silveira *et al.*, 2022). Applying common restoration concepts, which have been developed for forests to open ecosystems, can also aggravate the situation. These include afforestation and fire suppression in old-growth savannas and grasslands (Veldman *et al.*, 2019; Silveira *et al.*, 2020; Buisson *et al.*, 2021) where low tree cover and natural fires are necessary to maintain ecosystem function and high plant species diversity, especially of herbs and subshrubs (Durigan *et al.*, 2020; Wieczorkowski and Lehmann, 2022). Herbaceous species[2] represent 40% of the *Cerrado* flora (Reflora, 2020), highlighting that graminoids and forbs are central to recovering *Cerrado* plant diversity.

Restoration in the *Cerrado* is recent (<2 decades) relative to the Atlantic rainforest (>5 decades), but several approaches have been tested so far. The natural regeneration potential of *Cerrado* woody plants is higher than that of herbs (Cava *et al.*, 2018), although studies found some level of herbaceous flora recovery in former forest plantations after clear-cutting (Giles *et al.*, 2021; Horstmann, Sevilha and Vieira, 2023). Active restoration of the herbaceous layer through transferring hay from a donor site to a restoration site proved ineffective (Le Stradic, Buisson and Fernandes, 2014; Pilon, Buisson and Durigan, 2018), probably due to the fact dominant *Cerrado* grasses produce few and often embryoless seeds (Dayrell *et al.*, 2017; Fontenele and Miranda, 2022). Even though some *Cerrado* trees can form seed banks (Escobar and Cardoso, 2015), seed burial hampers seedling emergence among common *Cerrado* grasses (Fontenele *et al.*, 2020), suggesting a limited role for seed banks in restoration (Le Stradic, Fernandes and Buisson, 2018). The transplant of individual grass tussocks proved effective for recovering the herbaceous flora in experimental settings (Pilon *et al.*, 2019). However, plant transplants are resource-intensive, require well-conserved donor sites, and must be implemented immediately otherwise the plant dies, limiting the application of the method at scale. There are a few cases of restoration by planting nursery-grown grass seedlings in the *Cerrado* (Oliveira, Forti and Viani, 2022), but elevated costs make the technique

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[2] I define herbaceous as vascular plants that have no lignified stems aboveground. Herbs include graminoids, defined as grass-like plants with elongated blade-shaped leaves usually belonging to Poaceae, Cyperaceae, or Juncaceae families, and forbs, defined as herbaceous plants other than graminoids (Bond and Parr, 2010; Parr *et al.*, 2014).

unviable at scale and post-planting mortality is high due to root underdevelopment in pot-grown plants. Seeding is the main large-scale restoration technique in the *Cerrado* because seeds can be collected between different populations, stored for years, and shipped to the site at a low cost compared to other techniques (Sampaio *et al.*, 2019). However, the low proportion of viable seeds in *Cerrado* plant species can make seed-based restoration challenging in terms of recovering the species diversity and functions of reference ecosystems (Giles *et al.*, 2022). Although seed quality control is improving over time, a combination of different methodologies will likely be key to recovering the full diversity of life forms in the *Cerrado* (Pilon *et al.*, 2023).

In *Cerrado* and Brazil more widely, government incentives, NGO participation, and market demand shape the seed supply chain for restoration projects. Seed production consists of collection from natural populations (Schmidt *et al.*, 2019), which contrasts seed farming, common in North America (McCormick *et al.*, 2021) and Europe (De Vitis *et al.*, 2017), and under development in Australia (Gibson-Roy *et al.*, 2021). In 2001, Brazil's Ministry of Environment, through the National Environment Fund (FNMA 01/2001), invested up to US$ 500,000 to foster seed supply chains targeting native species. The incentive led to the creation of the "*Rede de Sementes do Cerrado*" (*Cerrado* Seed Network, RSC) in 2004. RSC receives seed requests from clients and redirects the orders to the "*Cerrado de Pé*" Association (ACP), a cooperative of approximately one hundred families of seed collectors. RSC sold more than 29 tons of seeds between 2018 and 2021, promoting the sustainable use of 900 hectares of native vegetation, the restoration of >600 hectares of degraded land, and income generation of more than US$ 200,000, of which 77% went directly to seed collectors affiliated to ACP. In 2007, The Socioenvironmental Institute (ISA), an NGO advocating for Indigenous rights, supported the creation of the "*Rede de Sementes do Xingu*" (*Xingu* Seeds Network, RSX) located at the *Cerrado*-Amazon transition (Campos-Filho *et al.*, 2013). Over the last 15 years, RSX sold approximately 300 tons of seeds, contributing to the restoration of 7,400 hectares and income generation of US$ 1,000,000 for associates, mainly Indigenous Peoples. Other *Cerrado* seed suppliers include *VerdeNovo* (VN), a market-driven business created in 2016, and "*Restauradores da RDS Nascentes Geraizeiras*" (RDS) created in 2017 with support from the NGO "*Bem Diverso*" and the Brazilian Agricultural Research Corporation (Embrapa).

Seed-based restoration is growing in the *Cerrado*, but climate change challenges its effectivity. The mean maximum temperature for October in the *Cerrado* increased by 4 °C between 1961 and 2019, a trend of 0.7 °C per decade (Hofmann *et al.*, 2021). Changes to the *Cerrado*'s climate are driven by regional warming and LULCC, as the conversion from savannas to pastures/croplands can increase the land surface temperature by an average of 1.9 °C (Rodrigues *et al.*, 2022). Climate change is also likely to affect plant phenology, which may disrupt the logistics of seed collection from wild populations (Buisson *et al.*, 2017). Moreover, species that occur in a given area might not persist there under future climates due to range shifts, adding complexity to species selection for seed mixes (Butterfield *et al.*, 2017). Finally, seeds collected locally might lack adaptive genetic variation to optimise the establishment of the population under a new climate. All of these potential changes call for climate-informed seed-provenancing guidelines (Havens *et al.*, 2015). Even though these questions are pressing, the fate of the *Cerrado* species under climate change scenarios remains poorly understood (Velazco *et al.*, 2019). Elevation plays a critical role in shaping the *Cerrado*'s climate, with lowlands being warmer than mountains (Sano *et al.*, 2019) (Figure 1.6). There is evidence that species can track climate change by migrating upslope (Parmesan and Yohe, 2003; Chen *et al.*, 2011), though this hypothesis remains untested in the *Cerrado*.

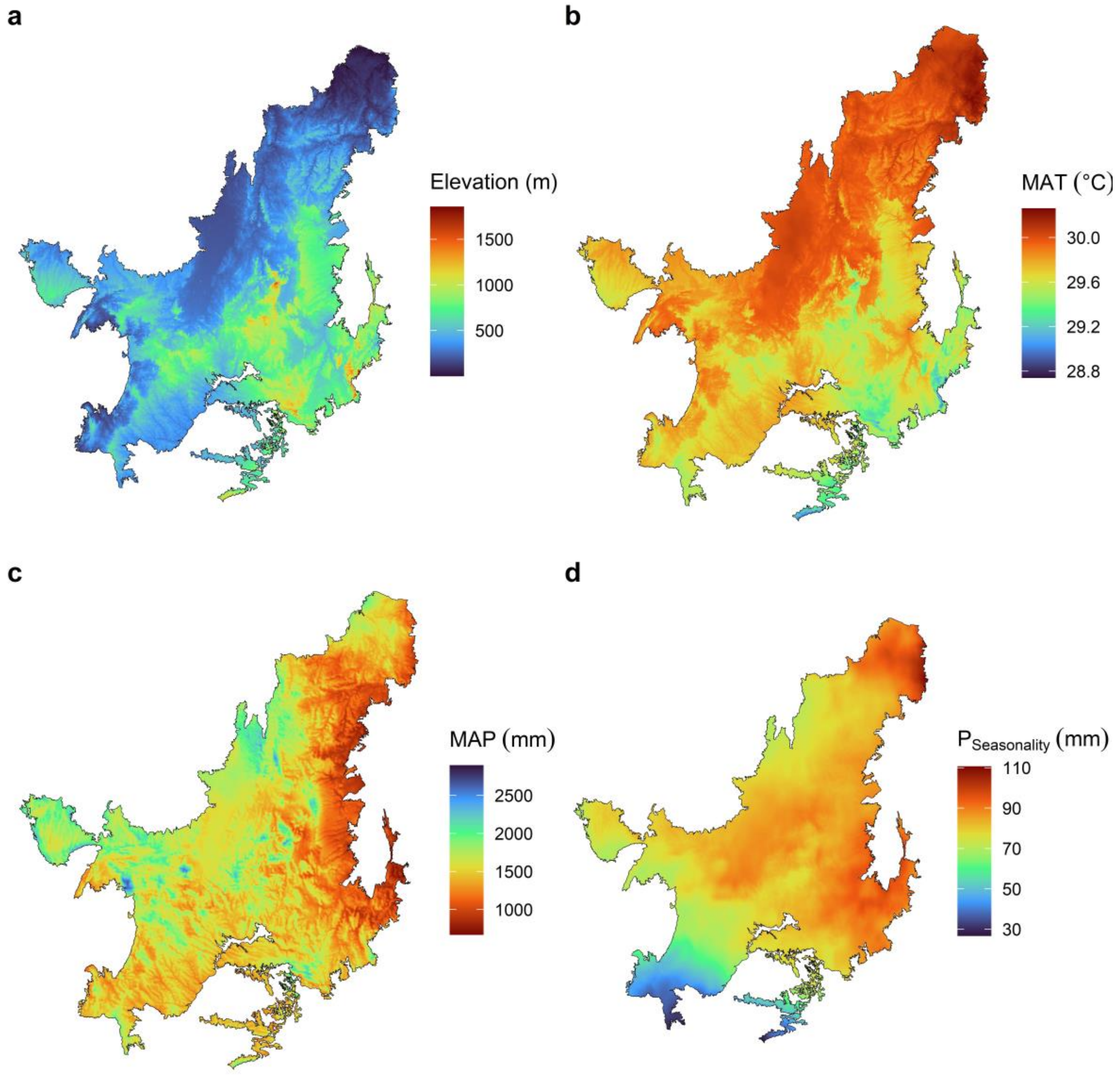

**Figure 1.6.** *Cerrado*'s elevational and climatic gradients. (**a**) Elevation in metres above the sea level derived from the Shuttle Radar Topographic Mission (SRTM) and (**b**) MAT, mean annual temperature, (**c**) MAP, mean annual precipitation, and (**d**) $P_{Seasonality}$, precipitation seasonality (coefficient of variation monthly precipitation), derived from CHELSA V2.1.

### 1.4. Thesis outline

The overarching goal of this thesis is to propose solutions to restore *Cerrado*'s degraded ecosystems at scale. The thesis is composed of five chapters (Figure 1.7). This chapter (Chapter 1) aimed to lay out the theoretical foundation and context for the remaining chapters. Chapters 2 to 4 are published or submitted manuscripts and therefore written in an article style. Their content is detailed in the section below. Chapter 5 summarizes the thesis findings and shares insights for future research. Lastly, the appendices include publications I contributed to during my doctoral studies and supplementary information from Chapters 2 to 4. I sought to write the chapters to be concise and practical, reflecting my aspiration to fill the research-implementation gap that motivated this thesis.

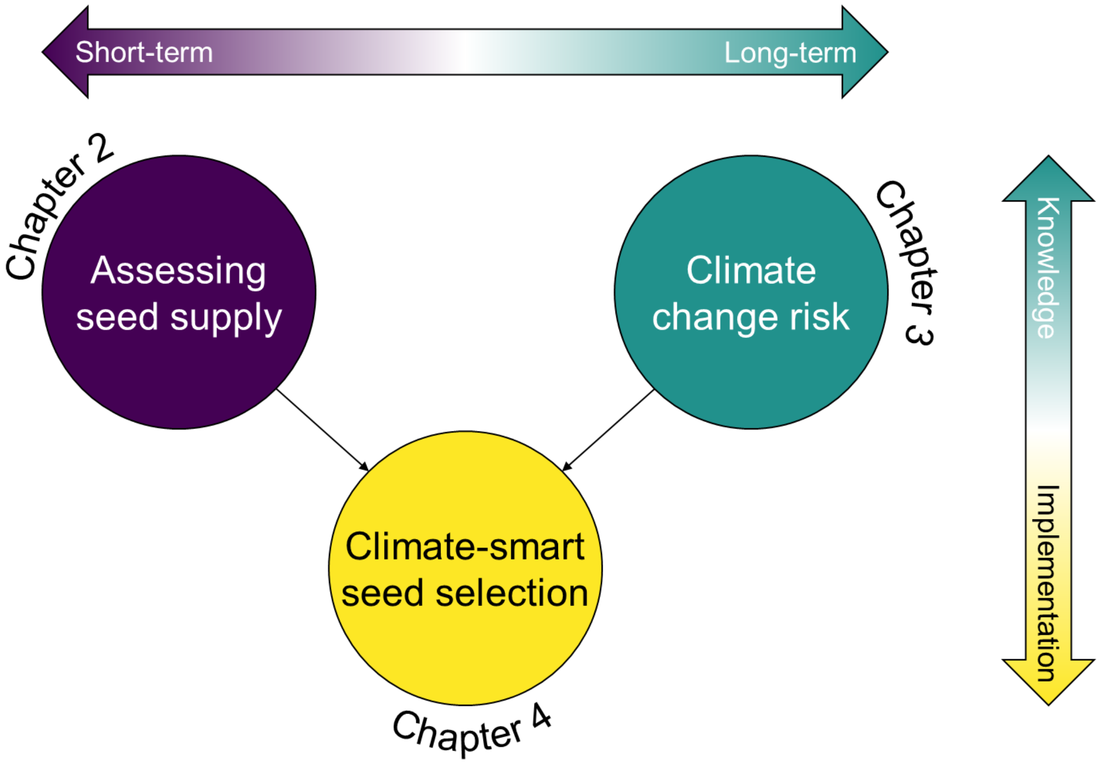

**Figure 1.7.** Graphical representation of the thesis structure. The circles represent Chapters 2 to 4 and the restoration challenge they address in the *Cerrado*. The black arrows represent data flow. The coloured arrows illustrate each chapter's timeframe (short-term or annual *vs*. long-term or decadal) and emphasis (filling knowledge *vs*. implementation gaps).

Chapters 2 to 4 vary in their timescale (short-term *vs*. long-term) and emphasis (knowledge vs. implementation) (Figure 1.7). In **Chapter 2**, I provide a snapshot of the diversity of plant species available for sale among major seed suppliers in the *Cerrado*. I collate data from four seed suppliers and analyse it against *Cerrado*-scale species richness and abundance estimates drawn from the literature. I ask how similar the species mixes commercialized by major seed suppliers are, whether there are biases among life forms and families, and if species typical of reference ecosystems are available for sale. Chapter 2 therefore addresses current seed supply limitations, specifically identifying the constraints to regaining species diversity in seed-based restoration projects in the *Cerrado*.

In **Chapter 3**, I predict the distribution of *c*. 7,400 *Cerrado* flowering plant species by 2040, fundamental information to future-proof conservation and restoration projects. I develop a Species Distribution Model pipeline considering warming of 1.5 and 4 °C by the end of the century. In this chapter, I test the hypothesis of upslope migration, where elevation plays a central role in shaping the changes in species ranges and the community's species richness and composition over time.

In contrast to Chapters 2 and 3, Chapter 4 emphasises the potential to implement changes to restoration planning at an intermediate timescale of years to decades. In **Chapter 4**, I introduce a tool to select seed sources following geographical *vs*. climate optimisations. The tool, named Climate Oriented Seed Sourcing Tool or COSST, draws data from Chapters 2 and 3 into a new framework. This framework tailors predictions for best-practice provenancing to the species and site of interest. I illustrate the tool in the *Cerrado,* but the methodology could apply to any terrestrial biome or ecosystem.

**Chapter 5** synthetizes the outcomes of this thesis across all chapters. I highlight how this thesis can help us to move forward in restoration science and practice and provide additional analyses that link Chapters 2 to 4. I finish by outlining questions that emerge from this thesis and will define our capacity to undertake large-scale restoration in the Brazilian *Cerrado* and elsewhere.

### 1.5. Significance of research

The research within this thesis aligns with pressing global and national restoration goals for this decade (2021–2030). The UN flagged 2021–2030 as the Decade on Ecosystem Restoration, an effort to catalyse action for protecting and revitalizing degraded ecosystems across the globe. The year 2030 also coincides with the deadline for the UN Sustainable Development Goals, a "shared blueprint for peace and prosperity for people and the planet", in which restoring degraded lands and reversing biodiversity loss plays a key role (https://sdgs.un.org/goals). To have a chance of bending the biodiversity loss curve by 2050, countries must mobilize unprecedented resources to scale up ecosystem restoration and protection in the current decade (Leclère *et al.*, 2020). In this context, Brazil pledged to restore an ambitious 12 million hectares by 2030 through the PLANAVEG (MMA, 2017). Following this, NGOs such as WWF, who jointly funded my PhD, have been acting intensively to promote ecosystem restoration in Brazil. For instance, supporting community-led seed suppliers in the *Cerrado* has been a flagship project within the WWF-Brazil Restoration Agenda. Promoting indigenous and local communities' rights and participation aligned to climate change mitigation and adaptation are integrative principles guiding the actions of all the organizations mentioned above. Such principles intersect this thesis since Chapters 2 and 4 focus on how seed supply chains, organized by indigenous and local communities, can support ecosystem restoration and Chapters 3 and 4 focus on how climate change will impact plant assemblages and how to foster climate adaptation in restoration through seed provenancing guidelines. I am confident the scientific advances of this thesis can help us scale up ecosystem restoration in the Brazilian *Cerrado* while improving people's livelihoods and building climate resilience. I hope this may contribute to enabling Brazil to meet national and international restoration goals and potentially inspire similar approaches in other parts of the globe.

# Chapter 2

Courtesy of Bruna Campos

# Chapter 2 – Towards diverse seed sourcing to upscale the Brazilian *Cerrado* restoration

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**Author contributions:** MCS, RTP, LR, and PM conceived the research; MCS gathered and analysed the data; MCS drafted the manuscript; all authors edited and gave input to the final version of the manuscript.

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## 2.1. Abstract

Seed markets are vital to upscale 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 suppliers 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 supplier. 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 suppliers 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.

## 2.2. 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, Gibson-Roy, *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). Supplying seeds of native species has emerged as a key strategy to achieve these national restoration targets (Urzedo *et al.*, 2021). Seed suppliers 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 the Brazilian seed supply network 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). 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 six 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, Ratter and Ribeiro, 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 suppliers 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 supplier. 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 to 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 suppliers?
2. How are life forms and plant families represented in the seed market?
3. Are dominant ground-layer species from old-growth open ecosystems available on the seed market?

## 2.3. Method

### 2.3.1. Seed harvesting sites

We mapped the centroid of the municipalities where the seed suppliers are active (Appendix 2.1). The municipalities were obtained from the RSX website (https://www.sementesdoxingu.org.br/biblioteca, *6º Boletim* – p. 2) and by directly contacting personnel from the RSC, VN, and RDS suppliers. 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”.

### 2.3.2. Species richness

We accessed the species list of each seed supplier by directly contacting them (VN and RDS) or through their websites (RSX and RSC) (Appendix 2.2). 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 supplier is in the transitional zone between the *Cerrado* and Amazon. Additionally, we checked whether the species turnover between the suppliers 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 suppliers (Karney, 2013). We also investigated whether the species richness of a given supplier might be a function of its age. The year of creation of each seed supplier 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).

### 2.3.3. 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 herbaria 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 platform (http://floradobrasil.jbrj.gov.br/) 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 made available by seed suppliers 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 suppliers for each life form and botanical family. We repeated the analysis within each seed supplier to verify whether the representation biases towards life forms or families were widespread among the suppliers.

#### 2.3.4. 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 analysed 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; 4 study sites). We ended up with 66 study sites from 25 publications (Appendix 2.3). We standardized the species name and removed all tree and liana species based on the Brazilian Flora 2020 (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, Cassia; 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 does not capture the importance of ecosystem engineering species and species with strong legacy effects. Yet, IVI is still useful for pinpointing species characteristic of reference ecosystems, which is the goal of this study.

### 2.3.5. RSC 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. We used total seed mass as a proxy for the quantity of seeds sold per species. We acknowledge, however, that seed mass changes across species, so the number of seeds per kilo will be species-specific. We focus on ground-layer species only, which controls for differences in seed mass as small light seeds are a common feature of Poales (Wang *et al.*, 2023), the lineage comprising typical ground-layer plants, such as grasses (Poaceae) and sedges (Cyperaceae). We followed the procedure mentioned in section 2.3.4 to classify ground-layer species.

## 2.4. Results

### 2.4.1. Geographic distribution of seed sourcing

The studied seed suppliers are located approximately from 9° S to 16° S (Figure 2.1). RSX was the biggest seed supplier in terms of the number of municipalities (18), followed by RSC (6), RDS (5), and VN (4). The current extension of the four seed suppliers 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).

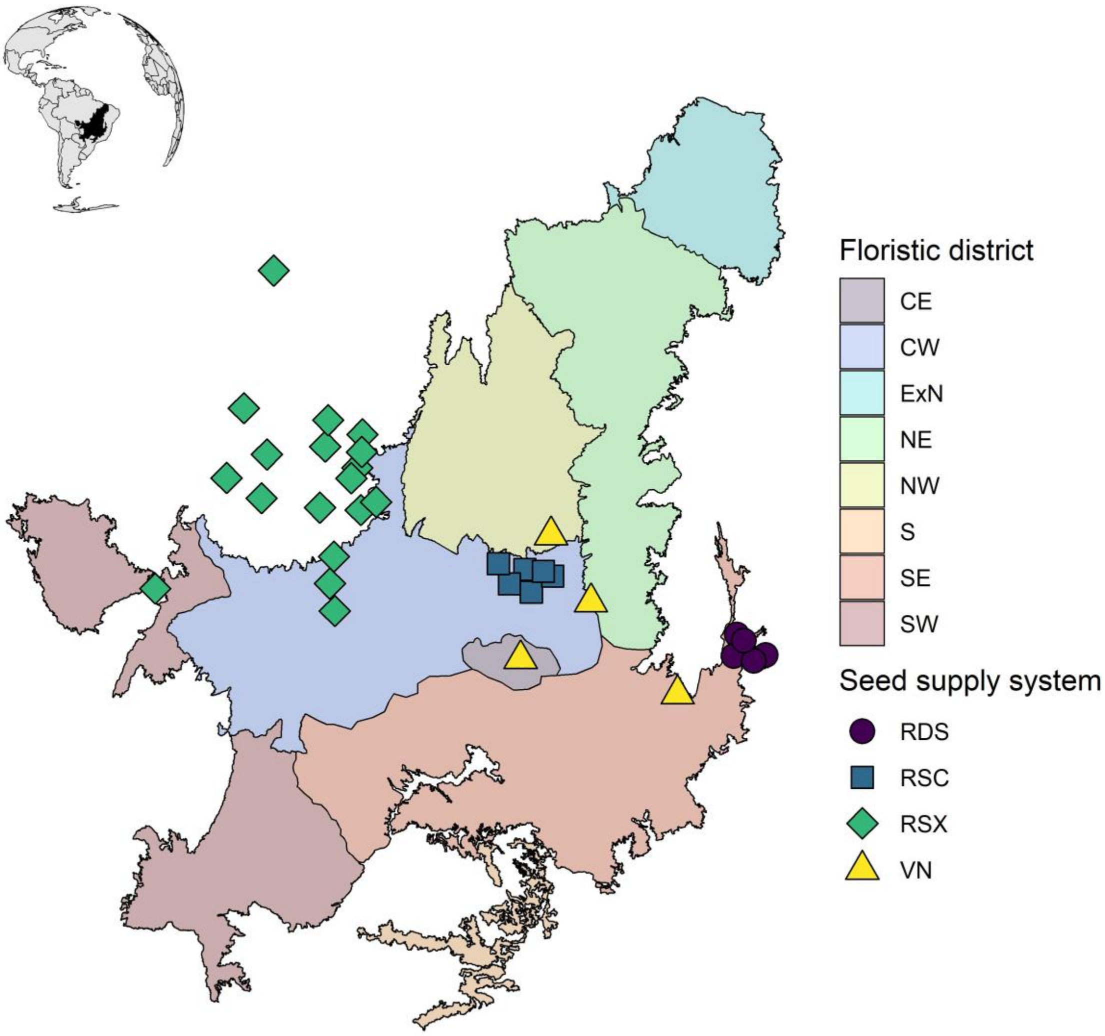

**Figure 2.1.** Geographical coverage of the main *Cerrado* seed suppliers for restoration. The points correspond to the centroid of the towns and cities with seed collection activities over the *Cerrado* region. The studied seed suppliers are the *Restauradores da RDS Nascentes Geraizeiras* (RDS), *Rede de Sementes do Xingu* (RSX; which also collects seeds outside of the *Cerrado* region), *Rede de Sementes do Cerrado* (RSC), and *VerdeNovo* (VN). Biogeographical districts depict areas with similar woody floras according to Françoso et al. (2020) and were represented by contrasting colours. The districts are central (CE), central-west (CW), external north (ExN), northeast (NE), northwest (NW), south (S), southeast (SE), and southwest districts (SW).

### 2.4.2. Floristic relationships

A total of 263 species were made available for restoration by the seed suppliers (Figure 2.2a). 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 suppliers. 167 species were found only in one supplier (i.e., unique species), representing around 63% of all traded species. The percentage of unique species per supplier ranged from 57% to 10% in the RSX and RSC suppliers, respectively. The VN supplier offered the greatest number of *Cerrado* species (165), followed by RSX (141), RSC (66), and RDS (48) suppliers. The number of shared species achieved its maximum (55) between the geographically closest suppliers (RSC and VN) and minimum (19) between the suppliers farthest apart (RSX and RDS) (Figure 2.2b). RSC was the oldest supplier (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 2.2c).

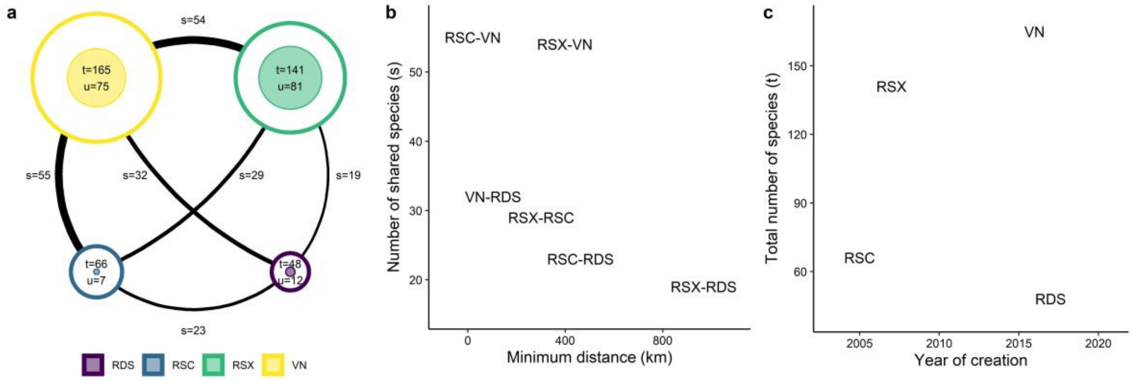

**Figure 2.2.** Floristic similarity between the *Cerrado* suppliers. (**a**) Diagram showing the number of total (t), unique (u), and shared (s) species between the suppliers. (**b**) Relationship between the number of shared species between a pair of seed suppliers and their minimum geographical distance. (**c**) Relationship between the total number of species of each seed supplier and the year of its creation. Unique species represent the ones traded by a single supplier. The size of the outer circle in panel **a** is proportional to t, the size of the inner circle to u, and the line thickness to s. The analysis includes only species that occur in the *Cerrado*. Seed suppliers were the *Restauradores da RDS Nascentes Geraizeiras* (RDS), *Rede de Sementes do Xingu* (RSX), *Rede de Sementes do Cerrado* (RSC), and *VerdeNovo* (VN).

### 2.4.3. Representativeness of life forms and families

Trees were the best-represented life form in the seed suppliers, while forbs were the worst according to the Brazilian Flora 2020 checklist (Figure 2.3a). 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 2.3b). 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 supplier was analysed separately (Figure 2.3c and d). All four suppliers had a good representation of trees and legumes and a lack of representation of forbs and orchids.

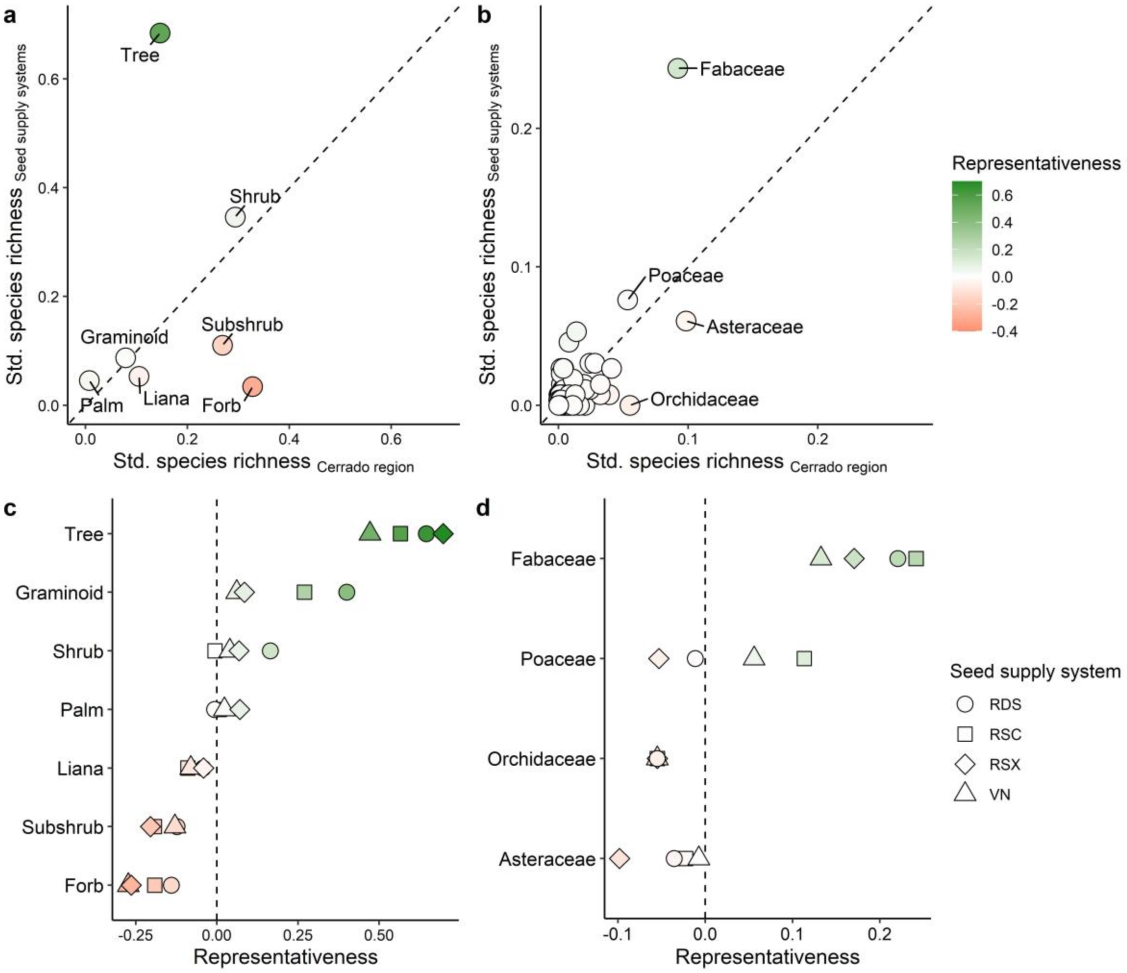
a
b
c
d
Std. species richness Seed supply systems
Std. species richness Cerrado region
Tree
Shrub
Graminoid
Subshrub
Palm
Liana
Forb
Fabaceae
Poaceae
Asteraceae
Orchidaceae
Representativeness
0.6
0.4
0.2
0.0
-0.2
-0.4
Tree
Graminoid
Shrub
Palm
Liana
Subshrub
Forb
-0.25
0.00
0.25
0.50
Representativeness
Fabaceae
Poaceae
Orchidaceae
Asteraceae
-0.1
0.0
0.1
0.2
Representativeness
Seed supply system
RDS
RSC
RSX
VN

**Figure 2.3.** Representativeness of the flora available for seed-based restoration compared to the *Cerrado* totals. Relationship between the number of species traded by the suppliers versus the richness across the *Cerrado* for each life form in panel **a** and botanic family in panel **b**. Difference between the observed and expected species richness (i.e., representativeness) for each life form in panel **c** and family in panel **d** per supplier. Species richness in panels **a** and **b** was standardized by the total number of species found in the *Cerrado* (x-axis) and available in the seed suppliers (y-axis). Representativeness in all panels consists of the difference between the standard species richness in the seed suppliers and the standard species richness in the *Cerrado*. The dashed line in panels **a** and **b** represents the 1:1 proportion. Representativeness > 0 indicates groups well represented by the seed suppliers given its richness in the *Cerrado*. Representativeness < 0 indicates groups lacking representation in the seed suppliers given its richness in the *Cerrado*. The top four species-rich families in the *Cerrado* are labelled in panel **b** and highlighted in panel **d**. Seed suppliers were the *Restauradores da RDS Nascentes Geraizeiras* (RDS), *Rede de Sementes do Xingu* (RSX), *Rede de Sementes do Cerrado* (RSC), and *VerdeNovo* (VN).

### 2.4.4. Dominant ground-layer species on the market

The seed suppliers traded 7 out of the 15 ground-layer species with the greatest Importance Value Index (IVI) among 66 *Cerrado* savanna sites (Figure 2.4a and b; Appendix 2.4). 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 sold. 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 2.4c; Appendix 2.5).

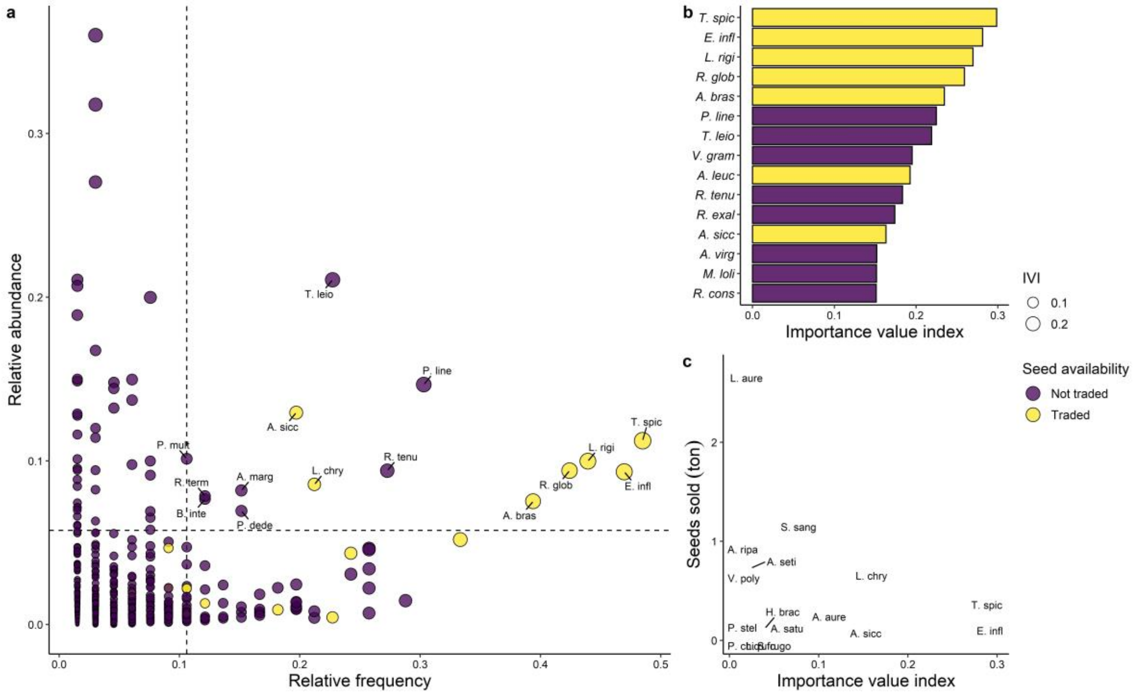

**Figure 2.4.** Availability of dominant ground-layer species among the seed suppliers. (**a**) The relationship between mean relative abundance and relative frequency of 1,108 ground-layer species over 66 old-growth open ecosystem sites over the *Cerrado*. (**b**) The top 15 species with the highest importance value index (IVI). (**c**) The relationship between the tons of seeds sold by the *Rede de Sementes do Cerrado* (RSC) from 2017 to 2019 per species and the species IVI. The species traded by the seed suppliers are coloured in yellow and the non-traded species are in purple. The point size in panel **a** is proportional to the IVI. The dashed line in panel **a** marks the 95th percentile of the mean relative abundance (y-axis) and relative frequency (x-axis). Species in panel **a** located at the top-right quadrat represent locally abundant and geographically widespread species, top-left locally abundant and geographically restricted, bottom-left locally and geographically rare, and bottom-right locally rare and geographically widespread. T. spic is an abbreviation of *Trachypogon spicatus*, E. infl *Echinolaena inflexa*, L. rigi *Lagenocarpus rigidus*, R. glob *Rhynchospora globosa*, A. bras *Axonopus brasiliensis*, P. line *Paspalum lineare*, T. leio *Tristachya leiostachya*, V. gram *Vellozia graminea*, A. leuc *Andropogon leucostachyus*, R. tenu *Rhynchospora tenuis*, R. exal *Rhynchospora exaltata*, A. sicc *Axonopus siccus*, A. purp *Axonopus purpusii*, A. virg *Andropogon virgatus*, M. loli *Mesosetum loliiforme*, L. aure *Lepidaploa aurea*, S. sang *Schizachyrium sanguineum*, A. ripa *Aristida riparia*, V. poly *Vernonanthura polyanthes*, A. seti *Aristida setifolia*, L. chry *Loudetiopsis chrysothrix*, H. brac *Hyparrhenia bracteata*, A. aure *Axonopus aureus*, P. stel *Paspalum stellatum*, L. rufo *Lepidaploa rufogrisea*, A. satu *Achyrocline satureioides*, P. chiq *Paepalanthus chiquitensis*, S. rugo *Senna rugosa*, B. inte *Byrsonima intermedia*, P. dede *Paspalum dedeccae*, P. mult *Paspalum multicaule*, and R. term *Rhynchospora terminalis*.

## 2.5. Discussion

We assessed the current locations of the major *Cerrado* seed suppliers and their species portfolio. We found that these suppliers 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, 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*.

### 2.5.1. *Cerrado*'s major seed suppliers have unique and complementary species portfolios

Each seed supplier traded a distinctive set of species, suggesting they are not interchangeable, as found in other seed supply systems[3] across the world (Atkinson *et al.*, 2021; Bosshard *et al.*, 2021). Consequently, expanding existing suppliers or creating new ones will probably increase the number of species available for seed-based restoration in the *Cerrado*. The seed suppliers were located in distinct biogeographical districts, which explains their floristic dissimilarity (Ratter *et al.*, 1996; Bridgewater, Ratter and Ribeiro, 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 suppliers were founded and their species richness. VN was created just ~7 years ago (2016) and already sells up to 160 species, suggesting the seed suppliers are flexible, and 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 suppliers can be key to diversifying the seed

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[3] I define a seed supply system as the body of individuals and organizations involved in the seed supply chain, including seed suppliers/vendors, restoration practitioners/implementers, policymakers, and government/nonprofit/academic facilitators.

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

### 2.5.2. Trees are overrepresented and forbs are underrepresented in the seed market

Trees are the best-represented life form in the seed suppliers 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 suppliers. 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 underlie this pattern found in all the seed suppliers. 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.

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

The species portfolio of the seed suppliers 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 (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 sales rank. Up to 80% of *T. spicatus* seeds can be empty (i.e., embryoless) (Zanetti *et al.*, 2020), explaining 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, Cruz-Lima, *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 two 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.

## 2.6. Conclusion

Our findings suggest that: (1) Brazilian *Cerrado* seed suppliers 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*; (3) sourcing seeds from 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 suppliers. 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 to survey local reference ecosystems as species with low IVI across the *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 suppliers 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 towards 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).

# Chapter 3

Courtesy of Rafael Oliveira

# Chapter 3 – Elevation modulates the impacts of climate change on the Brazilian *Cerrado* flora

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**Author contributions:** MS, LR, RTP, and PT designed the study. MS performed the analysis and drafted the manuscript. All the authors contributed to the final version of the article and approved its submission.

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## 3.1. Abstract

Climate change is causing species distribution to shift across the globe. Lowland taxa are moving upslope with warming, while montane species face extinction. We tested the hypothesis that elevation controls the future distribution of plant species in the Brazilian *Cerrado*, home of 3.5% of the Earth's flowering plants (*c*. 5,000 endemic species) in just 0.4% of the planet's land surface. We estimated geographical range shifts of 7,398 angiosperm species by 2040 using Species Distribution Models (SDMs). We stacked the SDMs to derive the temporal variations of species richness and composition over the *Cerrado*. Our results show that between 50–52% of the *Cerrado* flora will experience net range loss due to climate change. While montane species were more likely to lose range, range gain was more common among lowland taxa. We estimate that 68–73% of the *Cerrado* extent will face net species losses by 2040. Net species loss was more likely to occur below 743–798 metres above sea level. Virtually the entire *Cerrado* will experience some level of species replacement due to climate change and species turnover will intensify as elevation increases. Our findings suggest that upslope migration allows lowland plants to track climate change ("winners"), whereas montane taxa do not ("losers"). As species move upslope, lowlands become local extinction hotspots and mountains harbour novel plant assemblages. Therefore, elevation exerts a central role in shaping *Cerrado* flora responses to climate change and potentially the long-term efficacy of conservation and restoration efforts.

## 3.2. Introduction

Climate change is driving shifts in the distribution of species and ecosystems across the globe (Parmesan, 2006; Pecl *et al.*, 2017). Compared to pre-industrial levels, the Earth's surface temperature has increased by 1.1 °C and may exceed 4 °C by the end of the century (IPCC, 2023). Plant populations occurring outside their climate envelope are likely to undergo mass mortality events, resulting in geographical range loss (Sinervo *et al.*, 2010), a phenomenon that threatens one in six species globally (Urban, 2015). On the other hand, climate change may offer novel habitats for some species to migrate into, leading to range gains (Chen *et al.*, 2011). These contrasting responses to environmental change lead to the "winner-loser" dichotomy, which has been observed in multiple taxa (Bateman et al., 2016; Brodie et al., 2017; Prugh et al., 2018; Roeder et al., 2021; Smith et al., 2021). However, the drivers of the uneven response of species to the ongoing changes in climate remain unclear.

Elevation plays a key role in shaping how climate change impacts the range dynamics of species. Multiple lines of evidence point that species are shifting their distribution towards higher elevations with global warming, i.e., upslope migration (Chen et al., 2009, 2011; Feeley et al., 2011; Freeman et al., 2018; Girish & Srinivasan, 2022; Lenoir et al., 2008; Maharjan et al., 2022; Mamantov et al., 2021; Parmesan & Yohe, 2003; Rumpf et al., 2018; Vitasse et al., 2021). Upslope migration can allow species to track isotherms, but not all species are equally capable of moving upwards. Niche suitability often constrains the leading edge of lowland and mid-elevation species ranges. As climatic envelopes move upslope, such species may find migration opportunities at high elevations, but the distribution of montane species can be physically constrained if the leading edge of their range coincides with the peak of the mountain. Consequently, montane species may have a low migration potential due to the absence of suitable habitats (Dullinger *et al.*, 2012; Bell, Bradford and Lauenroth, 2014; Zu *et al.*, 2023). The elevation where a species occurs can underlie, then, whether it will become a "loser" or "winner" as climate changes.

Upslope migration can also change the number and identity of species in a given community. Species losses are expected to occur in lowlands if species are synchronously losing range near their lower elevational limit as temperatures increase (Ramirez-Villegas *et al.*, 2014). Similarly, we can anticipate species gains in mountain areas if species are systematically gaining range beyond their upper elevational limit (Walther, Beißner and Burga, 2005; Peyre *et al.*, 2020). The net outcome would be species turnover peaking at high elevations due to the immigration of low- and mid-elevation species (Thuiller *et al.*, 2011; Gibson-Reinemer, Sheldon and Rahel, 2015). At the same time, species richness is thought to decline at low elevations due to the loss of emigrant species (i.e., lowland biotic attrition) (Colwell *et al.*, 2008; Feeley and Silman, 2010). Evidence for upslope migration shaping species ranges and assemblages under climate change often relies on long-term ecological monitoring, data which is often lacking in the world's most biodiverse regions (Dornelas et al., 2018; Lenoir et al., 2020; Salguero-Gómez et al., 2015).

The Brazilian *Cerrado* host the most species-rich savannas in the globe, but its fate under climate change remains poorly known. *Cerrado* covers only 0.4% of the world's land area but it is home to 3.5% of all vascular plants on Earth (Freiberg *et al.*, 2020). Furthermore, 42% of the *c*. 12,000 flowering plants native to the *Cerrado* are endemic (Zappi *et al.*, 2015; Reflora, 2020). Weather stations spread across the region recorded maximum temperature increases as high as 4 °C from 1961 to 2019 (Hofmann *et al.*, 2021). Velazco et al. (2019) estimated that climate change can reduce 34–43% of the historical range of 1,553 *Cerrado* angiosperms. An outstanding question is whether elevation may underlie species- and site-specific responses to climate change. The main landforms in the *Cerrado* are plateaus reaching *c*. 1,800 metres above sea level (henceforth referred to as "mountains") and depressions starting from sea level (henceforth referred to as "lowlands") (Sano *et al.*, 2019; Lira-Martins *et al.*, 2022). Elevational gradients played a central role in shaping the origin and maintenance of the *Cerrado*'s remarkable plant diversity (Mews *et al.*, 2016; Mota *et al.*, 2018; Menegat *et al.*, 2019; Abadia *et al.*, 2023). It is less clear, however, whether elevation will also play a role in shaping the responses of the *Cerrado* flora to the contemporary changes in climate.

Here, we aim to unveil whether the effects of climate change on the *Cerrado* angiosperms depend on elevation. To do so, we fitted species distribution models (SDMs) for 7,967 *Cerrado* species at the South America scale using the MaxEnt algorithm and seven independent bioclimatic variables averaged from 1981 to 2010. We projected the SDMs to a smaller scale (Brazil) and transferred them to the 2011–2040 timeframe based on the projections of five Global Circulation Models (GCMs). We carried out the analyses considering two Shared Socioeconomic Pathways (SSP): a sustainability scenario limiting warming to 1.5 °C (SSP1) and a fossil-fuelled development scenario exceeding warming of 4 °C (SSP5). We, then, used the outputs from these simulations to test the following hypotheses.

1. Climate change will shrink the species’ range size with net range loss being more pronounced in montane species.
2. Species richness will decline under climate change with net species loss increasing towards lowland sites.
3. Climate change will lead to changes in species composition with temporal turnover increasing with elevation.

## 3.3. Material and methods

### 3.3.1. Study area

The *Cerrado* region extends over an area of 1.9 million km$^2$ (IBGE, 2019). The average mean annual temperature is 24 °C (18–28 °C) and the average annual precipitation is 1,359 mm (800–1,831 mm) (Nascimento and Novais, 2020). Precipitation is seasonal with monthly precipitation > 241 mm in Dec–Feb and < 40 mm in Jun–Aug. Elevation ranges from the sea level to 1,855 m, averaging 494 m (INPE, 2014). Most of the *Cerrado* is comprised of mid-elevation areas, the 1st elevation quantile being 294.4 m and the 3rd quantile being 677.7 m. *Cerrado* mountains fall into the pyramid mountain shape classification *sensu* Elsen & Tingley (2015), meaning that surface area decreases as elevation increases and mountaintop taxa have no higher-up habitat to migrate (i.e., “nowhere-to-go” situation). Conversely, mean annual temperature decreases with elevation.

### 3.3.2. Species occurrence and background data

We downloaded occurrence records for all terrestrial plant species (Embryophyta) available in the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/) and SpeciesLink (https://specieslink.net/) across South America. 50% of the occurrences date between 1985 (1st quantile) and 2008 (3rd quantile), the median being 1997. GBIF and SpeciesLink are repositories of herbarium data, which are likely to have georeferencing and taxonomic identification errors (Goodwin *et al.*, 2015; Zizka *et al.*, 2019). We applied a series of filters to minimize the chance of including erroneous occurrence records in our SDMs (See “Data cleaning” section in the Supplementary methods). We standardized the species names and filtered only angiosperm species according to the APG IV (2016) and those that occur in the Brazilian *Cerrado* using the function “get.taxa” from the R package “flora” (Carvalho, 2020) and removed species with ≤ 10 valid occurrence records. The final dataset consisted of 1,988,701 occurrence records (Appendix 3.2). We controlled for spatial sampling bias by retaining one presence record per 5 km pixel (i.e., thinning) using the function “thin” from the R package “spThin” (Aiello-Lammens et al., 2015). We used the MaxEnt algorithm to fit the SDMs. MaxEnt is a presence-only algorithm, but it requires generating points around the occurrence records (i.e., background points). To further control for bias, we coupled a sampling density map to MaxEnt background point generation to propagate the spatial bias of the presence data into the background data (Phillips *et al.*, 2009) (Appendix 3.10, S2; See “Bias-corrected background point generation” section in the Supplementary methods).

### 3.3.3. Climatic data

We downloaded 19 bioclimatic variables from CHELSA V2.1 (https://chelsa-climate.org/) averaged from 1981 to 2010 (baseline) at 30 arcsecs of resolution (*c*. 1 km near the equator) (Appendix 3.3). We first visually inspected the data and excluded the precipitation of the warmest (BIO18) and coldest quarter (BIO19) due to discontinuities that reflect methodological artefacts rather than biologically meaningful climatic gradients (Booth, 2022). For the 17 remaining variables, we used the Variance Inflation Factor (VIF) to remove highly correlated variables, which controls for collinearity issues and subsequent model overfitting (De Marco and Nóbrega, 2018). We applied the default settings of the function “vifstep” from the R package “usdm” (Naimi *et al.*, 2014), which retained seven out of the 17 bioclimatic variables (Appendix 3.4). We downloaded the seven independent variables at the 2011–2040 timeframe according to five Global Circulation Models (GCMs): GFDL-ESM4, UK-ESM1-0-LL, MPI-ESM1-2-HR, IPSL-CM6A-LR, and MRI-ESM2-0. Approximately 40% of the *Cerrado* flora is composed of herbaceous plants (*c*. 4,800 species), so the 2011–2040 timeframe choice aimed to match the relatively short time to maturation (i.e., from one to two years to flower) of most *Cerrado* angiosperms. We also considered different scenarios of global change, represented by the Shared Socioeconomic Pathways (SSPs). SSP1 corresponds to the sustainability scenario (optimistic), proportional to RCP2.6. SSP5 corresponds to the fossil-fuelled development scenario (pessimistic), proportional to RCP8.5 (Riahi *et al.*, 2017).

### 3.3.4. SDM training, evaluation, binarization, restriction, and transfer

We randomly split the presence data five times for each species into training (80%) and validation (20%) datasets. The five replicates account for the variability due to data splitting. We used the function “maxent” (default settings) from the R package “dismo” to fit the SDMs (Hijmans *et al.*, 2021). We fitted the MaxEnt models using the seven independent bioclimatic variables at 30 arcsecs resolution over South America. Even though our study area was the *Cerrado*, fitting the SDMs at this broader scale increases the chances of capturing the species’ full climatic niche, which improves the transferability of the SDMs over time (Chevalier *et al.*, 2022; Pang *et al.*, 2022).

We used the Continuous Boyce Index (CBI) to evaluate the goodness of fit of our SDMs. The CBI of each SDM replicate was computed separately. We used the function “contBoyce” from the R package “enmSdm” to determine CBI (Smith, 2021). We used CBI > 0.25 as the inclusion criteria, which is a conservative cut-off value since CBI > 0 would already indicate that the SDM performs better than random.

We projected the models to geographical space at a resolution of 150 arcsecs and across Brazil only to reduce the computational time (Appendix 3.12a). We binarized the niche suitability probability through a threshold that set apart suitable *vs*. unsuitable pixels (Appendix 3.12b). The threshold consisted of the 10th percentile of the niche suitability distribution of the training presence dataset (Radosavljevic and Anderson, 2014). This threshold represents the suitability cut-off that includes 90% of the highest-suitable presence points.

SDMs commonly overpredict the distribution of species. A posteriori spatial restriction routine can reduce SDM overprediction (Mendes *et al.*, 2020). We removed all suitable habitat patches that fell outside the species accessible area (i.e., 250 km radius buffer around presence points; Appendix 3.12c). Biologically, this correction removes habitat patches far from where the species have been observed to occur, i.e., areas theoretically less accessible by dispersal.

We projected our SDMs to the 2011–2040 timeframe using the forecasts of GFDL-ESM4, UK-ESM1-0-L, MPI-ESM1-2-HR, IPSL-CM6A-LR, and MRI-ESM2-0 GCMs under SSP1 and SSP5 scenarios. Then, we performed the same binarization and spatial restriction routines for the SDMs transferred to the future.

Finally, we averaged the SDMs projected using different GCMs into a single ensemble for each SSP.

### 3.3.5. Range size, species richness, and species composition

Range size represents the summed area where a given species can be found. We considered the sum of the suitable pixels obtained from the binary SDMs as the potential geographic range size (hereafter referred to as "range size"). The SDMs were projected across Brazil, hence the range size calculated here corresponds only to the species' distribution within the country. The temporal variation of the range size was expressed as "Δ range size". Δ range size was calculated in terms of percentage relative to the baseline (Equation 3.1).

$$\Delta\, range\ size\ (\%) = \frac{future\ range\ size - baseline\ range\ size}{baseline\ range\ size} \times 100 \qquad (3.1)$$

Where the *future range size* and *baseline range size* correspond to the range size estimated in the 2011–2040 and 1981–2010 periods, respectively.

Δ range size is the net difference between range size gains and losses. To get insight into Δ range size components, we also calculated range gain by summing the area that was unsuitable in the 1981–2010 period and became suitable in the 2011–2040 period. We calculated range loss using the same logic: the sum of the area that was suitable during 1981–2010 and became unsuitable during 2011–2040.

We stacked the binary SDMs (S-SDM) of all species with CBI > 0.25 into a single object using the "stack" function from the R package "raster" (Hijmans, 2021). We used the stacked map to estimate the temporal variation in species richness and composition (temporal turnover). Species richness was calculated by summing all the layers of the S-SDM. The temporal variation of the species richness was expressed as "Δ species richness" (Equation 3.2).

$$\Delta\, species\ richness = future\ species\ richness - baseline\ species\ richness \quad (3.2)$$

Where the *future species richness* and *baseline species richness* correspond to the species richness estimated in the 2011–2040 and 1981–2010 timeframes, respectively.

We used the same S-SDM to estimate the temporal species turnover. We used Simpson's index to quantify potential changes in species composition over time (hereafter referred to as the "species turnover") (Baselga, 2010). We first converted the S-SDM into a matrix where the rows were the pixels, the columns were the species, and the cells were filled with 1 when the pixel was suitable for the species and 0 when it was not. We contrasted the matrices derived from the 2011–2040 and 1981–2010 periods using the function "beta.temp" from the R package "betapart" (Baselga et al., 2021).

### 3.3.6. Elevation affiliation

We used the elevation affiliation to capture species' preferences across elevational gradients. We defined the elevation affiliation as the elevation where most of the species distribution is concentrated. We estimated the elevation affiliation of each studied species by calculating the median elevation of all valid presence points used to train and validate the SDMs. The elevation affiliation is a continuous index, so it avoids coercing the spectrum of elevation preferences into the binary lowland *vs*. montane classification. The occurrence records reflect only the species' historical elevation affiliation. So, to estimate future upslope migration rates, we first used the binary distribution maps of each species projected to the baseline (1981–2010) and future timeframes (2011–2040) to mask the elevation raster layer. The product represents the range of elevation that a given species is expected to experience over the baseline and future periods. We then extracted the elevation values for each pixel and calculated the 97.5th percentile per timeframe. We used the 97.5th percentile to represent the upper elevational limits of the species. The upslope migration rate consisted of the difference between the 97.5th percentile of the elevation affiliation in the future and the baseline timeframe. Finally, we converted the upslope migration rates to metres per decade by dividing the previous value by three, representing the number of decades between the mean point of baseline (1995) and future horizons (2025). The elevation data used over the entire study originated from the Shuttle Radar Topographic Mission (SRTM) retrieved from Brazil’s National Institute for Space Research (INPE) Ambdata project (INPE, 2014).

### 3.3.7. Data analysis

We ran a paired Student’s t-test to contrast the Δ range size, range gain, and range loss between SSP1 and SSP5 scenarios. We fitted linear regressions to test hypothesis 1: elevation affiliation negatively affects Δ range size. The sampling unit was the species. Additionally, we ran linear regressions where elevation affiliation predicts range gain and loss. We also ran paired Student’s t-tests to compare elevation affiliation in the future *vs*. baseline timeframe.

We ran a paired Student’s t-test to contrast the Δ species richness between SSP1 and SSP5 scenarios. We fitted linear regressions to test hypothesis 2: elevation positively affects Δ species richness. Elevation may covary with climatic anomalies, which can obscure the effects of elevation on Δ species richness. To account for that covariance, we performed an additional analysis that started by fitting a linear regression where the response was the Δ species richness and the predictors were the anomaly of the seven independent bioclimatic variables used in the study (anomaly = future – baseline). The sampling unit was 150 arcsec pixels across the *Cerrado*. We, then, fitted a second linear regression where the response variable was the residuals of the previous regression (Δ species richness ~ bioclimatic variables anomaly) and the predictor variable was the elevation. The residual variation of Δ species richness is independent of the climatic anomalies, so it can confirm whether elevation directly affects Δ species richness or not.

We ran a Student’s t-test to contrast the temporal species turnover (Simpson’s index) between SSP1 and SSP5 scenarios. We fitted linear regressions to test hypothesis 3: elevation positively affects species turnover. Same as before, to account for the effects of climatic anomalies on species turnover, we first estimated the effect of the bioclimatic variables’ anomaly on the temporal species turnover using linear regressions. We, then, fitted other linear regressions to unveil the effects of elevation on the residuals of the previous regression (species turnover ~ bioclimatic variables anomaly). The sampling unit remained 150 arcsec pixels across the *Cerrado*.

## 3.4. Results

### 3.4.1. Modelling species distribution

We fitted satisfactory SDMs (CBI > 0.25) for 7,398 species. 952 species were removed from the analysis due to poor model fit (CBI ≤ 0.25). The CBI of the 7,398 retained species averaged 0.72, indicating good model performance (Appendix 3.13). The 7,398 species represent 59.01% of the *Cerrado* angiosperm flora (12,052 species based on Reflora (2020)) and are spread over 174 families (94.05% of the *Cerrado* total). The precipitation of the driest month (BIO14) was the most important variable out of the seven bioclimatic variables used to fit the SDMs, followed by precipitation seasonality (BIO15; Appendix 3.14).

### 3.4.2. Direction and drivers of range shifts (hypothesis 1)

Our analyses predict that half of the studied *Cerrado* species will lose range by 2040. In terms of median values, range loss exceeded range gain under SSP1 (-9% *vs*. 6%) and SSP5 (-10.1% *vs*. 7.3%). Consequently, the median Δ range size was negative both under SSP1 (-0.4%) and SSP5 (-1.2%; Figure 3.1). Δ range size was significantly lower under SSP5 compared to SSP1 ($p = 0.01$; Appendix 3.5). 50.8% of the studied species showed a negative Δ range size under SSP1 (Figure 3.1). This percentage increased to 52% under SSP5. Our models predict that 152 species (SSP1) and 165 species (SSP5) will experience critical range contraction (i.e., Δ range size < -70%). *Cerrado* endemics accounted for 57.9% of the species with critical range contraction under SSP1 and 58.2% under SSP5.

Elevation affiliation had a negative effect on Δ range size under both scenarios of global change ($p < 0.001$; Figure 3.2). While range gain increased, range loss decreased with elevation affiliation ($p < 0.001$; Appendix 3.6; Appendix 3.15). Elevation affiliation had a median value of 587.1 m (95%CI: 103.1 –1,141.2 m). The subset of species with critical range contraction had a median elevation affiliation of 1,041.1 m (SSP1) and 1,030.6 m (SSP5). Maximum (97.5th percentile) elevation affiliation increased over time for 75.1% (SSP1) and 77.8% (SSP5) of the studied species. Median upslope migration rates were 5.8 m decade$^{-1}$ under SSP1 and 7.3 m decade$^{-1}$ under SSP5.

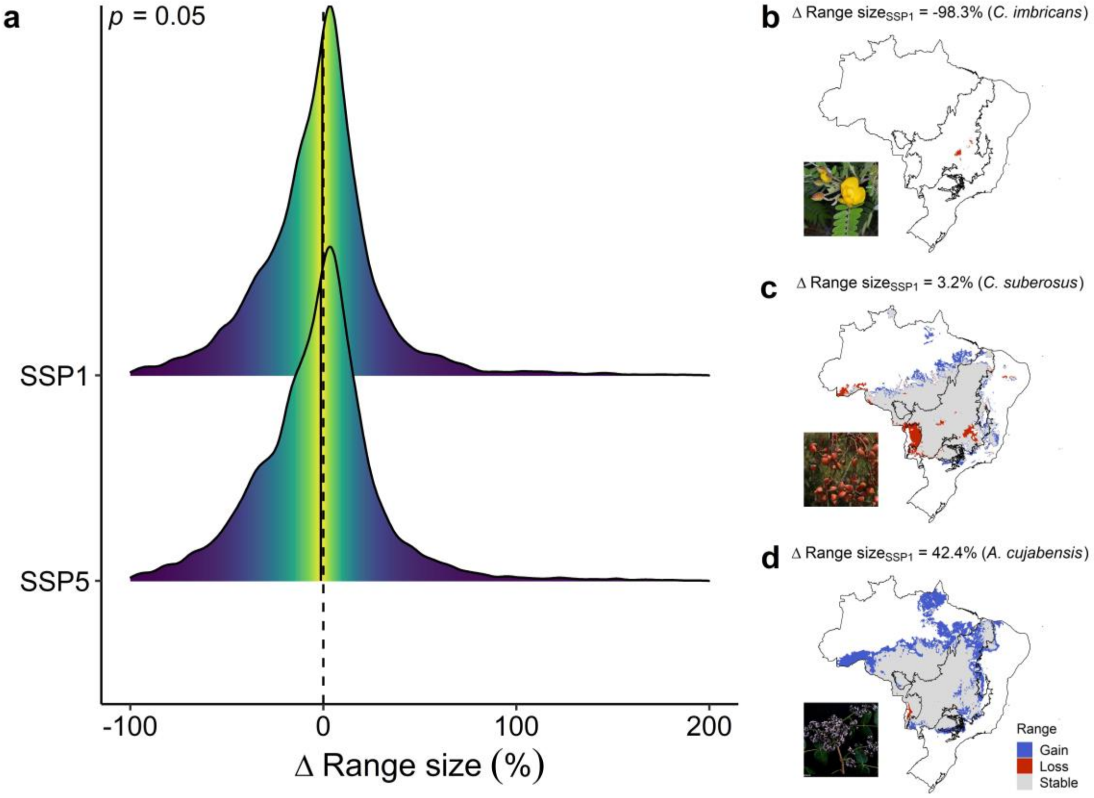
a
p = 0.05
SSP1
SSP5
-100
0
100
200
Δ Range size (%)
b
Δ Range size$_{SSP1}$ = -98.3% (C. imbricans)
c
Δ Range size$_{SSP1}$ = 3.2% (C. suberosus)
d
Δ Range size$_{SSP1}$ = 42.4% (A. cujabensis)
Range
Gain
Loss
Stable

**Figure 3.1.** Climate change impacts on the range size of *Cerrado* flowering plants. (**a**) The distribution of Δ range size for the 7,398 studied species and (**b–d**) species-specific examples. Δ range size represents the change in the potential geographic range size in the future (2011–2040) compared to the baseline (1981–2010) at the Brazil scale. Δ range size > 0 suggests range gain and Δ range size < 0 range loss. Δ range size was expressed in percentage relative to the baseline range size. The upper distribution in panel **a** corresponds to an optimistic scenario of global change (SSP1) and the lower distribution to a pessimistic scenario (SSP5). The distribution charts in panel **a** were coloured according to the tail probabilities. The dashed line marks the zero, i.e., no net change. The solid line indicates the median of the distribution. The x-axis of the panel **a** was limited to 200% to improve visualization which concealed 55 outlier species. The *p*-value at the panel **a** top right corner refers to the paired t-test comparing Δ range size under SSP1 *vs*. SSP5. Stable, gained, and lost range of (**b**) *Chamaecrista imbricans*, (**c**) *Connarus suberosus*, and (**d**) *Andira cujabensis* in the future *vs*. baseline timeframe. *C. imbricans* is a montane species (elevation affiliation = 1067 m), *C. suberosus* a mid-elevation species (elevation affiliation = 521.8 m), and *A. cujabensis* a lowland species (elevation affiliation = 391.6 m). The outer polygon depicts the Brazil border and the inner polygon the *Cerrado* limits. Δ Range size$_{\text{SSP1}}$ in panels **b–d** corresponds to the Δ range size under the SSP1.

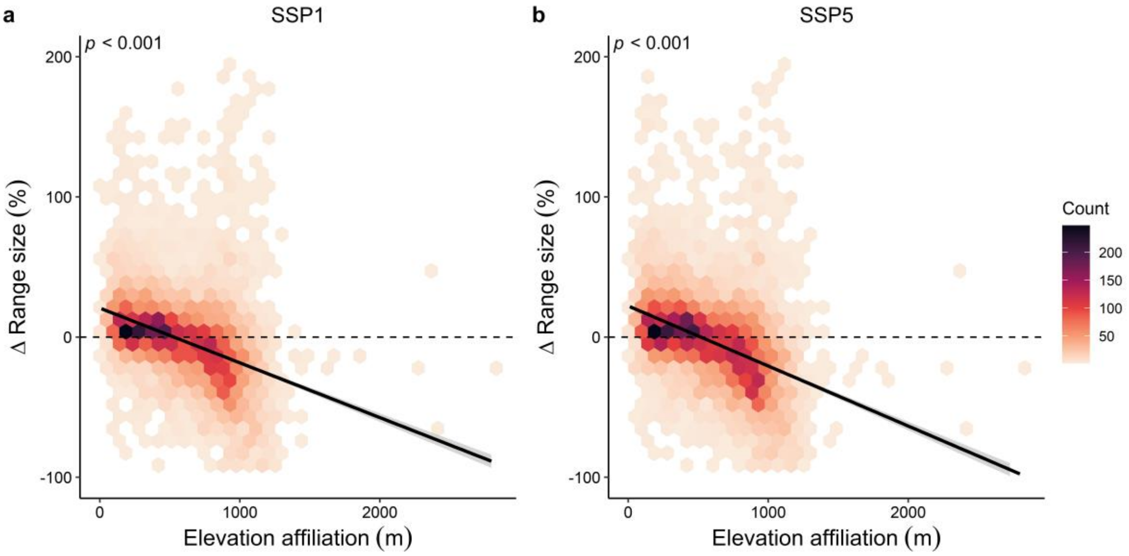

**Figure 3.2.** Relationship between range shift and elevation affiliation across *Cerrado* flowering plants. Δ range size was expressed in percentage relative to the baseline range size. Δ range size was calculated based on an (**a**) optimistic (SSP1) and (**b**) a pessimistic scenario of global change (SSP5). The solid line depicts the linear model fit. The *p*-value is shown at the top right corner. Each observation corresponds to a species. The hexagons' colour is proportional to the density of species in that area. The dashed line marks the zero, i.e., no net change. m.a.s.l. stands for metres above sea level. The X-axis was limited to 200% to improve visualization which concealed 32 outlier species.

### 3.4.3. Direction and drivers of species richness change (hypothesis 2)

Our models suggest that *c*. 70% of the *Cerrado* is expected to face climate-driven net species loss by 2040. Negative Δ species richness was projected to occur in 68.4% of the *Cerrado* area under SSP1 and 73.9% under SSP5 (Figure 3.3). The median potential species richness was 3,721 species per 150 arcsec pixel at the baseline timeframe. The median Δ species richness dropped from -71 species per 150 arcsec pixel under SSP1 (95%CI: -435–210 spp. pixel$^{-1}$) to -95 spp. pixel$^{-1}$ under SSP5 (95%CI: -469–204 spp. pixel$^{-1}$; $p < 0.001$; Appendix 3.7). Examples of regions with Δ species richness < -200 were the *Cuiabá* Depression (*Depressão Cuiabana*) and *Araguaia* Floodplain (*Planície do Araguaia*) lowlands. In contrast, the *Parecis* Plateau (*Serra dos Parecis*) and *Veadeiros* Plateau

(*Chapada dos Veadeiros*) mountains represent regions with Δ species richness > 200 species.

Elevation had a positive effect on Δ species richness under SSP1 and SSP5 ($p < 0.001$; Figure 3.4). The regression line predicted Δ species richness of -254.9 (SSP1) and -291.3 (SSP5) at sea level (i.e., elevation = 0; Appendix 3.8). Δ species richness tended to increase by one species when elevation increased by 2.9 m (SSP1) and 2.7 m (SSP5). Δ species richness was predicted to cross the zero at an elevation of 743.2 m (SSP1) and 798.9 m (SSP5). The positive relationship between Δ species richness and elevation remained statistically significant even after controlling for the effect of climatic anomalies on Δ species richness variation (Appendix 3.9).

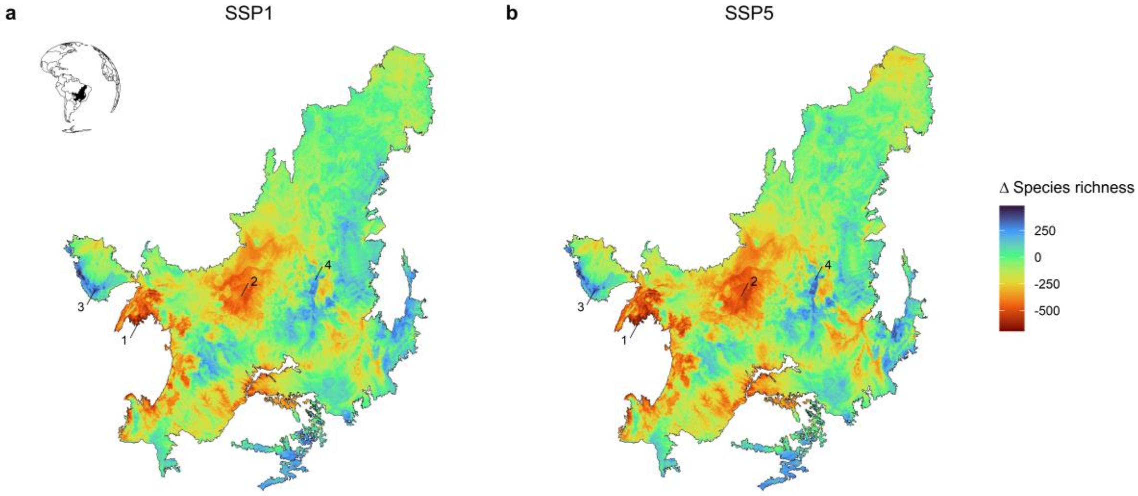

**Figure 3.3.** Temporal variation of floristic richness under climate change in the *Cerrado*. Δ species richness represents the change in potential species richness in the future (2011–2040) compared to the baseline (1981–2010). Δ species richness > 0 suggests species gain and Δ species richness < 0 species loss. Δ species richness was estimated based on an (**a**) optimistic (SSP1) and (**b**) a pessimistic scenario of global change (SSP5). Site-specific examples are labelled as follows: (1) *Cuiabá* Depression (*Depressão Cuiabana*) and (2) *Araguaia* Floodplain (*Planície do Araguaia*) exemplify lowlands with negative Δ species richness and (3) *Parecis* Plateau (*Serra dos Parecis*) and (4) *Veadeiros* Plateau (*Chapada dos Veadeiros*) exemplify mountains with positive Δ species richness.

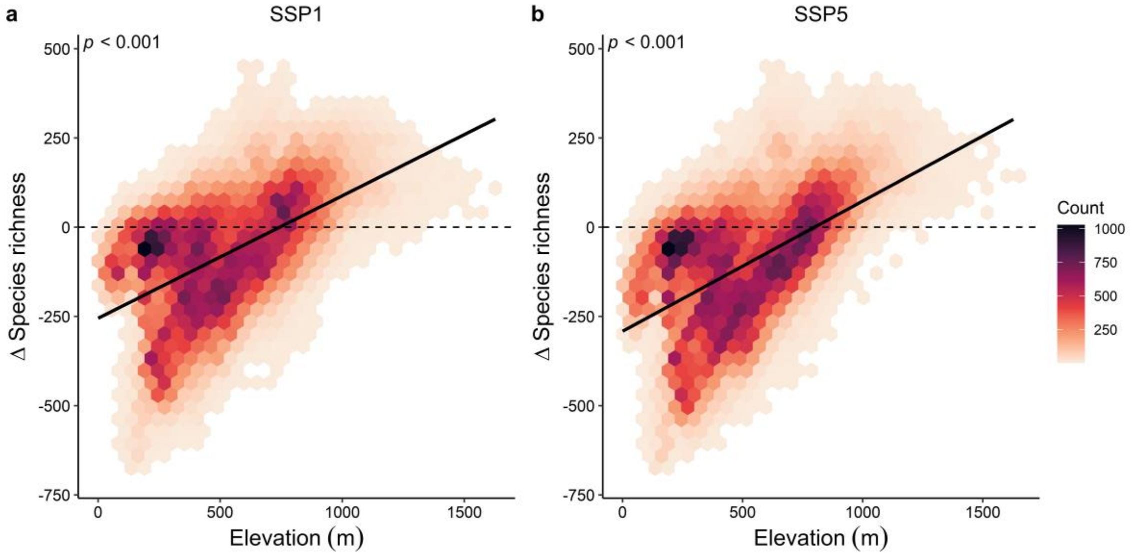

**Figure 3.4.** Effect of elevation on the temporal variation of floristic richness in the *Cerrado*. Δ species richness represents the change in potential species richness in the future (2011–2040) compared to the baseline (1981–2010). Δ species richness > 0 suggests species gain and Δ species richness < 0 species loss. Δ species richness was calculated based on an (**a**) optimistic (SSP1) and (**b**) a pessimistic scenario of global change (SSP5). The solid line depicts the line fitted to the relationship between the Δ species richness and the elevation. The *p*-value is shown at the top right corner. Each observation corresponds to a species. The hexagons' colour is proportional to the density of species in that area. The dashed line marks zero.

### 3.4.4. Direction and drivers of species temporal turnover (hypothesis 3)

We predict a shift in the composition of *Cerrado* angiosperm flora under climate change. The Simpson's turnover index was higher under SSP5 (median of 0.08) compared to SSP1 (median of 0.07; $p < 0.001$; Figure 3.5). The median turnover index was 5.5 (SSP1) and 5.1 times (SSP5) higher than the median nestedness index (Appendix 3.16). Regions showing the highest species turnover (> 0.1) included the Upper *São Francisco* Plateaus (*Serras do Alto São Francisco*) and *Parecis* Plateau (*Serra dos Parecis*). Meanwhile, the *Araguaia* Floodplain

(*Planície do Araguaia*) and *Paranã* Depression (*Vão do Paranã*) illustrate regions displaying the lowest species turnover values (< 0.05).

Elevation had a positive effect on species turnover under both SSPs ($p < 0.001$; Figure 3.6). Pixels at sea level (i.e., elevation = 0) tended to have a turnover index of 0.06 under SSP1 and SSP5 as inferred by the regression intercept (Appendix 3.8). Species turnover increased at a rate of $2.4 \times 10^{-5}$ per metre above sea level under SSP1 and $3.1 \times 10^{-5}$ under SSP5. The effect of elevation on species turnover remained positive and statistically significant after accounting for the effects of climatic anomalies on the turnover index (Appendix 3.9).

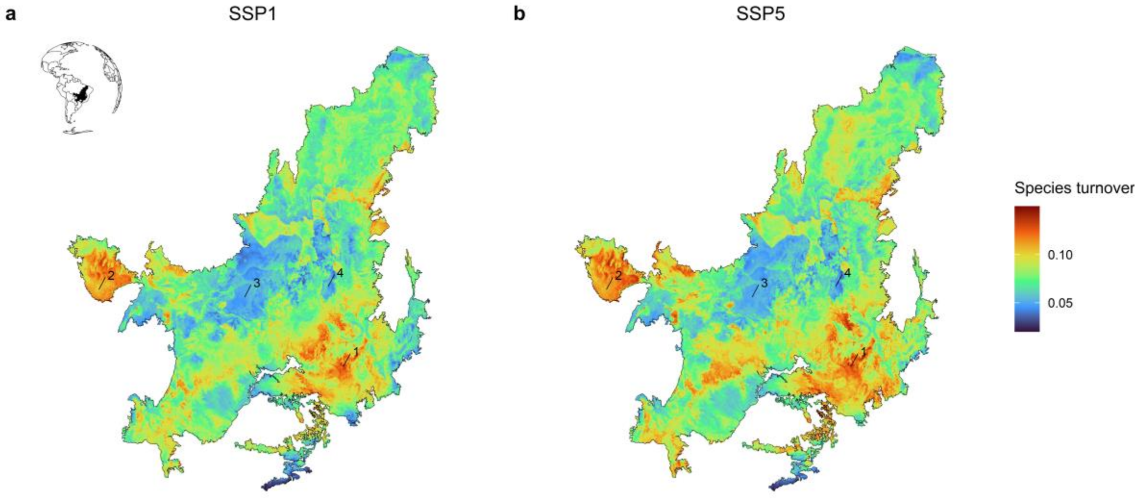

**Figure 3.5.** Temporal floristic turnover under climate change in the *Cerrado*. Species turnover represented by Simpson's index which reflects the species replacement in the future (2011–2040) compared to the baseline horizon (1981–2010). Turnover = 0 suggests no change in species composition and turnover = 1 suggests complete species replacement. Species turnover was estimated based on an (**a**) optimistic (SSP1) and (**b**) pessimistic scenario of global change (SSP5). Site-specific examples are labelled as follows: (1) Upper *São Francisco* Plateaus (*Serras do Alto São Francisco*) and (2) *Parecis* Plateau (*Serra dos Parecis*) exemplify mountains with high species turnover and (3) *Araguaia* Floodplain (*Planície do Araguaia*) and (4) *Paranã* Depression (*Vão do Paranã*) exemplify lowlands with low species turnover.

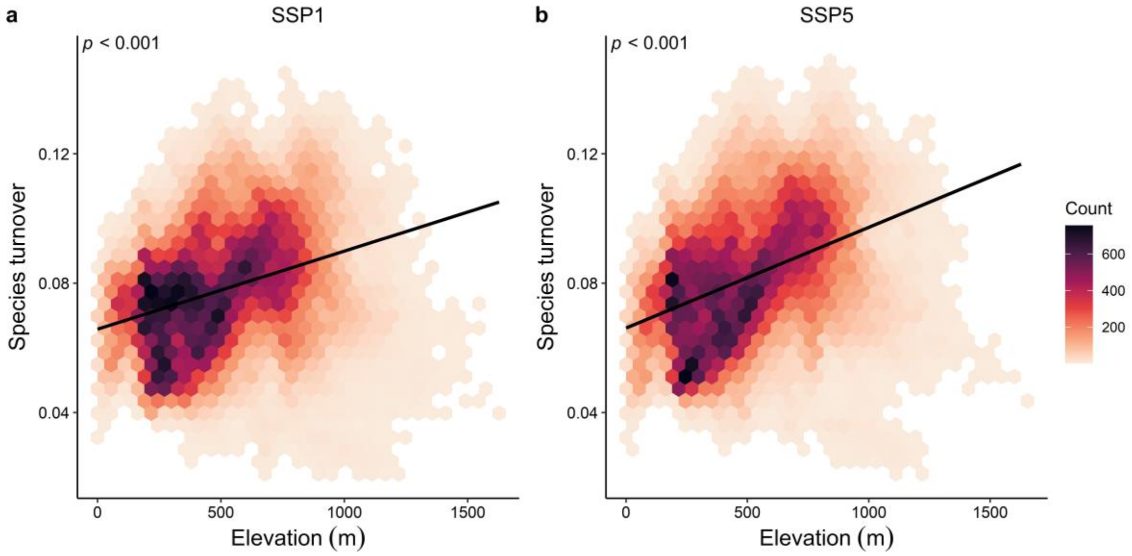

**Figure 3.6.** Effect of elevation on *Cerrado* temporal floristic turnover. Species turnover represented by Simpson's index which reflects the species replacement in the future (2011–2040) compared to the baseline horizon (1981–2010). Turnover = 0 suggests no change in species composition and turnover = 1 suggests complete species replacement. Species turnover was calculated based on (**a**) an optimistic (SSP1) and (**b**) a pessimistic scenario of global change (SSP5). The solid line depicts the line fitted to the relationship between the species turnover and the elevation. The *p*-value is shown at the top right corner. Each observation corresponds to a species. The hexagons' colour is proportional to the density of species in that area.

## 3.5. Discussion

Our results show that half of *Cerrado* plant species will experience range contraction by 2040. These range shifts translate to species losses, gains, and replacements at the community level. Elevation plays a key role in regulating how *Cerrado* angiosperms may respond to future climate change because as the ranges of montane species decrease, those of lowland species will increase. Up to three-quarters of *Cerrado* flowering plants will most likely have their ranges centred at higher elevations by 2040. Upslope migration rates are estimated at around 5–7 m decade$^{-1}$. At the community level, net species loss is predicted to peak in the lowlands, but mountains are likely to have a net species gain and be the hotspots of temporal species turnover. Finally, the more pessimistic climate change scenario (SSP5) leads to more net range loss, net species loss, and species replacement in the *Cerrado* relative to the more optimistic scenario (SSP1). We discuss below whether our data support our hypotheses and how our findings can inform conservation and restoration decision-making.

### 3.5.1. Montane species are more vulnerable to climate change than lowland species

We show that climate change will drive range shrinkage among *Cerrado* angiosperms and therefore data support hypothesis 1. However, the difference between species experiencing range loss *vs*. gain was small, only 0.8% (SSP1) to 2% (SSP5). At the global scale, the proportion of climate “winners” and “losers” tends to be similar across taxonomic groups and biomes (Dornelas *et al.*, 2019). Elevation affiliation emerges as a key modulator of how climate change impacts the range of *Cerrado* plant species. Range contractions are more likely to occur among montane species, potentially the future “losers” (Dullinger *et al.*, 2012). In the *Cerrado*, species facing a high risk of extinction (i.e., range contraction > 70%) were affiliated to elevations around 1,000 m (e.g., *Chamaecrista imbricans*, Figure 3.1b), but range expansion was common among species that typically occur at lower elevations (e.g., *Andira cujabensis*, Figure 1d), potentially the future “winners”. The land area often decreases as elevation increases in pyramid-shaped mountain ranges (the case of *Cerrado*). Hence, the lack of habitat higher up constrains the ability of montane species to migrate upslope at the rates that lowland species may do (Benito Garzón, Sánchez de Dios and Sainz Ollero, 2008; Bell, Bradford and Lauenroth, 2014). Alternatively, montane taxa could migrate to new mountains where they can find suitable habitats. However, mountain ranges are often disconnected (Flantua, Dea and Hooghiemstra, 2019), which tends to drive the patchy distribution of most montane species (Rahbek *et al.*, 2019). In the *Cerrado,* this habitat discontinuity constrains the ability of montane species to keep up with climate change by migrating latitudinally or longitudinally. Therefore, habitat shortage and patchiness probably synergistically drive the vulnerability of montane species to climate change in the *Cerrado*.

*Cerrado* flowering plants will need to move from five to seven metres upslope per decade to track climate change. This estimate aligns with a recent global systematic review reporting an average upslope migration rate of 6.9 m decade$^{-1}$ for plants (Rubenstein *et al.*, 2023). Even though lowland species show potential for migrating upwards, three factors may constrain their movement. First, dispersal and colonization limitations are common features of *Cerrado* plant assemblages (Le Stradic, Fernandes and Buisson, 2018; Arruda *et al.*, 2021). For instance, typical *Cerrado* families, such as the Poaceae and Melastomataceae, display a suit of traits that limit propagule movement and establishment. These include fire-triggered flowering (Pilon *et al.*, 2018; Fidelis and Zirondi, 2021; Zirondi, Ooi and Fidelis, 2021; Fontenele and Miranda, 2022), a high proportion of embryoless seeds (Le Stradic *et al.*, 2015; Kolb, Pilon and Durigan, 2016; Fontenele, Cruz-Lima, *et al.*, 2020), and seed dormancy (Silveira *et al.*, 2012; Dayrell *et al.*, 2017; Escobar, Silveira and Morellato, 2018). Secondly, several *Cerrado* plants are edaphic specialists and adapted to acidic, aluminium-rich, phosphorus-impoverished quartzite soils, typical of much of the *Cerrado* (Abrahão et al., 2019; Haridasan, 2008; Oliveira et al., 2015; Teodoro et al., 2019). These species may find suitable climate upslope, but not suitable edaphic conditions for their establishment and growth (Van De Ven, Weiss and Ernst, 2007). Thirdly, half of the *Cerrado* native vegetation cover has been converted to alternative land uses, mainly monoculture pastures and crops (Souza *et al.*, 2020; Mapbiomas, 2021), and the remaining native vegetation is often embedded in fragmented landscapes (Aguiar *et al.*, 2016; Rosan *et al.*, 2022). The lack of habitat quantity and connectivity can further hamper the chance of propagules dispersing to new sites. Therefore, upslope migration in the *Cerrado* will depend not only on the elevational affiliation of the species, but also on its dispersal abilities, edaphic requirements, and landscape configuration.

### 3.5.2. Lowlands are prone to climate-driven local extinctions

Net species losses will be widespread across the *Cerrado* by 2040 and particularly intense at lower elevations, in line with hypothesis 2. The range expansion predicted to happen among lowland species does not imply that lowlands will benefit from climate change. Lowland/mid-elevation species will lose range at low elevations, where they historically occurred, and expand their range upslope (e.g., *Connarus suberosus*) (Rumpf *et al.*, 2018). The result is net range gain for migrant species, but species richness declines for the assemblage from which these species migrated. The southwest part of the *Cerrado* offers a good example of these phenomena. Even though species losses were widespread across the region, net species losses were more intense at low elevations (e.g., *Cuiabá* Depression) compared to high-elevation areas (e.g., *Parecis* Plateau; Figure 3). The *Cerrado* lowland flora is, therefore, likely to harbour a subset of its historical species pool under climate change, supporting the lowland biotic attrition hypothesis (Colwell *et al.*, 2008; Bertrand *et al.*, 2011; Freeman *et al.*, 2018).

Two processes could offset future biotic attrition in the *Cerrado*'s lowlands. First, migration from other biomes leading to the arrival of non-*Cerrado* species adapted to warmer climates (see Anderson et al., 2012). Second, niche truncation where the modern climatic envelope of lowland species does not reflect their true fundamental niche (Feeley and Silman, 2010). Successful migrations of species from other biomes, such as seasonally tropical dry forests in the *Caatinga*, are unlikely as they do not possess fire and edaphic adaptations needed to thrive in fire-prone and P-impoverished savannas that cover *c*. 80% of the *Cerrado* (Simon and Pennington, 2012). Furthermore, even correcting for realized *vs.* fundamental niche mismatch was not enough to prevent widespread species loss in Amazon lowlands (Feeley and Silman, 2010). Assuming low cross-biome migration potential and low niche truncation, our findings suggest that climate change threatens low-elevation *Cerrado* areas by the erosion of local species pools as a consequence of upslope migration.

### 3.5.3. Mountains are likely to harbour a novel flora in a warmer world

Climate change will drive species replacement across the *Cerrado*, especially at higher elevations, consistent with hypothesis 3. The fact that mountains had net species gains coupled with species turnover further suggests that these regions can be refugia for species tracking climate change. Previous studies using hindcasted species distribution models suggested that *Cerrado* mountains played a role as refugia over past climatic events (Werneck *et al.*, 2012; Bueno *et al.*, 2017). Examples are the *Veadeiros* and Upper *São Francisco* Plateaus (Figures 3 and 5). However, Bueno et al. (2017) proposed refugia areas based on species affiliated with mid-elevation areas (500–700 m), such as *C. suberosus*, affiliated to elevations *c.* 522 m. The *Cerrado*'s mountain ranges may have provided climatic refugia primarily to low- and mid-elevation species, instead of montane ones, in the past. Our findings extend this idea to future climate change. While lowland species find climatic refugia upslope, mountains become unsuitable to present-day montane taxa, exposing them to extinction risk (Dullinger *et al.*, 2012; Freeman *et al.*, 2018).

The models suggest that the number of immigrating lowland species will exceed the number of montane species becoming locally extinct, leading to a net species gain in the *Cerrado* mountains. Transplant experiments and process-based simulations demonstrate that lowland species may outcompete montane species as they move uphill and lead to biotic homogenization (Svenning *et al.*, 2014; Alexander, Diez and Levine, 2015). Our estimates of species richness in the *Cerrado* mountains can be considered optimistic since our SDMs do not account for new competitive interactions that may emerge from upslope migration. *Cerrado* mountains are, therefore, prone to undergo a floristic turnover in the future, characterized by the arrival of lowland “refugee” taxa due to upslope migration and the decline of mountaintop “resident” taxa due to climatic suitability loss and potentially competitive exclusion.

### 3.5.4. Model assumptions and scope

Ecological models are simplified, yet useful representations of natural systems and SDMs are no different (Elith and Leathwick, 2009). We consider our predictions best-case scenarios due to two underlying assumptions. First, we assumed that *Cerrado* flowering plants can colonize new habitats by 2040 as long as they are within 250 km of a known occurrence point. Both unrestricted and no-dispersal scenarios are unrealistic, as no plant has either infinite or zero dispersal potential (Cain, Milligan and Strand, 2000; Nathan, 2006). The 250 km threshold lies in between unlimited and zero dispersal scenarios and is optimistic given maximal seed dispersal distance tends to be below 100 km (Poulsen et al., 2021, megafauna dispersal). Second, we assumed that only climatic suitability and proximity to an occurrence point constrain the movement of species through the landscape. It is known, however, that vegetation loss and fragmentation, which are extensive in the *Cerrado*, will certainly limit species dispersal (Ferraz *et al.*, 2021; Sousa *et al.*, 2021). Since the scope of our SDMs was to represent optimistic assumptions, we can then foresee the effects of climate change on the *Cerrado* flora under the best-case scenario. We show that climate change will put *Cerrado* angiosperms at risk even if there were no affiliation to particular soils and fire regimes or if these plants could move freely over an extensive area. Failing in the transition to a sustainable future (SSP1) will further intensify the impacts of climate change on the *Cerrado* flora. Specifically, range contractions, local extinctions, and species replacement are expected to occur even if we limit global warming to 1.5 °C (SSP1). All these responses will escalate in a 4 °C warmer future (SSP5). Global action towards climate change mitigation is, therefore, fundamental to reduce biodiversity loss that will happen in places such as the *Cerrado*.

### 3.5.5. Perspectives for conservation and restoration planning

Our data can assist conservation and restoration decision-makers in adapting to climate change. The species-specific distribution maps are useful to tailor conservation actions to species that are vulnerable to climate-driven extinction.

We flagged up to a hundred species facing range contractions exceeding 70% until 2040. For instance, the legume *C. imbricans* is expected to lose 98.3% of its range (Figure 1b), which will be restricted to a small habitat patch in Brazil's Central Plateau (*Planalto Central*). Conservation planners can target regions where the distribution of climate "loser" species, such as *C. imbricans*, will remain stable for the creation of protected areas (Groves *et al.*, 2012; Sales and Pires, 2023). Besides, the SDMs generated here can also guide assisted migration programmes, i.e., tracking climate change by introducing species in newly suitable habitats (Mclachlan *et al.*, 2007; Guisan *et al.*, 2013; Hällfors, Aikio and Schulman, 2017; McKone and Hernández, 2021).

Historical baselines may offer limited insight for selecting species for ecosystem restoration as species numbers and identities are changing over time due to climate change (Harris *et al.*, 2006; Hobbs, Higgs and Harris, 2009; Higgs *et al.*, 2014). S-SDMs can offer practitioners lists of species that will persist over time in a given area, thus boosting climate change resilience in restoration projects (Butterfield *et al.*, 2017; Fremout *et al.*, 2020). The species selection for restoration can be further refined by crossing S-SDM recommendations with the species available on the market as seeds and seedlings (Silva *et al.*, 2022; Coutinho, Carlucci and Cianciaruso, 2023). We have made available an R script based on the analyses presented here for (1) conservationists to visualize the current and future distribution of all the 7,398 species studied here, and (2) restoration practitioners to generate lists of species prone to occur in a specified coordinate in the future (2040).

### 3.6. Conclusion

Elevation mediates how *Cerrado* flora will respond to climate change. Approximately half of the species will lose range and half will gain range, meaning a balance between climate “winners” and “losers”. Moreover, range loss is more intense among montane species (“losers”) than lowland species (“winners”) since the latter can migrate upslope while the former cannot. Under climate change, lowlands are left with a diminished species pool as species losses surpass species gains. Conversely, the arrival of new species at high elevations outstrips the number of species going locally extinct, resulting in a net species gain and compositional turnover in the mountains. We anticipate that our predictions capture the best-case scenario of how climate change may impact *Cerrado* angiosperms. The realized impact will depend, among other factors, on whether we limit global warming to 1.5 °C as well as the dispersal ability of species and habitat quantity and connectivity. Climate change mitigation is key for safeguarding the integrity of *Cerrado* ecosystems in the long term. Additionally, we urge the incorporation of climate adaptation measures into conservation and restoration decision-making to increase climatic resilience in the *Cerrado*.

# Chapter 4

Courtesy of Bárbara Pacheco

# Chapter 4 – Operationalizing climate-oriented seed provenancing for ecosystem restoration: a case study in the Brazilian *Cerrado*

This chapter is **under review** in the Journal of Applied Ecology.

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### 4.1. Abstract

Seed provenance is a key step in ecological restoration planning especially under climate change. Seed provenance strategies range from the composite (reproducing natural gene flow) to the predictive (focusing on future climate adaptation) and climate-adjusted (a combination of the previous strategies). Yet, implementing different seed provenance strategies remains a challenge. To fill this methodological gap, we developed the **C**limate-**O**riented **S**eed **S**ourcing **T**ool (COSST), a framework capable of suggesting priority areas for seed collection and designing seed mixes from vendors according to the provenancing set by the user (composite, predictive, or climate-adjusted) and the restoration site. The tool derives its inputs from Species Distribution Models (SDMs), which require occurrence and climate data only. COSST accommodates multiple climatic variables with species-species weights based on the SDMs. The framework also accounts for uncertainties between climate forecasts used in the calculations. We demonstrated COSST flexibility using the Brazilian *Cerrado* as a case study. The tool was successful in tailoring the predictions across different provenance strategies, restoration sites, and focal species. It was possible to produce maps depicting the best areas for collecting seeds of a species to restore a given area as well as estimating the fraction of seeds to be purchased from different seed suppliers. Our framework has the potential to guide where to collect/buy seeds for species lacking genetic information, the case of a substantial proportion of the tropical flora, where ecosystem restoration is of paramount importance.

## 4.2. Introduction

Ecosystem restoration is fundamental to reducing and reversing biodiversity loss and the erosion of ecosystem services (IPBES, 2018; Leclère *et al.*, 2020). However, positive biodiversity outcomes require restoration projects to be successful over long periods in the face of continued climate change (Prober *et al.*, 2019; Zabin *et al.*, 2022). Extreme climatic events can push a restoration site back to a degraded state (Suding, Gross and Houseman, 2004; Qie *et al.*, 2019), making climate change a key challenge to restoring ecosystems worldwide (Frietsch *et al.*, 2023). Seeds are the main basis for active restoration on land and they carry part of the genetic pool of the population they were sourced from. Practitioners can take advantage of natural genetic variability to select seed genotypes more resilient to future climates and climate extremes (Broadhurst *et al.*, 2008; Hancock and Hughes, 2014; Havens *et al.*, 2015; Nolan *et al.*, 2023). The origin of seeds is known to affect seed germination rates (Gallagher and Wagenius, 2016; Lortie and Hierro, 2022), as well as survival (Gross, Fatemi and Simpson, 2017; Etterson *et al.*, 2020), growth (Gellie *et al.*, 2016; Notivol *et al.*, 2020), and phenology of adult plants (Giencke *et al.*, 2018; Rushing, Flint and Shaw, 2021; Bucharova *et al.*, 2022; Pizza, Foster and Brudvig, 2023; Woolridge *et al.*, 2023). Therefore, seed provenance decision-making has the potential to climate-proof restoration projects (Vitt *et al.*, 2022).

Seed provenancing guidelines have been debated in the ecological restoration community (Dupré la Tour, Labatut and Spiegelberger, 2020). Prioritizing local seed provenance (i.e., **local provenancing**) is a longstanding principle based on the assumption that local genotypes are adapted to local restoration site conditions. The concept of local is often subjective as nativity is a gradient rather than a discrete unit (Dupré la Tour, Labatut and Spiegelberger, 2020). Therefore, arbitrary buffers around the restoration site representing the “local population” often constrain seed supply capacity in detriment to conform with the local provenancing principles (Gibson-Roy *et al.*, 2021). Furthermore, the strict use of local seeds may come at the cost of inbreeding depression due to deleterious allele proliferation and loss of genetic variation (McKay *et al.*, 2005). Finally, local seeds might instead show maladaptation as local climate regimes depart from the conditions the genotypes evolved in (Wilczek *et al.*, 2014), jeopardizing restoration's long-term success.

Other strategies have been proposed as an alternative to local provenancing (Breed *et al.*, 2018). The **composite provenancing** addresses the genetic diversity issue by allowing the contribution of several populations to the seed mix (Aitken and Whitlock, 2013). In this strategy, the quantity of seeds collected from each population increases as one moves closer to the restoration site, mimicking natural genetic flow (Havens *et al.*, 2015). The **predictive provenancing** addresses the maladaptation issue by favouring seed collection in populations theoretically adapted to the future climate at the restoration site (Broadhurst *et al.*, 2008; Havens *et al.*, 2015). The predictive strategy has been criticized due to the risk of outbreeding depression (Bucharova *et al.*, 2019) and to aid that, the **climate-adjusted provenancing** was developed, which mixes local seeds with non-local seeds from populations that match the forecasted climate. The climate-adjusted provenancing lies in between the composite and predictive strategies, maximizing climate adaptiveness and genetic variation while minimising genetic risks (Prober *et al.*, 2015).

It remains a challenge to implement climate-oriented seed provenance strategies, such as climate-adjusted and predictive provenancing. Conventionally, seed transfer zones (i.e., areas sharing similar genomes) have been used to support provenancing decision-making (Jørgensen *et al.*, 2016; Durka *et al.*, 2017). Despite progress made in accounting for climate change when designing such zones (Shryock, DeFalco and Esque, 2018; Fremout *et al.*, 2021; Marinoni *et al.*, 2021), a fundamental limitation remains the availability of within-species genetic diversity data. The tropics are a key global target of restoration efforts (Strassburg *et al.*, 2020) but population-scale genetic information is especially scarce for tropical plant species. As an alternative to a genetic approach, mapping contemporary climates that are analogous to the predicted future climate at the restoration site may be useful to guide seed-sourcing decisions. However, the climate analogous approach often weights different aspects of climate evenly (e.g., annual rainfall, temperature), which are known to affect species differently (Harrison *et al.*, 2017; Harrison, 2021; St.Clair *et al.*, 2022). Furthermore, climatic forecasts vary considerably between Global Circulation Models (GCMs), which generates uncertainty in designing climate-smart seed mixes. Effective restoration planning requires, therefore, a novel seed-provenancing approach which encompasses species-specific sensitivities to different climatic variables, controls for climatic forecast uncertainties across the space, and is practical to implement.

Here we introduce the **C**limate-**O**riented **S**eed **S**ourcing **T**ool (COSST), a framework designed to operationalize seed provenance strategies for ecosystem restoration based on Species Distribution Models (SDMs). The tool provides seed-provenancing guidance in the absence of genetic and experimental data. COSST identifies priority areas for sourcing seeds to restore a target site specified by the user. When seed collection sites of commercial species are known, COSST can estimate the percentage of seeds to be purchased from different vendors. The tool allows the user to generate predictions based on three seed provenance strategies alternative to local provenancing: composite (not climate-oriented), predictive (fully climate-oriented), or climate-adjusted (balance between the previous ones). COSST weights climatic variables by their relative importance derived from SDMs and controls for the uncertainty in climate projections in the case of climate-adjusted provenancing. First, we describe the mathematical basis of the tool. Then, we demonstrate its applicability in the Brazilian *Cerrado*, a tropical global biodiversity hotspot. To exemplify its flexibility, we apply the tool to two actual restoration sites (~ 650 km apart), for single and multiple restoration-priority species (N = 3), and under the three focal provenance strategies.

## 4.3. Material and methods

### 4.3.1. The Climate-Oriented Seed Sourcing Tool (COSST)

The COSST framework (Figure 4.1) generates a raster layer where the cell values (i.e., COSST score) correspond to the priority of the pixel as a seed source given the species of interest and target site for restoration. The target site is defined as the place to be restored, while the sourcing site is the place where seeds will be collected. COSST produces three raster layers, one for each seed provenance strategy (composite, climate-adjusted, and predictive, see introduction for definitions). When commercial seed sources are known, the COSST score can be extracted at the source sites and the fraction of seeds that should be purchased from each seed vendor operating at these sites can be derived.

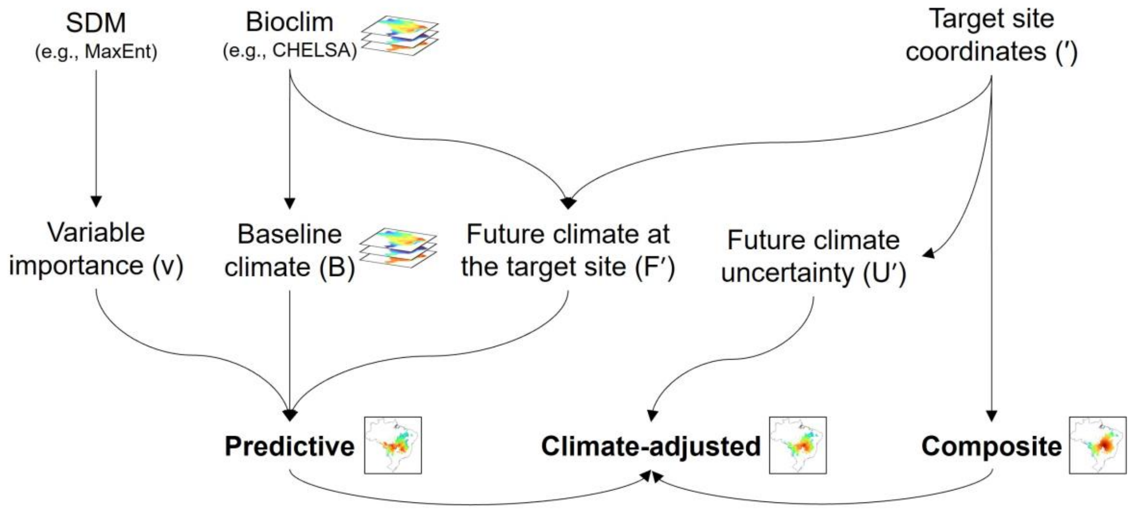


**Figure 4.1.** Climate-adjusted seed sourcing tool (COSST) data flow. Inputs consist of the species distribution model (SDM) outputs as well as bioclimatic layers (Bioclim) and the coordinates of the target site. The tool calculates a climate match layer (C) used to inform predictive provenancing and a geographical proximity layer (P) used to inform composite provenancing.

### 4.3.2. Input data

The first input to COSST are SDMs. Presence-only SDM algorithms, such as MaxEnt, require only species occurrence data and gridded layers of environmental data used to model the distribution of the species. Testing for multicollinearity amongst the environmental variables is essential to avoid overfitting SDMs. The SDM outputs used here are the species range map (R) and the relative importance of the environmental variables (v) to predicting R. R is the binary (or thresholded) projection of the SDM, representing the range of the species inferred from its climatic requirements. R sets the spatial scale of COSST predictions by default, but the user can reduce the scale of the predictions by cropping them *a posteriori*. In the case of MaxEnt, v corresponds to the permutation importance of the environmental variables. COSST also requires the same baseline bioclimatic data (B) used to run the SDMs (e.g., 1981–2010) and the same data for a future timeframe (F, e.g., 2011–2040). The last input to COSST is the target site coordinates.

### 4.3.3. Composite seed provenance strategy

COSST implements composite provenancing by calculating the Euclidean distance (D) between each potential seed source pixel and the target site. D is normalized and subtracted from 1, returning the proximity of each seed source pixel to the target site (Equation 4.1).

$$\mathrm{Composite} = 1 - scale(\mathrm{D}) \tag{4.1}$$

The normalization function rescales the data to vary between 0 and 1 (Equation 4.2).

$$scale(\mathrm{x}) = \frac{\mathrm{x} - \mathrm{x_{min}}}{\mathrm{x_{max}} - \mathrm{x_{min}}} \tag{4.2}$$

### 4.3.4. Predictive seed provenance strategy

COSST implements predictive provenancing by calculating the similarity between the future climate at the target site and the baseline climate at the seed source sites, hereafter the future climate match (C). We recommend that COSST is run with an average of GCMs forecasts. We first extract the future bioclimatic variables at the target site ($F_i'$) and subtract $F_i'$ (vector) from $B_i$ (raster). The product of which is normalized and inversed by subtracting it from 1 (Equation 4.3) to generate the climate match of variable *i* ($C_i$), corresponding to the similarity between the pixel's baseline climate and the target site's future climate (Equation 4.3).

$$\mathrm{C}_i = 1 - scale(|\mathrm{B}_i - \mathrm{F}_i'|) \tag{4.3}$$

Where *i* represents one of the 19 bioclimatic variables. $C_i$ values are multiplied by the bioclimatic variables derived from the SDM ($v_i$) to weigh each by their importance. Note that $v_i$ must be expressed as a fraction and not a percentage. The predictive provenancing optimization is achieved by summing and normalizing the bioclimatic layers (*n* being the number of variables; Equation 4.4).

$$\text{Predictive} = \sum_{i=1}^{n} \mathrm{C}_i \times \mathrm{v}_i \tag{4.4}$$

### 4.3.5. Climate-adjusted seed provenance strategy

COSST implements climate-adjusted provenancing by summing the composite *vs*. predictive provenancing scores. We included a climate uncertainty parameter (U′) defined as the standard deviation of the future climate at the target site across the GCMs. We used U′ to weight C, so the impact of future climate match for climate-adjusted provenancing decisions is lower in sites where the future climate is uncertain. The tool calculates the normalized standard deviation of each bioclimatic variable across GCMs ($\sigma F_i$). A $\sigma F_i$ equal to 1 corresponds to a pixel with the greatest GCM divergence for variable *i*. $\sigma F_i$ is multiplied by the importance of the bioclimatic variable *i* ($v_i$). We sum and normalise all bioclimatic variables (1 to *n*; Equation 4.5). Finally, COSST determines the uncertainty of climate forecasts at the target site (U′) by extracting U at the coordinate ′ (Equation 4.6).

$$\mathrm{U} = \sum_{i=1}^{n} scale(\sigma \mathrm{F}_i) \times \mathrm{v}_i \tag{4.5}$$

$$\mathrm{U}' = \mathrm{U} \cap {}' \tag{4.6}$$

The climate-adjusted provenancing score is given by Equation 4.7.

$$\text{Climate-adjusted} = scale\big((\text{Predictive} \times \text{U}') + \text{Composite}\big) \qquad (4.7)$$

### 4.3.6. Case study: The Brazilian *Cerrado*

We applied COSST to the Brazilian *Cerrado*, a region that covers a quarter of Brazil's territory. Tropical savannas and grasslands are the dominant biome in the *Cerrado* region, representing 78% of the vegetation cover before large-scale human occupation (Rodrigues *et al.*, 2022). About 12,000 flowering plant species are native to the *Cerrado* and 40% of this flora is endemic (Zappi *et al.*, 2015). However, half of the *Cerrado* native vegetation has been lost to cattle ranching and extensive agriculture (MapBiomas, 2023). The combination of high endemism levels and rapid land-use change has made the Brazilian *Cerrado* a global "hotspot" for biodiversity conservation (Myers *et al.*, 2000) and ecological restoration (Strassburg *et al.*, 2020). Brazil's ambition is to restore 2.1 Mha of *Cerrado* vegetation by 2030 (MMA, 2017). Seed suppliers led by indigenous peoples and local communities that harvest, process and sell seeds of native species (Schmidt *et al.*, 2019), play a major role in Brazil's ecosystem restoration strategy (Urzedo *et al.*, 2020). Local adaptation to climate has already been identified among *Cerrado* plants (Appendix 4.1), supporting the use of climate forecasts to underpin seed provenance decision-making. Therefore, providing practical guidelines on seed mix design, especially seed provenancing, will be key to achieving national restoration pledges.

### 4.3.7. Applying COSST to realistic scenarios

We demonstrate COSST using two examples: (example 1) mapping seed sourcing priority areas to restore a particular site and (example 2) estimating seed demand from multiple suppliers. In both examples, we explore the outcomes of different seed provenance strategies (composite, climate-adjusted, and predictive) for two target sites using first one and then three species. The two target sites are restoration projects 653 km apart. The first is a mining site in Niquelândia (State of Goiás; 14° 21' 0.3168" S 48° 24' 0.0468" W, 1,084 m.a.s.l.;

for more info, see https://www.rsc.org.br/aguascerratenses/). Mining activities in the region started approximately in 1994 and the soil remains exposed (MapBiomas, 2023). The second is an abandoned Eucalyptus plantation in Montezuma (State of Minas Gerais; 15° 20’ 10.8852” S 42° 24’ 34.6104” W, 1,105 m.a.s.l.; for more info, see https://www.coletoresgeraizeiros.com.br/). *Eucalyptus* sp. trees were planted approximately in 1997 and the plantation was abandoned in 2012 (MapBiomas, 2023).

We focus on the *Caryocar brasiliense* Cambess. (*pequi*) for the single-species examples because it is a key species for restoration due to its ecological and socioeconomic value. *Caryocar brasiliense* is a tree widespread in the *Cerrado* savannas and its fruit pulp and nuts are consumed across Brazil and their sale provides income to local communities. In addition to *C. brasiliense*, we focus on *Hymenaea stigonocarpa* Mart. ex Hayne (*jatobá-do-Cerrado*) and *Qualea grandiflora* Mart (pau-terra-grande) for the multi-species examples. These two species are widespread, common in *Cerrado* savannas (Bridgewater, Ratter and Ribeiro, 2004) and commonly traded by major *Cerrado* seed suppliers (*Restauradores da RDS Nascentes Geraizeiras* (RDS), *Rede de Sementes do Cerrado* (RSC), *Rede de Sementes do Xingu* (RSX), and *VerdeNovo* (VN); see Silva *et al.*, 2022). Both *H. stigonocarpa* and *Q. grandiflora* have uses, including timber, medicinal, and ornamental value (Ribeiro *et al.*, 2023). The precise location of the seed-sourcing sites of each species was not available, so we assumed that all species are collected across all the municipalities where the seed suppliers operate (Silva *et al.*, 2022).

### 4.3.8. Data processing and presentation

We use the MaxEnt algorithm to fit SDMs (Phillips and Dudík, 2008; Elith *et al.*, 2011; Phillips *et al.*, 2017). Please refer to Appendix 4.2 for the analytical pipeline and model specifications. We present the single-species example 1 by showing the COSST score, referred to as “seed sourcing priority areas”. We present the multi-species example 1 by binarizing the COSST score per species using a threshold of 0.75 (score 0–0.75 = 0, lower priority for seed sourcing and 0.75–1 = 1, higher priority for seed sourcing), summing up the binary layers, and excluding pixels equal to zero. The final map shows areas that are high priority for seed sourcing across multiple species. As an additional analysis, we ran a Pearson correlation to test the association between the COSST score calculated under different seed provenance strategies and for different species. We present the single-species example 2 by extracting the COSST score at the seed-sourcing sites and converting it into percentages. The multiple sourcing sites consisted of the centroid of the municipalities where the seed suppliers are active. We also sum the extracted COSST score per seed supplier to estimate the theoretical contribution of each vendor to the seed mix. We present the multi-species example 2 by repeating the previous step for the three species studied here. All analyses were made using the R environment (v.4.2.3).

## 4.4. Results

### 4.4.1. Example 1: Mapping seed sourcing priority areas

COSST was able to generate seed sourcing priority maps tailored to the seed provenancing and target site chosen by the user (Figure 4.2). Under predictive provenancing, the spatial distribution of COSST scores around each target site differs considerably. For example, for site 1 potential seed sourcing sites to the north of the target site have lower suitability (green shades) because their baseline climate does not match the target site's future climates. In contrast, for site 2, all nearby pixels (with savanna cover) show high scores. There is a positive correlation between the COSST score calculated under the composite and predictive provenancing, but the correlation coefficient is higher at site 2 ($r = 0.61$, $p < 0.001$), relative to site 1 ($r = 0.41$, $p < 0.001$; Appendix 4.3). The COSST prioritization developed for multiple species (N = 3) generates similar results to the prioritization based on one species (*C. brasiliense*; Figure 4.3). In fact, the Pearson correlation coefficients between the COSST score of *C. brasiliense vs*. *H. stigonocarpa* and *C. brasiliense vs*. *Q. grandiflora* are > 0.92 among all the seed provenancing and target site combinations ($p < 0.001$ for all comparisons).

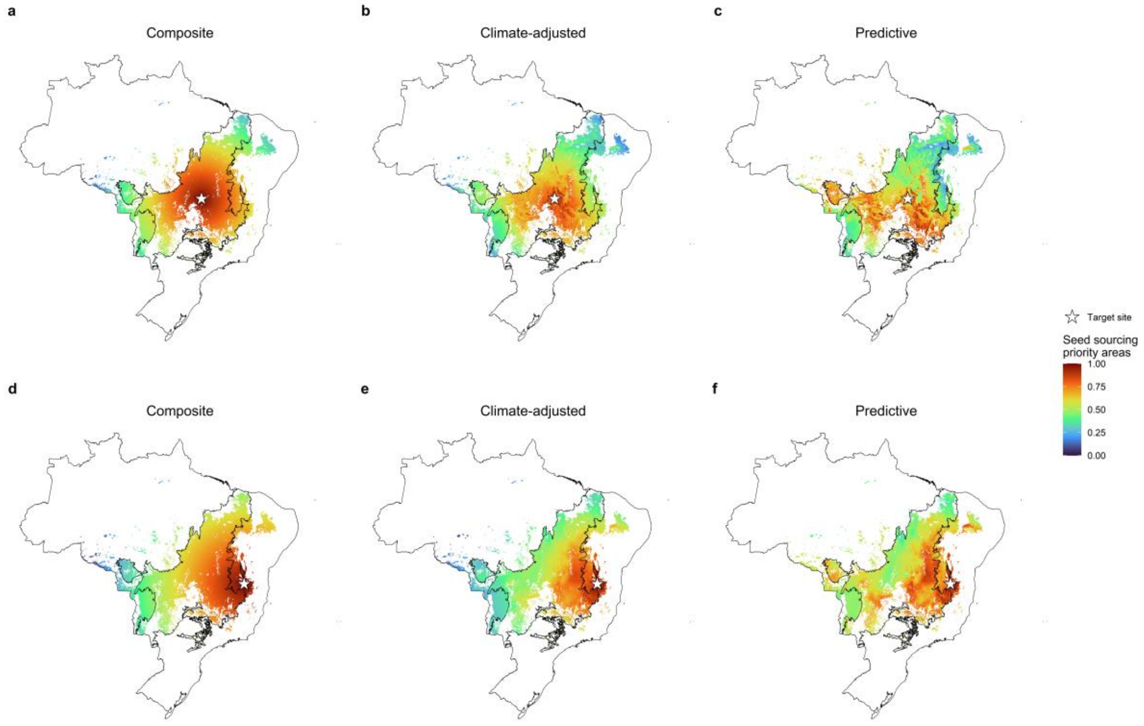


**Figure 4.2**. Priority areas for sourcing seed of *C. brasiliense* generated by COSST (Example 1, single-species). Predictions produced for (**a**–**c**) a mining site in Central *Cerrado* and (**d**–**f**) an abandoned Eucalyptus plantation in Eastern *Cerrado* and based on the (**a**, **d**) composite, (**b**, **e**) climate-adjusted, and (**c**, **f**) predictive seed provenance strategy. The coloured area represents the range of *C. brasiliense* excluding pixels with less than 10% of savanna and grassland cover in 2021. Warmer colours indicate high-priority areas and cooler colours low-priority areas. The star marks the location of the target site. The outer polygon delimits Brazil's boundaries and the inner polygon *Cerrado*'s boundaries.

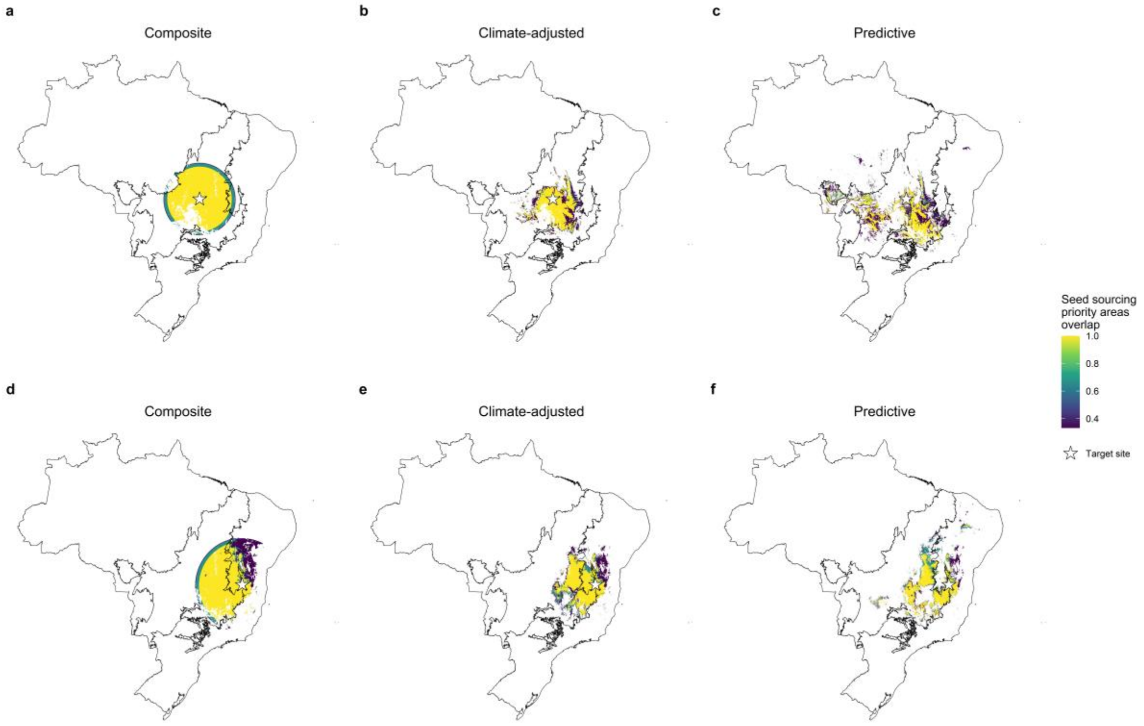


**Figure 4.3**. Priority areas for sourcing seeds of multiple species generated by COSST (Example 1, multi-species). The studied species were the *Caryocar brasiliense*, *Hymenaea stigonocarpa*, and *Qualea grandiflora*. Predictions produced for (**a**–**c**) a mining site in Central *Cerrado* and (**d**–**f**) an abandoned Eucalyptus plantation in Eastern *Cerrado* and based on the (**a**, **d**) composite, (**b**, **e**) climate-adjusted, and (**c**, **f**) predictive seed provenance strategy. The coloured area represents the overlap between single-species seed sourcing priority maps binarized using a 0.75 cutoff. Brighter colours indicate areas that are considered high priority for multiple species. The star marks the location of the target site. The outer polygon delimits Brazil's boundaries and the inner polygon *Cerrado*'s boundaries.

### 4.4.2. Example 2: Estimating seed demand per supplier

COSST was capable of designing seed mixes considering multiple seed suppliers, following different seed provenance strategies, and at different target sites. Considering a single species (*C. brasiliense*), RSC is the seed vendor closest to site 1 and RDS to site 2 (Figure 4.4). COSST suggests RSC be the main seed supplier for site 1 (total contribution of 31–33%) and RDS for site 2

(34.1–36.5%) regardless of the provenance strategy chosen (composite, climate-adjusted, or predictive). The greatest difference lay in the contribution of RDS to source seeds at site 1 under the composite (22.3%) *vs*. predictive provenance strategy (24.5%). The contribution of individual sourcing sites to the seed mix varies from *c*. 4.1–8.4% for site 1 and from *c*. 3.4–7.4% for site 2 considering the three seed provenance strategies, however, it should be considered that 13 out of 18 RSX sourcing sites and one out of six RSC sourcing sites fall outside *C. brasiliense* range (open points in Figure 4.4). Considering multiple species, RSC remains the principal vendor at site 1 and RDS at site 2 across all seed provenance strategies (Figure 4.5).

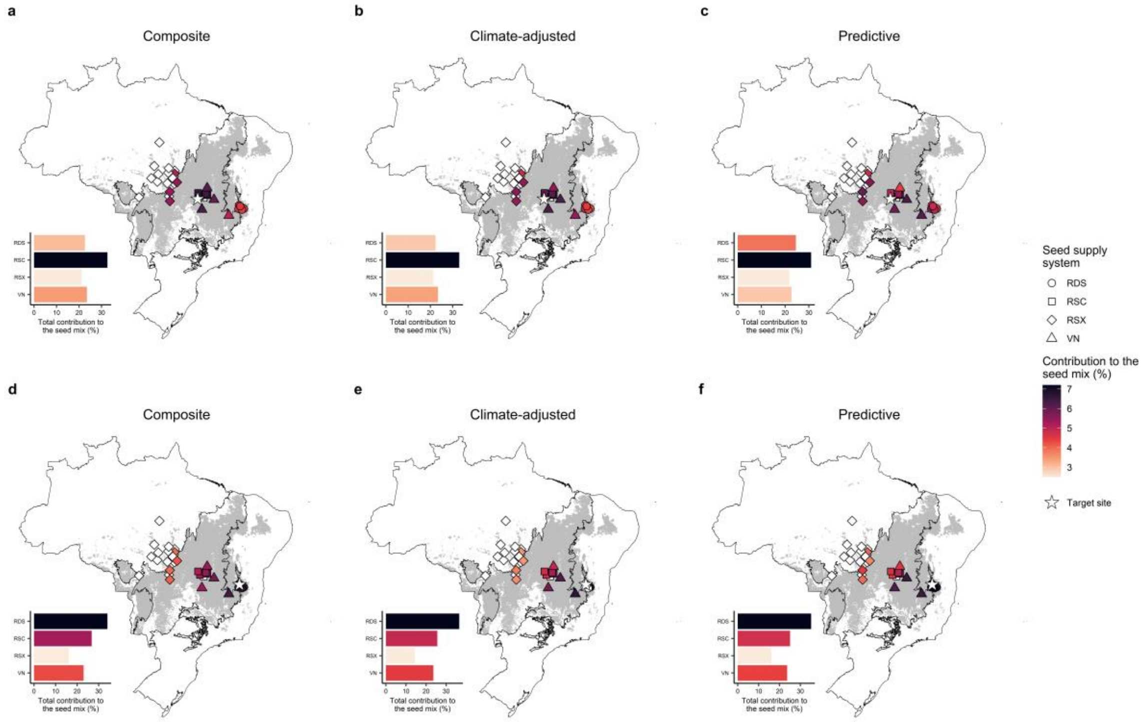


**Figure 4.4**. Seed contribution per supplier for *C. brasiliense* generated by COSST (Example 2, single-species). Predictions produced for (**a**–**c**) a mining site in Central *Cerrado* and (**d**–**f**) an abandoned Eucalyptus plantation in Eastern *Cerrado* and based on the (**a**, **d**) composite, (**b**, **e**) climate-adjusted, and (**c**, **f**) predictive seed provenance strategy. The area in grey represents the range of *C. brasiliense* excluding pixels with less than 10% of savanna and grassland cover in 2021. The points represent the *C. brasiliense* seed sourcing sites by four major seed suppliers in the *Cerrado*. The point colour is proportional to the contribution (%) of each sourcing site to the final seed mix. Open points represent sourcing sites outside the *C. brasiliense* range. Darker-coloured points represent high-contribution sourcing sites and white points represent sourcing sites outside the species range or with <10% of savanna and grassland cover. The insert graphs show the summed contribution of each seed supplier to the final seed mix. The star marks the location of the target site. The outer polygon delimits Brazil's boundaries and the inner polygon *Cerrado*'s boundaries. RDS stands for *Restauradores da RDS Nascentes Geraizeiras*, RSC *Rede de Sementes do Cerrado*, RSX *Rede de Sementes do Xingu*, and VN *VerdeNovo*.

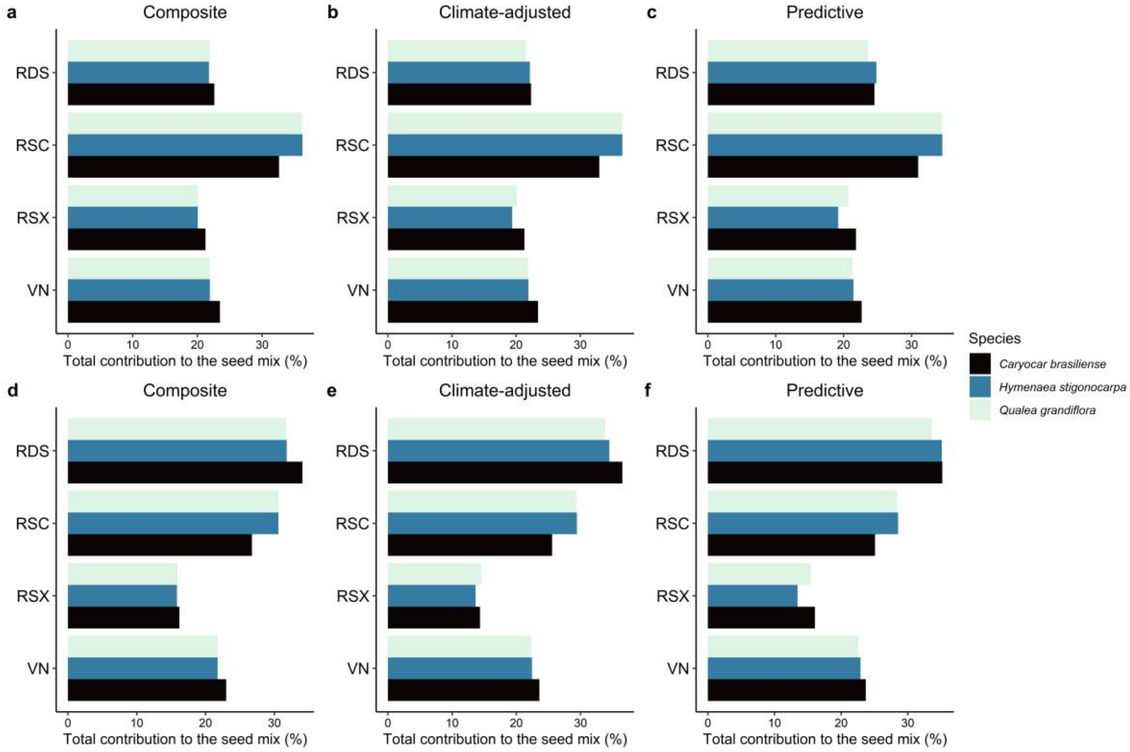


**Figure 4.5**. Seed contribution per supplier for multiple species generated by COSST (Example 2, multi-species). Predictions produced for (**a**–**c**) a mining site in Central *Cerrado* and (**d**–**f**) an abandoned Eucalyptus plantation in Eastern *Cerrado* and based on the (**a**, **d**) composite, (**b**, **e**) climate-adjusted, and (**c**, **f**) predictive seed provenance strategy. The bar shows the summed contribution (%) of each seed supplier to the final seed mix for each species. RDS stands for *Restauradores da RDS Nascentes Geraizeiras*, RSC *Rede de Sementes do Cerrado*, RSX *Rede de Sementes do Xingu*, and VN *VerdeNovo*.

## 4.5. Discussion

COSST strengths are threefold. First, the tool represents the multidimensionality and uncertainty of climatic regimes. Climate-adjusted and predictive seed provenance strategies have been conceptualized based on a single axis, such as mean annual temperature (Prober *et al.*, 2015). The accurate representation of climate requires accounting for multiple axes (e.g., temperature and rainfall) and across a range of metrics (e.g., mean, range, maximum, and minimum) as COSST does. Divergence among future climate predictions challenges the implementation of climate-adjusted and predictive strategies (St.Clair *et al.*, 2022). In the case of climate-adjusted strategy, COSST penalizes sites where the future climate is uncertain and favours the "local-is-best" approach instead. Second, the tool does not require empirical data other than the species occurrence. Common garden experiments are the best option to empirically test the adaptative superiority of different populations (Roybal and Butterfield, 2018; Lortie and Hierro, 2022) and genetic diversity data further provide valuable information about local adaptation (Collevatti *et al.*, 2019; Leal *et al.*, 2021). However, common garden and genetic data are far from being available for all the species relevant for restoration and COSST offers the best solution in the absence of these data. Third, the tool predictions are tailored for the focal species. Generic seed provenancing guidelines (e.g., provisory seed transfer zones) may fall short if there is no congruent population genetic structure among species, which is the case for Amazonian trees (Coronado *et al.*, 2019). COSST avoid this issue by focusing on species-specific climatic distances rather than generic polygons. Therefore, the novelty of our tool lies in its accessible inputs and customized outputs.

The main assumption of COSST is the prevalence of intraspecific adaptation to climate, especially when the user selects the climate-adjusted or predictive strategies. Evidence of climate adaptation exists for the *Cerrado* flora, but only for a handful of species (Appendix 1). The climate component of the tool may lose power if the genotypes of a species are not in equilibrium with their baseline climate (Wilczek *et al.*, 2014). Moreover, genotypes might be adapted to soil conditions rather than climate. However, we argue that our tool remains applicable even when the local adaptation assumptions are not met. For instance, in the case of *C. brasiliense*, COSST encourages some level of seed contribution from all potential sources regardless of the seed provenance strategy chosen. A small fraction of seeds from several populations amplifies genetic variation, which should increase adaptability and reduce the risk of inbreeding depression (McKay *et al.*, 2005; Kremer *et al.*, 2012). The predominance of local seeds reduces the risk of outbreeding depression due to the dilution of adaptive genes (genetic swamping) or the disruption of interacting gene networks and ploidy levels (hybrid breakdown) (Hufford and Mazer, 2003; Frankham *et al.*, 2011). In fact, when climate-adjusted provenancing is selected, geographical proximity will always be more influential on COSST estimates than the climate match since the latter is penalized by future climate uncertainty. Therefore, COSST augments genetic diversity regardless of the climate match optimization, the aspect of biological diversity most relevant for evolutionary rescue under climate change (Aitken and Whitlock, 2013).

Implementing the tool will depend on overcoming three challenges. First, precise information about seed provenance. Several countries use wild populations for seed production (Atkinson *et al.*, 2021; Bosshard *et al.*, 2021; Giacomini *et al.*, 2023), but the locations of these populations are often unavailable. Some suppliers are moving towards making these data available, for example, the Seeds of Success program (Haidet and Olwell, 2015; Barga *et al.*, 2020) and the Native Seed Vendors map (https://appliedeco.org/nativeseednetwork/find-seed/) in North America. A georeferenced map of seed sources where practitioners purchase seeds is essential for applying COSST at a large scale. Second, integrating seed provenance records with restoration outcomes. Our tool has the potential to improve the fitness of a species under climate change. To validate COSST and other seed mix design tools, it will be essential to monitor the ecological outcomes of the restoration intervention and relate it to the seed provenance decisions (Pedrini and Dixon, 2020; Pedrini, Gibson-Roy, *et al.*, 2020). Finally, seed storage technology and infrastructure must be strengthened. COSST encourages some level of seed transport over long distances. Hence, it is critical to develop techniques to ensure the viability of the seeds from harvesting to sowing (De Vitis *et al.*, 2020; Shaw *et al.*, 2020). For *Cerrado* species, such technologies may include storing the seeds in a cool and dark environment, as has been done in the *Rede de Sementes do Xingu*, the largest community-led seed supplier in Brazil (Schmidt *et al.*, 2019; Urzedo *et al.*, 2020).

Future research could increase the applicability of the tool even further by including seed production limitations and transport costs. Sites will differ in the volume of seeds that can be collected there due to differences in the size of the vegetation remnants, species abundance, and number of seed collectors (Pedrini, Gibson-Roy, *et al.*, 2020). Moreover, seeds can be produced ex-situ (e.g., native seed farms) (Gibson-Roy, 2023) or stored over time (De Vitis *et al.*, 2020), further increasing the seed production potential of a site. At present, COSST assumes that all sourcing sites have an equal seed production capacity. If seed production capacity is made available, it is possible to convert the COSST score into the volume/mass of seeds per sourcing site using the maximum seed production capacity as a cap. Also, seed batches may lack genetic variation if collected from small fragmented populations (Schlaepfer *et al.*, 2018; González *et al.*, 2020) at the periphery of the species range (Pironon *et al.*, 2017; Pfeilsticker *et al.*, 2021), e.g., beyond the area delimited by SDMs. On the other hand, leading/rear-edge populations may contain rare genes that can promote adaptation to climate change (Macdonald *et al.*, 2017; Gargano *et al.*, 2022). Habitat fragmentation can be included in COSST calculations (Harrison *et al.*, 2017), though range-wide studies are needed to unveil how population size and isolation affect genetic diversity. Another important consideration regards the additional costs to the restoration project by seed transport from multiple vendors (Schmidt *et al.*, 2019). Contrary to the strict local provenancing, the composite, climate-adjusted, and predictive strategies assume practitioners will purchase some degree of seeds from vendors far from the restoration site. Therefore, if such strategies are followed strictly, practitioners might buy fewer seeds per vendor to compensate for extra costs related to seed transport, which may lead to under-seeding. To avoid that, future work may aim to constrain COSST predictions by the budget and targeted seed volume/mass of the restoration projects.

## 4.6. Conclusion

COSST provides a novel and generalizable framework to translate seed provenancing principles into restoration planning. For instance, in the Brazilian *Cerrado*, COSST allowed us to identify potential areas for sourcing the seeds of a key species and to plan seed purchasing among existing seed suppliers. The tool can be applied to any terrestrial ecosystem given the flexibility of COSST's inputs derived from SDMs. The tool is likely most relevant in the tropics, where species-rich floras, from which population genetics is poorly known, pose a challenge for traditional provenancing tools, such as seed transfer zones. A better knowledge of the pervasiveness of local adaptation to climate will support COSST assumptions. Furthermore, the impact of the tool will depend on mapping wild populations where the seeds are being collected as well as advancing seed storage and transport techniques. By connecting theory and application, we hope our tool can help practitioners maximise ecosystem restoration success under a changing climate.

# Chapter 5

Courtesy of Ana Christina

# Chapter 5 – Synthesis

## 5.1. Summary of key findings

This thesis aimed to fill knowledge and implementation gaps that constrain large-scale ecosystem restoration in the *Cerrado*. I summarize below the key findings of Chapters 2 to 4 and how they link with the overall aim of the thesis.

In Chapter 2 “Towards diverse seed sourcing to upscale the Brazilian *Cerrado* restoration”, I found that more than 260 species were available for seed-based restoration in the *Cerrado* in 2021. The four seed suppliers studied were distributed across the centre of the *Cerrado* region. The suppliers were distinct in terms of the species they traded since >60% of the species were sold only by a single supplier. The seed market overrepresented trees and underrepresented forbs considering the *Cerrado* species pool. Finally, I confirmed that seeds from species typical of the *Cerrado*’s light-demanding ground layer were available for sale, but they did not feature among the top-selling species. The success of large-scale restoration will depend on accounting better for the remarkable species diversity (*c*. 12,000 species) and floristic turnover across the *Cerrado*. The outcomes of Chapter 2 have the potential to inform the seed sector on areas to expand into (e.g., South and North of the *Cerrado*) and species to include (e.g., forbs) in the upcoming years.

In Chapter 3 “Elevation modulates the impacts of climate change on the Brazilian *Cerrado* flora”, I found that responses of species and assemblages to climate change depend on elevation in the *Cerrado*. Half of the *c*. 7,400 *Cerrado* flowering plants for which I generated SDMs showed net range loss by 2040, with most of them tending to be montane species. Three-quarters of the species moved upslope at a rate of five to seven metres per decade. Net species losses were likely to occur in lowlands whereas net species gains and species turnovers were more pronounced in mountains. I found, therefore, a potential for *Cerrado* plants to respond to climate change through upslope migration. Understanding the basic mechanisms by which climate change affects species is the first step for applying climate adaptation principles to conservation and restoration planning. The conclusions and underlying data from Chapter 3 can guide the protection of

*Cerrado* areas that are climate refugia and the use of species likely to persist in the restoration site over the next decades.

In Chapter 4 “Operationalizing climate-oriented seed provenancing for ecosystem restoration: a case study in the Brazilian *Cerrado*”, I developed a framework to map seed collection sites and design seed mixes optimised for climate change. I used SDMs to delimit a species’ contemporary ranges and the relative importance of climatic variables in circumscribing this range. I then mapped areas within a species’ range that have a climate that matches the future predictions for the restoration site. I named the framework “Climate-Oriented Seed Sourcing Tool” (COSST) and illustrated two applications for single and multi-species at two sites in the *Cerrado*. The tool specifies predictions based on the seed provenance strategy chosen by the user and the species and site set by the user. It is expected the demand for seeds will increase in the upcoming years to meet ambitious restoration targets for the UN Decade on Ecosystem Restoration, which will likely increase the exchange of seeds across sites. The framework introduced in Chapter 4 can implement seed-provenancing concepts on the ground and help end-users find seed sources appropriate for the climate forecast for the next years or decades.

## 5.2. Cross-cutting questions

### 5.2.1. How to increase species and genetic diversity in restoration projects?

Chapters 2 and 4 highlight the risk of limited species and genetic diversity within restoration projects, as well as some of the current challenges for increasing these. The number and identity of species available for seeding or planting will define the diversity and functioning of ecosystems reassembled through active restoration (Coutinho *et al.*, 2019; Mazzochini *et al.*, 2023). To guarantee a range of possible outcomes, a range of species must be available on the market. In 2020, the *Caminhos da Semente* Initiative collated information on seed collection, storage, and processing for 835 species across Brazil, from which 208 were linked to a vendor. *Cerrado* species accounted for 143 out of these 208 commercially available species. These *Cerrado* species available for sale increased from 143 to 263 by 2021 (i.e., in just one year) looking only at four seed suppliers (Silva *et al.*, 2022). Moreover, the *Rede de Sementes do Cerrado* (RSC) included 18 additional species and *VerdeNovo* (VN) 25 additional species in their portfolios from 2021 to 2023 (Figure 5.1a). These numbers, then, point to a welcome trend of broadening the set of species commercialized by the seed supply sector. However, the proportion of herbaceous species in the seed portfolio only increased from 13% to 17% for the RSC network and actually decreased from 17% to 16% for the VN network between 2021 and 2023, showing the persistence of life form bias in the seed supply chain (Chapter 2; Figure 5.1b). VN is currently assessing the viability of commercializing seeds of several wet grassland species, such as *Andropogon virgatus*, *Cyperus aggregatus*, and *Rhynchospora rugosa* (Personal Communication, Bárbara Pacheco, 07/02/2024), which is an important step in sourcing the *Cerrado* herbaceous flora for restoration.

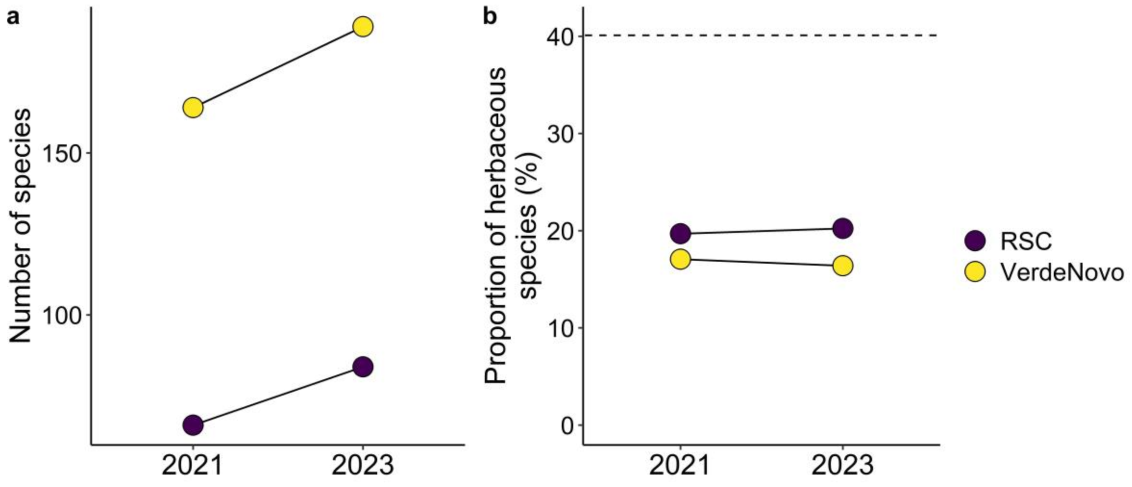


**Figure 5.1.** Changes in the species traded by two major *Cerrado* seed suppliers over time. (**a**) Total number of angiosperm species sold by *Rede de Sementes do Cerrado* (RSC) and *VerdeNovo* seed vendors from 2021 to 2023. (**b**) Proportion of herbaceous species in the species list of RSC and VerdeNovo in 2021 and 2023. The dashed line in panel b corresponds to the proportion of *Cerrado* species classified as herbaceous according to Reflora (2020).

Increasing species diversity in restoration projects, especially for the herbaceous component, will depend on aligning supply and demand. “Supply” refers to which species are available on the market and “demand” to the amount of seeds or seedlings bought per species. Supply and demand are intertwined because vendors tend to supply the species preferred by practitioners while practitioners tend to buy among the species supplied by the vendors. As a result of Chapter 2, I produced a spreadsheet ranking 1,108 species according to their dominance in the ground layer of 66 savanna and grassland sites across the *Cerrado*. In February 2023, I shared this spreadsheet with seed vendors aiming to help them source species with high ecological value but which are still overlooked for restoration. Alongside such connection of science with practice, developing standards and policies can further shape species’ offer and demand for restoration. I stress that standards and policies must accommodate the diversity of plant communities and ecosystems found in places such as the *Cerrado*. For instance, setting minimum species richness criteria might result in practitioners including inadequate species just to meet a target (Aronson *et al.*, 2011). Instead of set values, flexible tools can be key for supporting restoration planning and policymaking, for example where species lists are produced based on reference sites and ecosystem function targets combined with recommendations for extra species to include in the supply chain (Coutinho, Carlucci, and Cianciaruso, 2023).

Species diversity is important in the restoration process, but genetic diversity is also fundamental. The species list data I collated in Chapter 2, plus plant assemblage datasets (e.g., GrassSyn, Overbeck *et al.*, 2022), and functional trait databases (e.g., Mariano *et al.*, 2021) could all feed species diversity information into the Coutinho, Carlucci, and Cianciaruso (2023) tool to design species-rich seed or seedling mixes. However, the pathways to ensure genetic diversity among the seeds and seedlings used for restoring an area are less clear (though see Fremout *et al.*, 2022). The seed provenancing tool I introduced in Chapter 4, i.e., COSST, has the potential to help maximize genetic diversity in seed mixes by suggesting seed collection from multiple populations, though empirical validation is still needed. Given the astonishing number of species in the *Cerrado* flora, detailed range-wide genetic studies of each are not feasible. For such cases, COSST offers an option to design genetically diverse seed mixes based on the assumption that genetic variation in the seed mix should increase when seeds are sourced from populations geographically distant from each other. I stress that genetic research remains critical for restoration planning, and it could target species dominant in old-growth areas, such as *Trachypogon spicatus* and *Echinolaena inflexa* (see Chapter 2) or species with socioeconomic value such as *Syngonanthus nitens* (Schmidt, Figueiredo and Scariot, 2007).

A critical challenge to mainstream COSST or any other seed-sourcing tool is improving the traceability and transparency of the seed supply chain (Fremout *et al.*, 2022; St.Clair *et al.*, 2022). Brazil requires seed and seedling producers to upload their species lists in the National Seed and Seedling Registry (Renasem) system. The coordinates of the seed collection sites are uploaded in another system called the Inspection Management System (SIGEF). Some seed suppliers are therefore in the process of uploading their data to government platforms. However, the exact location of the seed collection activities is sensitive information for some collectors who are concerned about third parties overharvesting seeds on their land (Personal Communication, Maria Eduarda Camargo, 30/03/2021). Therefore, applying COSST in real-life situations depends on first mapping where the seeds are coming from, storing this information in an integrated and secure system, and making it available for the buyers at the end of the seed supply chain.

### 5.2.2. How will climate change impact the sustainability of restoration projects?

Climate change can push an ecosystem undergoing restoration to a degraded state via changes including the frequency, intensity, and length of drought, fire, or flood events (Zabin *et al.*, 2022). I reported in Chapter 3 that approximately 70% of the *Cerrado* area is expected to lose species while the remaining 30% will gain species by 2040. Lowlands are most likely to experience net species losses and mountains net species gains. Temporal changes in species composition showed the opposite pattern: high turnover in the mountains and low turnover in the lowlands. Therefore, climate change impacts on a restoration site in the *Cerrado* will depend on its elevation. Recovering historical species richness levels might be unachievable in low-elevation sites due to local extinctions under climate change. Examples are the Upper Paraguay and *Araguaia* River Basins where the *Xingu* and *Araguaia* seed collector networks are respectively active. These sites coincide with hotspots of climatic anomalies, adding to the need for practitioners to focus on a subset of species with the highest potential to resist forecasted changes in climate (e.g., *Caryocar brasiliense*, *Dipteryx alata*). The composition of the montane plant assemblages is likely to change in a way such that restoration might be able to recover historical species richness levels but not the historical species composition. Examples include the *Veadeiros* and *Espinhaço* Mountains, which are the focal regions of RSC and RDS seed suppliers, respectively. In this case, practitioners will likely need to consider the possibility of assisted migration from mid-elevation species and that montane species are prone to suffer range contractions.

Responses to climate change will be species-specific among key species for ecological restoration. There was a balance between climate “winners” and “losers” across the 7,398 *Cerrado* flowering plants studied in Chapter 3. The result was a median range shift (i.e., range size) of approximately -1% considering the most pessimistic global change scenario, SSP5. A net range loss of 1% is modest compared to other Brazilian regions, such as the Caatinga Seasonally Dry Tropical Forest, where this number was close to 40% in a modelling exercise for *c*. 3,000 angiosperms by 2060 under SSP5 (Moura *et al.*, 2023). Moura *et al.* (2023) made species movement assumptions that are more conservative than the ones adopted in Chapter 3 and projected the models to 2041–2060 and 2081–2100 timeframes versus 2011–2040 used here, which may explain the difference between the studies. I chose the 2011–2040 horizon to reflect climate conditions that most *Cerrado* species established through restoration will face considering their relatively short time to maturation. It is worth mentioning that global warming starts to diverge between the SSPs after 2050 (IPCC, 2023), which explains the modest variability in the Chapter 3 results between SSP1 and SSP5 (see Figure 5.2). I stress that Chapter 3 conclusions are more relevant in the context of near-future climate change, such as the timeframes required to limit global warming to 1.5 or 2 °C. Future studies will, however, be needed to assess the responses of the *Cerrado* flora from the middle to the end of the 21st century, especially if the focus is on long-lived organisms, such as trees.

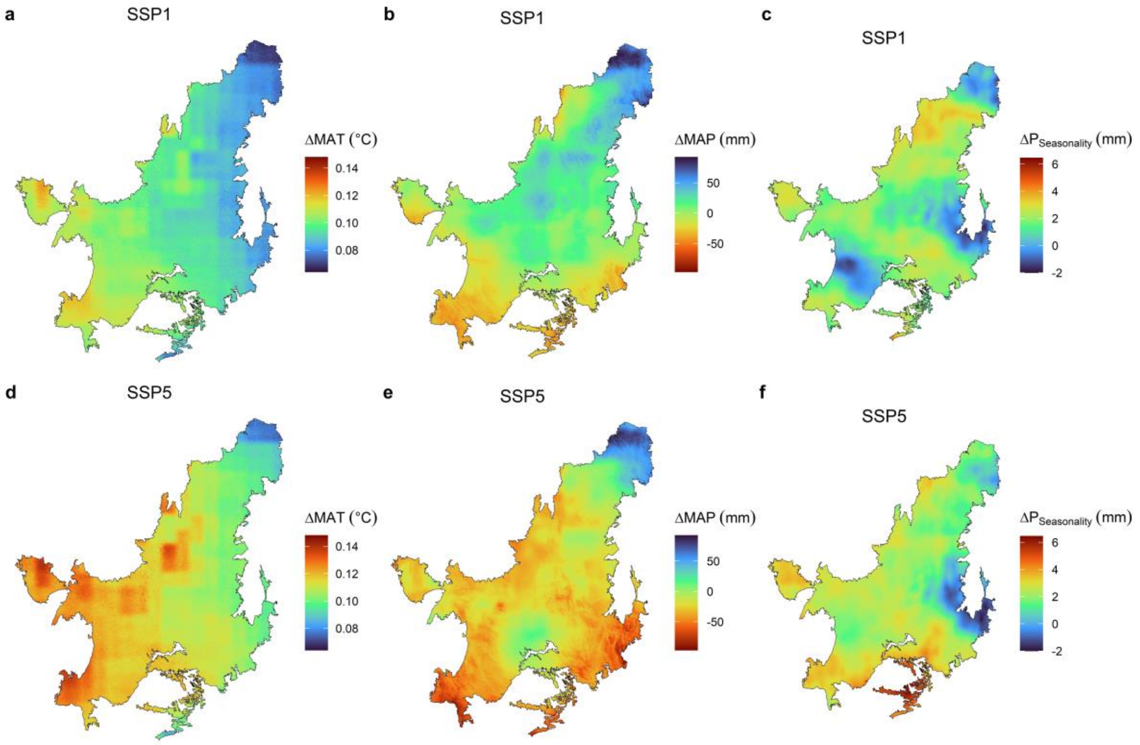


**Figure 5.2.** Near-future climate change in the Brazilian *Cerrado*. Climate anomalies (Δ) represent the difference between the 2011–2040 and the 1981–2010 averages. (**a, d**) Anomaly maps for mean annual temperature (MAP), (**b, e**) mean annual precipitation (MAP), and (**c, f**) precipitation seasonality between the (**a–c**) SSP1 and (**d–f**) SSP5 scenarios. The climatic data was retrieved from CHELSA V2.1 and 2011–2040 variables consist of the ensemble of GFDL-ESM4, UK-ESM1-0-L, MPI-ESM1-2-HR, IPSL-CM6A-LR, and MRI-ESM2-0 GCMs.

To explore the implications of climate winners and losers for the *Cerrado* restoration, I filtered the 263 species with seeds commercially available for restoration (Chapter 2) from the 7,398 species pool, resulting in a subset of 235 species with satisfactory SDMs (CBI > 0.25). I found that the median range shift was 3.6% for the species subset and it ranged from -87.5% (*Esenbeckia pumila*) to 123.6% (*Astrocaryum huaimi*) under SSP5 (Figure 5.3). In fact, 60% of the subset species had a positive range shift by 2040 (SSP5), showing that the species available in the seed supply chain are composed mostly of species expected to undergo future range expansion. The preponderance of climate winners on sale facilitates selecting species that will increase the chance of restoration succeeding in the long term.

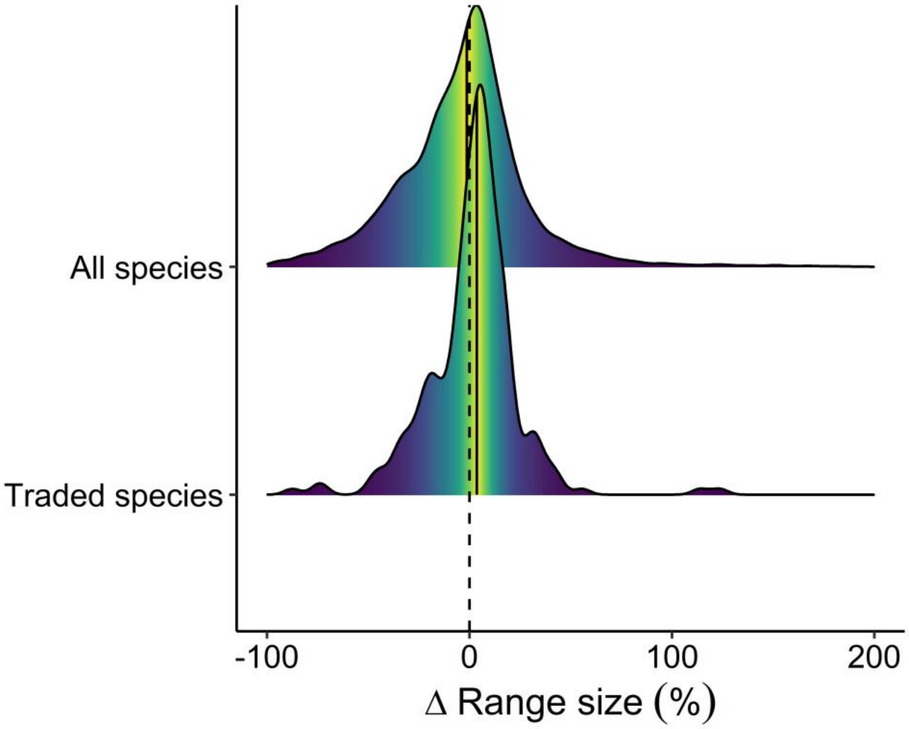


**Figure 5.3.** Climate change impacts on the range size of traded and non-traded *Cerrado* species in the seed supply chain. Δ range size represents the change in the potential geographic range size in the future (2011–2040) compared to the baseline (1981–2010) in Brazil under a pessimistic scenario (SSP5). The upper distribution "all species" corresponds to the 7,398 angiosperms studied in Chapter 3 and the lower distribution "traded species" corresponds to the 263 species with seeds commercially available for restoration (Chapter 2). Δ range size > 0 suggests range gain and Δ range size < 0 range loss. Δ range size was expressed in percentage relative to the baseline range size. The chart was coloured according to the tail probabilities. The dashed line marks zero, i.e., no net change. The solid line indicates the median of the distribution. The x-axis was limited to 200% to improve visualization which concealed 55 outlier species.

### 5.2.3. How to plan restoration projects under changing climate regimes?

Climate adaptation principles intersect all restoration stages, from improving soil health during site preparation (Fehmi, Rasmussen and Gallery, 2020), to selecting species/genotypes with the highest adaptive potential at the implementation phase (Fremout *et al.*, 2022) and re-establishing disturbance regimes post-sowing/planting (Young *et al.*, 2015). In this thesis, I focused on generating knowledge to support the design of seed mixes resilient to future climates. The first step consists of listing the species suitable for the restoration site in the future. I made available an R script in Chapter 3 that returns the potential species assemblage in the 2011–2040 timeframe considering sustainable (SSP1) and fossil-fuelled development (SSP5) scenarios for the *Cerrado*. The user can further constrain the list by the species available for sale as seeds, using information from Chapter 2. If the user wants to avoid any introduction (i.e., species unsuitable for contemporary climate but suitable for future climate), it is also possible to use species assemblages generated in the 1981–2010 timeframe to filter only species likely to occur today and in the next decades. At this stage, the user would have a regional species pool, but the local assemblage would be a subset of the regional pool defined by ecological filters other than climate (e.g., soils) and the restoration goal. One option is using species selection tools as proposed by Coutinho, Carlucci and Cianciaruso (2023) that use traits and reference communities to suggest species lists or another from Laughlin *et al.* (2018) that uses traits to suggest species abundances in revegetation projects. However, trait data in the *Cerrado* is scarce relative to other regions in Brazil, such as the Atlantic rainforest (Mariano *et al.*, 2021). Alternatively, the assemblage dataset I compiled in Chapter 2 can further guide practitioners to target species that are abundant in old-growth reference sites while designing seed mixes for restoration (Figure 5.4).

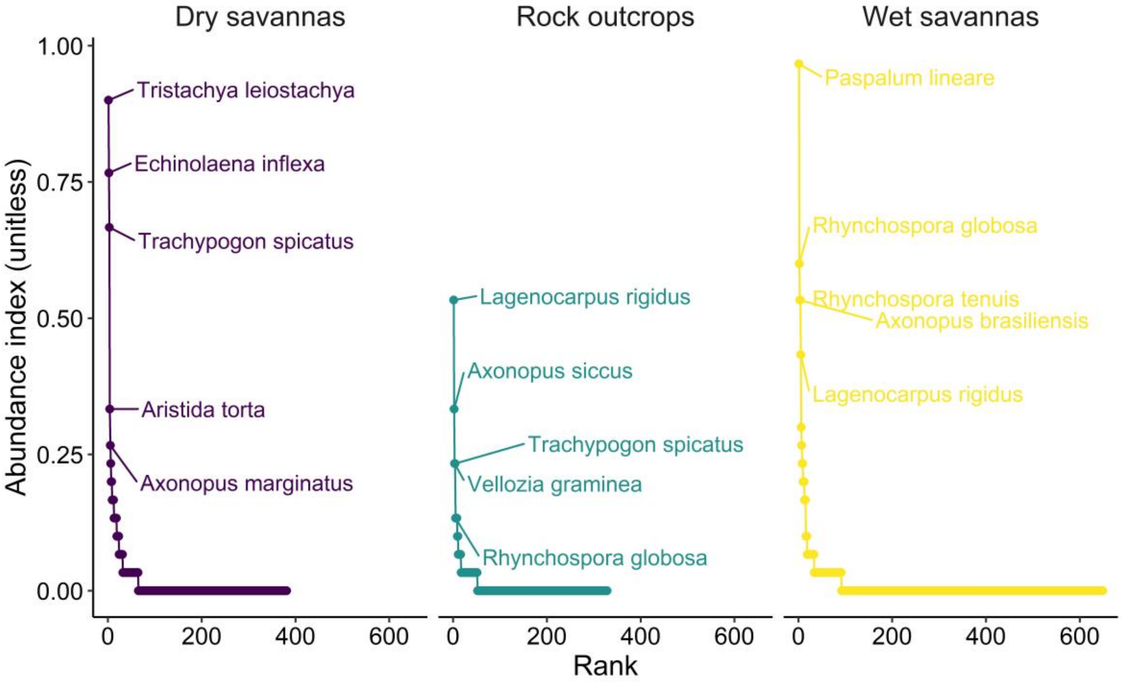


**Figure 5.4.** Rank-abundance curves for major vegetation types extracted from 27 studies (75 sites) with openly available abundance data across the *Cerrado*. The top five abundant species per vegetation type were identified.

After deciding on the species list, restoration practitioners can take another step to future-proof their projects by selecting seed/seedling batches adapted to future climates. I automated this decision in Chapter 4 and discussed some implementation challenges in Section 5.2.1. Users can directly use the COSST tool I developed, but it currently requires basic knowledge of R software, which a significant number of restoration practitioners do not have. The same limitation applies to the species selection steps I discussed above. Alternatively, there is a noteworthy opportunity to embed the climate-smart species/genotype selection developed for this thesis into *Redário*, a nationwide coalition of seed vendors for ecosystem restoration in Brazil (Urzedo, Westerlaken and Gabrys, 2023). *Redário* connects 24 major seed suppliers bringing together *c*. 1,200 individual seed collectors. Over the past years, *Redário* has been centralizing seed purchase requests and bridging customers and seed suppliers. *Redário* also provides basic technical assistance, helping practitioners decide on the species and seed sources for their mixes. Including all the climate-proofing steps I discussed so far in *Redário* decision-making would help practitioners maximize the chance of success of restoration projects under climate change without requiring developing programming skills.

### 5.2.4. Are the conclusions drawn here only relevant to the Brazilian *Cerrado*?

This thesis focused on the *Cerrado*, but the findings and approaches are generalizable to other regions in the world. I found a bias towards sourcing tree species to the detriment of herbaceous species among seed vendors across the *Cerrado* (Chapter 2). Similarly, Andres *et al.* (2023) independently reported the same bias in the Australian native seed market. They listed approximately 3,000 commercial species and the proportion of trees on sale was higher than would be expected based on the regional species pool across all major Australian vegetation types, including Eucalyptus-dominated savannas, whilst the proportion of herbs was lower. Savannas and grasslands cover up to 40% of the globe and half of them are degraded (Bardgett *et al.*, 2021). Recovering savanna and grassland biomes globally will require making herbaceous species a priority in the restoration seed supply chain, which is not yet the case in Brazil and Australia (Silva *et al.*, 2022; Andres *et al.*, 2023).

I found potential for upslope migration as a strategy for plants to track climate change in the *Cerrado* (Chapter 3). There is also compelling evidence supporting the occurrence of upslope migration in mountain ranges such as the Andes (Feeley *et al.*, 2011), the Alps (Vitasse *et al.*, 2021), and the Himalayas (Girish and Srinivasan, 2022). Ensslin *et al.* (2018) carried out a reciprocal transplant experiment between grasses from lowland and montane African savannas and found that lowland species established at high elevations whereas montane species could not establish at low elevations. These results support the potential for upslope migration among lowland taxa rather than montane taxa, as I also found in Brazil through a modelling approach.

Finally, the seed-sourcing tool I designed in Chapter 4 is general because it applies to any plant species to which SDMs can be fitted.

## 5.3. Impact among decisionmakers and practitioners

The scientific outputs of this thesis yielded impact even though the project is in progress. First, I collaborated with the Spatial Intelligence Working Group of the Araticum Alliance for the *Cerrado* Restoration to make available current and future distribution maps for key species for restoration. The data came from Chapters 2 and 3 and the maps can be accessed at https://araticum.lapig.iesa.ufg.br/ (Layers > Climate adaptation; Figure 5.5). This is the first step in selecting species that have the potential to survive under climate change in a given restoration site. Second, I contributed to the Restoration Plan for the Pantanal Headwaters Landscape, a report led by WWF-Brazil identifying strategies to restore upstream *Cerrado* areas that supply water to the Pantanal Wetland (Maioli, 2023). Figure 13 of the Restoration Plan shows areas expected to experience intense local extinctions and species gains, which can guide restoration practitioners in anticipating the impact of climate change in their projects. Lastly, I was invited to co-organize the Seed Mix Design Workshop at the 10th World Conference on Ecological Restoration (SER2023) in Darwin, Australia. I had the opportunity to present the outcomes of Chapters 2 and 4 to a broad audience including representatives of research institutions, the seed supply sector, non-profits, and governments.

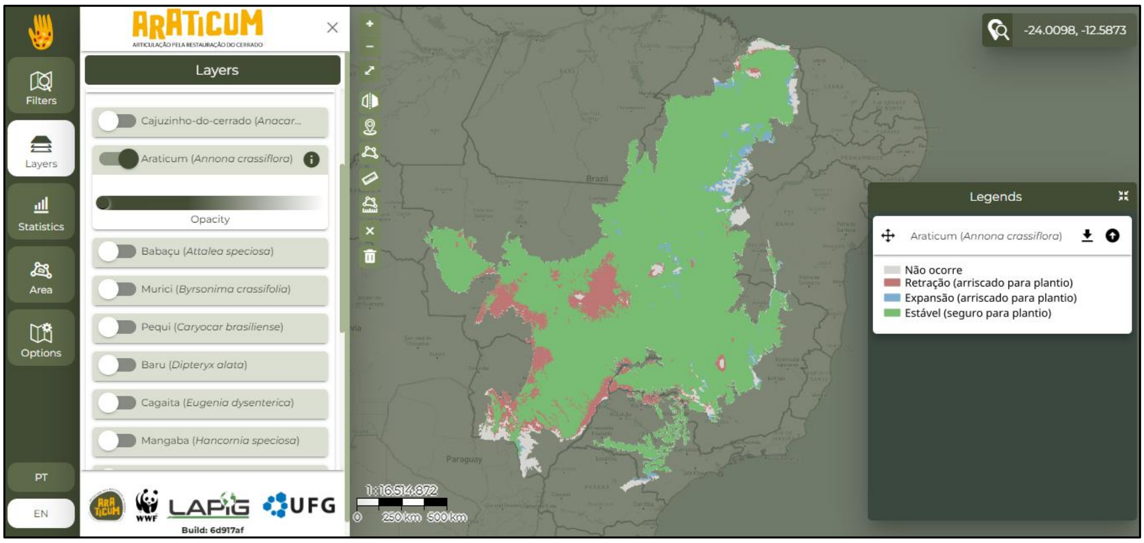


**Figure 5.5.** Range shifts of ten key species for restoration available on the *Araticum* Alliance online platform (https://araticum.lapig.iesa.ufg.br/). The green area corresponds to the stable range until 2040, blue range expansion, red range contraction, and grey unsuitable areas for the occurrence of the species. The species selected is *Annona crassiflora* and the nine other species are *Anacardium humile*, *Attalea speciosa*, *Byrsonima crassifolia*, *Caryocar brasiliense*, *Dipteryx alata*, *Eugenia dysenterica*, *Hancornia speciosa*, *Syagrus oleracea*, and *Syngonanthus nitens*. The layers originate from Chapter 3.

### 5.4. Aspirations for future research

I generated new scientific knowledge on the supply chain (Chapters 2 and 4) and climate adaptation (Chapters 3 and 4) for ecosystem restoration in the Brazilian *Cerrado*. The theoretical and applied outcomes of this thesis are a step towards implementing large-scale restoration projects in Brazil and elsewhere. Additional questions arose from Chapters 2 to 4. I identified three directions for future research to move forward national and international restoration agendas.

**1) Reversing life form biases in the seed supply chain:** Improving seed supply chains will depend on unveiling the drivers of the underrepresentation of herbaceous species among seed vendors in countries such as Brazil (Silva *et al.*, 2022) and Australia (Andres *et al.*, 2023). Stakeholder interviews may help us to understand their perspectives on herbaceous plant diversity and how such values result in the limited supply and demand of herbaceous plants for restoration. Furthermore, stakeholders' choices may also be linked to the biases in policies regulating restoration (Aronson *et al.*, 2011; Urzedo *et al.*, 2019). An example is Brazil's Forest Code, the nationwide policy that regulates ecosystem restoration on private land. The Forest Code specifically requires the restoration of forests alongside watercourses, though no similar requirement is made for non-forest ecosystems. This biome awareness disparity (Silveira *et al.*, 2022) may underpin the supply and demand for a greater diversity of trees rather than herbaceous species for seed-based ecosystem restoration.

**2) Assessing climate risks in restoration projects:** SDM data offers opportunities to quantify the risks of selecting inappropriate species for restoration under future climates (Simonson *et al.*, 2021; Sandoval-Martínez *et al.*, 2023). The findings of Chapter 3 point to the pervasive impacts of climate change on the *Cerrado* flora. The first step for assessing risk in current restoration projects would be investigating the percentage of species used in seed mixes that are unlikely to survive in the restoration site in the upcoming decades. This information, combined with the cost of buying and seeding such species, would help anticipate risks of failure in ongoing projects due to species-climate mismatches. The second step would be automatizing a tool for restoration practitioners to contrast their species lists with SDM forecasts per species per site. This would be a recommendation for species that are suitable/unsuitable for the restoration site today and in the future. The tool Diversity for Restoration (D4R) (Fremout *et al.*, 2022) combines SDMs and provisory seed transfer zones for planning restoration in several countries and extending or developing similar tools for Brazil should be a priority.

**3) Linking seed origin to restoration success:** Two complementary approaches can guide the selection of the best seed sources for successful restoration. First, controlled experiments are critical to test empirically the existence of local adaptation and the superiority of a particular population in each site or environmental condition. Such experiments can involve growing plants originating from multiple populations together (i.e., common garden) or growing plants from two or more populations in their native and alternative environment (i.e., reciprocal transplant) (Hufford and Mazer, 2003; Villemereuil *et al.*, 2016; Lortie and Hierro, 2022). Common garden and reciprocal transplant experiments can become even more relevant for restoration planning if coupled with the manipulation of abiotic conditions, such as simulated droughts or warming (Notivol *et al.*, 2020). Second, restoration projects often source plant material from different vendors, creating a natural experiment where researchers can test whether the origin of the seeds used in the mix will affect success at the species level inferred by germination, growth, reproduction, and/or survival rates (Pizza, Foster and Brudvig, 2023). Both controlled and natural experiments would provide valuable information to test whether the predictions of tools based on climatic analogues (e.g., COSST) or seed transfer zones (e.g., D4R) hold up in real situations (Miller *et al.*, 2011).

## 5.5. Concluding statement

Within this thesis, I have shown that large-scale ecosystem restoration in the Brazilian *Cerrado* should move towards incorporating more of its native species-rich flora, whilst accounting for future climate change threats. I identified the need to expand the number of species available for restoration as seed, especially herbaceous species. I also highlighted the mismatch between the species used in seed mixes *versus* the ones typical of old-growth areas. Moving forward, I argue that restoring diverse plant communities depends not only on seed availability but also on the long-term persistence of adult plants in the face of the ongoing climate change. In this regard, I found that climate change will reshape the *Cerrado* flora by 2040, including those species currently used in restoration projects. Finally, I moved the focus from species to populations and introduced a new framework to future-proof restoration by strategic seed collection among natural populations. Taken together, I hope these findings will contribute to combating and reversing land degradation in the Brazilian *Cerrado* biodiversity hotspot.

# Appendices

Courtesy of Bruna Campos

## Appendices

### Appendix 1 – Other publications (2021–2024)

First-authored peer-reviewed articles

- Silva, M. C., Melo, F. P. L. and Berg, E. (2021) ‘Changes in tree size, not species diversity, underlie the low above-ground biomass in natural forest edges’, Journal of Vegetation Science, 32(2), pp. 1–10. doi: 10.1111/jvs.13003.
- Silva, M. C. et al. (2021) ‘The enemy within: the effects of mistletoe parasitism on infected and uninfected host branches’, Plant Ecology, 222(5), pp. 639–645. doi: 10.1007/s11258-021-01132-6.
- Silva, M. C. et al. (2023) ‘From leaves to the whole tree: Mistletoe effects on the productivity, water relations, and demography of a Neotropical savanna tree’, Austral Ecology, (November), pp. 1–18. doi: 10.1111/aec.13461.

Co-authored peer-reviewed articles

- Giles, A. L. et al. (2022) ‘How effective is direct seeding to restore the functional composition of neotropical savannas?’, Restoration Ecology, 30(1), pp. 1–13. doi: 10.1111/rec.13474.
- Toone, T. A. et al. (2023) ‘Inclusive restoration: ten recommendations to support LGBTQ+ researchers in restoration science’, Restoration Ecology, 31(3). doi: 10.1111/rec.13743.
- Zanne, A. E. et al. (2022) ‘Termite sensitivity to temperature affects global wood decay rates’, Science, 377(6613), pp. 1440–1444. doi: 10.1126/science.abo3856.
- Mattos, C. R. C. et al. (2023) ‘Rainfall and topographic position determine tree embolism resistance in Amazônia and *Cerrado* sites’, Environmental Research Letters, 18(11), p. 114009. doi: 10.1088/1748-9326/ad0064.

Participation in reports

- Maioli, V. (2023) ‘Restoration Plan for the Pantanal Headwaters Landscape’. WWF-Brazil, Agroicone e AEGEA. ISBN:978-65-89267-04-1. https://wwfbrnew.awsassets.panda.org/downloads/lab-wwf-cabeceiraspantanal-restauracao-en-web.pdf.

Participation in science communication articles

- Yeung, P. (2023) ‘What’s at stake is the life of every being’: Saving the Brazilian *Cerrado*. Mongabay. https://news.mongabay.com/2021/02/whats-at-stake-is-the-life-of-every-being-saving-the-brazilian-*Cerrado*/ (Accessed on 01/12/2023).

# Appendix 2 – Supplementary material to chapter 2

## Appendix 2.1

Coordinates of the municipalities with seed collection activities by the *Rede de Sementes do Xingu* (RSX), *Rede de Sementes do Cerrado* (RSC), *VerdeNovo* (VN), and *Restauradores da RDS Nascentes Geraizeiras* (RDS) seed suppliers.

| Municipality | State | System | Longitude | Latitude |
|---|---|---|---|---|
| Alto Paraíso De Goiás | Goiás | RSC | -47.53503772 | -14.182979 |
| Cavalcante | Goiás | RSC | -47.69610637 | -13.63483414 |
| Colinas Do Sul | Goiás | RSC | -48.0751276 | -13.98491512 |
| Minaçu | Goiás | RSC | -48.34883188 | -13.49910784 |
| Nova Roma | Goiás | RSC | -47.01075126 | -13.80060515 |
| Teresina De Goiás | Goiás | RSC | -47.23753839 | -13.68240294 |
| Berizal | Minas Gerais | RDS | -41.76177286 | -15.6841129 |
| Montezuma | Minas Gerais | RDS | -42.46950384 | -15.19126449 |
| Rio Pardo De Minas | Minas Gerais | RDS | -42.55130263 | -15.70886514 |
| Taiobeiras | Minas Gerais | RDS | -42.05603136 | -15.82451771 |
| Vargem Grande Do Rio Pardo | Minas Gerais | RDS | -42.29891709 | -15.34071607 |
| Altamira | Pará | RSX | -53.88526356 | -6.481083979 |
| Água Boa | Mato Grosso | RSX | -52.50035535 | -13.97768503 |
| Bom Jesus Do Araguaia | Mato Grosso | RSX | -51.73961317 | -12.21782322 |
| Canabrava Do Norte | Mato Grosso | RSX | -51.82360578 | -11.20158473 |
| Canarana | Mato Grosso | RSX | -52.39930011 | -13.32992514 |
| Cláudia | Mato Grosso | RSX | -55.0477153 | -11.44814074 |
| Confresa | Mato Grosso | RSX | -51.69860128 | -10.40419775 |
| Diamantino | Mato Grosso | RSX | -56.80503644 | -14.09601894 |
| Feliz Natal | Mato Grosso | RSX | -54.18326992 | -11.93276047 |
| Guarantã Do Norte | Mato Grosso | RSX | -54.62106729 | -9.776326752 |
| Marcelândia | Mato Grosso | RSX | -54.05324038 | -10.88634417 |
| Nova Xavantina | Mato Grosso | RSX | -52.3802024 | -14.63454855 |
| Porto Alegre Do Norte | Mato Grosso | RSX | -51.71372724 | -10.82630332 |
| Querência | Mato Grosso | RSX | -52.74426224 | -12.15835764 |
| São José Do Xingu | Mato Grosso | RSX | -52.61688835 | -10.69640213 |
| Santa Cruz Do Xingu | Mato Grosso | RSX | -52.54143126 | -10.06447375 |
| São Félix Do Araguaia | Mato Grosso | RSX | -51.97052293 | -11.45543052 |
| Serra Nova Dourada | Mato Grosso | RSX | -51.36210558 | -12.02297925 |
| Arraias | Tocantins | VN | -47.04765564 | -12.8170917 |
| Montes Claros | Minas Gerais | VN | -43.92876318 | -16.62032554 |
| Mambaí | Goiás | VN | -46.06677873 | -14.41939181 |
| Brasília | Distrito Federal | VN | -47.79684133 | -15.7814442 |

## Appendix 2.2

Species with seeds traded by the main *Cerrado* seed suppliers. “1” means the species is traded by the respective supplier. RDS: *Restauradores da RDS Nascentes Geraizeiras*, RSC: *Rede de Sementes do Cerrado*, RSX: *Rede de Sementes do Xingu*, VN: *VerdeNovo*.

| **Species** | **RDS** | **RSC** | **RSX** | **VN** |
|---|---|---|---|---|
| *Abuta grandifolia* | | | 1 | |
| *Achyrocline satureioides* | 1 | 1 | | 1 |
| *Acrocomia aculeata* | | | 1 | 1 |
| *Actinocephalus polyanthus* | | | | 1 |
| *Aegiphila verticillata* | | | | 1 |
| *Aldama bracteata* | | | | 1 |
| *Aldama filifolia* | | | | 1 |
| *Aldama robusta* | | | | 1 |
| *Alibertia edulis* | | | 1 | |
| *Amburana cearensis* | | 1 | | 1 |
| *Anacardium humile* | | 1 | 1 | 1 |
| *Anacardium occidentale* | | 1 | 1 | 1 |
| *Anadenanthera colubrina* | 1 | 1 | 1 | 1 |
| *Andira cujabensis* | | | 1 | |
| *Andira fraxinifolia* | | 1 | | |
| *Andira vermifuga* | | 1 | 1 | |
| *Andropogon bicornis* | | | | 1 |
| *Andropogon fastigiatus* | | 1 | | 1 |
| *Andropogon leucostachyus* | | | | 1 |
| *Anemopaegma glaucum* | 1 | | | 1 |
| *Annona coriacea* | | | 1 | |
| *Annona crassiflora* | 1 | | 1 | 1 |
| *Annona muricata* | | | 1 | |
| *Apeiba tibourbou* | | | 1 | 1 |
| *Apuleia leiocarpa* | | | 1 | |
| *Aristida gibbosa* | | 1 | | 1 |
| *Aristida recurvata* | | | | 1 |
| *Aristida riparia* | 1 | 1 | | 1 |
| *Aristida setifolia* | 1 | | | |
| *Aspidosperma macrocarpon* | | | 1 | |
| *Aspidosperma macrocarpum* | | | | 1 |
| *Aspidosperma subincanum* | | | 1 | |
| *Aspidosperma tomentosum* | 1 | | | 1 |
| *Astrocaryum huaimi* | | | 1 | |
| *Astronium fraxinifolium* | 1 | 1 | 1 | 1 |
| *Astronium urundeuva* | 1 | 1 | 1 | 1 |
| *Attalea speciosa* | | | 1 | |
| *Axonopus aureus* | | 1 | | 1 |
| *Axonopus brasiliensis* | | | | 1 |
| *Axonopus siccus* | | 1 | | 1 |
| *Baccharis dracunculifolia* | | | | 1 |

| | | | | |
|---|---|---|---|---|
| *Bactris acanthocarpa* | | | 1 | |
| *Bauhinia campestris* | | | 1 | |
| *Bauhinia dumosa* | | | | 1 |
| *Bauhinia forficata* | | | | 1 |
| *Bellucia grossularioides* | | | 1 | |
| *Bixa orellana* | | | 1 | 1 |
| *Bowdichia virgilioides* | | 1 | 1 | 1 |
| *Brosimum gaudichaudii* | | | 1 | |
| *Buchenavia tetraphylla* | | | 1 | |
| *Buchenavia tomentosa* | | 1 | 1 | 1 |
| *Byrsonima basiloba* | | | | 1 |
| *Byrsonima coccolobifolia* | | | 1 | |
| *Byrsonima cydoniifolia* | | | 1 | |
| *Byrsonima verbascifolia* | | | 1 | |
| *Calliandra dysantha* | | | | 1 |
| *Calophyllum brasiliense* | | | 1 | 1 |
| *Carica papaya* | | | 1 | |
| *Cariniana estrellensis* | | | | 1 |
| *Cariniana rubra* | | | | 1 |
| *Caryocar brasiliense* | 1 | 1 | 1 | 1 |
| *Casearia sylvestris* | | | | 1 |
| *Cassia ferruginea* | | | | 1 |
| *Cecropia pachystachya* | | | 1 | 1 |
| *Cedrela fissilis* | | | 1 | |
| *Ceiba speciosa* | | | 1 | |
| *Centrolobium tomentosum* | | | | 1 |
| *Chaetocarpus echinocarpus* | | | 1 | |
| *Chamaecrista orbiculata* | | 1 | | |
| *Chresta exsucca* | | | | 1 |
| *Chresta sphaerocephala* | | | | 1 |
| *Chromolaena maximiliani* | | | | 1 |
| *Clitoria fairchildiana* | | | 1 | |
| *Cochlospermum regium* | | | | 1 |
| *Combretum leprosum* | | | | 1 |
| *Connarus suberosus* | | | | 1 |
| *Copaifera langsdorffii* | 1 | 1 | 1 | 1 |
| *Copaifera marginata* | | | 1 | |
| *Cordia alliodora* | | 1 | | |
| *Cordia trichotoma* | | | | 1 |
| *Cordiera macrophylla* | | | 1 | |
| *Couepia grandiflora* | | | 1 | |
| *Ctenium cirrosum* | | | | 1 |
| *Cucurbita pepo* | | | 1 | |
| *Cupania vernalis* | | | | 1 |
| *Curatella americana* | | | 1 | 1 |
| *Cybistax antisyphilitica* | | | 1 | 1 |
| *Dalbergia miscolobium* | 1 | | | 1 |
| *Delonix regia* | | | | 1 |
| *Didymopanax macrocarpus* | | | | 1 |
| *Dilodendron bipinnatum* | | | | 1 |

|  |  |  |  |  |
|---|---|---|---|---|
| *Dimorphandra mollis* |  | 1 | 1 | 1 |
| *Dioclea virgata* |  |  | 1 |  |
| *Diospyros lasiocalyx* |  |  | 1 |  |
| *Dipteryx alata* |  | 1 | 1 | 1 |
| *Duguetia furfuracea* | 1 |  |  |  |
| *Duguetia marcgraviana* |  |  | 1 |  |
| *Dyckia brasiliana* |  |  |  | 1 |
| *Echinolaena inflexa* |  | 1 |  | 1 |
| *Emmotum nitens* |  | 1 | 1 | 1 |
| *Enterolobium contortisiliquum* | 1 | 1 |  | 1 |
| *Enterolobium gummiferum* |  | 1 |  | 1 |
| *Enterolobium schomburgkii* |  |  | 1 |  |
| *Enterolobium timbouva* |  |  | 1 |  |
| *Eremanthus erythropappus* |  |  |  | 1 |
| *Eremanthus glomerulatus* |  | 1 |  |  |
| *Eremanthus uniflorus* |  | 1 |  |  |
| *Eriotheca gracilipes* |  |  | 1 |  |
| *Eriotheca pubescens* |  |  |  | 1 |
| *Esenbeckia pumila* |  |  |  | 1 |
| *Eugenia dysenterica* | 1 |  | 1 | 1 |
| *Eugenia punicifolia* |  |  |  | 1 |
| *Euterpe edulis* |  |  |  | 1 |
| *Euterpe oleracea* |  |  | 1 |  |
| *Fridericia platyphylla* |  | 1 |  | 1 |
| *Genipa americana* |  |  | 1 | 1 |
| *Guazuma ulmifolia* | 1 | 1 | 1 | 1 |
| *Gymnopogon foliosus* |  |  |  | 1 |
| *Hancornia speciosa* | 1 |  | 1 | 1 |
| *Handroanthus heptaphyllus* |  |  |  | 1 |
| *Handroanthus impetiginosus* | 1 | 1 | 1 | 1 |
| *Handroanthus ochraceus* | 1 |  | 1 |  |
| *Handroanthus serratifolius* |  |  | 1 | 1 |
| *Himatanthus articulatus* |  |  | 1 |  |
| *Himatanthus obovatus* |  |  | 1 | 1 |
| *Humiria balsamifera* |  |  | 1 |  |
| *Hymenaea courbaril* | 1 | 1 | 1 | 1 |
| *Hymenaea stigonocarpa* | 1 | 1 | 1 | 1 |
| *Hyparrhenia bracteata* |  | 1 |  |  |
| *Hyptis dictyodea* |  |  |  | 1 |
| *Inga edulis* |  |  | 1 | 1 |
| *Inga heterophylla* |  |  | 1 |  |
| *Inga laurina* |  |  | 1 | 1 |
| *Inga thibaudiana* |  |  | 1 |  |
| *Jacaranda brasiliana* |  | 1 |  | 1 |
| *Jacaranda cuspidifolia* |  |  | 1 |  |
| *Jacaranda ulei* |  | 1 |  | 1 |
| *Kielmeyera abdita* |  |  |  | 1 |
| *Kielmeyera coriacea* | 1 | 1 |  | 1 |
| *Kielmeyera speciosa* |  |  |  | 1 |
| *Lafoensia pacari* |  | 1 | 1 | 1 |

| | | | | |
|---|---|---|---|---|
| *Lagenocarpus rigidus* | | | | 1 |
| *Lepidaploa aurea* | | 1 | | 1 |
| *Lepidaploa rufogrisea* | 1 | | | 1 |
| *Leptolobium dasycarpum* | | | | 1 |
| *Libidibia ferrea* | | | | 1 |
| *Licania micrantha* | | | 1 | |
| *Lippia lupulina* | | | | 1 |
| *Loudetiopsis chrysothrix* | | 1 | | 1 |
| *Luehea divaricata* | | 1 | | |
| *Luetzelburgia auriculata* | | | | 1 |
| *Mabea fistulifera* | | | 1 | 1 |
| *Mabea paniculata* | | | 1 | |
| *Machaerium acutifolium* | | | 1 | |
| *Machaerium hirtum* | | | | 1 |
| *Machaerium opacum* | 1 | 1 | | 1 |
| *Maclura tinctoria* | | | 1 | |
| *Magonia pubescens* | 1 | 1 | 1 | 1 |
| *Mauritia flexuosa* | | | 1 | 1 |
| *Mauritiella armata* | | | 1 | 1 |
| *Mezilaurus crassiramea* | | | 1 | |
| *Miconia ligustroides* | | | | 1 |
| *Mimosa claussenii* | | 1 | | 1 |
| *Mimosa gemmulata* | 1 | | | |
| *Mouriri acutiflora* | | | 1 | |
| *Mouriri apiranga* | | | 1 | |
| *Mouriri elliptica* | | | 1 | |
| *Mucuna pruriens* | | | 1 | |
| *Myrsine guianensis* | | | | 1 |
| *Odontadenia hypoglauca* | | | | 1 |
| *Oenocarpus distichus* | | | 1 | |
| *Ormosia arborea* | | | | 1 |
| *Ormosia excelsa* | | | 1 | |
| *Ouratea hexasperma* | | | | 1 |
| *Paepalanthus chiquitensis* | | 1 | | 1 |
| *Parinari obtusifolia* | | | | 1 |
| *Paspalum eucomum* | | | | 1 |
| *Paspalum stellatum* | | 1 | | 1 |
| *Passiflora cincinnata* | 1 | | | |
| *Passiflora edulis* | | | 1 | |
| *Passiflora setacea* | 1 | | | |
| *Peltogyne confertiflora* | | | 1 | |
| *Pera heteranthera* | | | 1 | |
| *Peritassa campestris* | 1 | | 1 | |
| *Peritassa laevigata* | | | 1 | |
| *Physocalymma scaberrimum* | | | 1 | 1 |
| *Plathymenia reticulata* | 1 | | 1 | 1 |
| *Platypodium elegans* | | | 1 | 1 |
| *Pleroma candolleanum* | | | | 1 |
| *Pleroma stenocarpum* | | | | 1 |
| *Pouteria macrophylla* | | | 1 | |

| | | | | |
|---|---|---|---|---|
| *Pouteria ramiflora* | | | 1 | |
| *Pseudobombax tomentosum* | | | 1 | 1 |
| *Pseudobrickellia brasiliensis* | | | | 1 |
| *Pseudotrimezia juncifolia* | | | | 1 |
| *Psidium guajava* | | | 1 | |
| *Pterodon emarginatus* | | 1 | | 1 |
| *Pterodon pubescens* | | | 1 | |
| *Pterogyne nitens* | | | 1 | 1 |
| *Pyrostegia venusta* | | | 1 | |
| *Qualea grandiflora* | 1 | 1 | 1 | 1 |
| *Qualea parviflora* | 1 | 1 | | |
| *Rhynchospora globosa* | | | | 1 |
| *Rhynchospora speciosa* | | | | 1 |
| *Sabicea brasiliensis* | | | | 1 |
| *Salvertia convallariodora* | | | 1 | |
| *Samanea saman* | | | 1 | |
| *Sapindus saponaria* | | | | 1 |
| *Schinopsis brasiliensis* | 1 | | | 1 |
| *Schinus terebinthifolia* | | | | 1 |
| *Schizachyrium sanguineum* | | 1 | | 1 |
| *Senegalia langsdorffii* | 1 | | | |
| *Senegalia polyphylla* | | 1 | 1 | 1 |
| *Senna alata* | | 1 | 1 | 1 |
| *Senna cana* | 1 | | | |
| *Senna obtusifolia* | | | 1 | |
| *Senna rugosa* | 1 | | | 1 |
| *Simarouba amara* | | | 1 | |
| *Simarouba versicolor* | | 1 | 1 | |
| *Siparuna guianensis* | | | 1 | |
| *Smilax goyazana* | | | | 1 |
| *Solanum crinitum* | | | 1 | |
| *Solanum lycocarpum* | 1 | 1 | | 1 |
| *Sorghastrum setosum* | | | | 1 |
| *Spondias mombin* | | | 1 | |
| *Stachytarpheta longispicata* | | | | 1 |
| *Sterculia striata* | | 1 | 1 | 1 |
| *Strychnos pseudoquina* | | | 1 | |
| *Stryphnodendron adstringens* | 1 | 1 | | 1 |
| *Stryphnodendron fissuratum* | | | | 1 |
| *Stryphnodendron rotundifolium* | | | 1 | |
| *Swietenia macrophylla* | | | 1 | 1 |
| *Syagrus flexuosa* | | | 1 | |
| *Syagrus oleracea* | | 1 | 1 | 1 |
| *Syagrus romanzoffiana* | | | 1 | |
| *Tabebuia aurea* | | 1 | 1 | 1 |
| *Tabebuia roseoalba* | | | 1 | 1 |
| *Tachigali aurea* | 1 | 1 | | 1 |
| *Tachigali subvelutina* | 1 | | 1 | |
| *Tachigali vulgaris* | | 1 | 1 | |
| *Talisia esculenta* | | | 1 | |

| | | | | |
|---|---|---|---|---|
| *Tamarindus indica* | | | 1 | |
| *Terminalia argentea* | 1 | 1 | 1 | 1 |
| *Terminalia fagifolia* | 1 | 1 | | 1 |
| *Terminalia glabrescens* | | | | 1 |
| *Trachypogon spicatus* | | 1 | | 1 |
| *Trema micrantha* | | | 1 | |
| *Trichogonia prancei* | | | | 1 |
| *Triplaris americana* | | | | 1 |
| *Triplaris gardneriana* | | | | 1 |
| *Vatairea macrocarpa* | | 1 | 1 | 1 |
| *Vernonanthura polyanthes* | 1 | 1 | | 2 |
| *Virola sebifera* | | | 1 | 1 |
| *Vismia japurensis* | | | 1 | |
| *Vitex panshiniana* | | | 1 | |
| *Vochysia divergens* | | | 1 | |
| *Vochysia haenkeana* | | | 1 | |
| *Vochysia rufa* | | | | 1 |
| *Vochysia thyrsoidea* | | | | 1 |
| *Xylopia aromatica* | | | 1 | 1 |
| *Xylopia sericea* | | | 1 | |
| *Zanthoxylum rhoifolium* | | | 1 | 1 |
| *Zeyheria montana* | | 1 | | 1 |

## Appendix 2.3

The details of the 66 study sites from 25 publications used to rank *Cerrado* species according to their dominance in the ground layer.

| First author name | Publication year | Vegetation type | Link |
|---|---|---|---|
| Aianã Francisco Santos Pereira | 2010 | Rock outcrop | https://www.locus.ufv.br/bitstream/123456789/2540/1/texto%20completo.pdf |
| Aianã Francisco Santos Pereira | 2010 | Rock outcrop | https://www.locus.ufv.br/bitstream/123456789/2540/1/texto%20completo.pdf |
| Chesterton Ulysses Orlando Eugênio | 2011 | Grassland | https://repositorio.unb.br/bitstream/10482/8655/3/2011_CherstertonUlyssesOrlandoEugenio.pdf |
| Chesterton Ulysses Orlando Eugênio | 2011 | Flooded grassland | https://repositorio.unb.br/bitstream/10482/8655/3/2011_CherstertonUlyssesOrlandoEugenio.pdf |
| Chesterton Ulysses Orlando Eugênio | 2011 | Flooded grassland | https://repositorio.unb.br/bitstream/10482/8655/3/2011_CherstertonUlyssesOrlandoEugenio.pdf |
| Chesterton Ulysses Orlando Eugênio | 2016 | Palm swamp | https://repositorio.unb.br/bitstream/10482/22737/1/2016_ChestertonUlyssesOrlandoEugenio.pdf |
| Chesterton Ulysses Orlando Eugênio | 2016 | Palm swamp | https://repositorio.unb.br/bitstream/10482/22737/1/2016_ChestertonUlyssesOrlandoEugenio.pdf |
| Chesterton Ulysses Orlando Eugênio | 2016 | Palm swamp | https://repositorio.unb.br/bitstream/10482/22737/1/2016_ChestertonUlyssesOrlandoEugenio.pdf |
| Chesterton Ulysses Orlando Eugênio | 2016 | Palm swamp | https://repositorio.unb.br/bitstream/10482/22737/1/2016_ChestertonUlyssesOrlandoEugenio.pdf |
| Diogo Pereira da Silva | 2016 | Palm swamp | https://repositorio.unb.br/bitstream/10482/22419/1/2016_DiogoPereiradaSilva.pdf |
| Diogo Pereira da Silva | 2016 | Palm swamp | https://repositorio.unb.br/bitstream/10482/22419/1/2016_DiogoPereiradaSilva.pdf |
| Diogo Pereira da Silva | 2016 | Palm swamp | https://repositorio.unb.br/bitstream/10482/22419/1/2016_DiogoPereiradaSilva.pdf |
| Diogo Pereira da Silva | 2016 | Palm swamp | https://repositorio.unb.br/bitstream/10482/22419/1/2016_DiogoPereiradaSilva.pdf |
| Emilia Pinto Braga | 2010 | Savanna | https://repositorio.unb.br/bitstream/10482/6926/1/2010_EmiliaPintoBraga.pdf |
| Fernanda de Carvalho | 2010 | Rock outcrop | http://pos.icb.ufmg.br/pgecologia/teses/T67_Fernanda_de_Carvalho.pdf |

|  |  |  |  |
|---|---|---|---|
| Fernanda de Carvalho | 2010 | Flooded grassland | http://pos.icb.ufmg.br/pgecologia/teses/T67_Fernanda_de_Carvalho.pdf |
| Fernanda de Carvalho | 2010 | Rock outcrop | http://pos.icb.ufmg.br/pgecologia/teses/T67_Fernanda_de_Carvalho.pdf |
| Fernanda de Carvalho | 2010 | Savanna | http://pos.icb.ufmg.br/pgecologia/teses/T67_Fernanda_de_Carvalho.pdf |
| Fernanda de Carvalho | 2010 | Rock outcrop | http://pos.icb.ufmg.br/pgecologia/teses/T67_Fernanda_de_Carvalho.pdf |
| Gabriella Ferreira de Souza | 2021 | Savanna | https://link.springer.com/article/10.1007/s40415-020-00672-x |
| Guilherme de Medeiros Antar | 2015 | Grassland | https://teses.usp.br/teses/disponiveis/41/41132/tde-08032016-135410/publico/Guilherme_Antar.pdf |
| Guilherme de Medeiros Antar | 2015 | Grassland | https://teses.usp.br/teses/disponiveis/41/41132/tde-08032016-135410/publico/Guilherme_Antar.pdf |
| Guilherme de Medeiros Antar | 2015 | Grassland | https://teses.usp.br/teses/disponiveis/41/41132/tde-08032016-135410/publico/Guilherme_Antar.pdf |
| Guilherme de Medeiros Antar | 2015 | Grassland | https://teses.usp.br/teses/disponiveis/41/41132/tde-08032016-135410/publico/Guilherme_Antar.pdf |
| Halina Soares Jancoski | 2010 | Flooded grassland | https://repositorio.unb.br/bitstream/10482/7328/1/2010_HalinaSoaresJancoski.pdf |
| Igor Aurélio Silva | 2010 | Grassland | https://link.springer.com/article/10.1556/ComEc.11.2010.1.14#SecESM1 |
| Igor Aurélio Silva | 2010 | Grassland | https://link.springer.com/article/10.1556/ComEc.11.2010.1.14#SecESM1 |
| Igor Aurélio Silva | 2010 | Grassland | https://link.springer.com/article/10.1556/ComEc.11.2010.1.14#SecESM1 |
| João Luis Sanches Tannus | 2007 | Flooded grassland | https://repositorio.unesp.br/bitstream/handle/11449/100640/tannus_jls_dr_rcla.pdf?sequence=1&isAllowed=y |
| Marcelo Leandro Bueno | 2014 | Flooded grassland | https://www.scielo.br/scielo.php?script=sci_arttext&pid=S1519-69842014000200325&lng=en&tlng=en |
| Marco Antônio Batalha | 1997 | Savanna | https://teses.usp.br/teses/disponiveis/41/41134/tde-01082001-083840/publico/Batalha.pdf |
| Marco Antônio Batalha | 1997 | Grassland | https://teses.usp.br/teses/disponiveis/41/41134/tde-01082001-083840/publico/Batalha.pdf |
| Marcus Vinícius Cianciaruso | 2005 | Flooded grassland | https://repositorio.ufscar.br/bitstream/handle/ufscar/2111/607.pdf?sequence=1&isAllowed=y |
| Marcus Vinícius Cianciaruso | 2005 | Grassland | https://repositorio.ufscar.br/bitstream/handle/ufscar/2111/607.pdf?sequence=1&isAllowed=y |

| | | | |
|---|---|---|---|
| Marta Regina Barrotto do Carmo | 2006 | Grassland | https://repositorio.unesp.br/bitstream/handle/11449/100628/carmo_mrb_dr_rcla.pdf?sequence=1&isAllowed=y |
| Marta Regina Barrotto do Carmo | 2006 | Flooded grassland | https://repositorio.unesp.br/bitstream/handle/11449/100628/carmo_mrb_dr_rcla.pdf?sequence=1&isAllowed=y |
| Marta Regina Barrotto do Carmo | 2006 | Rock outcrop | https://repositorio.unesp.br/bitstream/handle/11449/100628/carmo_mrb_dr_rcla.pdf?sequence=1&isAllowed=y |
| Mercedes Maria da Cunha Bustamante | 2012 | Savanna | https://link.springer.com/article/10.1007/s11258-012-0042-4 |
| Mônica Gabrielle Paêlo | 2013 | Flooded grassland | https://ri.ufmt.br/bitstream/1/1713/1/DISS_2013_M%c3%b4nica%20Gabrielle%20Pa%c3%aalo.pdf |
| Mônica Gabrielle Paêlo | 2013 | Flooded grassland | https://ri.ufmt.br/bitstream/1/1713/1/DISS_2013_M%c3%b4nica%20Gabrielle%20Pa%c3%aalo.pdf |
| Mônica Gabrielle Paêlo | 2013 | Flooded grassland | https://ri.ufmt.br/bitstream/1/1713/1/DISS_2013_M%c3%b4nica%20Gabrielle%20Pa%c3%aalo.pdf |
| Mônica Gabrielle Paêlo | 2013 | Flooded grassland | https://ri.ufmt.br/bitstream/1/1713/1/DISS_2013_M%c3%b4nica%20Gabrielle%20Pa%c3%aalo.pdf |
| Natália Rodrigues Bijos | 2017 | Palm swamp | https://www.sciencedirect.com/science/article/pii/S0367253017333522?via%3Dihub |
| Natália Rodrigues Bijos | 2017 | Palm swamp | https://www.sciencedirect.com/science/article/pii/S0367253017333522?via%3Dihub |
| Natália Rodrigues Bijos | 2017 | Palm swamp | https://www.sciencedirect.com/science/article/pii/S0367253017333522?via%3Dihub |
| Natália Rodrigues Bijos | 2017 | Palm swamp | https://www.sciencedirect.com/science/article/pii/S0367253017333522?via%3Dihub |
| Natália Rodrigues Bijos | 2017 | Palm swamp | https://www.sciencedirect.com/science/article/pii/S0367253017333522?via%3Dihub |
| Paula Alves Oliveira | 2015 | Rock outcrop | http://acervo.ufvjm.edu.br/jspui/bitstream/1/1036/1/paula_alves_oliveira.pdf |
| Paula Alves Oliveira | 2015 | Rock outcrop | http://acervo.ufvjm.edu.br/jspui/bitstream/1/1036/1/paula_alves_oliveira.pdf |
| Paula Alves Oliveira | 2015 | Rock outcrop | http://acervo.ufvjm.edu.br/jspui/bitstream/1/1036/1/paula_alves_oliveira.pdf |
| Rafael de Oliveira Xavier | 2019 | Flooded grassland | https://link.springer.com/article/10.1007/s00442-019-04423-y |
| Rafael de Oliveira Xavier | 2019 | Grassland | https://link.springer.com/article/10.1007/s00442-019-04423-y |
| Rafael de Oliveira Xavier | 2019 | Grassland | https://link.springer.com/article/10.1007/s00442-019-04423-y |

| | | | |
|---|---|---|---|
| Rafael de Oliveira Xavier | 2019 | Grassland | https://link.springer.com/article/10.1007/s00442-019-04423-y |
| Rafael de Oliveira Xavier | 2019 | Savanna | https://link.springer.com/article/10.1007/s00442-019-04423-y |
| Rodolfo Cesar Real de Abreu | 2013 | Grassland | https://teses.usp.br/teses/disponiveis/18/18139/tde-23092013-085713/publico/TeseRodolfoCesarRealDeAbreu.pdf |
| Soizig Anne Le Stradic | 2012 | Rock outcrop | https://repositorio.ufmg.br/handle/1843/BUOS-96WF5S |
| Soizig Anne Le Stradic | 2012 | Rock outcrop | https://repositorio.ufmg.br/handle/1843/BUOS-96WF5S |
| Sonielle Pereira Paro | 2013 | Savanna | https://www.locus.ufv.br/bitstream/123456789/2550/1/texto%20completo.pdf |
| Sonielle Pereira Paro | 2013 | Savanna | https://www.locus.ufv.br/bitstream/123456789/2550/1/texto%20completo.pdf |
| Sonielle Pereira Paro | 2013 | Savanna | https://www.locus.ufv.br/bitstream/123456789/2550/1/texto%20completo.pdf |
| Suzana Neves Moreira | 2015 | Palm swamp | https://repositorio.ufmg.br/bitstream/1843/BUBD-A35JZ6/1/tese_suzanamoreira_final.pdf |
| Thiago de Roure Bandeira de Mello | 2012 | Flooded grassland | https://repositorio.unb.br/bitstream/10482/12515/1/2012_ThiagodeRoureBandeiradeMello.pdf |
| Thiago de Roure Bandeira de Mello | 2012 | Flooded grassland | https://repositorio.unb.br/bitstream/10482/12515/1/2012_ThiagodeRoureBandeiradeMello.pdf |
| Thiago de Roure Bandeira de Mello | 2012 | Rock outcrop | https://repositorio.unb.br/bitstream/10482/12515/1/2012_ThiagodeRoureBandeiradeMello.pdf |
| Thiago de Roure Bandeira de Mello | 2012 | Rock outcrop | https://repositorio.unb.br/bitstream/10482/12515/1/2012_ThiagodeRoureBandeiradeMello.pdf |

## Appendix 2.4

The top 15 species with the highest importance value index (IVI) on the ground layer of 66 study sites in the *Cerrado*. IVI corresponds to the mean of the abundance index and relative frequency. Seed availability regards whether the species is being traded or not among the studied seed suppliers.

| **Species** | **Mean abundance index** | **Relative frequency** | **Importance value index** | **Seed availability** |
|---|---|---|---|---|
| *Trachypogon spicatus* | 0.112305 | 0.484848 | 0.298577 | Traded |
| *Echinolaena inflexa* | 0.093308 | 0.469697 | 0.281503 | Traded |
| *Lagenocarpus rigidus* | 0.099787 | 0.439394 | 0.26959 | Traded |
| *Rhynchospora globosa* | 0.093994 | 0.424242 | 0.259118 | Traded |
| *Axonopus brasiliensis* | 0.075282 | 0.393939 | 0.234611 | Traded |
| *Paspalum lineare* | 0.146647 | 0.30303 | 0.224839 | Not traded |
| *Tristachya leiostachya* | 0.210658 | 0.227273 | 0.218965 | Not traded |
| *Vellozia graminea* | 0.360064 | 0.030303 | 0.195184 | Not traded |
| *Andropogon leucostachyus* | 0.051978 | 0.333333 | 0.192655 | Traded |
| *Rhynchospora tenuis* | 0.094032 | 0.272727 | 0.18338 | Not traded |
| *Rhynchospora exaltata* | 0.317732 | 0.030303 | 0.174018 | Not traded |
| *Axonopus siccus* | 0.129434 | 0.19697 | 0.163202 | Traded |
| *Andropogon virgatus* | 0.046527 | 0.257576 | 0.152051 | Not traded |
| *Mesosetum loliiforme* | 0.045746 | 0.257576 | 0.151661 | Not traded |
| *Rhynchospora consanguinea* | 0.014531 | 0.287879 | 0.151205 | Not traded |

## Appendix 2.5

The amount of seeds sold per species by the *Rede de Sementes do Cerrado* (RSC) from 2017 to 2019 alongside their importance value index. IVI corresponds to the mean of the abundance index and relative frequency calculated over 66 study sites in the *Cerrado*.

| **Species** | **Mean abundance index** | **Relative frequency** | **Importance value index** | **Seeds sold (ton)** |
|---|---|---|---|---|
| *Lepidaploa aurea* | 0.002403 | 0.015152 | 0.008777 | 2.74665 |
| *Schizachyrium sanguineum* | 0.012898 | 0.121212 | 0.067055 | 1.04945 |
| *Aristida riparia* | 0.00347 | 0.030303 | 0.016887 | 0.8228 |
| *Vernonanthura polyanthes* | 8.02E-06 | 0.015152 | 0.00758 | 0.750462 |
| *Aristida setifolia* | 0.018499 | 0.030303 | 0.024401 | 0.7312 |
| *Loudetiopsis chrysothrix* | 0.085626 | 0.212121 | 0.148874 | 0.55835 |
| *Trachypogon spicatus* | 0.112305 | 0.484848 | 0.298577 | 0.2623 |
| *Axonopus siccus* | 0.129434 | 0.19697 | 0.163202 | 0.1702 |
| *Hyparrhenia bracteata* | 0.019053 | 0.060606 | 0.039829 | 0.12215 |
| *Axonopus aureus* | 0.009011 | 0.181818 | 0.095415 | 0.1118 |
| *Paspalum stellatum* | 0.001404 | 0.030303 | 0.015853 | 0.0322 |
| *Lepidaploa rufogrisea* | 0.004715 | 0.045455 | 0.025085 | 0.0272 |
| *Achyrocline satureioides* | 0.021847 | 0.106061 | 0.063954 | 0.024 |
| *Paepalanthus chiquitensis* | 0.001376 | 0.015152 | 0.008264 | 0.01 |
| *Echinolaena inflexa* | 0.093308 | 0.469697 | 0.281503 | 0.000785 |
| *Senna rugosa* | 0.006808 | 0.106061 | 0.056434 | 0.0005 |

# Appendix 3 – Supplementary material to chapter 3

## Appendix 3.1 – Supplementary methods

### *Cerrado* edaphic and vegetation description

The *Cerrado* is roughly three times the size of France. Ferralsols are the predominant soil group (covering 44% of the *Cerrado* area), followed by Arenosols (21%), Plinthosols (10%), and Cambisols (10%) (Sano *et al.*, 2019; Lira-Martins *et al.*, 2022). Edaphic conditions vary on a fine scale, with mosaics of rock outcrops, well-drained soils, and seasonally waterlogged soils coexisting within 1 km$^2$ (Abrahão *et al.*, 2019). Savannas historically covered 57% of the *Cerrado* (Rodrigues *et al.*, 2022) and consist of open-canopy vegetation with a continuous herbaceous layer (Ribeiro and Walter, 1998). Grasslands and forests were the second most common vegetation type, both covering 21% of the *Cerrado* according to historical reconstructions (Rodrigues *et al.*, 2022). Savannas and grasslands are fire-prone and occur on well-drained deep acidic Al-rich soils (*cerrado sensu stricto*, *campo sujo*, *campo limpo*), seasonally waterlogged soils (*vereda*, *campo úmido*), and rock outcrops (*Cerrado rupestre*, *campo rupestre*). Forests are fire-sensitive and occur on well-drained alkaline nutrient-rich soils (*mata seca*), alongside watercourses (*mata de galeria*, *mata riparia*), and in fire-excluded areas (*cerradão*).

### Data cleaning

Firstly, we removed all records containing missing coordinates and coordinates outside the planetary boundaries. Secondly, we flagged and excluded potential errors (e.g., coordinates in the ocean, the centroid of municipalities) using the function “clean_coordinates” from the R package “CoordinateCleaner” (Zizka *et al.*, 2019). Thirdly, we removed all records without identification at the species level or falling outside South America.

### MaxEnt additional information

MaxEnt performance generally exceeds that of the other algorithms, such as generalized linear and additive models (Elith *et al.*, 2006; Valavi *et al.*, 2022), especially for species with few occurrence records. Furthermore, MaxEnt can fit non-linear relationships by transforming predictor variables (i.e., features) and can smooth out the model prediction by the use of regularization parameters (e.g., $L_1$/Lasso) (Phillips and Dudík, 2008; Elith *et al.*, 2011). Lastly, MaxEnt has a lower computation time than alternative algorithms (Valavi *et al.*, 2022), which is critical when large numbers of SDMs need to be fitted, as was required for this study.

Previous studies have recommended controlling MaxEnt regularization parameters and features to balance model complexity and goodness-of-fit (i.e., tuning) (Anderson and Gonzalez, 2011; Radosavljevic and Anderson, 2014). Yet, Valavi et al. (2022) showed that there is no statistically significant difference between tuned and default MaxEnt models, although the former increases the computational time and uses more memory than the latter. Therefore, we used MaxEnt default settings to allow us to fit SDMs for thousands of species in a time- and memory-efficient way.

### Bias-corrected background point generation

The density of presence records is often biased towards areas close to research institutions, roads, and human settlements (Oliveira et al., 2016; Reddy & Dávalos, 2003). Ignoring sampling biases can lead to SDMs that assume high environmental suitability in oversampled sites and low environmental suitability in undersampled sites (Phillips *et al.*, 2009; Kramer-Schadt *et al.*, 2013). Therefore, spatially biased presence data translates into a biased representation of the species' environmental niche, adding uncertainty when transferring the model to a new timeframe (Radosavljevic and Anderson, 2014). MaxEnt requires additional input data named "background points" which consists of a set of points capturing the whole range of environmental conditions that a species is expected to experience within its accessible area (i.e., theoretical area accessed through dispersal). Background points are usually randomly generated inside the species' accessible area. We calculated the density of presence points per pixel and generated background points as a function of this density layer (Appendix 3.10).

Therefore, background points will be most likely to be allocated in well-sampled areas, which reduces the chance of assuming niche unsuitability when the lack of presence points is due to under-sampling.

We produced the sampling density layer by creating a grid at the resolution of 30 arcsecs and applying a function to count the number of cleaned presence records of all terrestrial plants available on GBIF and SpeciesLink per grid cell for South America. The taxonomic and spatial scope of the sampling density layer aimed to capture sampling biases across multiple taxa at once and at the extent where the SDMs were fitted (S. America). We constructed the accessible area of each species by drawing circles of 250 km of radius around each presence point following Moonlight et al. (2020) (Appendix 3.11a, b). We, then, used the function “sampleRast” from the R package “enmSdm” (Smith, 2021) to produce 10,000 background points within the species’ accessible area. We set the argument “prob = TRUE” which made the probability of placing a point proportional to the density of presence records at that pixel (Appendix 3.11c, d).

### Environmental predictor assumptions

We assumed climate to be the main driver of the distribution of *Cerrado* plants, but we acknowledge that soils and fire regimes also control their occurrence and abundance (Lira-Martins *et al.*, 2022). Edaphic and fire spatial products do exist for the near-present timeframe (Andela *et al.*, 2019; Batjes, Ribeiro and van Oostrum, 2020). We did not include such environmental layers in our modelling because, to the best of our knowledge, such layers are not available for the future time horizon (2011–2040) and global change scenarios (SSP1 and SSP5) used here. Furthermore, inaccurate georeferencing propagates more uncertainty to the model output when soil and fire variables are used as input data alongside climate. The climate varies on coarse scales while soils and fire regimes vary on a much finer scale. In the case of the *Cerrado*, the climate varies over kilometres (Nascimento and Novais, 2020) whereas different soil types and fire regimes can be a few metres apart from each other, often spatially structured as a complex mosaic (Lira-Martins *et al.*, 2022). Therefore, an imprecise coordinate is more likely to fall within its true climate than its true soil type and fire regime. By focusing on the climatic niche only, our models avoid the issues described above, but are more likely to overestimate species ranges, and therefore give an optimistic perspective of species potential range size.

### Grided climatic products

CHELSA climatologies are based on statistical downscaling of atmospheric temperature and precipitation data from ERA-Interim Reanalysis. Downscaled climatologies often yield more accurate climatic projections compared to climatologies based on the interpolation of weather stations (e.g., WorldClim) (Karger *et al.*, 2017). In this study, we used the following seven bioclimatic variables along with their biological significance.

- Mean diurnal temperature range (BIO2): The thermal oscillation an organism experiences during the day.
- Isothermality (BIO3): The magnitude of daily thermal oscillations (day-to-night) relative to annual thermal oscillations (summer-to-winter).
- Mean temperature of the wettest quarter (BIO8): The average temperature an organism experiences during the wettest season (e.g., summer in the tropics).
- Mean temperature of the driest quarter (BIO9): The average temperature an organism experiences during the driest season (e.g., winter in the tropics).
- Precipitation of the wettest month (BIO13): The maximum rainfall an organism experiences at the peak of the wettest season (e.g., summer in the tropics).
- Precipitation of the driest month (BIO14): The minimum rainfall an organism experiences at the peak of the driest season (e.g., winter in the tropics).
- Precipitation seasonality (BIO15): The magnitude of rainfall oscillation an organism experiences over the course of the year.

Global Circulation Models (GCMs) differ in their future climate projections, which propagates uncertainty into SDMs transferred to the future (Steen *et al.*, 2017;

Thuiller *et al.*, 2019). We accounted for this uncertainty by downloading the forecasts of five competing GCMs: the Geophysical Fluid Dynamics Laboratory's Earth System Model Version 4 (GFDL-ESM4) (Dunne *et al.*, 2020), the U.K.'s Earth System Model Version 1-0-LL (UK-ESM1-0-LL) (Sellar *et al.*, 2019), Max Planck Institute Earth System Model (MPI-ESM1-2-HR) (Gutjahr *et al.*, 2019), Institut Pierre-Simon Laplace Climate Model (IPSL-CM6A-LR) (Boucher *et al.*, 2020), and Meteorological Research Institute Earth System Model (MRI-ESM2-0) (Yukimoto *et al.*, 2019).

## Continuous Boyce Index (CBI) additional information

CBI is a presence-only statistic ranging from -1 to 1 (Boyce *et al.*, 2002; Hirzel *et al.*, 2006). The closer the CBI to 1, the higher the model capacity to predict the species to occur where the validation dataset shows so. CBI around 0 means the SDM predictive power is no better than what would be expected by chance. Negative CBI implies the models are paradoxically predicting the species to occur in places far from where the validation presences were registered, hence, a poor SDM performance. CBI has been reported to be unaffected by species' prevalence, i.e., the percentage of the presence data belonging to a species (Hirzel *et al.*, 2006). That makes CBI a robust performance metric for evaluating SDMs fitted to rare species, a common feature in the *Cerrado*.

## Appendix 3.2

The number of presence records per data processing stage.

| Stage | Dataset | Number of records |
|---|---|---|
| Raw data | GBIF | 9,108,756 |
| | SpeciesLink | 7,682,847 |
| Remove records missing coordinates | GBIF | 5,664,438 |
| | SpeciesLink | 7,682,846 |
| Merge datasets | Merged* | 13,347,284 |
| Remove records outside the planetary boundary (90° S/N, 180° W/E) | Merged* | 13,347,281 |
| Remove potential errors according to CoodinateCleaner | Merged* | 6,068,634 |
| Remove records missing the species determination | Merged* | 5,470,890 |
| Remove species that are not native in the *Cerrado* | Merged* | 2,204,404 |
| Remove records outside South America | Merged* | 2,167,263 |
| Remove species with 10 or fewer records | Merged* | 2,156,244 |
| Remove non-angiosperms (e.g., mosses, ferns, conifers) | Merged* | 1,988,701 |

* GBIF + SpeciesLink

## Appendix 3.3

List of the bioclimatic variables downloaded from Chelsa V2.1. Note that the rainfall unit “kg $m^{-2}$” is equivalent to “mm”.

| Code | Bioclimatic variable | Unit |
|---|---|---|
| BIO1 | Mean annual air temperature | °C |
| BIO2 | Mean diurnal air temperature range | °C |
| BIO3 | Isothermality | °C |
| BIO4 | Temperature seasonality | °C |
| BIO5 | Mean daily maximum air temperature of the warmest month | °C |
| BIO6 | Mean daily minimum air temperature of the coldest month | °C |
| BIO7 | Annual range of air temperature | °C |
| BIO8 | Mean daily mean air temperatures of the wettest quarter | °C |
| BIO9 | Mean daily mean air temperatures of the driest quarter | °C |
| BIO10 | Mean daily mean air temperatures of the warmest quarter | °C |
| BIO11 | Mean daily mean air temperatures of the coldest quarter | °C |
| BIO12 | Annual accumulated precipitation | kg $m^{-2}$ $year^{-1}$ |
| BIO13 | Accumulated precipitation of the wettest month | kg $m^{-2}$ $month^{-1}$ |
| BIO14 | Accumulated precipitation of the driest month | kg $m^{-2}$ $month^{-1}$ |
| BIO15 | Precipitation seasonality | kg $m^{-2}$ |
| BIO16 | Mean monthly accumulated precipitation of the wettest quarter | kg $m^{-2}$ $month^{-1}$ |
| BIO17 | Mean monthly accumulated precipitation of the driest quarter | kg $m^{-2}$ $month^{-1}$ |
| BIO18 | Mean monthly accumulated precipitation of the warmest quarter | kg $m^{-2}$ $month^{-1}$ |
| BIO19 | Mean monthly accumulated precipitation of the coldest quarter | kg $m^{-2}$ $month^{-1}$ |

## Appendix 3.4

The Variance Inflation Factor after excluding collinear bioclimatic variables (i.e., VIF > 10). See Appendix 3.3 for the full name of the variables.

| Code | VIF |
|---|---|
| BIO2 | 2.3 |
| BIO3 | 2 |
| BIO8 | 2.2 |
| BIO9 | 3.5 |
| BIO13 | 2.5 |
| BIO14 | 3 |
| BIO15 | 2.5 |

## Appendix 3.5

The output of the paired Student’s t-tests contrasting range size components between SSP1 and SSP5 scenarios. The unit was the species. Range size was expressed as the percentage of the baseline range size. *t* refers to the *t*-value, d.f. to the degrees of freedom, and *p* to the *p*-value.

| **Variable** | ***t*** | **d.f.** | ***p*** |
|---|---|---|---|
| Shift (Δ) | 2.4 | 7389 | 0.01 |
| Gain | 0.4 | 7389 | 0.7 |
| Loss | -30.8 | 7389 | < 0.001 |

## Appendix 3.6

Drivers of range size. Coefficients of the linear model fitted to Δ range size, range gain, and range loss predicted by the elevation affiliation in m.a.s.l. (metres above the sea level). The unit was the species. Range was expressed as the percentage of the baseline range size (%). The linear models were fitted under an optimistic global change scenario (SSP1) and a pessimistic scenario (SSP5). SE represents the standard error, *t* the *t*-value, and *p* the *p*-value.

| | | **SSP1** | | | **SSP5** | | |
|---|---|---|---|---|---|---|---|
| **Variable** | **Coefficient** | **Estimate (± SE)** | ***t*** | ***p*** | **Estimate (± SE)** | ***t*** | ***p*** |
| Shift (Δ) | Intercept | 26.8 (1) | 21.5 | < 0.001 | 23.8 (1) | 23.9 | < 0.001 |
| | Elevation affiliation | $-3.7 \times 10^{-2}$ ($2 \times 10^{-3}$) | -17.9 | < 0.001 | $-4.3 \times 10^{-2}$ ($1.4 \times 10^{-3}$) | -28.9 | < 0.001 |
| Gain | Intercept | 17.1 (1.6) | 10.3 | < 0.001 | 21.1 (0.8) | 25.2 | < 0.001 |
| | Elevation affiliation | $-2.4 \times 10^{-3}$ ($2.4 \times 10^{-3}$) | -1 | 0.33 | $-9.6 \times 10^{-3}$ ($1.2 \times 10^{-3}$) | -7.7 | < 0.001 |
| Loss | Intercept | -2.9 ($3.9 \times 10^{-1}$) | -7.3 | < 0.001 | -2.7 ($4 \times 10^{-1}$) | -6.6 | < 0.001 |
| | Elevation affiliation | $3.1 \times 10^{-2}$ ($5.8 \times 10^{-4}$) | 53.9 | < 0.001 | $3.3 \times 10^{-2}$ ($6 \times 10^{-4}$) | 55.1 | < 0.001 |

## Appendix 3.7

The output of the Student’s t-tests comparing Δ species richness and temporal species turnover (Simpson’s index) between SSP1 and SSP5 scenarios. The unit was the pixel. *t* corresponds to the *t*-value, d.f. to the degrees of freedom, and *p* to the *p*-value.

| **Variable** | ***t*** | **d.f.** | ***p*** |
|---|---|---|---|
| Δ species richness | 218.5 | 95754 | < 0.001 |
| Species turnover | -167.5 | 95754 | < 0.001 |

## Appendix 3.8

Drivers of temporal changes in species richness and turnover. Coefficients of the linear regression fitted to Δ species richness and temporal species turnover (Simpson's index). The predictor of the Δ species richness and temporal species turnover was the elevation in metres above the sea level (m.a.s.l.). The regressions were fitted under an optimistic global change scenario (SSP1) and a pessimistic scenario (SSP5). The unit was the pixel. SE represents the standard error, *t* the *t*-value, and *p* the *p*-value.

| | | **SSP1** | | | **SSP5** | | |
|---|---|---|---|---|---|---|---|
| **Variable** | **Coefficient** | **Estimate (± SE)** | ***t*** | ***p*** | **Estimate (± SE)** | ***t*** | ***p*** |
| Δ species richness | Intercept | -254.9 (1) | -251.6 | < 0.001 | -291.3 (1) | -278 | < 0.001 |
| | Elevation | $3.4 \times 10^{-1}$ ($1.8 \times 10^{-3}$) | 187.1 | < 0.001 | $3.6 \times 10^{-1}$ ($1.9 \times 10^{-3}$) | 192.3 | < 0.001 |
| Species turnover | Intercept | $6.6 \times 10^{-2}$ ($1.2 \times 10^{-4}$) | 533.4 | < 0.001 | $6.6 \times 10^{-2}$ ($1.2 \times 10^{-4}$) | 519.8 | < 0.001 |
| | Elevation | $2.4 \times 10^{-5}$ ($2.2 \times 10^{-7}$) | 108.2 | < 0.001 | $3.1 \times 10^{-5}$ ($2.3 \times 10^{-7}$) | 135.3 | < 0.001 |

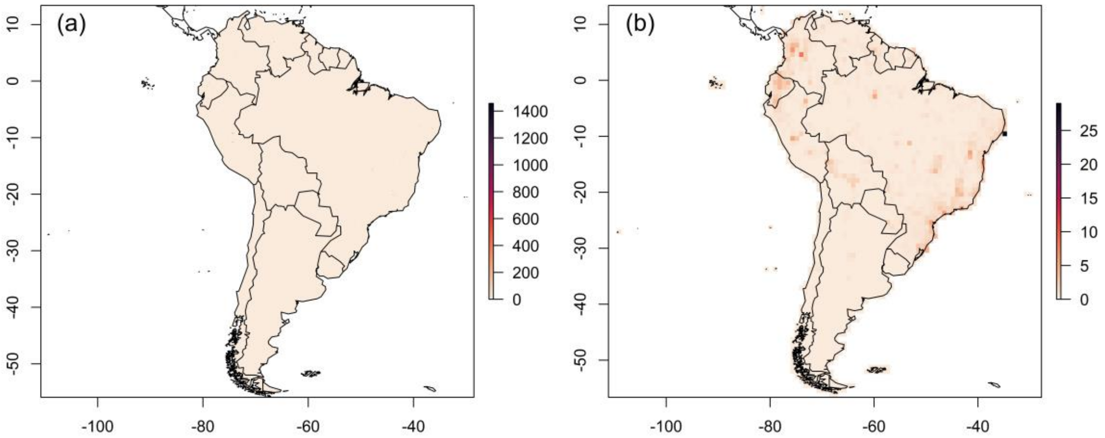
## Appendix 3.9

Drivers of temporal changes in species richness and turnover controlling for climatic anomalies. Coefficients of the linear regression fitted to Δ species $\text{richness}_{\text{residuals}}$ and temporal species $\text{turnover}_{\text{residuals}}$ (Simpson's index). The predictor variable was the elevation in metres above the sea level (m.a.s.l.). The regressions were fitted under an optimistic global change scenario (SSP1) and a pessimistic scenario (SSP5). The unit was the pixel. SE represents the standard error, *t* the *t*-value, and *p* the *p*-value.

| | | **SSP1** | | | **SSP5** | | |
|---|---|---|---|---|---|---|---|
| **Variable** | **Coefficient** | **Estimate (± SE)** | ***t*** | ***p*** | **Estimate (± SE)** | ***t*** | ***p*** |
| Δ species richness | Intercept | -161.7 (0.9) | -175.6 | < 0.001 | -165.6 (0.9) | -172.1 | < 0.001 |
| | Elevation | $3.3 \times 10^{-1}$ ($1.7 \times 10^{-3}$) | 196.1 | < 0.001 | $3.4 \times 10^{-1}$ ($1.7 \times 10^{-3}$) | 192.2 | < 0.001 |
| Species turnover | Intercept | $-9.7 \times 10^{-3}$ ($1 \times 10^{-4}$) | -94.3 | < 0.001 | $-1.3 \times 10^{-2}$ ($1.1 \times 10^{-4}$) | -114.5 | < 0.001 |
| | Elevation | $2 \times 10^{-5}$ ($1.9 \times 10^{-7}$) | 105.3 | < 0.001 | $2.6 \times 10^{-5}$ ($2 \times 10^{-7}$) | 127.9 | < 0.001 |

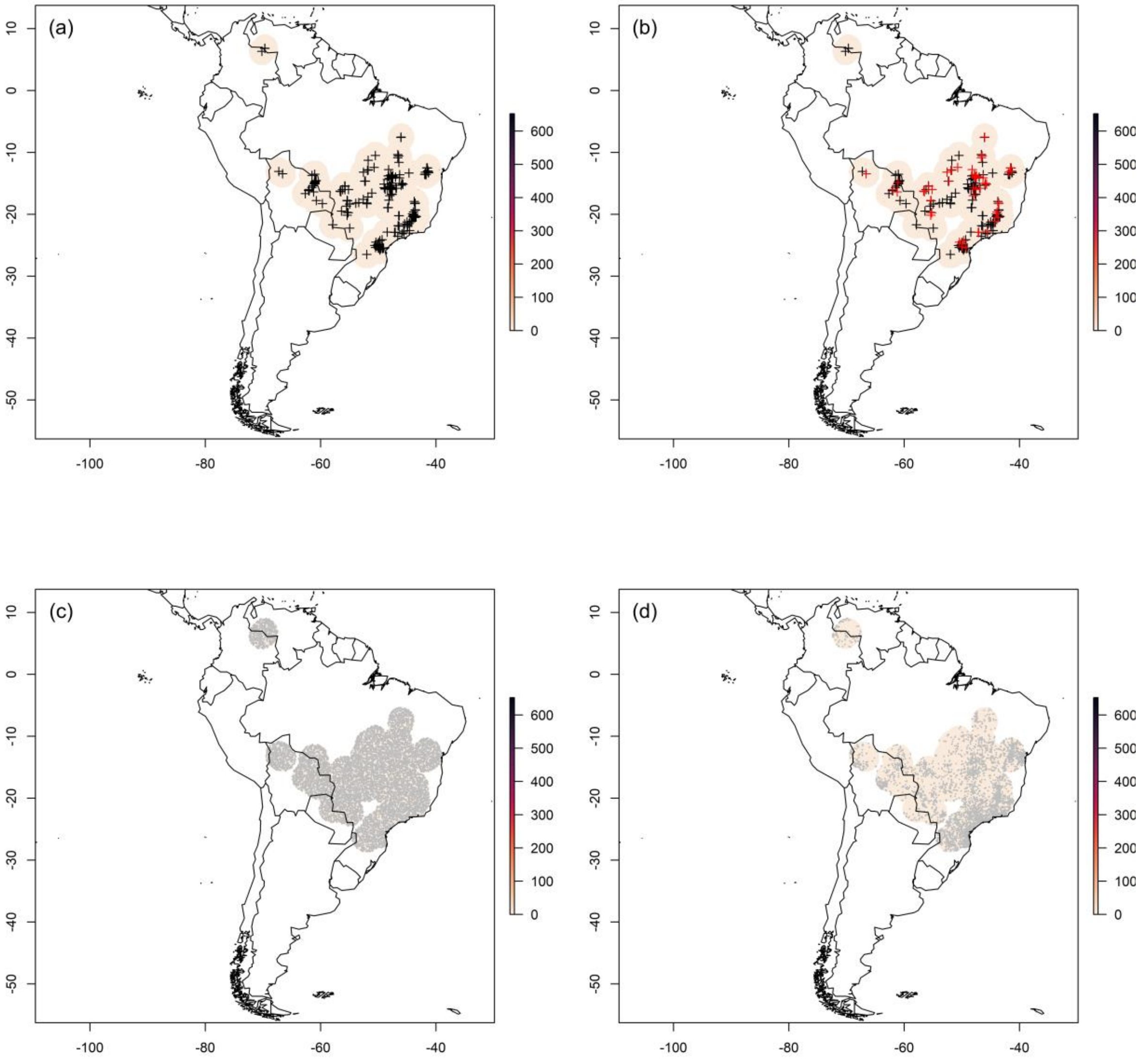
**Appendix 3.10**

The density of GBIF and SpeciesLink plant presence records over South America. (**a**) The sampling density map at 30 arcsec resolution was used to generate background points. (**b**) The map was reduced at the 300 arcsec resolution to aid visualization.



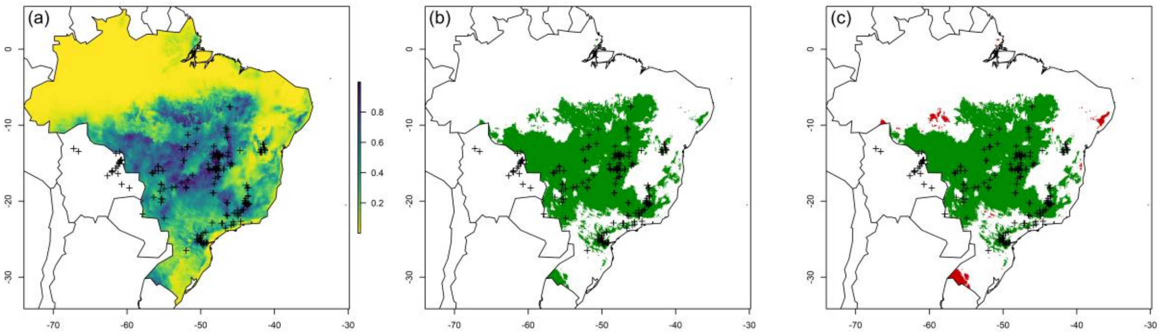
## Appendix 3.11

Illustration of presence and background points for the species *Paspalum lineare*. (**a**) Presence records are displayed on top of the sampling density map masked by the species' accessible area (250 km buffer). (**b**) Presence data random split between training (80%, in black) and validation data (20%, in red). (**c**) 10,000 background points were generated randomly. (**d**) 10,000 background points were generated as a function of the sampling density map.



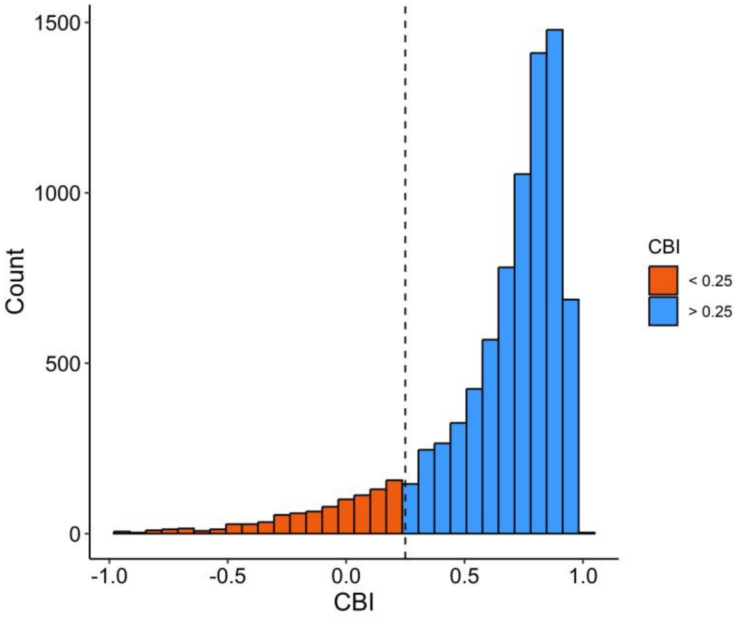
## Appendix 3.12

Illustration of MaxEnt output for the species *Paspalum lineare*. (**a**) Continuous suitability probability projected at the Brazil extent and 150 arcsec of resolution. (**b**) Species' range after binarization. (**c**) Species' range after spatial restriction (green – spatially restricted range; red – marginal habitat patches removed during the restriction).



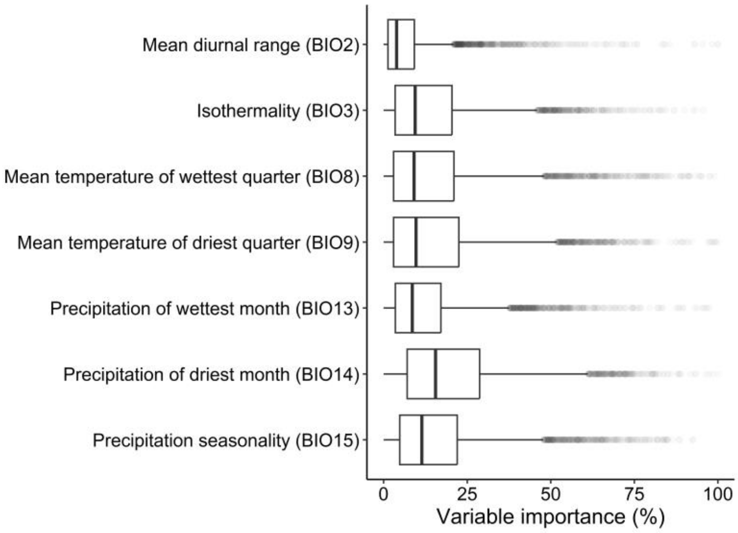
## Appendix 3.13

Distribution of the Continuous Boyce Index (CBI) values. CBI > 0.25 suggest good model performance and it was coloured in blue whereas CBI < 0.25 suggests the opposite (in red). The dashed line marks the 0.25 threshold.



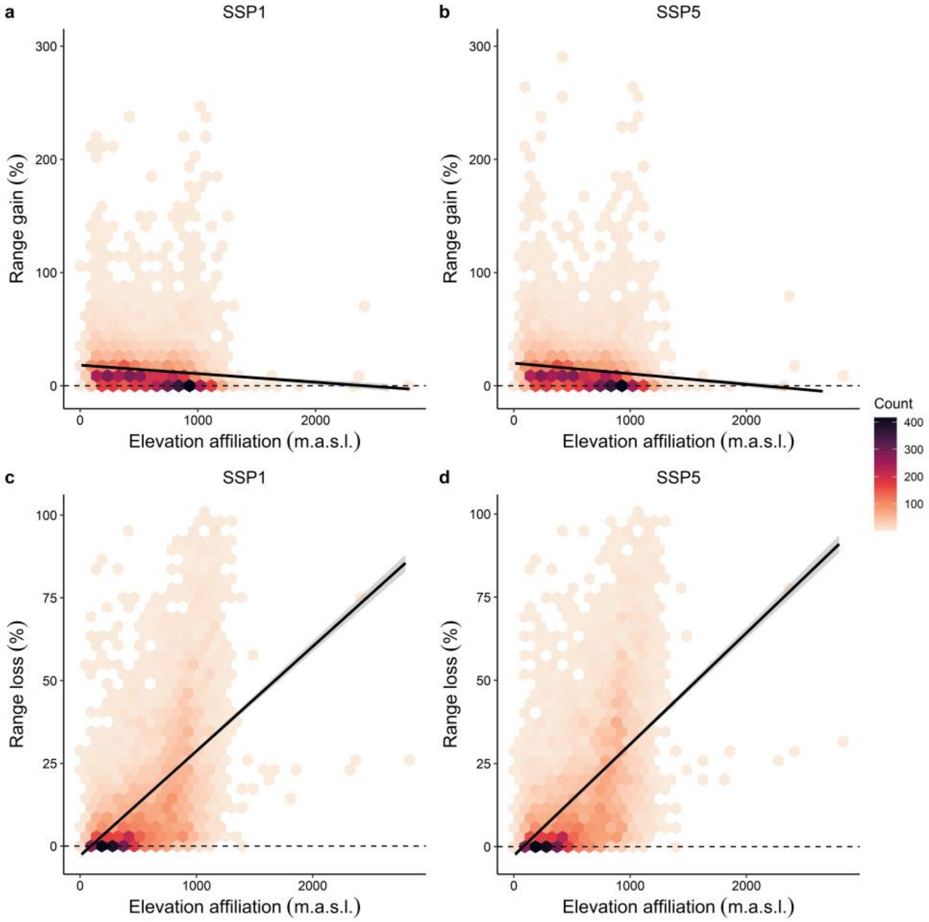
## Appendix 3.14

Permutation importance of the seven bioclimatic variables used to fit the SDMs. Each observation corresponds to a species.



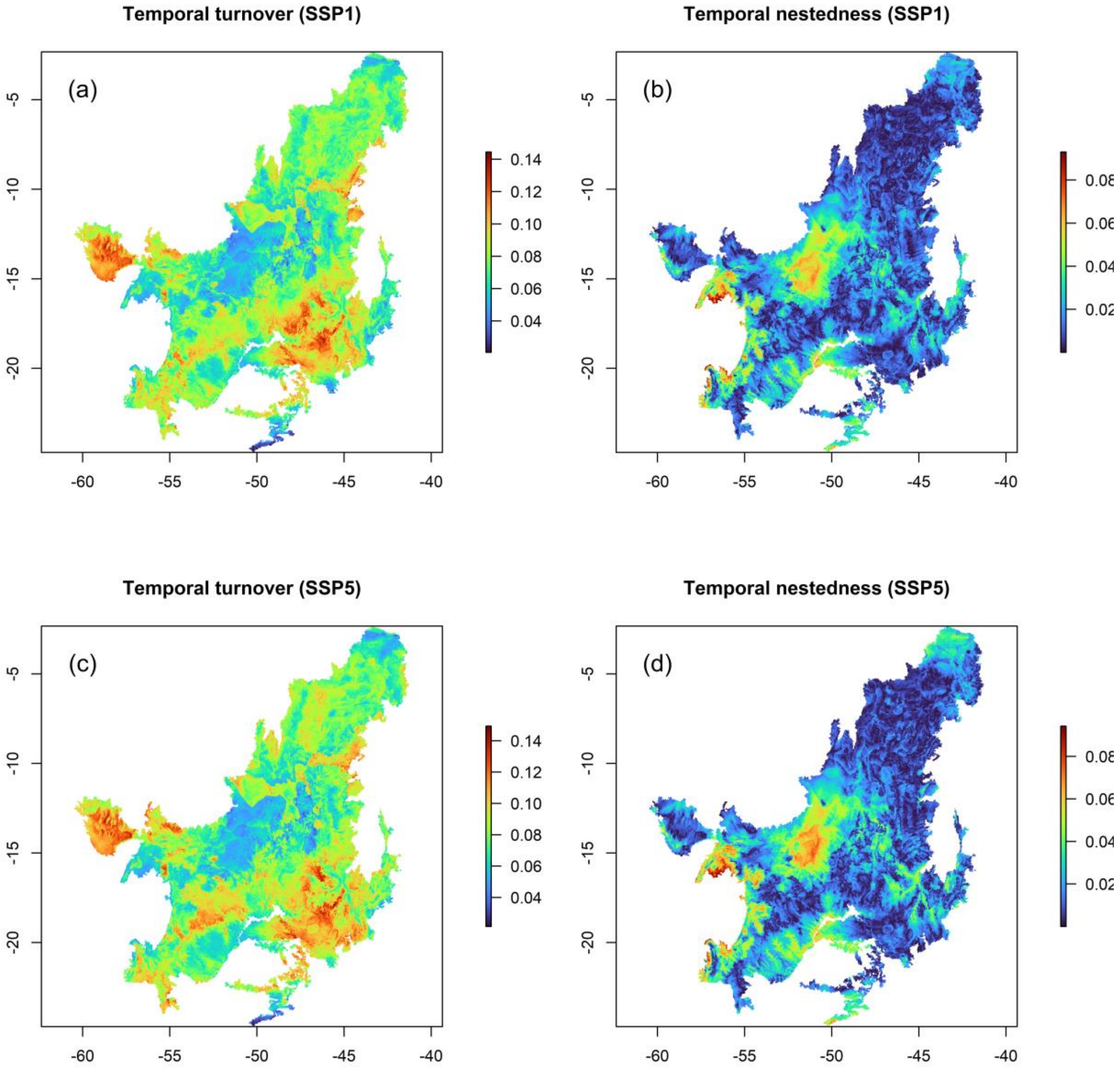
## Appendix 3.15

Relationship between range gain and loss and the elevation affiliation. Range gain and loss were expressed as the percentage relative to the baseline range size. Range size and gain were calculated based on (**a, c**) an optimistic (SSP1) and (**b, d**) a pessimistic scenario of global change (SSP5). The solid line depicts the linear model fit. Each observation corresponds to a species. The hexagons' colour is proportional to the density of species in that area. The dashed line marks the zero, i.e., no net change. m.a.s.l. stands for metres above the sea level. Panels (**a, b**) x-axis were limited to 300% to improve visualization which concealed 16 outlier species.



## Appendix 3.16

Turnover and nestedness components of the Sørensen index. (**a, c**) Turnover corresponds to the fraction of the Sørensen index driven by species replacement and (**b, d**) nestedness corresponds to the fraction of the Sørensen index driven by species loss. Sørensen turnover and nestedness components were estimated under (**a, b**) an optimistic (SSP1) and (**c, d**) a pessimistic scenario of global change (SSP5).

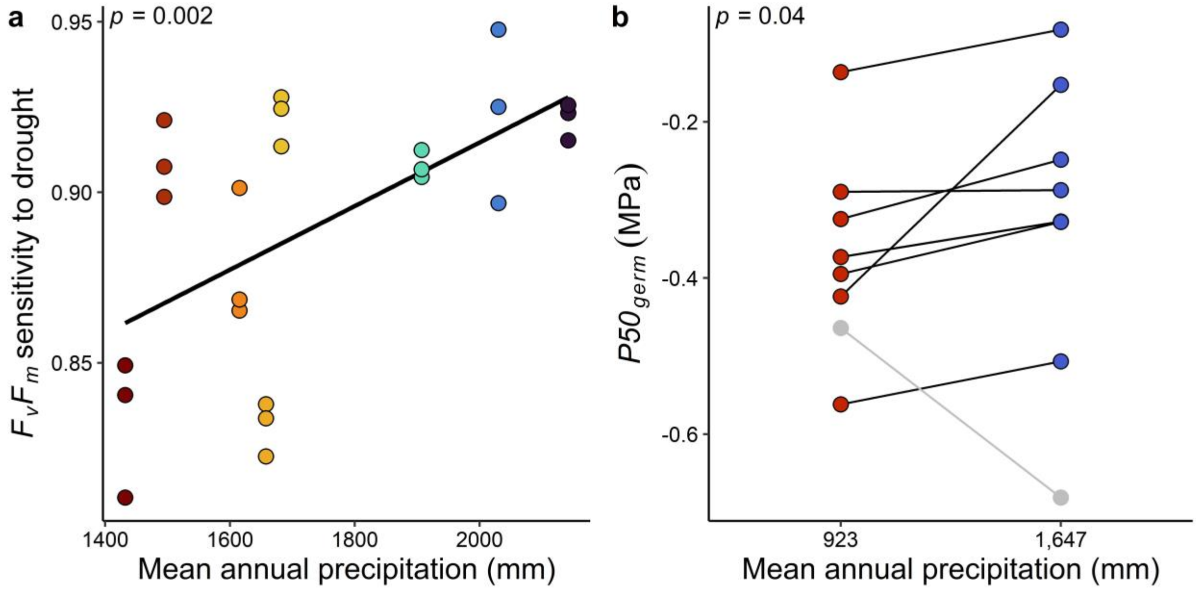


## Appendix 4.1 – Evidence of local adaptation in the Brazilian *Cerrado*.

Proof of intraspecific adaptation to climate is still scarce for the *Cerrado* flora. Yet, we handpicked two study cases that exemplify between-population adaptation to rainfall regimes.

**Photosynthesis sensitivity to drought:** Leal et al. (2021) sampled individuals of *Pitcairnia lanuginosa* (Bromeliaceae) from eight populations across the *Cerrado*. The individuals were grown in a greenhouse for a year and half of them were submitted to a simulated drought (no watering for a month). The sensitivity of the photosystem to drought was assessed by the difference in the maximal photochemical efficiency ($F_vF_m$) between control and drought conditions divided by the control mean. We crossed the $F_vF_m$ drought sensitivity of each population with CHELSA 2.1 MAP estimates. $F_vF_m$ sensitivity to simulated drought increased with annual precipitation ($p$ = 0.002, Box Fig. 1a). Therefore, Leal et al. (2021) data shows that populations that evolved under a dry climate have a more drought-resistant photosystem than populations native to wet parts of the *Cerrado*.

**Germination sensitivity to moisture:** Costa (2019) collected seeds from eight tree species from a wet origin (*Cerrado*-Amazon Rainforest ecotone) and a dry origin (*Cerrado*-Caatinga Seasonally Dry Forest ecotone). The germination (%) of a hundred seeds per species per origin was monitored over two months across a water potential gradient (0, -0.2, -0.4, -0.6, and -0.8 MPa). Based on Costa et al. (2019) data, we estimated the water potential at 50% of germination ($P50_{germ}$). Ecologically, a more negative $P50_{germ}$ means seeds that tolerate drier conditions at the germination phase. Seven out of eight species showed a more negative $P50_{germ}$ in seeds native to the dry site than seeds from the wet site ($p$ = 0.04, Box Fig. 1b). Costa (2019) data then provide evidence of drought-resistant seeds in tree populations that evolved in dry regions in the *Cerrado*.



Evidence of intraspecific adaptation to rainfall in the *Cerrado* flora. (**a**) Sensitivity of maximal photochemical efficiency ($F_vF_m$) to a simulated drought *vs*. the native rainfall of eight *Pitcairnia lanuginosa* populations. The line represents the regression fit along with its respective *p*-value at the top-left corner. (**b**) Water potential at the loss of 50% of germination capacity ($P50_{germ}$) in seeds collected from an arid and humid site in eight woody species. The *p*-value at the top-left corner refers to a paired t-test after excluding the outlier species *Plathymenia reticulata* (in grey).

## Appendix 4 – Supplementary material to chapter 4

### Appendix 4.2 – Input data and settings of the Species Distribution Models

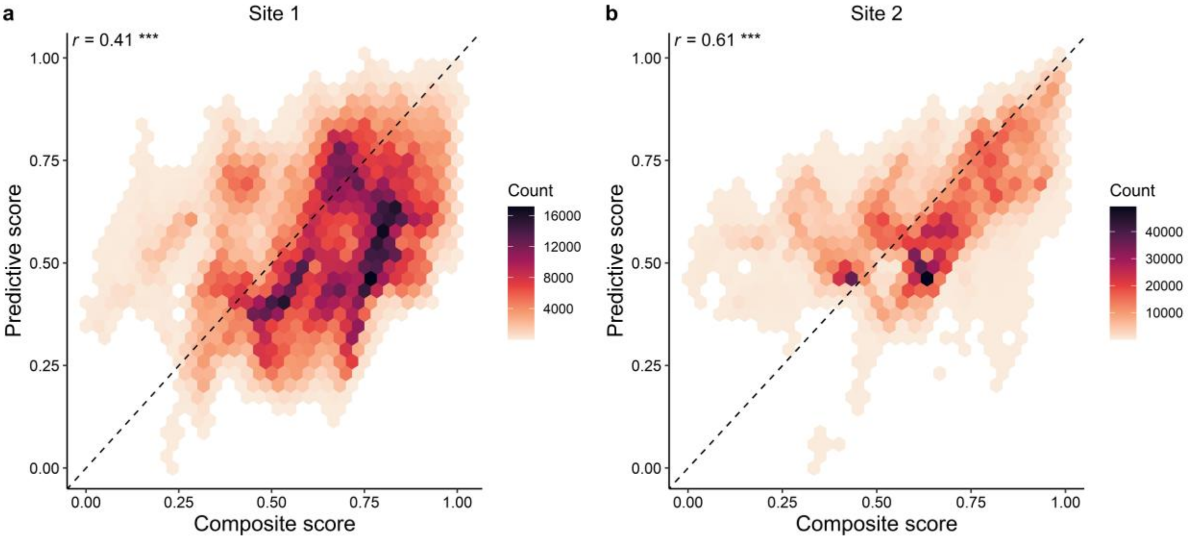
The SDMs are fit at the South America extent which exceeds the known distribution of the three studied species allowing the models to capture their full climatic niche. We download occurrence records from the Global Biodiversity Information Facility (GBIF) and SpeciesLink and remove dubious coordinates using the R package "CoordinateCleaner" (Zizka *et al.*, 2019). We retain one occurrence per 5 km grain to control for spatial sampling biases using the R package "spThin" (Aiello-Lammens *et al.*, 2015). We download bioclimatic variables (BIO) averaged from 1981 to 2010 at a resolution of 30 arcsecs from CHELSA V2.1 (Karger *et al.*, 2017). We remove auto-correlated variables according to the Variance Inflation Factor (VIF) using the R package "usdm" and visual inspections which reduces the number of layers from 19 to seven (BIO2, 3, 8, 9, 13, 14, and 15). We fit five models per species based on the random split of the occurrences into the training (80%) and validation (20%) datasets. We generate 10,000 background points in buffers of a 250 km radius around occurrences. The point generation is proportional to the sampling density of terrestrial plants across S. America to further control for sampling biases (Phillips *et al.*, 2009; Kramer-Schadt *et al.*, 2013).

We fit the MaxEnt models using the R package "dismo" (Hijmans *et al.*, 2021) and assess the goodness-of-fit using the Continuous Boyce Index (CBI) from the R package "enmSdm" (Smith, 2021). We project the SDMs to the extent of Brazil at a resolution of 150 arcsecs and average the five replicates. We delimit the species range (R) by binarizing the SDM projection using the 10th percentile of the niche probability of the training occurrences. We remove habitat patches more than 250 km apart from an occurrence to control for model overprediction (Mendes *et al.*, 2020). We restrict our analyses to pixels with more than 10% of savanna and grassland cover based on MapBiomas v.7.1 to reduce range overestimation. We extract the permutation importance (v) of each one of the seven bioclimatic variables used to fit the SDMs. We also download the seven bioclimatic variables averaged for the 2011–2040 period under the Shared Socio-economic Pathway 5 (SSP5, global warming exceeding 4 °C by 2100) from CHELSA V2.1. We average the forecasts of five GCMs (GFDL-ESM4, UKESM1-

0-LL, MPI-ESM1-2-HR, IPSL-CM6A-LR, and MRI-ESM2-0) and reduce the resolution to 150 arcsecs.

## Appendix 4.3

Relationship between the COSST score calculated under the predictive (y-axis) and composite provenancing (x-axis) for *C. brasiliensis*. Predictions produced for (**a**) a mining site in Central *Cerrado* and (**b**) an abandoned Eucalyptus plantation in Eastern *Cerrado*. Pearson's correlation coefficient (*r*) is displayed in the top-left corner. Each observation corresponds to 150 arcsec pixels within the *C. brasiliensis* range. The darker the hexagon, the higher the number of observations. The dashed line marks the 1:1 ratio. *** means *p*-value < 0.001.



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