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# What to expect from restored Cerrado grasslands? Indicators and reference values from pristine ecosystems

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**Open ecosystems are disappearing worldwide, requiring urgent restoration efforts. However, limited knowledge of their structure and composition hinders the assessment of restoration success. We aimed to establish reference values for plant community attributes in undisturbed native grasslands to guide restoration. In an unprecedented data collection, we sampled 14 remnants under different climate, soil, and fire regimes, representing a broad portion of the Brazilian savanna (except the least converted northern). We assessed plant community composition, richness at different scales, ground cover by functional groups, and aboveground biomass. From the 794 species recorded, half were unique occurrences, and few were present in over 70% of the sampled areas. Richness ranged from 9 to 22 species/m$^2$ and 53 to 130 in 30 m$^2$. Grasses (22–80%) and non-grasses (9–45%) did not cover the ground entirely, leaving 4–56% exposed. Biomass ranged from 57 to 715 g/m$^2$. Because species composition is variable, finding a "reference set" of species for the whole Cerrado is not possible. Regional subsets and key functional guilds are recommended instead. The number of species/m$^2$ is a good proxy for diversity, and species/30 m$^2$ is a good reference for total richness. Biomass is an unreliable indicator due to the broad natural range independent of integrity. The maximum biomass, however, should never be surpassed. Structural targets should include grasses, non-grasses, and bare soil within the reference range, but achieving pristine plant richness may be unrealistic in most cases. Strong efforts should focus on conservation rather than restoration, once recovering all the reference's attributes is difficult.**

**Key words:** community structure, conservation, growth forms, reference ecosystem, restoration, species diversity

### Implications for Practice

- Assessing grassland restoration success relies on reference values from pristine areas for easy-to-measure and accurate indicators obtained by standardized sampling methods.
- Because pristine grasslands are variable in structure and diversity, a broad range of reference values is needed for each indicator. Falling outside the range would be worrisome.
- Richness per m$^2$, richness in 30 m$^2$, ground cover by native grasses and non-grasses, total vegetation cover, and bare soil percentage can be considered good indicators to assess how far a restored grassland is from the reference range.
- A standardized "reference species composition" does not exist. Provided that restoration includes native species from the regional pool and reaches the expected proportion between growth forms, it can be assumed adequate.

## Introduction

The escalating degradation of ecosystems, coupled with the urgent need to mitigate the effects of climate change, has elevated the importance of ecosystem conservation and restoration to an unprecedented global priority (Suding et al. 2015; Temperton et al. 2019). Ecological restoration aims to restore an ecosystem's key characteristics, including its biodiversity and ecological functions, to conditions that existed prior to degradation (Jordan et al. 1987; SER 2004). The knowledge to assess, plan, implement, manage, and monitor restoration processes relies on multiple sources and field restoration experiments (Gann et al. 2019). Although all terrestrial biomes are experiencing human-induced environmental change, grasslands and savannas have been historically overlooked in both restoration and conservation strategies (Veldman et al. 2015; Silveira et al. 2022). As a result, open ecosystems face obstacles regarding the absence of reference ecosystems and the lack of established protocols for restoration, as well as an unsystematic evaluation of the techniques currently employed (Medeiros et al. 2024).

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The reference ecosystem is frequently highlighted as a crucial element in pre-project planning, serving to establish management goals and outline best practices (Gann et al. 2019). It is also vital for evaluating project success, as post-restoration monitoring measures the progress of the developing ecosystem toward the reference conditions (Rey Benayas et al. 2009; Wortley et al. 2013). So, effective restoration of open ecosystems requires, first, understanding their function, structure, diversity, and floristic composition (Buisson et al. 2019). Second, it calls for a well-defined set of goals and objectives, aligned with the features of pristine ecosystems, along with appropriate medium- and long-term indicators to be applied (Prach et al. 2019). Also, given the heterogeneity of open ecosystems, establishing regional ranges for indicators, instead of a simple average, can be essential in setting realistic restoration targets (Buisson et al. 2020; Shackelford et al. 2021; Oliver et al. 2023). Setting goals toward the natural state of reference ecosystems helps preventing misguided actions that could drive restoration to unexpected outcomes.

Plant species in tropical grasslands and savannas assemble slowly (Nerlekar & Veldman 2020). Once degraded and without intervention, these ecosystems cannot regain their biodiversity, structural integrity, and functional capabilities, such as fire resilience, species interactions, carbon and nutrient cycling, and rain infiltration (Pilon et al. 2023). The Cerrado represents the tropical savanna biome in Brazil, and its open ecosystems are characterized by a dominant grassy layer with rare or scattered trees and shrubs (Overbeck et al. 2022). This biodiversity hotspot (Murphy et al. 2016) occupied originally 20% of the country (2 million $km^2$), but half was already converted to agricultural land uses at astonishing rates. Although the biome gained more attention recently and restoration efforts have grown significantly even in open ecosystems (e.g. Ferreira et al. 2015; Pellizzaro et al. 2017; Assis et al. 2021), we still do not have the means to measure how far we are from effectively recovering a degraded ecosystem (Medeiros et al. 2024). Without adequate assessment of the restoration effectiveness, a plethora of unacceptable interventions named "grassland restoration" has been found in the real world. Examples are tree planting where trees do not belong (afforestation); misguided carbon-based actions to enhance aerial biomass (Veldman et al. 2015; Parr et al. 2024), ignoring that these fire-prone ecosystems will eventually burn and their carbon is naturally stored belowground; "restored grassy vegetation" composed of native ruderals and exotic grasses (Pilon et al. 2023); and pristine riparian grasslands mapped as degraded riparian forests. Therefore, besides threats such as land conversion directly reducing the remnants (RAD 2023), fire suppression leading to woody encroachment (Durigan & Ratter 2016), and biological invasions severely reducing the diversity of grasses and forbs (Foxcroft et al. 2010; Bardgett et al. 2021), grasslands face additional risks. Misguided and ineffective restoration interventions, driven by a lack of knowledge about their structure, biodiversity, functioning, and ecosystem services, also threaten these ecosystems.

In this scenario, selecting robust indicators and making available reference values for key descriptors of pristine remnants can be the first steps to effectively guide efforts toward successful restoration of open ecosystems. Indicators serve as measurable proxies for ecosystem health, helping to track progress and adjust management strategies. However, identifying appropriate indicators and establishing reference values is particularly challenging in open ecosystems due to their high diversity at different scales, the naturally heterogenous community structure, and the lack of standardized sampling procedure. We here aimed to provide a robust characterization of pristine Cerrado grasslands, using different indicators to assess their structure, plant richness, and composition. We then explored the plant community descriptors as indicators of restoration effectiveness by their strengths and weaknesses to measure how far the ecosystems under restoration are from the reference ecosystems.

## Methods

We conducted a broad characterization of pristine Cerrado grasslands that could be considered reference ecosystems in the context of restoration, regarding their structure, floristic composition, and diversity. The descriptors obtained from the extensive field data collection were explored as indicators by their adequacy as surrogates not only for the ecosystem properties but also for its functionality.

### Study Sites

We assessed 14 natural remnants (Table S1; Fig. 1) preserving Cerrado open ecosystems on well-drained terrains in the states of São Paulo, Minas Gerais, Paraná, Mato Grosso do Sul, and Goiás, the states where Cerrado vegetation has been more severely degraded. The northern states with Cerrado vegetation (Tocantins, Bahia, Maranhão, Mato Grosso, and Piauí) were not assessed, mainly due to the comparatively low land conversion, with generally more than 60% remaining (Carvalho et al. 2008), far beyond what is required by law (20–35%), and thus rarely candidates for restoration.

The vegetation in all study sites presents a continuous ground layer composed of grasses, forbs, and subshrubs, and a reduced or absent canopy cover, not surpassing 20%, measured by the line-intercept method (Canfield 1941). Throughout the text, we use the generic term "grasslands" to refer to the studied vegetation. We aimed to select areas representing natural grasslands where the vegetation has never been disrupted by mechanization, invasive plants, or any other form of degradation. Despite cattle grazing being the historical land use for centuries in the whole Cerrado biome (Dias 2006), we sampled only areas from where cattle were excluded for a long time. Fire is a natural factor in grassy Cerrado vegetation, with variable frequency among our study sites (from 0 to 14 times in 35 years). Such pristine open ecosystems are commonly referred to in international literature as "old-growth grasslands" (Veldman et al. 2015).

### Data Collection

In each of the selected sites, we demarcated a 100 m × 100 m area within which we sampled 30 plots grouped into three 100 m transects (sampling scheme in Fig. 2).

At each site, we recorded all plant species across the entire 1 ha area and sampled the plant community in the 30 plots.

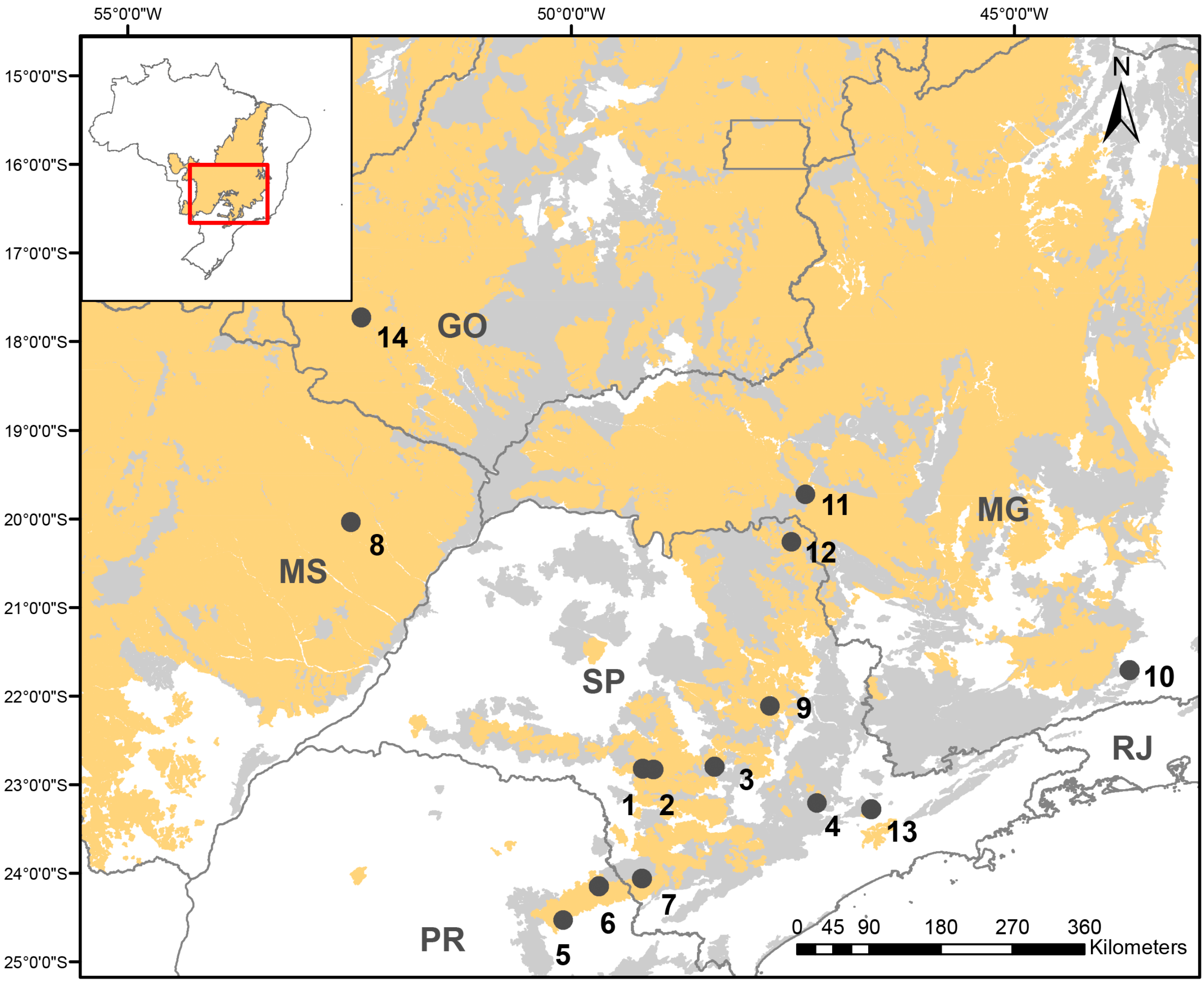


Figure 1. Location of the 14 study sites: The numbers on the map correspond to the codes of the sites described in Table S1. As a background is the Cerrado biome (orange) and transition zones (gray), where the open ecosystems of the Cerrado form a mosaic with the surrounding Atlantic forest.

### Floristic Survey

For the comprehensive floristic survey of the 1 ha area, we recorded species present in the patch using the method proposed by Filgueiras et al. (1994). We recorded all observed plant species at regular time intervals during walks covering the entire sampling area, stopping data collection when fewer than five new species were added during two consecutive intervals of 15 minutes. Most plant species were identified to the species level in the field. In the other cases, botanical material was collected for later identification (based on literature, herbarium specimen comparison, and consultation with experts). Voucher specimens were deposited at the University of Campinas Herbarium and Dom Bento José Pickel Herbarium. Species were classified according to their growth forms, including trees, shrubs, subshrubs, forbs, palms, climbers, arborescent ferns, grasses, and sedges (Durigan et al. 2018; Flora do Brasil 2020; Pilon et al. 2021).

### Plant Community Sampling

Within each transect, we established 10 circular 1-m$^2$ plots for plant community sampling, with a 10-m spacing between the central points of the plots (see Fig. 2), totaling 30 plots. Within each plot, we visually estimated the percentage cover of grasses (including sedges), non-grasses (forbs, shrubs, subshrubs, trees, climbers, and palms), and bare soil (litter included). All plant species were recorded, and cover was visually estimated per species (percentage of the plot occupied by each species), following a method adapted from Wikum and Shanholtzer (1978).

Aboveground biomass was collected from five of the 30 plots systematically predefined. From one quarter (randomly selected) of the plot area, we collected live or dead biomass still attached to the plant base, excluding litter and any stems thicker than 6 mm in diameter (Newberry et al. 2020). The collected biomass was placed in properly labeled tissue-non-tissue

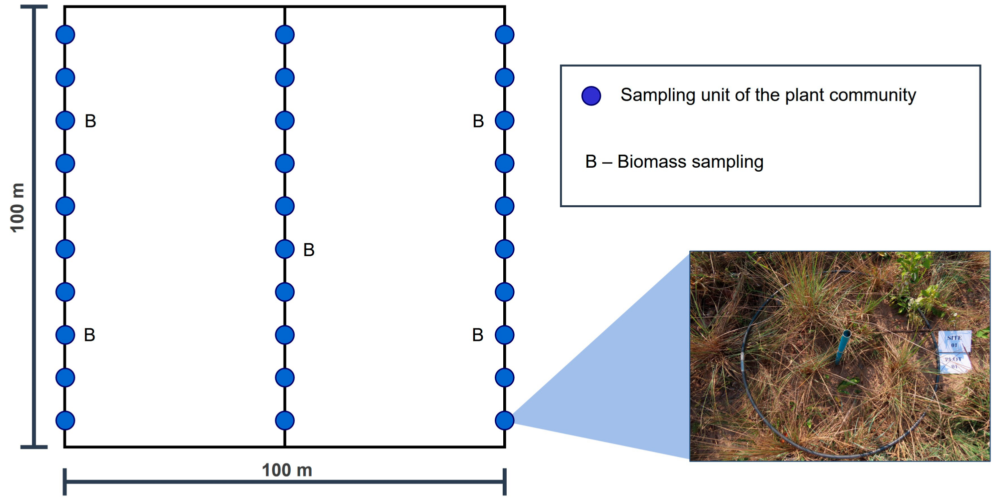


Figure 2. Sampling scheme. In detail, one of the sampling plots of the plant community, bounded by a polyvinyl chloride (PVC) hose circle with an area of 1 $m^2$.

(TNT) bags and oven-dried until constant weight. The bags containing biomass were weighed on an electronic scale with a precision of 0.1 g. After weighing, the plant material was discarded, and the empty bag was weighed to determine the net dry biomass.

### Data Analyses

We used the Pearson correlation coefficient to assess the correlation between (1) richness in the 30 plots and total richness; (2) aboveground biomass and grasses cover. Data normality assumptions were tested prior to the analyses.

Analyses were carried out in the R Software (version 4.3.1; R Core Team 2023), and figures were created using the package *ggplot2* (Wickham 2016).

## Results

### Plant Species Composition and Relative Abundance

In the 14 sites sampled, we recorded 794 plant species, belonging to 87 families. The top five families with the highest numbers of species, in descending order, were Asteraceae (19%), Fabaceae (11%), Poaceae (11%), Myrtaceae (5%), and Melastomataceae (4%). The proportion of growth forms among the total sampled species is distributed as follows, in descending order: 32% subshrubs, 23% forbs, 15% shrubs, 11% grasses, 12% trees, 3% climbers, 3% sedges, 1% palms, and 0.1% arborescent ferns (listed in Table S2). It is worth noting that some species can exhibit more than one growth form (Fig. S1; *Byrsonima verbascifolia*, *Kielmeyera rubriflora*, *Licania humilis*, *Ouratea spectabilis*, and *Psidium laruotteanum* are examples ranging from subshrubs up to mid-size trees). In this study, these species were categorized as the most common form observed during sampling. Only 2% of the species sampled could not be identified even at the family level, and 4% were identified only at the family level or even at the genus level. No species was found in all sites, and only nine species occurred in more than 70% of the study areas (Table S2). Among the top 10 most frequent, six were grasses, two were shrubs, one was a forb, and one was a subshrub. On the other hand, 53% of the species were recorded in only one of the study sites. The five most abundant species at each site were selected, totaling 38 species across the 14 sites, of which 50% were grasses (Table S3).

### Range of Reference Values for Structure and Plant Richness of Cerrado Grasslands

The ground cover by vegetation ranged from 44 to 94%, with an average of 80% (Fig. 3). When separated by plant types, grasses cover varied from 22 to 80% (mean of 53%), and non-grasses cover ranged from 9 to 45% (mean of 27%; Fig. 3). The proportion of bare soil plus litter ranged from 4 to 56% (mean of 19.5%; Fig. 3). The species richness of plants in 1 $m^2$ ranged from 9 to 22 species (average among the 30 plots within each location), with an overall average of 15 species per $m^2$ across all locations (Fig. 4). The species richness in the 30 sampled plots ranged from 53 to 130, with an average of 92 species (Fig. 4). The total number of species sampled per site ranged from 93 to 190 (average of 138 species; Table S2; Fig. 4). The species richness in the 30 plots and the total number of species were highly correlated ($r^2 = 0.88$, $p < 0.01$). The average biomass varied from 57 to 715 g/$m^2$ (mean of 466 g/$m^2$) and was correlated to grasses cover ($r^2 = 0.62$; $p < 0.02$).

## Discussion

Setting realistic restoration goals for open ecosystems is particularly challenging due to the inherent heterogeneity of the vegetation and the scarcity of standardized studies that cover large, diverse natural areas. Restoration success is more often defined as a shift toward an existing or pre-existing functional ecosystem rather than just the improvement from the degraded state (Wortley et al. 2013). Knowing the floristic composition, community structure, and diversity of the reference ecosystems, based on robust data collected over extensive areas, is crucial for improving and guiding current and future restoration and

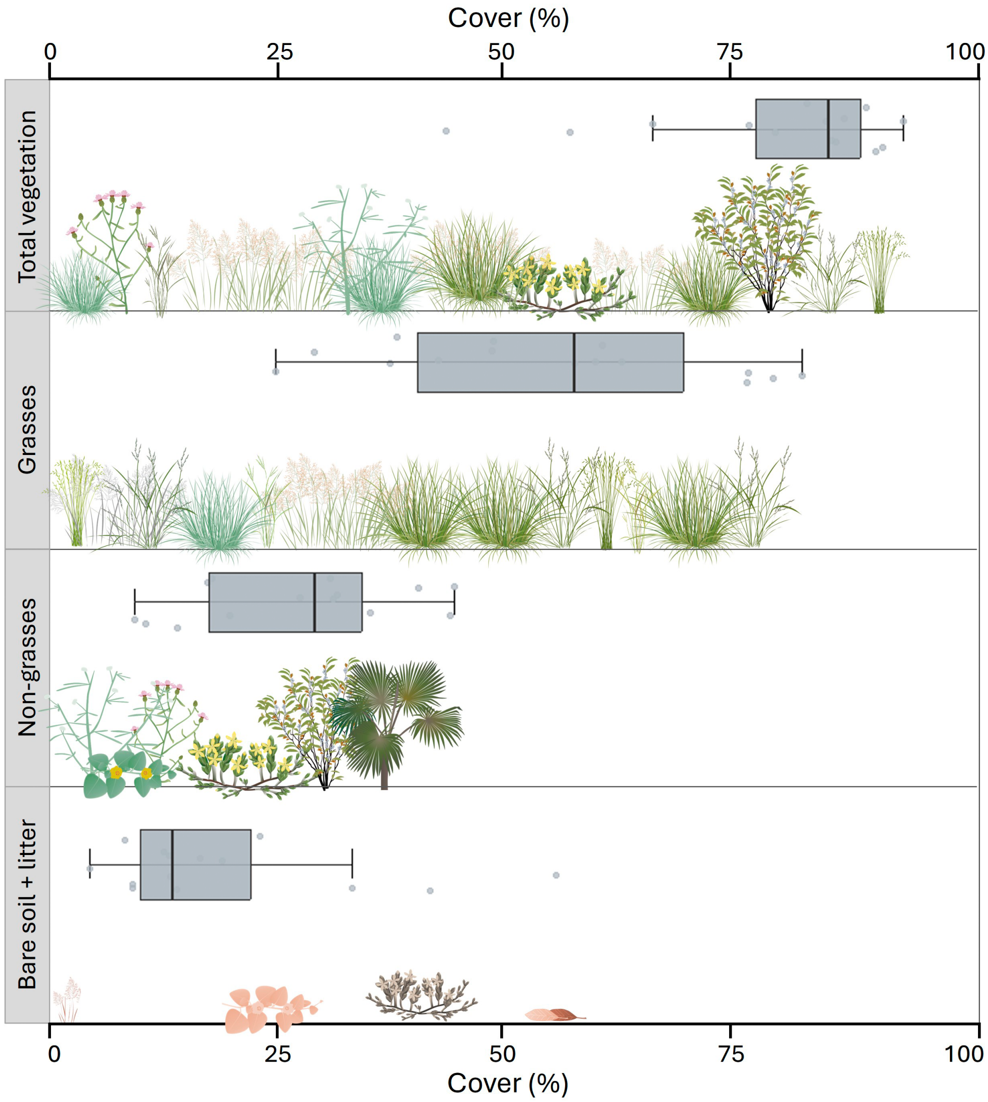


Figure 3. Range of ground cover percentage of plant communities in 14 Cerrado grasslands. Total vegetation (grasses + non-grasses); grasses, non-grasses; bare soil + litter. Each small circle represents the average value calculated among the 30 sampled plots in one site. The thicker central line represents the median, and the box boundaries are the 25 and 75% quartiles. The vertical lines represent the minimum and maximum observations.

conservation efforts. Whether or not the reference values for the indicators are achievable and could be established as restoration goals is another issue.

The difficulty of restoration can vary greatly depending on preceding land uses; moreover, because what is left from the original community in the soil (seed bank or underground structure able to resprout) depends on former land use (Le Stradic et al. 2018). In addition, the techniques applied are also a source of variation in the restoration outcomes. A meta-analysis in Cerrado open ecosystems covering 82 data sets (Pilon et al. 2023) has shown that different restoration techniques drive plant communities to different sets of growth forms. Active restoration based on topsoil translocation, transplant, or seeding performed better than passive restoration for most growth forms analyzed. However, in all cases using natural ecosystems for comparison, the results obtained for richness and functional composition are by far lower than the reference standards (Pilon et al. 2023). That has strong implications for public policies on a local, national, or global scale, since the irreplaceability of an ecosystem should be taken as a decisive argument against its conversion. Comparison with reference standards provides, definitely, the most robust evidence on the limitations of restoration to reestablish an ecosystem resembling undisturbed natural grasslands. In this study, we explored a range of indicators using conserved grasslands as reference ecosystems, aiming to find good indicators to assess restoration success. Some descriptors, such as richness per $m^2$, richness in 30 $m^2$, total vegetation cover, and percentage of bare soil, are reliable indicators for assessing how closely restored areas resemble reference ecosystems. Other attributes of the plant communities, however, like floristic composition, aboveground biomass, and total richness, were less reliable as indicators, with limitations for their applicability.

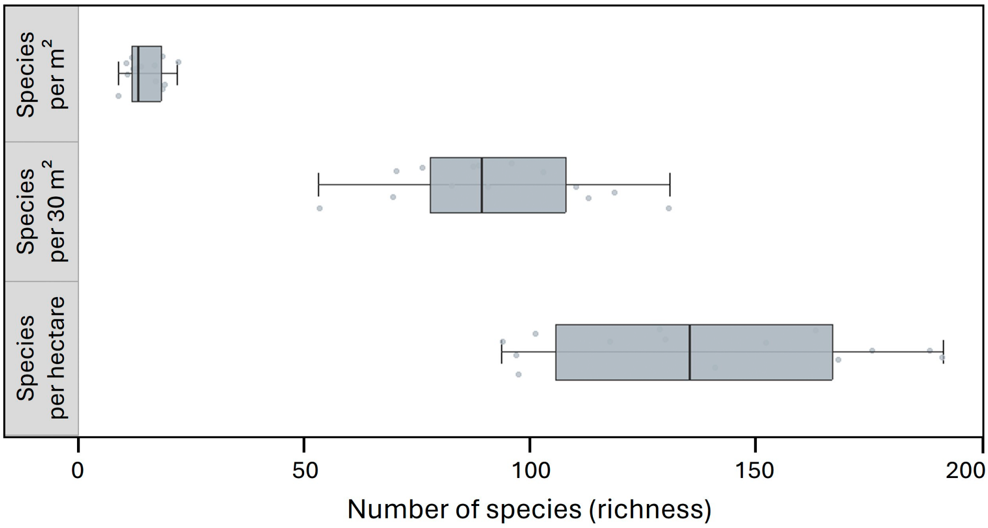


Figure 4. Range of plant species richness in three different scales of plant communities in 14 Cerrado grasslands. Each small circle represents the value for one site (the average value among the 30 plots in one site in the case of species per m$^2$). The thicker central line represents the median, and the box boundaries are the 25 and 75% quartiles. The vertical lines represent the minimum and maximum observations.

### Suitable Indicators to Assess Tropical Grassland Restoration

Restoration goals should be established in terms of ecosystem attributes that can be effectively assessed through reliable indicators (Ruiz-Jaen & Aide 2005). As Dale and Beyeler (2001) argue, no single ecological indicator can fully capture all aspects of what needs to be evaluated. However, a few well-selected indicators are best; one or too many will lead to analytical or logistically based failures (Prach et al. 2019). Good indicators should be easily obtained, exhibit sensitivity to system stressors, and respond to those stresses in a predictable way. Additionally, they should be forward-looking, capable of predicting changes that management actions can prevent (Dale & Beyeler 2001). For restoration purposes, the indicators selected for monitoring should also serve as reliable proxies for ecosystem services, such as provisioning fresh water (quality and quantity), carbon storage and sequestration, providing habitat for wild plants and animals, among many others (Bardgett et al. 2021). From the plant community attributes assessed, we consider as the most important the structure of the ground layer and plant species richness, which can be assessed by the following indicators.

**Growth-form Proportion.** It refers to roughly partitioning the ground layer between grasses and non-grasses, both fundamental components of tropical grasslands. Recovering the growth-form proportion is critical not only to replicate the aspect of tropical grasslands but also for ensuring the resilience of these ecosystems in the face of environmental changes. If promoting a diverse array of growth forms, restoration efforts can enhance the stability of ecological processes such as nutrient cycling, soil stabilization, and biodiversity conservation. Each growth form plays a specific role in supporting ecosystem services (Pilon et al. 2023): grasses are key to maintain the fire regime (Bond 2021) and enhance water infiltration, as the lack of a closed canopy allows more rain to reach the soil directly rather than being intercepted (Hino et al. 1987; Baudena & Rietkerk 2013; Honda & Durigan 2016); shrubs and subshrubs enhance carbon storage and can resprout after disturbance (Pausas et al. 2018; Pilon et al. 2021; Faleiro et al. 2022); forbs maintain pollinator networks (Oliveira & Gibbs 2002). Therefore, achieving a balanced proportion of growth forms might be essential for the long-term sustainability and functionality of restored grasslands, as growth-form diversity is linked to underground structure and diverse responses to disturbances (Pilon et al. 2021; Bombo et al. 2022). Estimating the ground cover percentage by native grasses and non-grasses is an easy task in the field. Additionally, this community descriptor is sensitive to exotic plant invasion and woody encroachment, as these threats can severely impact open ecosystems by altering vegetation structure through competition (Damasceno & Fidelis 2023) and excessive shading of sun-loving species (Pilon et al. 2021; Souza et al. 2022). This sensitivity makes growth-form proportion a valuable indicator for assessing restoration progress, as it can quickly reflect shifts in ecosystem balance in response to threats and/or management interventions.

**Richness Per Square Meter.** The number of native plant species in 1 m$^2$ has been widely used to represent grassland diversity. This indicator has already been a piece of essential information to support conservation planning and management interventions (Wilson et al. 2012; Menezes et al. 2018), and we argue that it is the best indicator to assess plant diversity in grassland restoration. Grasslands have predictable responses to disturbances such as fire frequency (Palmquist et al. 2014; Lebbink et al. 2018; Antar et al. 2022), frost (Joshi et al. 2018; Pilon et al. 2022), drought (Moran et al. 2014; de Vries et al. 2016; Carroll et al. 2021), biological invasions (Abreu & Durigan 2011; Damasceno et al. 2018; Dresseno et al. 2018), fire suppression

(Rodrigues & Fidelis 2022), and woody encroachment (Ratajczak et al. 2012; Wieczorkowski & Lehmann 2022). Changes in plant richness per $m^2$, therefore, reflect the dynamic nature of these ecosystems and detect positive or negative forces impairing a grassland undergoing restoration. Moreover, assessing native species richness does not necessarily require specialized taxonomic knowledge; it can be effectively gauged using morphotypes, allowing for broader participation and application in restoration efforts. This makes species richness not only a practical but also a robust indicator for tracking restoration progress. Invasive exotic species must be recognized and, ideally, ruderals should also be quantified, because these species can rapidly colonize degraded and restored areas, hindering colonization by target species (Coutinho et al. 2019; Nerlekar & Veldman 2020).

**Richness at the Site Level (30 $m^2$).** Thirty 1-$m^2$ plots spread over 1 ha were enough to provide a good representation of plant community composition of the pristine grasslands (28–70%, about half the species on average). It is a valuable metric also for capturing species turnover across wider areas, enabling the detection of the most common species within a community. This measure can fluctuate over time, increasing with factors like fire frequency (Wieczorkowski et al. 2024) or decreasing due to fire suppression (Rodrigues & Fidelis 2022), woody encroachment (Souza et al. 2022; Wieczorkowski & Lehmann 2022), and biological invasions (Pivello et al. 1999; Damasceno et al. 2018). If compiling a species list within a defined area, it can also provide insights into functional diversity, as ecosystems with high functional diversity have higher overall functionality (Lavorel et al. 2013). A functionally diverse ecosystem tends to be more resilient to natural disturbances, invasions, and other forms of degradation. This makes site-level richness a key indicator for assessing ecosystem health and stability of grasslands being restored.

**Total Vegetation Cover and Bare Soil.** This refers to quantifying the portion of the ground exposed to direct sunlight or covered by plants, both crucial to the functioning of tropical grasslands (Pinheiro et al. 2022). The recovery of vegetation structure plays a crucial role in enhancing environmental conditions, facilitating the colonization by plants and animals, and supporting ecological processes like nutrient cycling, rain interception, and defense against invaders (Ruiz-Jaen & Aide 2005; Llorens & Domingo 2007). In open ecosystems, such as tropical savannas and grasslands, bare soil and litter do not necessarily indicate a degraded ecosystem; for example, pristine grasslands sampled had an average bare soil and litter cover of 20%, ranging from 4 to 56%. Instead, unoccupied surfaces provide opportunities for seed arrival and germination or even resprouting from underground structures, particularly for sun-loving specialist species that thrive in these environments (Pinheiro et al. 2022). These species require open space, free from the shade of trees or the dense cover of large grass tussocks, to successfully grow and maintain the ecological balance of these plant communities. Many ecosystem services, including carbon sequestration (Zhou et al. 2023), soil protection against erosion (Zhao et al. 2020), and water infiltration (Honda & Durigan 2016), are closely tied to vegetation structure. Notably, quantifying the ground cover by native vegetation and bare soil/litter is an easily measurable indicator that provides clear evidence of an ecosystem progressing in restoration, gradually building resilience and self-sustainability (Ruiz-Jaen & Aide 2005; Llorens & Domingo 2007).

### Descriptors That Are Less Reliable as Indicators for Restored Grasslands

While reliable indicators are crucial for assessing restoration success, it is important to recognize that not all ecosystem descriptors meet these stringent criteria. Less reliable indicators refer to descriptors that fail to capture the complexity of ecosystem processes or may not respond predictably to environmental stressors and time (Dale & Beyeler 2001). These descriptors could be overly sensitive to short-term fluctuations, leading to misleading conclusions about long-term restoration progress. Additionally, some descriptors may lack clear linkages to ecosystem services or may be difficult to measure consistently, making them less useful for guiding adaptive management strategies. As a result, relying on descriptors that are less robust indicators could hinder the ability to accurately assess and achieve restoration goals, ultimately compromising the effectiveness of restoration projects. From the plant community attributes assessed, we consider as the less reliable the following indicators.

**Floristic Composition.** We identified a group of widely distributed or highly abundant species that are likely to be found in natural Brazilian grasslands. However, we cannot designate them as "indicator species of Cerrado open ecosystems" because some of these species occur in other types of grasslands outside the Cerrado biome. A quick search in the SpeciesLink database (2023) shows, among the most frequent species found, that *Chaptalia integerrima*, *Elionurus muticus*, and *Trachypogon spicatus*, for instance, occur in all Brazilian biomes except the Amazon region. *Andropogon leucostachyus* and *Eragrostis lugens* are found throughout Brazil, treated as ruderal or even as weed (Lorenzi 2008). Additionally, some ruderal and generalist species that prioritize seed reproduction over resprouting, are usually killed by fire and end up relying only on the germination of seeds dispersed previously (Grime et al. 1988; Pausas & Keeley 2014; Fontenele & Miranda 2024). Thus, the presence of these species does not necessarily indicate a natural grassland, and they should not be considered as target species in restoration efforts. The large variation in community composition among sites and the high proportion of rare species and unique occurrences reinforce the fragility of this descriptor to be used as a restoration target.

**Total Richness (1 ha).** The number of native plant species recorded in 1 ha, although potentially providing a broader survey than the thirty 1-$m^2$ plots, is not practical or a reliable indicator due to the difficulty in accurately capturing all species, particularly within the herbaceous layer. This descriptor is labor-intensive, often requiring specialized botanical knowledge even using morphotypes. While the 1 ha survey can yield a general sense of richness, it does not provide the same precision as the richness estimate derived from the thirty 1-$m^2$ plots, which is not influenced by varying levels of sampling effort and observer expertise. Still, the additional richness gained by surveying an entire hectare does not justify the extensive effort required, especially given that species richness measured within the 30 plots is strongly correlated with total site richness.

**Aboveground Biomass.** Aboveground biomass was considered a less reliable indicator in tropical grasslands due to ecological factors, such as seasonality (Sala et al. 2012; Pillay & Ward 2022), fire events (Le Stradic et al. 2021), and frost (Hoffmann et al. 2019; Pilon et al. 2022), which seasonally or randomly change the biomass over time within a site. For instance, natural factors like fire reduce biomass by consuming plant material, while frost increases dead biomass accumulation (Fidelis et al. 2013). A good indicator must have clear direction, respond to stress, and increase over time in a predictable manner (Dale & Beyeler 2001). Aboveground biomass varies naturally in tropical grasslands, and, very importantly, the amount is not clearly related to the ecosystem's health. Low biomass does not necessarily indicate a degraded grassland, nor does high biomass confirm a pristine or fully restored ecosystem. Additionally, our field observations suggest that differences in floristic composition significantly contribute to biomass variation. This was partially confirmed by the correlation between grass cover and biomass: the greater the grass cover, the higher the biomass. Many species in the Cerrado form aggregated populations (Pausas et al. 2018; Zemunik et al. 2018; Maracahipes et al. 2024), leading to substantial spatial variation in biomass accumulation within the same plant community. Besides the ecological aspects, determining aboveground biomass is destructive, time-consuming, and requires infrastructure for storing, drying, and weighing the samples.

### Are the Reference Values From Pristine Grasslands Achievable?

Although there is consensus on the need for reference values from old-growth grasslands to drive restoration planning and to assess restoration success (Buisson et al. 2022), it must be clear that matching the reference should not be the restoration target for all indicators. Reaching all attributes of a pristine reference is not a feasible goal for restoration interventions (Hobbs 2007; Shackelford et al. 2021). Among all community descriptors explored, the most clearly achievable is aboveground biomass due to its established protocols and quantifiable measurements, and the most unachievable is the precise plant community composition, which largely varies among sites. However, biomass is not reliable as an indicator, as explained above, because neither high nor low biomass directly correlates with positive or negative restoration outcomes, and especially because it is very sensitive to different abiotic natural factors (e.g. fire, seasonality, frost). Regarding community composition, the long list of species recorded in pristine grasslands in our study serves as a guide for nurseries and seed collectors or even to categorize the species in a restored site as target or non-target. However, the precise species composition of a restored grassland is simply a mobile target, impossible to reach.

Among the numerical indicators, especially those quantifying plant richness and diversity of the pristine grasslands, are likely unachievable, while for structural indicators (ground cover and proportions between growth forms), the restoration target can be within the range of reference values. Because relevant ecosystem services (e.g. groundwater recharge, water provisioning, soil erosion control, and carbon storage) are strongly related to vegetation structure (Bengtsson et al. 2019; Zhao et al. 2020), reaching the reference values means restoration success.

The high diversity of plants and growth forms found in the pristine grasslands surveyed is by far above what has been found in the restoration of the Brazilian savanna (Cava et al. 2018; Pilon et al. 2023; Wiederhecker et al. 2024). Constraints encompass ecological and technological limitations to propagate endemic species, the level of habitat degradation, the naturally harsh environmental conditions of savannas—which result in very low or null seedling survival (Buisson et al. 2020)—and the naturally slow assembly rate of grasslands (Nerlekar & Veldman 2020). Most Cerrado endemic species have specialized requirements for establishment and growth, which are often absent in disturbed environments. Additionally, the slow recovery of species interactions, soil conditions, and microclimate further hampers the restoration process. As a result, achieving the high richness and diversity seen in reference open ecosystems is an extremely long-term goal, at least a century, and possibly even millennia to fully recover species richness (Nerlekar & Veldman 2020). This extended time frame makes diversity descriptors less reliable as immediate indicators of restoration success, as they cannot realistically be achieved within the duration of typical restoration projects.

The total vegetation cover can be readily achieved through various active restoration techniques. However, the critical question is whether the species that establish are the desired target species or non-target species (exotics and ruderals) that do not align with restoration goals. In open ecosystems, the general structure is characterized by a continuous grass layer interspersed with scattered woody elements (Veldman et al. 2015), which depends on a specific proportion between grasses and non-grasses. It is well known that once the native grasses are lost, they are challenging to reestablish on their own, often requiring interventions such as tussock transplantation or direct seeding to successfully colonize the area (Pilon et al. 2019, 2023). On the other hand, the ground cover by non-grasses can be easier to restore, as pine cultivation (Faleiro et al. 2022) and biological invasion do not completely eliminate these species (Assis et al. 2021). Many of these plants possess robust underground structures that can remain dormant for large periods, waiting for favorable conditions to resprout (Faleiro et al. 2022).

### On the Use of Pristine Grasslands as Reference for Restoration Assessment

When setting the goal for Cerrado grassland restoration, one crucial factor must be ensured: tree canopy cover should not exceed

20%, as vegetation surpassing this threshold is classified as savanna (Ribeiro & Walter 2008). Additionally, both cover and biomass of the ground layer should not exceed the top limit of pristine grasslands. Current restoration techniques are notably effective in promoting tree establishment (Pilon et al. 2023), and this effectiveness can be further amplified by undesirable woody encroachment, a significant issue in areas where fire suppression occurs (Stevens et al. 2017; Wieczorkowski & Lehmann 2022). Given that trees can recover through natural regeneration (Cava et al. 2018) and woody encroachment already is a global phenomenon (Stevens et al. 2017), focusing on tree planting should not be the primary concern in grassland restoration projects. In fact, projects that involve tree planting should be approached with caution—or even avoided—in open ecosystems. Such interventions not only alter the original vegetation structure (Parr et al. 2014) but also have broader consequences: they can negatively impact carbon storage (Berthrong et al. 2012), water regulation (Honda & Durigan 2016), tourism (Gray & Bond 2013), fire regimes (Rosan et al. 2019), and biodiversity of both fauna (Furtado et al. 2021) and flora (Abreu et al. 2017; Souza et al. 2022).

While some indicators are achievable, restoration success should also emphasize the recovery of minimum levels of ecological complexity, which underpins the ecosystem's ability to sustain essential processes (Prach et al. 2019). In some cases, degraded ecosystems may not fully reach the reference values even in the long term. However, if the plant community's structural complexity and composition are restored to a minimum level that supports key ecosystem services and a substantial portion of its historical biodiversity, habitat functionality can still be reestablished (Chaves et al. 2015). This minimum complexity, however, is still to be determined for tropical grasslands, and that requires evidence-based information. If the species composition is a subset from the large pool of old-growth grasslands instead of a high diversity of ruderals and exotics, and the functional proportions and fire resilience are recovered, we can consider that the ecosystem trajectory follows the right way.

In this study, we provided an overview of ecological indicators and their reliability to assess grassland restoration success, along with the range of reference values from pristine ecosystems. We identified effective descriptors, though some exhibited considerable variability—an expected but often overlooked aspect of native vegetation (Oliver et al. 2023). The simplicity of measuring certain descriptors does not guarantee their utility and that their reference values will be fully restored in practice. However, using reference values can significantly improve the assessment and support planning of restoration efforts by clearly defining the status, measuring the distance from what existed, evaluating the need for interventions, and setting realistic goals for the future.

Ultimately, priority should be given to the conservation of remaining natural undisturbed ecosystems instead of allowing their conversion. Especially given that restoration efforts, however extensive, cannot fully recover all the ecological attributes and complexity of pristine grasslands. Indicators and reference standards developed here can also serve to assess the degree of conservation in protected areas, helping to identify any gradual degradation and allowing for timely intervention. This approach reinforces the need for proactive conservation strategies that ensure the protection of these ecosystems' unique biodiversity and ecological functions, particularly in the face of increasing threats such as land conversion, climate change, and habitat fragmentation.

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## Supporting Information

The following information may be found in the online version of this article:

**Figure S1.** Reproductive adults of *Byrsonima verbascifolia* in the Cerrado, presenting different life forms.
**Table S1.** Location of sampling areas in natural grassland regions within the Cerrado.
**Table S2**. Plant species categorized by family, growth form, and occurrence across different sites, along with the total number of sites in which each species was recorded.
**Table S3**. Relative cover of the five most abundant species occurring at each site.

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