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What is the current status of phenological studies of herbaceous species from tropical dry forests and savannas in the Neotropical region?

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ABSTRACT

Phenology studies the life cycle of living beings, relating them to emerging environmental changes. Although dry tropical forests and savanna formations in Neotropics harbor rich diversity and endemism of herbaceous plants, this component has received less attention in phenological studies. Therefore, understanding its dynamics is crucial for comprehending the functioning of these ecosystems and for promoting effective conservation strategies. In this study, we conducted a comprehensive scientific mapping of phenological studies on herbaceous species undertaken in the dry forests and savannas of the Neotropical region over 11 years (2009-2020). Our results highlight a concentration of studies in 2011 (24%) and within the Cerrado Biome (38%), primarily through direct observations in natural environments (96%) and in short-term studies (76%). Many studies did not detail the plant's life form (62%), with a predominance of community studies (80%) focusing on reproductive phenophases. Correlations between phenophases and abiotic factors were common (76%), while biotic factors were less explored (28%). We recommend comprehensive studies that consider the diversity of herbaceous species (both annual and perennial) in Neotropics, incorporating longer-term experiments to observe subsequent generations of annual species and the various growth stages of perennial herbs. The intricate interactions within herbaceous populations deserve attention and offer valuable insights into understanding Neotropical transformations. Prioritizing the relationship between herbaceous phenology and biotic and environmental factors is essential for understanding the dynamics of different vegetation formations and their future in the face of predicted climate change.

Keywords: Climate change, Caatinga, Cerrado, Chaco, phenophases.

Introduction

Phenology is an environmental science that focuses on monitoring, understanding, and predicting the life cycles of living organisms, correlating them with environmental changes (Aguiar et al., 2024; Morellato et al., 2024; Santos et al., 2025). Phenological studies are pivotal in researching, documenting, and managing biodiversity, thereby becoming an indispensable tool for natural systems conservation (Morellato et al., 2016, 2018).

Plant phenological responses are extremely sensitive to climate, and their phenological feedback impacts climatic patterns at regional and global scales, both in the short and long term (Richardson et al., 2013). Consequently, the analysis of plant phenology emerges as an essential tool to monitor potential variations in the ecology of plant species in the face of climatic fluctuations (Abernethy et al., 2018; Silva-Filha et al., 2025), allowing projections on future scenarios of tropical forest functioning (Knapp et al., 2018; Aguiar et al., 2024).

Despite the advances made, phenological studies in tropical dry forests (TDFs) remain underrepresented (Santos et al., 2025), and within these investigations, herbaceous species have received less attention (e.g., Morellato et al., 2018; Morellato et al., 2024), as well as in savanna formations of the Neotropical region. Comprehensive reviews conducted in the region so far have seldom provided a detailed description or specifically focused on the herbaceous stratum (Morellato et al., 2013; Mendoza et al., 2017; Aguiar et al., 2023). While many recent landscape-level studies have employed innovative technologies like satellite remote sensing, phenocams, and other digital tools to attain large-scale results of vegetative responses within the plant community (Abernethy et al., 2018; Alberton et al., 2019; Santos et al., 2025), it is noteworthy that such studies have concealed a range of specific responses from herbaceous populations, particularly those related to their reproductive cycles. Our study centers on this critical point, emphasizing the need for a more detailed and comprehensive analysis of these phenological studies concerning herbaceous species, while also setting goals for future research.

It is important to highlight that herbaceous species not only dominate a significant portion of the landscape in dry tropical forests and savannas of the Neotropical region but also exhibit a high degree of endemism (Santos et al., 2013; Banda-R et al., 2016; Florentín et al., 2022). They are present in the early stages of ecological succession, playing a crucial role in habitat recovery (Le Stradic et al., 2017; Aguiar et al., 2020) by preparing the soil for the establishment of secondary species. In this scenario, we emphasize that incorporating herbaceous species into phenological studies broadens the understanding of their dynamics and the impacts of climate change and human activities on the natural ecosystems of the Neotropical region. Based on these premises, we conducted a comprehensive scientific mapping of phenological studies on herbaceous species carried out in tropical dry forests and savannas of the Neotropical region over 11 years (2009–2020). The central objective of this review is to synthesize the current state of knowledge on these studies by examining which vegetation types or biomes were addressed, the average duration of the investigations, whether the life form of the species was reported, the level of analysis adopted (population or community), the phenophases considered, and the existence of correlations with biotic or abiotic factors.

Material and Methods

The Neotropical region encompasses a vast area including Central America, South America, and the Caribbean islands, with a variety of ecosystems ranging from humid tropical forests to deserts, including savannas, seasonal tropical forests, mangroves, and a wide diversity of vegetation (Myers et al., 2000; Ríos-Touma & Ramírez, 2019). The "seasonally dry" Neotropical Forest, also known as the "dry forest," is a widely distributed and fragmented biome that spans from Mexico to Argentina and throughout the Caribbean. It stands as one of the most globally threatened forests, with less than 10% of its original extent remaining in many countries (Banda-R et al., 2016).

Savannas constitute an extensive biome, distributed in two major belts located north and south of the Amazon Rainforest: the Llanos to the north (Colombia and Venezuela) and the Cerrado to the south (Brazil and Bolivia) (Nepomuceno et al., 2020; Jaramillo, 2023). In this biome, fire plays a crucial role in the global distribution of species and in defining its boundaries with forests (Gold et al., 2023). From an evolutionary perspective, tropical dry forests are significantly older than savannas in the Neotropics, with the latter considered relatively recent formations (Jaramillo, 2023).

Based on Whittaker's diagram (1975), which depicts the diversity of major terrestrial biomes in relation to monthly precipitation and temperature, this review focuses on the "dry" or "seasonally dry" tropical forests of the Neotropical region, as well as on savanna formations. These ecosystems are also characterized by pronounced climatic seasonality (distinct dry and wet seasons), low precipitation levels (≤ 1,800 mm; Banda-R et al., 2016, with some exceptions), and specific physiognomies or vegetation types.

Considering scientific mapping, we conducted an article search using the "Web of Science" citation database. The following Portuguese and English descriptors were used: "neotropic," "tropical forest," "dry tropical forest," "dry forest," "savanna," "seasonally dry forest," "semi-arid," "phenology," "herbaceous," "herb," "grass." All descriptors were used in the "topic" search fields, not specifying the location of the search in articles, which could be in the title, abstract, or throughout the body of the article. We used Boolean operators "or" and "and." "Google Scholar" was used to search for articles in Brazilian national journals that are generally not present in the "Web of Science".

We set an 11-year search period and filtered the studies from the following knowledge areas and subareas related to Botany, Ecology, and related fields. After a preliminary reading of the title, abstract, and methods, based on the following inclusion criteria, the selected studies were: a) studies published between 2009 and 2020; b) selection of studies conducted in dry tropical forests and savannas in the Neotropical region, considering the terminologies used in the studies and rainfall indices as inclusion criteria; c) presence of data and vegetative and/or reproductive phenological methodologies in these studies; d) native herbaceous plants as the subject of study.

Considering these studies, we analyzed the following points: i) which ecosystem or biome was studied; ii) the duration of the studies (short-term: up to one year; long-term: over one year); iii) if they described the life form (annual and/or perennial); iv) if the studies were at the population or community level; v) which phenophases were analyzed (vegetative and reproductive); vi) if correlations between phenophases and biotic or abiotic factors were made. Statistica software was used to perform descriptive statistical analyses and construct the graphs.

Results

Over the past 11 years, the highest number of publications focusing on phenological studies of the herbaceous component in the Neotropical (savanna and tropical dry forest biomes) region was in 2011, accounting for only 24% of the published studies (Figure 1a, Table 1). We observed a decrease in studies from 2012 to 2018, with a maximum decrease of 8% (Figure 1a). Other pioneering studies have provided a comprehensive historical description of phenological research in Central and South America (Morellato et al., 2013; Mendoza et al., 2017; Morellato et al., 2024; Santos et al., 2025) or, regionally, in northeastern Brazil (Aguiar et al., 2023); however, little description has been provided for herbaceous species. This scenario might be associated with limited resource allocation or less attention directed towards the herbaceous community.

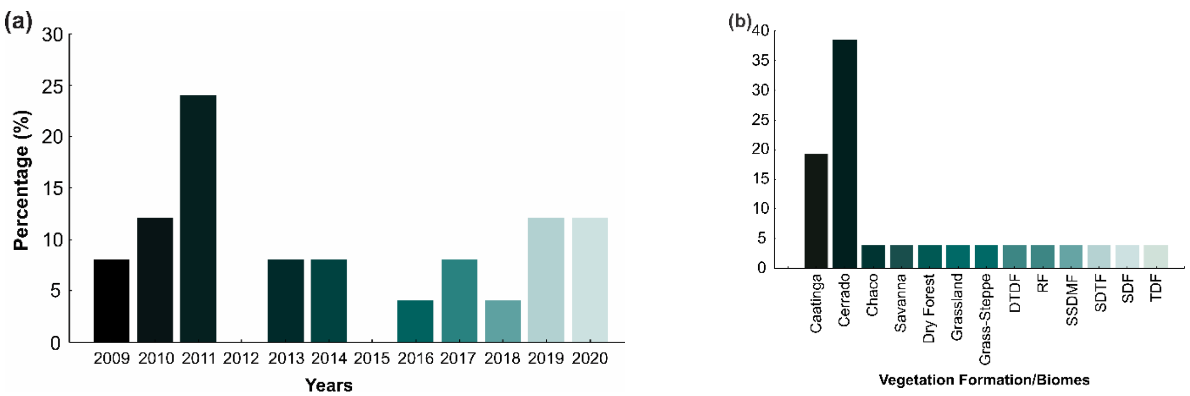

Figure 1. Scientific mapping of phenological studies conducted in the dry forests of the Neotropical region (2009-2020). Percentage of phenological studies according to (a) year of publication and (b) Vegetation Formation/biomes/forests where they were conducted. DTDF = Deciduous Tropical Dry Forest; RF = Riparian Forests; SSDMF = Seasonal Semi-Deciduous Montane Forest; SDTF = Seasonally Dry Tropical Forest; SDF = Semideciduous Dry Forest; TDF = Tropical Dry Forest. Font: Aguiar (2025).

The locations where the studies were conducted include environmental protection areas, national parks, private natural heritage reserves (PNHRs), ecological stations, mountain ranges, and forest fragments. Among the biomes or vegetation types where the research was carried out, the Cerrado stands out with approximately 38% of the studies (Faria & Araújo, 2010; Rocha et al., 2016), followed by the Caatinga with 19% (Quirino & Machado, 2014), and the Chaco, together with other vegetation types, representing only 8% (Torres & Galetto, 2011) (Figure 1b, Table 1). The higher number of studies in the Cerrado can be attributed to its vast extent, as it represents the largest savanna area in South America, encompassing much of central Brazil (Nepomuceno et al., 2020; Jaramillo, 2023).

Table 1. Summary of Phenological Studies of Herbaceous Species from Tropical Dry Forests and Savannas in the Neotropical Region (2009-2020): Central research questions, Life cycles, Vegetation classification, and Area precipitation. NI = Not Informed. Font: Aguiar (2025).

Author/Year	Central research question	Life cycles	Vegetation classification	Area precipitation
Florêncio et al. (2009)	How does the vegetative and reproductive phenology of herbaceous plants vary among intact, reforested, and burned Cerrado areas?	NI	Cerrado	NI
Dutra et al. (2009)	How are the reproductive phenology and floral and dispersal syndromes of Leguminosae related to climatic seasonality in the rocky fields of the Itacolomi State Park?	NI	Cerrado (Rocky Grassland)	Average monthly precipitation 125 mm
Faria & Araújo (2010)	What are the ornithophilous plant species of Serra da Bodoquena, what is their phenological dynamics, and how do interactions and visitation patterns by hummingbirds occur in different habitats of the region?	NI	Cerrado (Savanna)	Total annual rainfall is roughly 1500 mm
Lesica & Kittelson (2010)	How does the first flowering date of herbaceous plants in a semi-arid prairie of the Rocky Mountains vary over time, and how are these changes associated with temperature and precipitation, especially in comparison with temperate humid systems?	Perennial and Annual	Grassland (Prairie)	The average annual precipitation was 337 mm
Martini et al. (2010)	How does the reproductive and vegetative phenology of 10 species from the Campos ecosystem in Paraná occur, and how are meteorological variables (temperature, precipitation, relative humidity, and photoperiod) associated with their phenophases?	NI	Grass-Steppe (Campos)	Average annual precipitation of 1,571.28 mm
Ramírez & Briceño (2011)	How are the reproductive phenology patterns of herbaceous–shrubby communities in the Gran Sabana Plateau influenced by climate, plant life-forms, and soil properties?	Perennial and Annual	Great Savanna	Annual precipitation rates vary between 1815 mm and 3400 mm $year^{-1}$
Torres & Galetto (2011)	How do climatic factors, plant traits, plant–animal interactions, and phylogenetic relationships influence the flowering phenodynamics of co-occurring Asteraceae species in the Chaco Serrano forests of central Argentina?	Annual and Perennial	Chaco	Annual total rainfall over 10 years averaged 866 mm
Neves & Damasceno-Júnior (2011)	What are the phenological patterns of a campo sujo community in the Urucum plateau after a fire event, and how are these patterns related to rainfall seasonality and to the different dispersal syndromes of the species?	NI	Cerrado	Annual rainfall of about 1,120 mm

Silva et al. (2011)	What are the main determinants of phenological patterns in Cerrado and riparian forest communities, soil water availability, climatic variables, or phylogenetic relationships, and how do these factors influence reproductive peaks and the synchronization among species?	NI	Cerrado / Riparian Forests	The average annual rainfall is 1,339 mm
Rossato & Kolb (2011)	Which climatic variables determine the vegetative and reproductive phenological patterns of a *P. venusta* population in a cerradão in the state of São Paulo?	NI	Cerrado	Average annual precipitation of 1,400 mm
Araújo et al. (2011)	How are the reproductive phenology, floral biology, and pollination mechanisms of *Allamanda blanchetii* characterized in the Caatinga?	NI	Caatinga	Average annual precipitation around 500 mm to 800 mm
Ferreira & Consolaro (2013)	What are the phenological strategies, pollination syndromes, and dispersal syndromes of understory species in an urban forest fragment, and how are these patterns distributed throughout the year?	NI	Semideciduous Dry Forest	NI
Parente et al. (2013)	What is the effect of different stocking rates in a continuous goat grazing system on the structure of herbaceous species and soil cover in a Caatinga area in northeastern Brazil?	NI (short life cycle)	Caatinga	Average annual precipitation around 400 mm
Ramos (2014)	How do habitat filtering and interspecific competition influence the phenological diversity of a grass assemblage in the Neotropical savanna?	Perennial	Cerrado	Accumulated precipitation during the study period (January to March) was 1,152 mm
Leal & Moraes (2014)	What is the reproductive phenology and spatial distribution of Oeceoclades maculata in the Cerrado of Mogi Guaçu, São Paulo?	NI	Cerrado	Rainfall does not exceed 30 mm during the driest month (July)
Rocha et al. (2016)	How does the reproductive phenology of rupestrian grassland vegetation vary along the altitudinal gradient of Serra do Cipó?	NI	Cerrado / Rocky Grasslands	Precipitation ranges from 821 mm to 1,420 mm, depending on the Cerrado vegetation physiognomy
Cortés-Flores (2017)	How do flowering phenology, growth forms, and pollination syndromes vary among species in a dry tropical forest?	Annual and Perennial	Dry Forest	The total annual precipitation is 564 mm, with most rainfall concentrated between July and September
Quirinoa & Machado (2017)	What are the pollination syndromes and how does the seasonality of floral resources occur in a plant community of the Paraíba Caatinga?	NI	Caatinga	Rainfall is extremely irregular and usually totals less than 600 mm . year^{-1}
Le Stradic et al. (2018)	How does the reproductive phenology of two coexisting	Perennial	Cerrado / Rocky Grasslands	The average annual precipitation is 1,622 mm

	Neotropical montane grasslands vary between rocky and sandy soils			
Cortés-Flores (2019)	How do abiotic factors, plant functional traits, and phylogeny influence fruiting phenology in a tropical dry forest community?	NI	Seasonally Dry Tropical Forest	Mean annual precipitation is 564 mm with a marked seasonality (83% of the precipitation between June and September)
Lopes et al. (2019)	What are the reproductive phenological patterns of *D. burchellii*, an herbaceous climber, and how are they associated with abiotic variables?	NI	Seasonal Semi-Deciduous Montane Forest	Average annual rainfall is 1,221 mm
Alberton et al. (2019)	How do leaf phenology and the growing season vary among seasonally dry Neotropical ecosystems, and what are their main environmental drivers?	NI	Cerrado and Caatinga	Caatinga - average annual precipitation about 260 mm. Cerrado - mean annual precipitation ranges from 1,150 mm to 1,478 mm
Palomeque et al. (2020)	How do floristic diversity, biomass, and pasture productivity in secondary tropical dry forest vegetation respond to Voisin grazing management?	NI	Deciduous Tropical Dry Forest	The average annual precipitation is < 1000 mm, and rainfall mainly occurs in the summer
Aguiar et al. (2020)	What is the effect of reduced soil water availability on the growth and reproduction of a drought-tolerant herbaceous plant?	Perennial	Caatinga	Average annual rainfall of 662,3 mm
Cortés-Flores et al. (2020)	To what extent are seed germination patterns and seedling types in a Neotropical dry forest shaped by plant life-history traits and phylogeny?	NI	Tropical Dry Forest	Total annual precipitation of 564 mm

It is important to note that, in addition to the extent of the main biomes (Cerrado and Caatinga), several other vegetation types were also reported, although with very low representation (each accounting for a single study). These include different savanna extensions, such as grasslands and steppes, riparian forests, as well as various types of tropical dry forest vegetation, such as deciduous tropical dry forest (DTDF), semi-deciduous dry forest (SDF), seasonal semi-deciduous montane forest (SSDMF), and seasonally dry tropical forest (SDTF) (Figure 1b, Table 1). It is important to note that some studies were limited to more general descriptions of the biome, such as savanna (3%) and tropical dry forest (TDF) (3%) (Figure 1b). The precipitation range across Neotropical vegetation types is remarkably wide, varying from extremely dry environments such as the Caatinga (<300 mm annually) to humid savanna formations in the Gran Sabana (up to 3400 mm annually). This high climatic heterogeneity present in tropical dry forests and savannas (Table 1) makes direct comparisons between regions particularly challenging. This is because the herbaceous stratum can respond differently to local rainfall patterns, reflecting its adaptive strategies of tolerance or avoidance under the stressful conditions of drought (Aguiar et al., 2020, 2024).

Most studies (96%) conducted direct phenological observations in natural environments (Cortes-Flores et al., 2019), while only 4% were carried out in controlled environments, such as greenhouses (e.g., Aguiar et al., 2020). It is important to highlight the growing number of studies focused on monitoring the phenological responses of herbaceous plants, although research in controlled environments remains relatively limited (Stuble et al., 2021; Aguiar et al., 2024).

Most studies are short-term (76%), not exceeding one year of monitoring (Figure 2a), which may be related to the rapid life cycle of these herbaceous species (Aguiar et al., 2020; Souza et al., 2020). A significant portion of the studies did not specify the life form of herbaceous species (62%) (Figure 2b). Only 24% of the studies specified the use of perennial species as the subject of study, followed by 13% for annual species (Figure 2b). It is noteworthy that there were studies involving herbaceous components, both transient (annuals) and permanent (perennials), as well as tree species (Ramírez & Briceno, 2011; Quirino & Machado, 2014). The identification of life cycles in herbaceous plants (annual or perennial) is essential, as these differences are associated with traits that influence ecosystem functioning. A marked difference is observed in the proportion of annuals relative to perennials across biomes, with the prevalence of annual plants (70–80%) increasing in warmer and drier regions, as well as in environments subjected to greater climatic unpredictability, where they tend to replace or coexist with perennials (Poppenwimer et al., 2023). Community studies stood out, representing 80% of the studies (Figure 2c), and many of these involved the herbaceous-shrub-tree stratum.

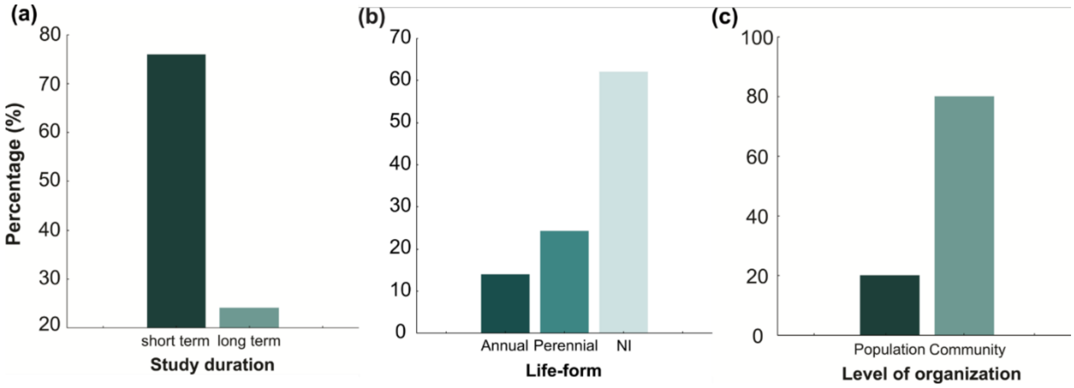

Figure 2. Scientific mapping of phenological studies in dry forests of the Neotropical region (2009-2020). Percentage of phenological studies according to (a) monitoring duration, (b) life-form of herbaceous species, and (c) sampled organizational level in the studies. NI = not informed. Font: Aguiar (2025).

The reproductive phenophases were the most investigated, with the flowering phenophase present in 96% of the conducted studies, followed by fruiting (68%) (Figure 3a) (Ramírez & Briceno, 2011). Vegetative phenophases were the least investigated, with budding, senescence, and leaf abscission combined accounting for less than 16% of these studies (Figure 3a) (Alberton et al., 2019). Most studies correlated vegetative and reproductive phenophases with abiotic factors (76%), while biotic factors (28%) were less frequently correlated (Figure 3b). The study of leafing and leaf-fall phenology of herbaceous plants provides insights into the key processes that drive photosynthetic gains, which can be allocated to reproductive activities and, at the end of the cycle, to nutrient resorption in many perennial plants (Mašková et al., 2022; Aguiar et al., 2020, 2024). These resorbed nutrients are then translocated to support the rapid growth of perennials at the onset of the following rainy season, when favorable environmental conditions are established. Our review highlights that such responses remain largely underrepresented in dry forests and savannas, although they are comparatively better characterized in temperate forests (Abernethy et al., 2018).

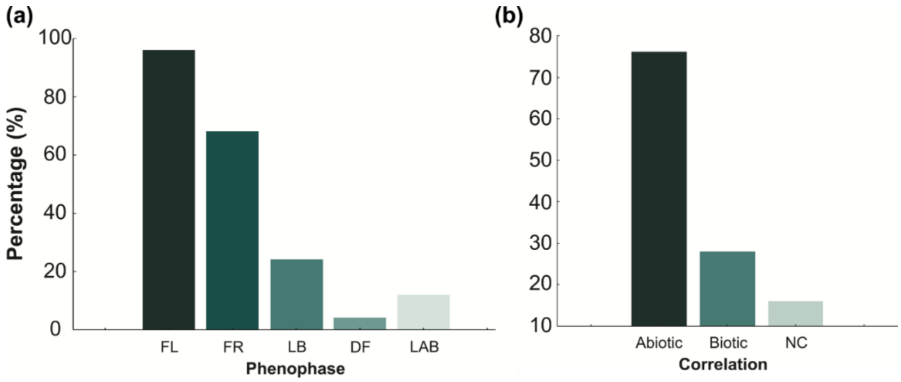

Figure 3. Scientific mapping of phenological studies in dry forests of the Neotropical region (2009-2020). Percentage of phenological studies according to (a) Investigated phenophases, (b) Correlations between phenophases and biotic and/or abiotic factors. NC = No correlation. FL = flowering; FR = Fruiting; LB = Leaf

budding; DF = Dispersion of fruits or seeds; LAB = Leaf abscission and senescence. Font: Aguiar, B.A.S. (2025).

Less attention to the correlations between phenophases and biotic factors represents a limitation in understanding the strategies that species adopt for their establishment and survival, such as: (i) in leaf dynamics, allowing them to escape both drought and damage caused by herbivory; (ii) in the synchronization between flowering and pollinators, as well as in fruiting and seed dispersal by dispersers, which promote the reproductive success of herbaceous plants (Morelato et al., 2016).

Conclusion

A limited number of studies have been observed, even though their distribution has been gradual over the years. These findings indicate that the investment in understanding the life cycle phases of the herbaceous component in Neotropical dry forests and savannas, along with its correlations to climate change, remains insufficient.

The Cerrado, a representative savanna biome, has been the focus of most of these studies, followed by the Caatinga. However, greater attention is needed for other savanna formations in the region, as well as for various types of tropical dry forest vegetation that have received less focus (approximately 3%). Our results emphasize the importance of standardizing terminology and classifying vegetation formations within their respective biomes in these studies. This enables accurate comparisons and promotes significant advancements in the phenological research of herbaceous plants in the Neotropics.

Since most of the analyzed studies are short-term, primarily due to the relatively short life cycle of the herbaceous species that predominate in these ecosystems, we recommend conducting more long-term studies, either in the field or under controlled conditions. Such studies could monitor successive generations of annual herbaceous species and different growth and reproductive stages of perennial plants, elucidating the mechanisms through which adaptive responses are stabilized by epigenetic mechanisms and transmitted as environmental memory across generations.

Community-level studies were more frequent and, although they included herbaceous species, they were not exclusively focused on these plants. In addition, we found that the life form of herbaceous plants was often not clearly specified in these studies. Consequently, comparisons may be inaccurate when different life cycles are not properly described, for instance, species that complete their cycle within a single season versus those capable of persisting through multiple consecutive dry seasons. This gap highlights the need for a more detailed investigation of intra-individual responses (at the population level) and among functional groups, to identify response patterns in herbaceous plants.

Another concern observed is that the study of vegetative phenophases, which are critical for reproductive timing, has received less attention. Additionally, correlations with biotic factors could be further emphasized in future studies, particularly for annual and perennial herbaceous plants.

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