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Reference wet grasslands to support conservation and restoration assessments in the Brazilian Savanna

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Abstract

Introduction: Grassy wetlands of the Cerrado provide key ecosystem services but remain largely overlooked and are rapidly disappearing, threatened by land use change and climate-driven changes in hydrological cycles. As restoration initiatives are urgent, reference ecosystems and robust indicators are essential to guide conservation and restoration efforts.
Objectives: We aimed to provide reference values of adequate ecological indicators to assess both the ecological integrity of pristine wet grasslands and the effectiveness of restoration interventions.
Methods: We sampled 15 pristine remnants in southeastern Brazil and assessed plant community composition, species richness at multiple scales, ground cover by functional groups, water-table depth, and aboveground biomass.
Results: In total, we recorded 306 plant species. Mean richness per 1 m^2 plot ranged from 6 to 14 species (mean = 9). Richness at 30 m^2 ranged from 36 to 73 (mean = 53), whereas total richness ranged from 47 to 92 species (mean = 70). Biomass ranged from 380 to 844 g/m^2 (mean = 618), with total vegetation cover from 72 to 97% (mean = 87%).
Conclusions: Owing to their hydrological setting, these wet grasslands host a distinctive flora, including *Acisanthera alsinaefolia*, *Chaetogastra gracilis*, and *Xyris jupicai*, which occurred in all sampled sites and can serve as practical reference species for restoration monitoring. Richness per m^2 or at 30 m^2, along with ground cover, are reliable indicators, effectively capturing community diversity, structure, and associated ecosystem services. Total species richness per site and biomass largely vary among sites and require time-consuming sampling, limiting their reliability as indicators.

Implications for Practice: Our synthesis provides a practical framework to guide restoration monitoring and indicator selection across sites, facilitating the selection of efficient and comparable metrics. The consistent structural attributes observed across pristine wet grasslands support the use of well-defined reference ranges: richness per m^2, richness in 30 m^2, and total vegetation cover can be considered reliable indicators to assess how far a restored wet grassland is from the reference range. Because the water table is the primary driver of these ecosystems, its temporal dynamics must be explicitly considered when monitoring conservation and restoration outcomes.

Key words: Cerrado, growth forms, indicators, reference ecosystem, reference values, wetlands

Introduction

Assessing the ecological integrity of natural ecosystems and the success of restoration initiatives requires clear, objective, and ecologically meaningful indicators (Ruiz-Jaen & Aide 2005; Gann et al. 2019). Because ecosystems are complex and dynamic, such assessments cannot rely on exhaustive measurements of all components, but instead depend on a small, well-chosen set of indicators capable of capturing key ecological processes and ecosystem functions (Dale & Beyeler 2001; Ruiz-Jaen & Aide 2005). The use of reference ecosystems is central to this approach, as they provide reference values that allow the evaluation of conservation status and restoration trajectories (Gann et al. 2019). The development and application of ecological indicators have long been recognized as central to evaluating ecosystem conditions and guiding restoration efforts (Ruiz-Jaen & Aide 2005). Indicators are most informative when explicitly linked to clearly defined goals, rather than used as generic measures of recovery (Hobbs 2007; Hallett et al. 2013). Effective indicators should be ecologically meaningful, sensitive to disturbance and management, easy to measure, and capable of integrating complex ecological processes while minimizing natural variability (Dale & Beyeler 2001). For this reason, a small, carefully selected set of indicators is often more effective than extensive metric lists, particularly in open ecosystems and wetlands, where strong environmental filters shape community structure and function (Prach et al. 2019).

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Dynamic hydrological regimes in wetlands can complicate both conservation assessment and restoration, making the selection of reliable indicators more challenging. These hydrological regimes also shape grassy vegetation in wetlands, which is distinguished by its unique plant species composition and ecosystem functioning (Blom & Voesenek 1996; Zedler & Kercher 2005). In the Brazilian savanna (Cerrado), wetlands are represented by wet grasslands (*campos úmidos*, *veredas*), open vegetation types dominated by herbaceous species, especially graminoids, with sparse or absent woody cover, associated with seasonally waterlogged or poorly drained soils (Munhoz & Felfili 2007; Ribeiro & Walter 2008). Owing to their outstanding role in ecosystem service provision, wetlands are among global priorities for conservation and restoration (Finlayson et al. 2005; Costanza et al. 2014). Despite their ecological importance, wet grasslands are rapidly disappearing due to land-use conversion, which alters fire regimes and hydrological cycles (Joyce 2014; Kingsford et al. 2021; Fluet-Chouinard et al. 2023).

Ecological restoration is a key strategy to recover ecosystem structure and function, yet restoring wet grasslands remains challenging (Pilon et al. 2023; Medeiros et al. 2024). In practice, restoration efforts in these ecosystems are limited, and commonly used approaches, particularly tree planting, are inadequate for these herbaceous-dominated systems (Durigan 2025). Beyond these constraints, a more fundamental gap persists: the absence of robust, widely applicable indicators and reference values to assess the ecological integrity of wet grasslands and to evaluate recovery trajectories (Zedler 2000; Taddeo & Dronova 2018). Such criteria, however, are often not based on comparisons with reference ecosystems (Moreno-Mateos et al. 2012; Herb & Finlayson 2023). The absence of adequate indicators and reference values represents a major obstacle for decision-making, including vegetation suppression, prioritization of conservation and restoration actions (Grasel et al. 2019; Durigan et al. 2022), and for diagnosing degradation within protected areas (Newall & Fisk 2023).

In this study, we provide reliable ecological indicators and a range of reference values for wet grasslands in the Brazilian Cerrado, to guide (i) the assessment of their integrity in the conservation context, and (ii) the evaluation of their restoration success, based on deviation from reference conditions. We present a comprehensive characterization of a large set of pristine Cerrado wet grasslands, using multiple indicators to evaluate their structure (aboveground biomass, ground cover by graminoids and non-graminoids), plant richness, species composition, and hydrological conditions (water-table depth). We then assess the potential of these descriptors as indicators of ecosystem integrity and restoration success, discussing their strengths and limitations in capturing the trajectory toward reference conditions.

Methods

Study Sites

We surveyed 15 natural remnants (hereafter “sites”) of open Cerrado ecosystems occurring in wetlands (wet grasslands) in São Paulo State (Table S1; Fig. 1). The study sites were selected to represent pristine wet grasslands where vegetation has not been disrupted by mechanization, invasive species, or other forms of degradation, although wildfires have occurred in most sites over recent decades. Fire, however, is a natural driver in grassy Cerrado vegetation, including wet grasslands (Schmidt et al. 2017; Durigan et al. 2022).

The study region includes areas classified as Cfa and Cwa climates, with a marked wet season from October to March and a drier season from April to September (Alvares et al. 2013). Wet grasslands occur on poorly drained, hydromorphic soils, acidic, with a high content of organic matter and carbon (Verona et al. 2026), where seasonal oscillations of the water table lead to soil waterlogging during and just after the rainy season. These ecosystems are therefore not permanently flooded; instead, their structure and functioning are primarily controlled by groundwater emergence and shallow water tables.

Plant Community Sampling

At each site, independently of the area occupied by the wet grassland patch, we sampled the plant community within 30 circular plots of 1-m^2 to represent the dominant species of each site, the average number of species per square meter (alpha diversity), the ground cover by plants and bare soil, and to obtain the average ratio between non-graminoids and graminoids. We followed the standardized sampling protocol adopted by the broader research project and allowing comparability with previous assessments of Cerrado grasslands, including dry grasslands surveyed by Campos et al. (2025a). Sampling standardization allows robust comparison between ecosystems being restored and reference ecosystems. The 30 plots were arranged in three transects of 10 plots each (see Fig. 1) to represent distinct hydrological conditions within the site, determined by topographic variation or landscape position that influences the level of waterlogging and, therefore, the plant community (Munhoz et al. 2008). To obtain the site-level richness and composition as possible indicators, we additionally recorded plant species occurring outside the plots.

In each plot, we visually estimated the percentage cover of graminoids (including Poaceae, Cyperaceae, Juncaceae, and Xyridaceae), non-graminoids (forbs, subshrubs, shrubs, trees, ferns, climbers, and palms), and bare soil (including litter). All vascular plant species within the plot were identified, and their cover was visually estimated as a percentage, following an adaptation of the method proposed by Wikum and Shanholtzer (1978).

Aboveground biomass was collected in nine 0.25-m^2 subplots and included live and recently dead plant material still attached to the plant base, excluding detached litter and stems thicker than 6 mm in diameter (Newberry et al. 2020; Campos et al. 2025a). Graminoid and non-graminoid biomass were separated, stored in labeled paper bags, oven-dried at 60°C until constant weight, and weighed using a digital scale with a precision of 0.1 g. All measurements were taken during the rainy season across all sites.

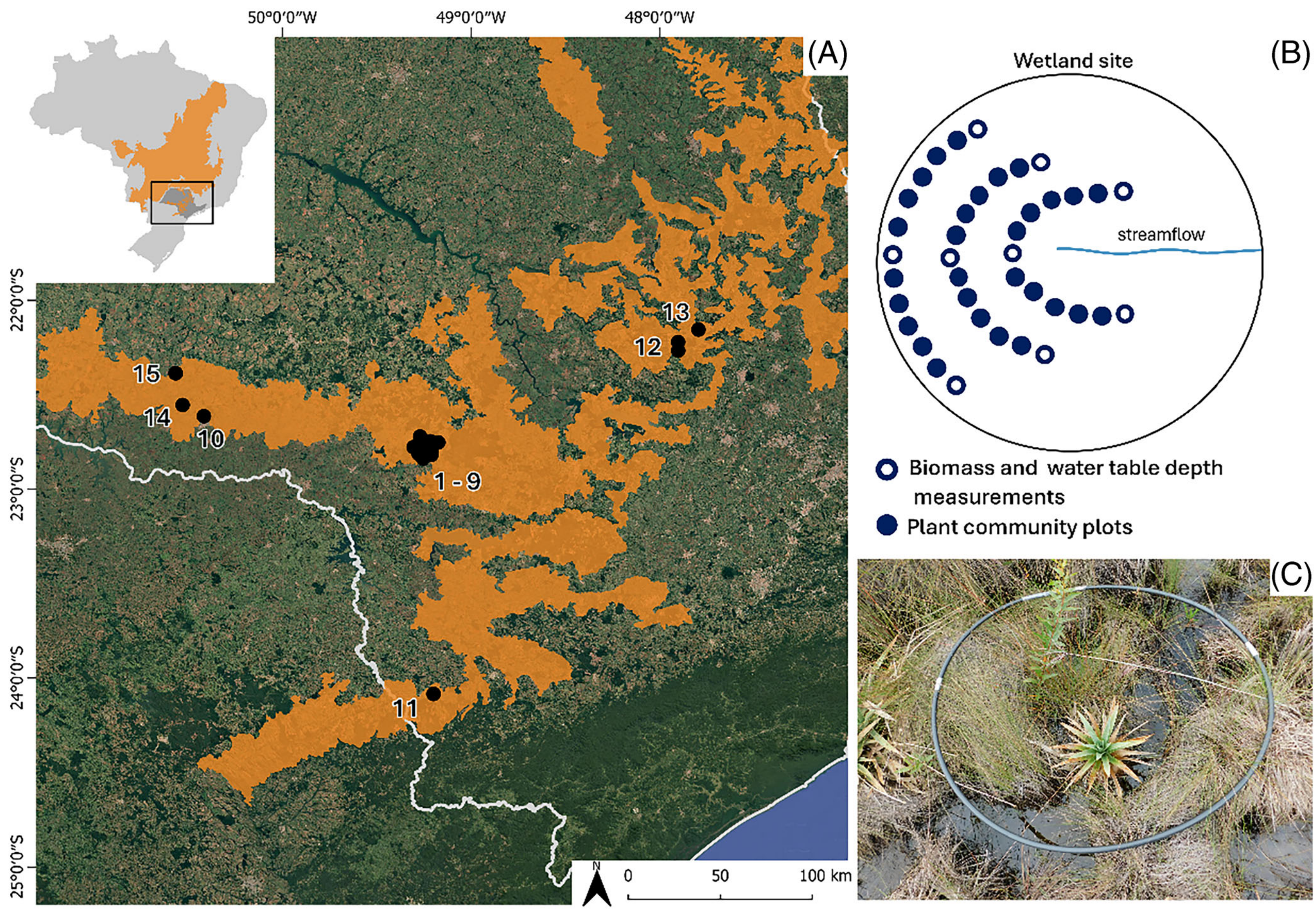

Figure 1. Location of the 15 wet-grassland sites (A). Numbers correspond to site codes described in Table S1. The Cerrado biome is shown in orange. Sampling design within a wetland site (B). Detail of a vegetation plot (1 m^2) used for plant community sampling, bounded by a polyvinyl chloride (PVC) hose (C).

Floristic Survey Beyond the Plots

To record additional species not captured within the plots, allowing a broader view of species richness and species composition per site, we conducted a general floristic survey using the "rapid survey" method proposed by Filgueiras et al. (1994). During systematic walks across the entire wet grassland patch, we recorded all observed vascular plant species at regular time intervals. Sampling was concluded when fewer than five new species were observed during two consecutive 15-minute intervals.

Most plant species were identified to the species level in the field. When identification was not possible on-site, botanical material was collected for later determination based on literature, herbarium specimen comparisons, and consultation with experts. Voucher specimens were deposited in the University of Campinas Herbarium and the Dom Bento José Pickel Herbarium.

Species were classified into growth forms, including trees, shrubs, subshrubs, forbs, palms, climbers, arborescent ferns, grasses, and sedges, following Pilon et al. (2021), Durigan et al. (2018), and Flora do Brasil (2026). In addition, species were classified according to their habitat preference as wet, dry, or wet/dry, based on the environmental conditions reported in the literature. Species classified as wet occur exclusively in hydromorphic soils or wet grasslands; species classified as dry occur more frequently in non-hydromorphic soils, and wet/dry habitat refers to species recorded in both conditions. This classification was supported by descriptions provided by Durigan et al. (2018), Sano et al. (2008), and by additional information from the SpeciesLink database, where we verified the habitat descriptions in herbarium specimen labels.

Water-Table Depth Measurements

Water-table depth was measured in the nine systematically predefined plots where aboveground biomass was collected, aiming to characterize the range of hydrological conditions of reference wet grasslands. For each site, we used the mean water-table depth across the nine wells as a site-level descriptor of hydrological conditions. All measurements were taken during the end of the rainy season, when the maximum elevation occurs, ensuring consistency in the hydrological stage across all sites, and because the maximum elevation of the water table is the major filter influencing the plant community (Ribeiro et al. 2021).

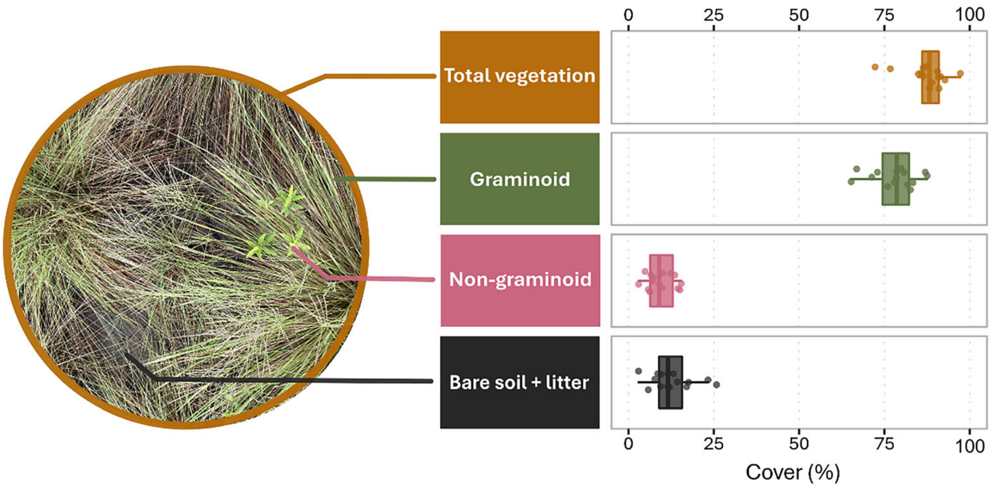

Figure 2. Range of ground cover percentage of plant communities in 15 Cerrado wet grasslands. Total vegetation (graminoid + non-graminoid cover); graminoids, non-graminoids; bare soil + litter. Each small circle represents the average value calculated across the 30 sampled plots within each site. The thicker central line represents the median, and the box boundaries are the 25 and 75% quartiles.

Indicators

For each site, we obtained a single value for each indicator. Species richness was quantified at three spatial scales: (i) richness per 1 m^2 plot, calculated at the plot level and averaged per site; (ii) richness at 30 m^2, defined as the cumulative number of species recorded across the 30 plots within each site; and (iii) total species richness per site, corresponding to the total number of species recorded per site, including both plot-based sampling and the floristic survey conducted beyond the plots. Ground cover metrics (total vegetation cover, graminoid, non-graminoid, and bare soil + litter cover) were calculated as mean values across the 30 plots sampled within each site. Aboveground biomass (g/m^2) and water-table depth were calculated as means across the nine sampling points per site. Reference values for each indicator were defined as the range of site-level values observed across the 15 pristine wet grasslands and are graphically presented using boxplots.

To support indicators selection, we conducted a qualitative–quantitative assessment of each metric based on its ecological meaning, feasibility, precision, sensitivity to disturbance or restoration, and relevance for conservation and restoration purposes. Each indicator was scored on a five-point ordinal scale. Scores reflect field experience, methodological constraints, and evidence from the literature on grassland and wetland functioning.

We used Pearson's correlation coefficient to assess correlations and potential redundancy among indicators. Data normality assumptions were tested prior to the analysis. All analyses were conducted in R version 4.3.1 (R Core Team 2023), and figures were produced using the ggplot2 package (Wickham 2016).

Results

Plant Species Composition

We recorded a total of 306 plant species belonging to 73 families across the 15 wet grassland sites, including both plot-based sampling and floristic surveys. The six families with the highest number of species were Poaceae (16%), Asteraceae (14%), Cyperaceae (9%), Melastomataceae (7%), Xyridaceae (5%), and Fabaceae (4%). We found a set of species exclusive to wetlands (waterlogged conditions) that occurred across all sites, comprising: *Acisanthera alsinaefolia*, *Chaetogastra gracilis*, and *Xyris jupicai* (Table S2). Several species were recorded in more than 70% of the sites, such as *Comanthera xeranthemoides*, *Desmoscelis villosa*, *Lagenocarpus rigidus*, *Ludwigia nervosa*, *Miconia chamissois*, *Palhinhaea cernua*, *Paspalum cordatum*, *Rhynchospora globosa*, *Rhynchospora rugosa*, *Scleria hirtella*, *Trichanthecium schwackeanum*, and *Xyris savanensis*. Other species occurred in most sites but were also found under well-drained conditions, including *Andropogon leucostachyus*, *Axonopus siccus*, *Anthaenantia lanata*, *Andropogon virgatus*, *Axonopus marginatus* (Table S3). In contrast, 136 species (44%) were recorded in only a single site.

Regarding growth forms, most of the species were forbs (38%), followed by graminoids (28%), subshrubs (12%), shrubs (7%), trees (7%), climbers (3%), and palms (0.3%). Species typical of dry grasslands were also present (17%), but specialists in waterlogged conditions (47%) and those tolerant of both wet and dry soils (33%) predominated.

Range and Average of Reference Values per Indicator

The ground cover by vegetation (as opposed to bare soil or litter) ranged from 25 to 100%, with an average of 87% (Fig. 2). Graminoid cover ranged from 20% to 100%, with a mean of 78% per plot. Non-graminoid cover ranged from 0% to 58%, with an average of 9%. The proportion of bare soil plus litter ranged from 0% to 50%, with a mean of 5%. The ratio of non-graminoid to graminoid cover (NG:G) ranged from 0.03 to 0.21 (mean = 0.12). Species richness per 1-m^2 plot ranged from 6 to 14 species (average among the 30 plots within each site), with a mean of 9 species per m^2 across all sites. Richness per

30 m^2 (i.e., cumulative richness across the 30 plots) ranged from 36 to 73 (mean = 53). Total species richness per site (i.e., total number of species per site considering the floristic survey) ranged from 47 to 92 (mean = 70) (Fig. 3).

The average aboveground biomass across sites ranged from 142 to 1,512 g/m^2, with a mean of 618 g/m^2. Graminoid biomass ranged from 140 to 1,504 g/m^2 (mean = 605 g/m^2), and non-graminoid biomass from 0 to 244 g/m^2 (mean = 12 g/m^2). Water-table depth ranged from 8 cm above the soil surface to more than 100 cm below, with an average depth of 21 cm across all sites at the end of the rainy season. In search of redundancy between indicators, we found species richness at 30 m^2 was correlated with the total number of species ($r^2 = 0.61$; $p < 0.01$). Aboveground biomass was not correlated with vegetation cover ($r^2 = 0.08$; $p = 0.30$).

Indicator's Relevance and Quality to Inform Conservation and Restoration

Indicator scores showed clear differences across evaluation criteria, while also reflecting trade-offs between indicators. Here, we summarize overall indicator performance across feasibility, precision, predictability, and relevance (Table 1). Plot-level richness (1-m^2), 30 m^2 richness, native plant cover (%), and water-table depth during the rainy season consistently received the highest scores across most criteria due to strong performance across criteria for both conservation and restoration. In contrast, total species richness per site and aboveground biomass received lower scores for feasibility and precision due to potential limitations for routine application. Indicators based on species composition, such as indicator species presence, had intermediate performance but lower predictability compared to structural metrics.

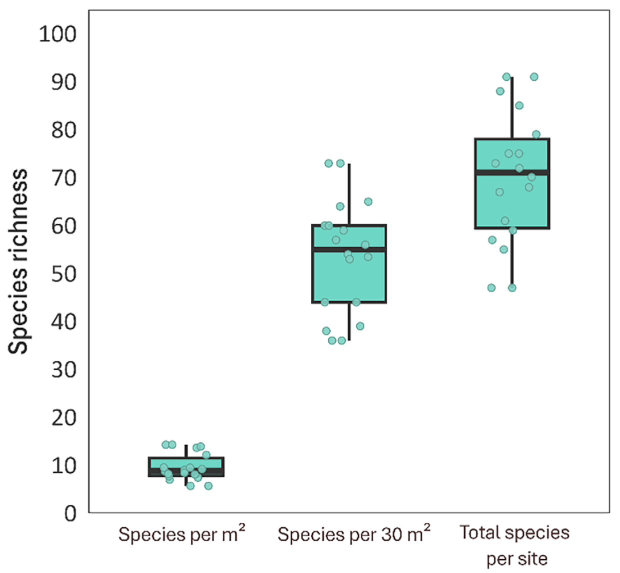

Figure 3. Range of plant species richness at three different spatial scales of plant communities in 15 Cerrado wet grassland sites. The thicker central line represents the median, and the box boundaries are the 25 and 75% quartiles.

Discussion

Pristine ecosystems provide the baseline for rebuilding resilient systems, and setting clear goals is crucial for advancing restoration ecology in a world of rapid, unpredictable environmental change (Pilon et al. 2023). We evaluated a range of indicators using well-conserved wet grasslands to test their potential for assessing restoration success. In wetlands, indicators should link abiotic conditions to biotic responses, translating hydrological and edaphic gradients into measurable biological parameters (Rosenthal 2003). Effective indicators must also be simple, measurable, and sensitive to key stressors such as altered hydrology, fire-regime changes, biological invasions, and overgrazing (Spellerberg 2005; Caro 2010).

Some descriptors, such as total vegetation cover, growth-form proportions, floristic composition, and plot and 30 m^2 species richness, are good indicators, particularly informative for integrity evaluation, diagnosing progress in restoration interventions, and guiding adaptive management. Other attributes, such as aboveground biomass, show pronounced variability in pristine wet grasslands and do not represent ecosystem integrity or restoration success. Richness per site, despite being relevant for biological conservation at the site level, strongly depends on exhaustive inventories, which are impossible to standardize when comparing multiple sites or when quantifying changes over time. In terms of setting restoration goals, studies have shown that reaching the total richness is not a feasible goal. These indicators, therefore, are better reserved for complementary interpretation.

Suitable Indicators to Assess Wet Grassland Restoration

A small, well-selected set of indicators can represent key ecological processes (Prach et al. 2019) and biological values. Good indicators should be ecologically relevant, easy to measure, respond predictably to disturbance and management, integrate multiple ecosystem components, have known responses to anthropogenic pressures and temporal dynamics, and exhibit low natural variability (Dale & Beyeler 2001; Taddeo & Dronova 2018). Beyond these general attributes, indicators must also be feasible to apply across spatial and temporal scales and linked to measurable ecological functions, ensuring both conceptual and operational robustness (Taddeo & Dronova 2018). In wet grasslands, indicators should also capture the hydrological functioning that supports ecosystem integrity and the services derived from that functioning, including freshwater provisioning, carbon storage, and habitat maintenance (Rosenthal 2003; Casanova et al. 2023). Based on the attributes assessed, total plant cover, growth-form proportions, plot- and 30 m^2 plant species richness, and floristic composition emerged as the most informative indicators for tracking the recovery of Cerrado wet grasslands.

Vegetation Cover. Vegetation cover is a simple and powerful indicator of restoration progress (Ruiz-Jaen & Aide 2005; Taddeo & Dronova 2018). It corresponds to the percentage of the ground surface that is occupied by vegetation, indirectly

Table 1. Indicators' relevance and quality for conservation and restoration. Scores range from 1 (low) to 5 (high).

Indicator	*Ecological Meaning or Surrogacy*	*Facility to Measure*	*Precision*	*Predictability of Changes Over Time in Response to Disturbance or Restoration*	*Relevance for Conservation*	*Relevance for Restoration*
Plot-level richness (1-m^2)	Alpha diversity, resilience, pollination	5	5	5	5	5
30 m^2 richness	Community diversity, pollination	4	5	5	5	4
Total species richness per site	Species richness pollination	2	2	5	4	3
Indicator species presence	Keystone species	3	3	2	4	3
Native plant cover (total %)	Community structure, absence of invasive plants, soil protection against erosion, Albedo, disturbance, water infiltration	5	4	5	4	5
NG:G (ratio)	Functional diversity, habitat diversity	3	3	1	2	3
Grass cover %	Flammability, forage availability for grazers	4	4	3	3	3
Non-grass cover %	Pollination	4	4	3	2	2
Bare soil + litter %	Favorable for germination and re-sprouting	5	4	5	3	4
Aboveground biomass (g/m^2)	Net primary productivity, carbon storage, light competition, rain interception	1	2	3	3	3
Water-table depth in the rainy season (cm)	Hydrological functioning, environmental filter	4	3	5	5	5

indicating the ground percentage exposed to direct sunlight (Pinheiro et al. 2022). Ground cover by vegetation is directly related to soil erosion control, surface water dynamics, infiltration and storage (Kim & Jackson 2012; Honda & Durigan 2016), as well as habitat provisioning for small animals. Although our sampling sites are located in Southern Cerrado and nearby regions, previous studies in other regions have consistently described Cerrado wetlands as ecosystems with dense herbaceous vegetation and high cover of grasses and sedges (Munhoz et al. 2008; Miranda Santos & Munhoz 2012), and contrast with dry Cerrado grasslands, where bare soil plus litter may be much higher, ranging from 4 to 56% and averaging approximately 20% (Campos et al. 2025a). This suggests that wet grasslands are relatively homogeneous across the biome, in contrast to dry Cerrado grasslands, which show greater heterogeneity in vegetation cover and bare soil. Yet, high cover should not be interpreted as complete cover. This consistent difference between dry and wet grasslands is highly important when planning or assessing Cerrado grasslands restoration. In the end state of wet grassland restoration, a small portion of bare soil or litter is expected (around 5%), as observed in the reference ecosystems, to allow germination and resprouting of native plants. Vegetation cover expressed in percentage of the ground occupied by each cover class is straightforward and easy to measure in the field, making it a practical indicator for monitoring both ecosystem integrity and restoration success.

Growth-Form Proportion. Growth-form proportion refers to the relative cover of graminoids (Poaceae, Cyperaceae, Xyridaceae) versus non-graminoids (forbs, subshrubs, shrubs, climbers, and palms). In our reference sites, graminoids accounted for most of the vegetation cover, whereas non-graminoids were consistently lower. Beyond the floristic composition (dominant taxa), the dominant functional groups in Cerrado wet grasslands are also relatively homogeneous across regions, with graminoids consistently prevailing (Guimarães et al. 2002; Munhoz et al. 2008; Miranda Santos & Munhoz 2012). Previous studies in Cerrado wetlands have shown Poaceae and Cyperaceae with the highest absolute cover in veredas, and the dominant species were often graminoids such as *Paspalum*, *Lagenocarpus*, *Axonopus*, *Rhynchospora*, and *Xyris* (Araújo et al. 2002; Munhoz et al. 2008; Bijos et al. 2017). In dry grasslands, graminoids dominate but are accompanied by substantial non-graminoid and bare soil cover (Campos et al. 2025a). In contrast, we found a clear predominance of graminoids and low cover of non-graminoids and bare soil in the wet grasslands. This structural pattern is not only distinctive of wet grasslands but also fundamental for maintaining their hydrological processes (Bullock & Acreman 2003), as dense graminoid cover influences water infiltration, storage, and surface dynamics (Kim & Jackson 2012; Honda & Durigan 2016). Under shallow or fluctuating water tables, graminoids form dense tussocks that sustain fire regimes while maintaining an open, light-rich herbaceous layer and contribute to fuel continuity for fire-prone grassland dynamics (Fidelis et al. 2013; Bond 2021). Non-graminoids add complementary functions, such as pollination networks and diversity (Oliveira & Gibbs 2002; Pilon et al. 2023), yet they typically occur at lower cover in hydromorphic settings.

Because it integrates structure and function and is quick to assess in the field, not depending on species identification, growth-form proportion is a reliable restoration indicator. It is sensitive to multiple pressures, including biological invasions, woody encroachment, and shifts in hydrological or fire regimes, which can rapidly alter the balance among growth forms and compromise ecosystem functioning (Damasceno et al. 2018; Souza et al. 2022). Monitoring the proportion of growth forms in restored sites can therefore provide a practical measure of whether restoration efforts are recovering the structure and functional attributes of reference ecosystems. Re-establishing the expected dominance of graminoids with limited non-graminoid and maintaining a certain proportion of bare soil should be considered a central target for restoration in Cerrado wet grasslands. In pristine areas, deviations from the expected proportions may be a sign of ongoing degradation processes.

Richness per 1 m^2 Plot. Wet grasslands in the Cerrado naturally host fewer species than their dry-grassland counterparts (Campos et al. 2025a), and our data reflect this context: richness per plot varied widely considering all plots from all sites, from a single species in extremely waterlogged plots to more than 20 species in others. Despite considerable variation among plots, the mean richness per 1 m^2 per site showed moderate variation among sites (≈9 species per m^2). The observed variability among plots highlights the strong influence of water-table dynamics, which can favor the dominance of a few highly adapted graminoids. Consequently, low richness does not necessarily indicate degradation but may reflect more restrictive environmental filtering (Brinson 1993).

The average richness per 1 m^2 within a site is a valuable indicator because it responds predictably to disturbance, management, and anthropogenic pressures, showing consistent temporal patterns in relation to fire frequency (Fidelis et al. 2013; Rodrigues & Fidelis 2022; Campos et al. 2025b), frost (Pilon et al. 2022), drought (Brotherton & Joyce 2015; Joyce et al. 2016), biological invasions (Joyce 2014; Lázaro-Lobo & Ervin 2021), and woody encroachment (Souza et al. 2022; Wieczorkowski & Lehmann 2022). Counting plant species per 1-m^2 plot is an easy task that does not necessarily require specialized taxonomic knowledge. It simply involves counting distinct species within the plot, provided that exotic species can be detected and recorded.

Richness per 30 m^2. Richness accumulated across thirty 1-m^2 plots was also considered a reliable indicator, providing an integrated view of community composition and heterogeneity within each site. Values in the reference sites reflected the influence of hydrological gradients and microtopographic variation on community assembly. Within-site heterogeneity in water-table depth often leads researchers to sample transects of different sizes rather than discrete plots (Munhoz et al. 2008; Rolon et al. 2011; Bijos et al. 2017), hindering direct comparisons and complicating the establishment of standardized richness values. Standardizing the sampling effort can provide valuable information, enabling further ecological community analyses such as functional diversity, and consequently the assessment of ecosystem stability and resilience (Lavorel et al. 2013). Nevertheless, these studies highlight the importance of allocating sampling units along the entire hydrological gradient to adequately capture the species diversity of wet grasslands.

Floristic Composition. Floristic composition is often included in wetland definitions because, differently from dry grasslands (Campos et al. 2025a), these ecosystems host distinctive groups of species (Cowardin et al. 1979; Ramsar Convention Secretariat 2010; Junk et al. 2013). In the Cerrado, a small set of families, genera, and species can be used to recognize wet grasslands (Durigan et al. 2022). Plant species occurring in wet ecosystems can serve as valuable tools for linking abiotic conditions to biotic responses, translating hydrological and edaphic gradients into measurable biological parameters (Rosenthal 2003). Although we acknowledge the difficulties of identifying small herbaceous plants, many diagnostic taxa are relatively easy to recognize and can be used to ensure integrity or to monitor restoration progress.These taxa are typically restricted to wet grasslands and serve as reliable indicators of waterlogged conditions: the families Cyperaceae (especially *Rhynchospora tenuis*, *Lagenocarpus rigidus*, *Scleria hirtella*, *Rhynchospora globosa*, *Rhynchospora rugosa*), Eriocaulaceae (e.g. the genera *Eriocaulon, Paepalanthus, Syngonanthus*, and *Comanthera*), Lycopodiaceae (e.g. *Palhinhaea*), Melastomataceae (especially *Acisanthera alsinaefolia, Chaetogastra gracilis, Desmoscelis villosa*), Poaceae (e.g. *Paspalum cordatum, Trichanthecium schwackeanum*), Onagraceae (e.g. *Ludwigia*), and Xyridaceae (*Abolboda* and *Xyris*), many of which are adapted to a wide range of hydrological conditions, and occur across broad geographical regions. The recurrence of these taxa in our study is consistent with broader floristic assessments of Cerrado wet ecosystems, such as those conducted by Bijos et al. (2017) and Silva et al. (2017). This agreement suggests that, despite local variation at a fine scale, wet grasslands share a recognizable floristic core across the Cerrado. Silva et al. (2017) further demonstrated that this flora is distinct from that of drier Cerrado vegetation types.

In contrast, several widespread species occurring across both wet and dry grasslands (wet/dry taxa) can also play important roles, particularly in restoration. These include grasses such as *Andropogon virgatus, Anthaenantia lanata, Axonopus siccus, Axonopus marginatus*, and *Trachypogon vestitus*, which tolerate seasonal fluctuations in water availability and can rapidly establish under variable hydrological conditions. They are likely the most successful when used in restoration due to their adaptation to a broad range of environmental conditions. Therefore, floristic composition offers both diagnostic and monitoring potential, allowing practitioners to distinguish restored wetlands from those dominated by ruderal or invasive species. The total list of species recorded in the 15 wet grasslands sampled can serve as a menu for restoration planning in wet grasslands of the Cerrado. Species not mentioned are either very rare or do not occur in wet grasslands of the broader study region.

Less Reliable Indicators for Restored Wet Grasslands

In contrast to the set of reliable indicators, some descriptors show high variability in their responses, are difficult to measure, or fail to capture the full complexity of ecosystem processes (Dale & Beyeler 2001). Indicators with high natural variability or weak connections to ecosystem functioning may have limited applicability for monitoring restoration outcomes, even when conceptually sound (Taddeo & Dronova 2018). In this context, we consider the total species richness per site and aboveground biomass as less reliable indicators for assessing ecosystem integrity and restoration outcomes in wet grasslands because they are highly variable, operationally demanding, and weakly linked to restoration trajectories.

Total Species Richness per Site. The richness obtained from the floristic inventory was considered less reliable as an indicator of restoration progress. This metric integrates species from multiple microhabitats and often includes taxa from ecotonal or adjacent dry-grassland areas, potentially inflating species counts and obscuring site-level patterns. Total richness was strongly correlated with richness at 30 m^2, indicating substantial redundancy between these indicators. Moreover, total richness is highly sensitive to sampling effort and identification accuracy, particularly in diverse herbaceous layers where morphologically similar species coexist. Practical challenges further constrain the use of richness as an indicator in wet grasslands. Even when morphotype-based approaches are employed, the high similarity among species in the herbaceous layer makes accurate identification difficult, particularly for observers not specialized in herbaceous communities. In such cases, surveying larger areas will naturally yield more species, but the additional richness does not justify the extra effort, as richness within smaller plots closely mirrors overall richness at 30 m^2.

Aboveground Biomass. Aboveground biomass exhibited high variability across sites and sampling periods, consistent with previous evidence that biomass in tropical grasslands is strongly influenced by short-term environmental fluctuations, including seasonal dynamics, fire, and frost (Fidelis et al. 2013; Hoffmann et al. 2019; Campos et al. 2025b). These drivers can either reduce or increase biomass irrespective of restoration success, as fire removes standing biomass while frost can promote the accumulation of dead material (Fidelis et al. 2013; Pilon et al. 2022). As a result, biomass values may shift substantially over short time scales without corresponding changes in vegetation structure or species composition. In our study, aboveground biomass was weakly correlated with vegetation cover, graminoid cover, and plant richness, indicating that it does not consistently track key components of vegetation recovery or ecosystem condition. This lack of surrogacy limits its usefulness as an indicator, since effective indicators are expected to respond to environmental stressors and management interventions in a predictable and directional manner (Dale & Beyeler 2001). Furthermore, biomass estimation relies on destructive sampling and requires laboratory infrastructure for drying and weighing plant material, making it a logistically demanding and time-consuming metric.

Groundwater Dependence

Hydrology is the primary driver of wetland existence and functioning, determining not only the persistence of these ecosystems but also the composition and dynamics of their flora and fauna (Casanova et al. 2023). Because natural wetlands contract and expand with temporal and spatial variability in water availability, resilience depends on the capacity to accommodate such fluctuations (Xavier et al. 2019). In this context, seeking to define a fixed endpoint for restoration is problematic, since the ecological character of wetlands is inherently dynamic (Casanova et al. 2023). In our study, water-table depth ranged from aboveground flooding to values exceeding 1 m deep, underscoring that reference conditions should be understood as ranges rather than fixed targets, consistent with calls for realistic and flexible goals in restoration ecology (Hobbs 2007). In the Cerrado ecoregion, shallow groundwater dependence makes hydrological conditions a critical abiotic constraint for wet grasslands' persistence and restoration. The water table integrates hydrological functioning, soil redox conditions, and plant-available water, thereby shaping biogeochemical processes and species composition (Baird & Low 2022). Oscillations in water-table depth are central to grassland maintenance in the Cerrado, mediating alternative woodland–grassland states (Ribeiro et al. 2021). Our results illustrate the strong oscillations in water-table depth, which highlight the complexity of hydrological restoration: it requires re-establishing not only vegetation but also the abiotic conditions that sustain ecosystem resilience.

Short periods of soil saturation (even on the order of days) can alter species' composition and maintain characteristic vegetation (National Research Council 1995). Such oscillations are expected when rainfall and temperature fall within typical ranges and surrounding land use supports recharge. Departures from this pattern (e.g. substantial water-table declines under normal rainfall) can indicate watershed processes requiring management (Jackson et al. 2005; Kim & Jackson 2012). In this case, the scale of restoration projects needs to consider entire catchments or substantial landscapes to restore natural functions (Joyce et al. 2016). Accordingly, water-table monitoring is a pragmatic, cost-effective indicator of wetland condition (Baird & Low 2022).

Using Reference Values (and What to Expect) from Pristine Wet Grasslands

Because structure and composition are tightly constrained by hydrology, and hydrology itself varies across seasons, years, landscape positions, and catchments, reference conditions are best conceived as a range of values (Zedler 2000; Zedler 2007;

Casanova et al. 2023). In many contexts, not all indicators of reference sites will be reached (Hobbs 2007), especially where groundwater recharge is damaged, hydrological connectivity is disrupted, or propagule pressure from exotics is high. In many cases, wetlands can be restored when appropriate hydrology is returned (Casanova et al. 2023); and this often implies recognition of processes in the catchment area, not only *in situ* (Jobbágy & Jackson 2004; Kim & Jackson 2012).

Within this hydrological framework, plant richness values and structural indicators (ground cover and growth-form proportions) are achievable targets, as restoration outcomes can realistically fall within the reference range. Because key ecosystem services, such as groundwater recharge, water provisioning, soil erosion control, and carbon storage, are strongly linked to vegetation structure (Zhang et al. 2001; Bengtsson et al. 2019), achieving these structural reference values represents ecological success. A predominance of graminoids combined with low bare-soil cover is a key condition for sustaining hydrological processes and may serve as an indicator of re-established water-table oscillations, given that dry grasslands typically have a higher proportion of bare soil (Campos et al. 2025a). Plot- and 30 m^2 richness can be used as indicators within the reference range to track the restoration process and offer realistic and ecologically meaningful support for adaptive management. At the same time, these reference values can be used to identify conserved sites, which must be treated as conservation priorities. Many wet grasslands remain under-recognized due to their subtle topography or seasonal dynamics. Strengthening recognition with floristic diagnostics, plot-scale richness, and simple water-table monitoring helps to improve mapping and ensure that conserved sites are identified, protected, and used to guide restoration trajectories.

Finally, the presence and cover of invasive exotic species adapted to waterlogged conditions, particularly *Pinus* species, constitute a leading indicator of degradation in wet grasslands (Rolon et al. 2011). Because invasives rapidly increase shading, they disrupt the balance among growth forms, suppressing the herbaceous layer and consequently altering fire behavior (Abreu & Durigan 2011; Brewer et al. 2018). They also alter hydrological feedback by lowering the water table (Zhang et al. 2001). Therefore, exotic species should be routinely monitored and used as actionable triggers for management interventions. In practice, pairing floristic diagnostics and growth-form proportions with an explicit exotics metric (e.g. % ground cover) provides an early-warning signal as the system moves toward (or away from) the reference indicators.

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Supporting Information

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

Table S1. Location of sampling areas in natural wet 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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