ENVIRONMENTAL RESEARCH
LETTERS

TOPICAL REVIEW • OPEN ACCESS

Integrating approaches and methodologies into phenological research in Neotropical dry forests: a systematic review

To cite this article: Maria Maraíza Pereira Dos Santos *et al* 2025 *Environ. Res. Lett.* **20** 083002

IOP Publishing Environ. Res. Lett. 20 (2025) 083002 https://doi.org/10.1088/1748-9326/ade9e2

ENVIRONMENTAL RESEARCH
LETTERS

RECEIVED
31 March 2025

REVISED
25 June 2025

ACCEPTED FOR PUBLICATION
30 June 2025

PUBLISHED
17 July 2025

TOPICAL REVIEW

Integrating approaches and methodologies into phenological research in Neotropical dry forests: a systematic review

Maria Maraíza Pereira Dos Santos[1,2,*], Leonor Patrícia Cerdeira Morellato[1,*], Thieres George Freire da Silva[2], Alexandre Maniçoba da Rosa Ferraz Jardim[1], Carlos André Alves de Souza[2], Wilma Roberta Dos Santos[2] and Luciana Sandra Bastos de Souza[2,*]

[1] Center for Research on Biodiversity Dynamics and Climate Change and Department of Biodiversity, Phenology Lab, São Paulo State University (UNESP), Biosciences Institute, Rio Claro, São Paulo, Brazil
[2] Academic Unit of Serra Talhada, Federal Rural University of Pernambuco, Serra Talhada, Pernambuco, Brazil
[*] Authors to whom any correspondence should be addressed.

E-mail: maria.maraiza@unesp.br, patricia.morellato@unesp.br, sanddrabastos@hotmail.com, sanddrabastos@yahoo.com.br, thieres.silva@ufrpe.br, alexandremrfj@gmail.com, carlosandre08_@msn.com and wilma.roberta@ufrpe.br

Keywords: Caatinga, leaf phenology, phenocams, environmental triggers, climate change

Abstract

Phenological shifts are increasingly recognized as tangible indicators of plant responses to climate change. Tropical dry forests (TDFs), in particular, are key ecosystems for unraveling the mechanisms driving phenological dynamics, given their crucial role in biodiversity conservation and carbon balance. Although phenological research has advanced rapidly in recent decades in tandem with new methodological innovations, TDFs remain underrepresented. Consequently, the extent to which recent approaches have improved our understanding of leaf changes is still poorly understood. Here, we conducted a comprehensive literature review of phenology in seasonally dry tropical forests (SDTFs) in the Neotropics using Web of Science and Scopus databases up to December 2024. We aimed to synthesize methodological advances, environmental drivers, and functional traits related to phenology, providing insights about mechanisms underlying phenological shifts in Neotropical SDTFs. We documented a significant expansion in phenology research in Neotropical SDTFs over the last decade, with a concentration of studies in South America, particularly Brazil, followed by Central America. Despite these advances, long-term studies remain scarce, limiting our ability to detect interannual variability and long-term trends. The integration of high-resolution monitoring tools, such as phenocameras, has enhanced data collection across spatial and temporal scales, improving our ability to track phenological changes. Furthermore, plant functional traits such as wood density and leaf characteristics associated with deciduousness are key for understanding drought adaptation strategies in dry forests. Given the strong dependence of SDTFs phenological patterns on climate variability, predictive models that incorporate phenological observations, plant functional traits, and climate data will be further crucial for refining our understanding of adaptive mechanisms and improving forecasts of vegetation responses in dry forests. By highlighting research gaps and future directions, this synthesis provides a foundation to improve conservation efforts and climate resilience assessments in seasonally dry tropical ecosystems.

1. Introduction

Seasonal shifts in phenology are increasingly recognized as key indicators of species responses to emerging environmental changes, especially global warming (Rosenzweig *et al* 2008). Consequently, phenology research has experienced rapid growth in recent decades, providing essential information on how species and ecosystems may be impacted by the effects of climate change (Cleland *et al* 2007, Piao *et al* 2019a, Inouye 2022, Hassan *et al* 2024, Morellato *et al* 2024, Schwartz 2024). Noticeable alterations in phenology include variations in the synchrony of leaf patterns (Pau *et al* 2010), which can have far-reaching effects on carbon balance and ecosystem resilience (Walther *et al* 2002, Morellato *et al* 2016, Sakai and Kitajima 2019). At the individual level, phenological changes can impact fitness and population distribution patterns (Zettlemoyer and DeMarche 2022). However, these responses do not occur uniformly across the ecosystems (Inouye 2022) and are often based on short-term observations, covering up to three years (Morellato *et al* 2024). This bias may limit our interpretations of tropical regions (Schwartz 2003, Morellato *et al* 2016, Staggemeier *et al* 2020), where phenological patterns are driven by interactions between multiple environmental factors (e.g. rainfall, solar radiation, photoperiod), plant-animal interactions and species-specific functional strategies (Mendoza *et al* 2017, Piao *et al* 2019b, Staggemeier *et al* 2020, Fagundes *et al* 2022). Furthermore, identifying the factors influencing long-term phenological responses remains a significant challenge, particularly in tropical dry ecosystems, which are notably underrepresented in current phenological research (Abernethy *et al* 2018, Sheldon 2019, Morellato *et al* 2024).

Tropical dry forests (TDFs) account for approximately 42% of the tropical and subtropical forest area worldwide (Murphy and Lugo 1986) with the Neotropics hosting the second largest extent of dry lands (Ocón *et al* 2021). The TDFs occur in disjunct fragments, within a complex of vegetation types, influenced by local climate, soil, and topography conditions (Banda *et al* 2016). The Brazilian Caatinga represents the largest seasonally dry tropical forest (SDTFs) in the Neotropics, a vegetational type located in the semi-arid region, of Northeast Brazil, with about 912 529 km^2 (Banda *et al* 2016, Silva *et al* 2017) and biogeographically determined as part of the 'dry diagonal' of open vegetation (Neves *et al* 2015). Several terms have been used to refer to these locations, such as dry forest, deciduous dry forest, besides the local name Caatinga or caatingas, and the widely diffused SDTFs (Prado 2003, Silva *et al* 2017, Singh and Chaturvedi 2018). Collectively, these terms encompass ecosystems that are marked by pronounced seasonality of rainfall, leading to annual drought cycles and often exposing vegetation to water deficit conditions (Murphy and Lugo 1986). While broader definitions may include diverse formations such as forests within grassland, shrubland, and savanna ecosystems (Cerrado), and Chaco vegetation (Pennington *et al* 2000, Linares-Palomino *et al* 2011, Mendoza *et al* 2017), in this review, we adopted a restricted definition, referring to Neotropical TDFs as ecosystems where annual precipitation is less than 1600 mm, and a dry season lasting at least five to six months (Murphy and Lugo 1986, Sánchez-Azofeifa *et al* 2005). These conditions define the leaf exchange patterns of plants, and most of species are deciduous, losing all their leaves during the dry season and flushing synchronously with the onset of the rainy season (Kushwaha *et al* 2011). However, the existence of evergreen species and the occurrence of flushing and flowering during the dry season in some species reveal the complexity of phenological patterns in SDTFs (Borchert and Rivera 2001). Furthermore, this variability is not restricted to visually detected leaf changes but involves plant-specific ecophysiological mechanisms that are still poorly understood in SDTFs (Vico *et al* 2015). Consequently, attributing phenological shifts to climate change in dry tropics remains particularly challenging (Fitchett *et al* 2015, Abernethy *et al* 2018).

The strong dependence of the phenological patterns of dry communities on climate variability highlights the importance of accurate and continuous monitoring (Alberton *et al* 2019, Sheldon 2019), especially considering projections of increasing temperature and aridity for these environments (Gutiérrez *et al* 2014, Seneviratne *et al* 2021). These changes could make dry communities even more vulnerable to significant variations in their seasonal hydrological cycles, thus affecting key vegetation-mediated processes, including phenology (Vico *et al* 2015, Jardim *et al* 2023, Santos *et al* 2024). Therefore, in addition to documenting patterns such as interannual variations within communities, which are common focuses in phenological research, it is crucial to consider the mechanisms underlying vegetation phenological change, including the role of individual strategies, and their environmental drivers (Rafferty and Nabity 2017, Zettlemoyer and DeMarche 2022).

Although new tools and methodologies have made it possible to take a crucial step in this direction, providing data in different temporal and spatial scales (Abernethy *et al* 2018, Stan and Sanchez-Azofeifa 2019, Morellato *et al* 2024), the latest syntheses on TDFs do not integrate these specific advances in phenology research (Stan and Sanchez-Azofeifa 2019). Specifically how these approaches contribute to unraveling the mechanisms underlying leaf changes is still poorly understood (Jin *et al* 2024), and are particularly useful for identifying the drivers of long-term phenological change across multiple scales, as well as for significantly improving predictive modeling capabilities (Tang *et al* 2016). Therefore, this review aims to synthesize current research on the phenology of Neotropical SDTFs, addressing the main methodologies to assess patterns, environmental triggers and ecological traits related to phenological strategies in SDTFs.

2. Review methodology

2.1. Search strategy and selection of studies

To provide an encompassing perspective overview of leaf phenology research on TDFs, we conducted a literature search on the Web of Science and Scopus databases, using the following search terms: 'phenology*' OR "leaf phenology*' OR "leafing' AND 'Trop* dry forest' OR 'Neotrop* dry forest' OR 'SDTF' OR 'deciduous dry forest' OR 'Caatinga', in English, Portuguese and Spanish. We queried titles, abstracts, and keywords for all articles published up to December 2024. The search strategy and study selection process adhered to the standard requirements outlined in the PRISMA Statement (Preferred Reporting Items for Systematic Reviews and Meta-Analyses—Page *et al* (2021); figure 1). Duplicate publications were removed using Mendeley software. Articles identified through the search were assessed according to the following eligibility criteria: (i) the study addressed leaf phenology, (ii) was conducted in native vegetation types within Neotropical seasonally dry forests, and (iii) did not involve the monitoring of agricultural, crop, or introduced species. Studies that did not meet these inclusion criteria were excluded. Additionally, studies focused on reproductive phenology (flowering and fruiting) as well as those on plant-animal interactions (pollination, frugivory, seed dispersal) were excluded unless they also include information on leaf phenology.

2.2. Datasets

The studies selected to compose the analysis were classified based on their methodological approach and focus of studies. Methodologically, the studies were categorized as observational (direct and indirect monitoring), experimental (observed and manipulative), or ecological modeling involving the use of statistical, theoretical, or mechanistic models to assess pheno-climatic shifts (Zhao *et al* 2013). The studies were classified according to the main ecological questions addressed in research, considering the assessment of patterns, including where leaf phenology was used as proxy to productivity, climatic or non-climatic drivers of phenology, or impacts of climate change on phenology. To systematically assess how phenological research has been conducted in STDFs, we extracted information on spatial coverage (e.g. single-site vs. multi-site studies), monitoring methods (direct field observations, herbaria, near-surface remote sensing, e.g. phenocams, land surface phenology), as these influence the temporal resolution and scale of phenological measurements. Ultimately, we selected datasets of the largest seasonally dry Neotropical forest—the Caatinga—to discuss predominant patterns and phenological strategies of vegetation, and we identified key information about the main environmental triggers related to phenology and how ecological traits were incorporated into phenological assessments considering anatomical, morphological, ecophysiological, or biochemical traits (de Freitas *et al* 2024).

3. Results and discussion

3.1. Trends in phenological research in TDFs

We identified a total of 104 articles eligible for the synthesis of this review (figure 1, the dataset is publicly available on Zenodo at https://zenodo.org/records/15660935) (Santos *et al* 2025). Overall, 64% of studies focused on patterns ($n = 67$), and 27% assessed the climatic and others environmental drivers of leaf phenology ($n = 28$) (figure 2(A)). Yet, few papers (9%, $n = 9$ studies) addressed the effects of climate change and the responses of plants to weather extreme events (Butz *et al* 2018, Castro *et al* 2018, Parker *et al* 2018, Huang *et al* 2021). In addition, 94% of studies were based on direct and indirect observations and/or monitoring technics ($n = 98$), followed by plant experimental approach ($n = 4$) and a few studies using phenological modeling ($n = 2$) (figure 2(A)). Experimental studies typically investigated how water availability affects the phenology, productivity, and adaptive strategies of trees in TDFs (Díaz and Granadillo 2005, Gutiérrez-Soto *et al* 2008, Hayden *et al* 2010, Sánchez *et al* 2020). Modeling studies, on the other hand, have focused on assessing pheno-climatic shifts or parameterization of methods to monitor seasonal patterns of vegetation (Silva *et al* 2018, Silva Filho *et al* 2020). The observational studies are explored in the next section.

Our research covered the main phenological datasets in Neotropical SDTFs, expanding previous syntheses focused only on community studies on reproductive phenology (Mendoza *et al* 2017, Morellato *et al* 2024). Although the current review still showed a low density of studies (1 study per $\sim$ 80 000 km^2), considering the extensive distribution of TDFs in the Neotropical region, 70 studies (approximately 67% of all datasets) were carried out in the last 10 years, which suggests a growing effort to understand the patterns of dry tropical communities (figure 2(B)). These datasets remain unevenly distributed, concentrating mainly in the South (64%), and Central America (20%) (figure 2(C)). In South America, Brazil dominates the phenological research scenario, contributing 74 datasets, followed by Colombia (3), Argentina (2), Venezuela (2), Bolivia (2), and Ecuador (1). This dominance is no coincidence; Brazil's extensive dry vegetation cover, represented mainly by semi-desertic and xeric wood/shrublands (Caatinga), makes it a focal point for TDF research (Portillo-Quintero and Sánchez-Azofeifa 2010, Morellato *et al* 2024). In Central America, studies carried on dry forests in Costa Rica (e.g. Guanacaste) and Mexico (e.g. Chamela and Yucatán) also contribute significantly to the datasets (24 and

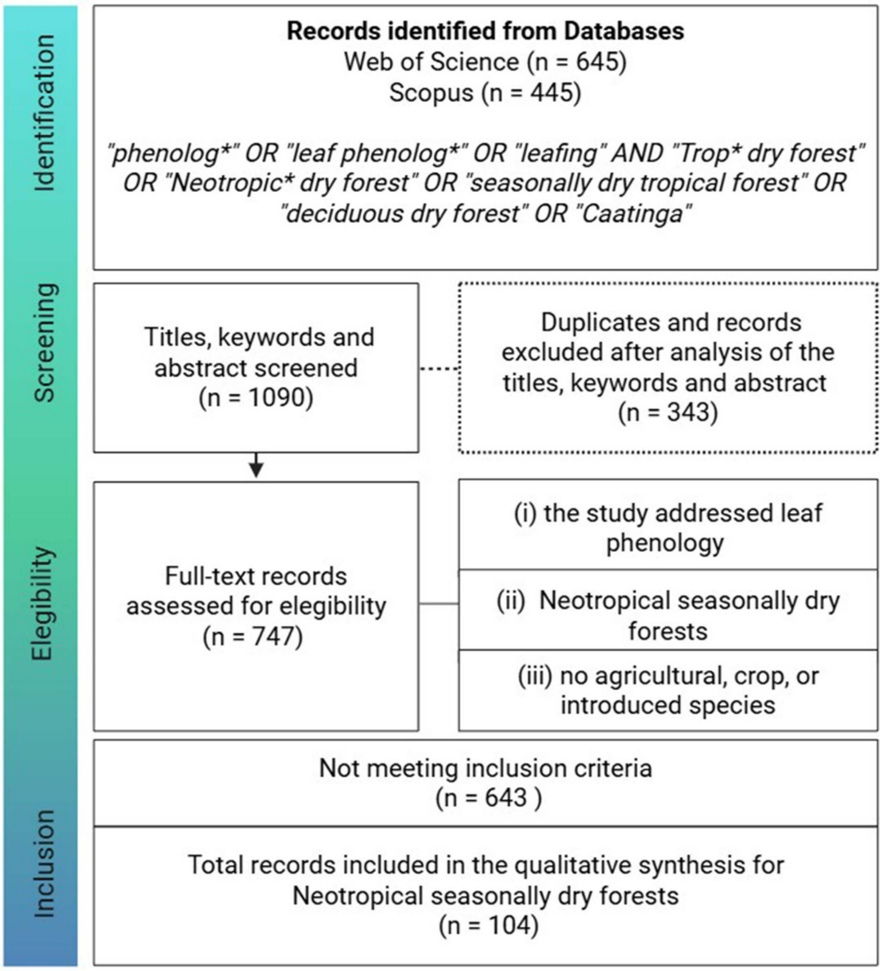

Figure 1. Flowchart of the search strategy and selection process for studies on phenology in Neotropical seasonally dry forests. The studies were retrieved from the Web of Science and Scopus database using specific keywords and filtered based on relevance and inclusion criteria.

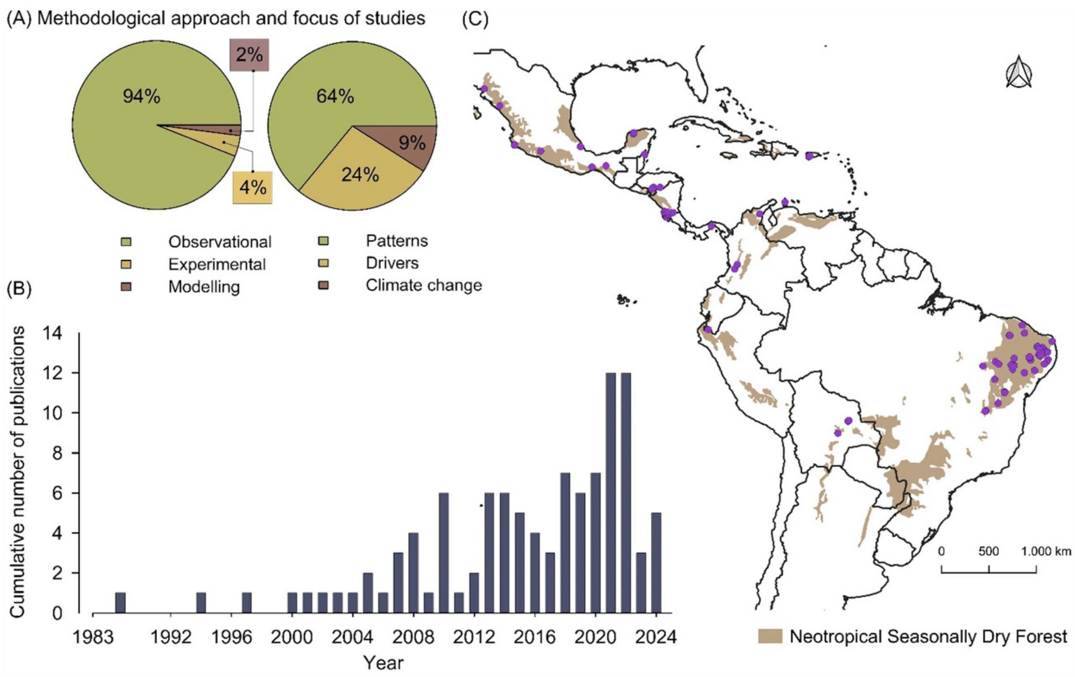

Figure 2. Spatial and temporal distribution of the number of publications and approaches applied to phenological research in Neotropical dry forests until December 2024. The purple dots on the map indicate the study site locations.

20, respectively). In terms of temporal coverage (i.e. number of years of study), it varies from one year to 26 years of monitoring, with ten long-term datasets and five studies (>10 years of observations) (Silva Filho *et al* 2020, de Jesus *et al* 2021, Medeiros *et al* 2022).

3.2. Measuring phenology in STDFs

The methodologies of the sample provide different levels of detail regarding phenological patterns according to their spatial scale. In this survey, we identified 79 studies based on individual-based observations, 6 studies using near-surface measurements, and 15 studies employing land surface phenology, which are often collected across regional and local scales. In addition, 4 studies used a multi-scale approach (i.e. combining two or more methods of observation). Below, we briefly discuss the main monitoring techniques used to characterize phenology in TDFs, providing examples of their applications and focus of studies.

3.2.1. Individual-based observations

3.2.1.1. Direct human observations

Studies involving the method of direct observations of phenology experienced a rise in the tropics around the 1990s and it is still a widely used method, providing high-resolution data on species and community patterns (Abernethy *et al* 2018, Morellato *et al* 2024). While direct observations of phenology are valuable to understanding the fine-scale spatial dynamics of individual plants and for climate change studies (Abernethy *et al* 2018, Morellato *et al* 2024), this method is also subject to some shortcomings. First, the method is often limited by low temporal frequency (Morellato *et al* 2013, 2024), ranging from weekly or fortnightly (e.g. Valdez-Hernández *et al* 2010, Parente *et al* 2012, Cardenas-Henao *et al* 2017) to monthly campaigns (most studies in TDFs). In addition, as the approach typically involves interpretation by the observer, who records the presence or absence of the phenophase of previously marked or unmarked individuals (Fournier 1974, D'Eça-Neves and Morellato 2004, Hudson and Keatley 2010, Mendoza *et al* 2017), it is subject to observer biases in detection and identification of species and phenophase (Primack *et al* 2023). Despite its limitations, the sampling method allowed addressing different research objectives in phenology studies in dry communities. The studies include descriptive approaches regarding the influence of climatic seasonality on leaf and reproductive patterns (Luna-Nieves *et al* 2022, Costa *et al* 2022), the role of leaf age on the timing of leaf shedding (Gutiérrez-Soto *et al* 2008), interannual variations in leafing behaviors (Villalobos *et al* 2013), and leaf plants strategies related to herbivory (Chaves and Avalos 2006, Sloan *et al* 2007, Silva *et al* 2020). More recent studies have also leveraged observational data to explore phenological responses to climate change (Aguiar *et al* 2024). Furthermore, the use of direct observations by local observers for monitoring the phenological patterns exemplifies the integration of citizen science into phenological research in TDFs (Neto *et al* 2013). Finally, several studies are concerned about traits associated to leaf phenology in dry forest, especially hydraulic and woody density and anatomy (Lima *et al* 2012, 2021, Worbes *et al* 2013, da Silva e Teodoro *et al* 2022, Neves *et al* 2022) which have proven to be important tools to understand mechanisms closely related to leaf phenology in TDFs.

3.2.1.2. Herbaria

Herbarium collections, long regarded as essential tools for species discovery and identification (Bebber *et al* 2010) also harbor ecological data on seasonal patterns of plants, yet remain largely untapped, including in tropical ecosystems, regardless the increasing number of published research using herbarium records (Willis *et al* 2017, Park *et al* 2023). The digitization of herbarium specimens has significantly enhanced our ability to assess the phenological responses of vegetation to climate change (Park *et al* 2023, Zhu and Song 2023) and to understand the phenological mechanisms driving individual species (Davis *et al* 2015). Nevertheless, the use of these data is still limited in tropical regions, where sampling encounter both temporal and spatial challenges (Daru *et al* 2018, Park *et al* 2023). Additionally, the high diversity of species in tropical areas presents challenges related to taxonomic uncertainty, which can impact data interpretation and comparability (Guedes *et al* 2025). Despite this, two studies from our dataset utilized herbarium specimens to classify phenological stages from different dry forest locations, establishing comparisons regarding species leafing (Orellana *et al* 2020) and flowering time patterns (Borchert and Rivera 2001). Using over 1673 biological collections originating from the Neotropics (South and Central America, Mexico, Colombia and Venezuela), Borchert and Rivera (2001) identified four important flowering patterns associated with leaf exchange strategies which reveal distinct plant adaptations to the specific seasonal conditions of dry tropical forests. Orellana *et al* (2020) concluded that field observations and herbarium collections were similar and complementary, providing clues about seasonality and the relationship between leaf changes in Caatinga forests. Recognizing these potentialities and overcoming limitations, future studies should leverage herbarium collections to complement and expand field phenological research in TDFs.

3.2.2. Land surface phenology

Phenological patterns extracted from satellites or remote sensing tools, known as land surface phenology are well established in TDFs, providing comprehensive spatial information (Adole *et al* 2016). This approach relies on global sensors with medium to high spatial resolution, such as the Moderate Resolution Imaging Spectroradiometer and Landsat (Rankine *et al* 2017, Mas and de Araújo 2021), to detect changes in vegetation. Tracking seasonal patterns in TDFs are based on spectral vegetation indices, such as Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI), providing dynamics of vegetation seasonal greening (de Jesus *et al* 2021). NDVI/Landsat time series were also associated with climatic variables (El Niño and La Niña) allowing them to describe the phenological patterns in dry seasonal communities (Silva *et al* 2018). Furthermore, Medeiros *et al* (2022) used long-term time series (20 years) to estimate phenological greenness parameters in Caatinga cultivation areas, relating them to environmental determinants. Ultimately, vegetation indices adequately described interannual variations in the forest's response to environmental factors, and gross primary production, providing information about ecosystem functions related to phenology (Costa *et al* 2022). Despite wide application, the method has a low temporal resolution as an important limitation, revealing significant discrepancies between the phenological transition dates obtained from near surface monitoring (see next section) when estimating the duration of the growing season (Rankine *et al* 2017, Sanchez-Azofeifa *et al* 2024). However, increasing efforts have been dedicated to integrating high temporal resolution time series obtained by digital cameras to improve the definition of landscape phenology transition dates detected by remote sensing, demonstrating a promising approach to monitoring of tropical dry vegetations (Ramos *et al* 2023). Ultimately, we have to mention the potential of the new high-resolution sensor that may help to better define deciduate and tree crown seasonality (Wang *et al* 2023, Song *et al* 2024).

3.2.3. Near-remote phenology (phenocameras)

Near-remote phenology using digital repeat photography or phenocameras provides fine-frequency (daily) data of the community level and several individuals and plant species (Brown *et al* 2016, Alberton *et al* 2017) effectively bridging the spatial and temporal gap between satellite and human direct observations (Browning *et al* 2017). The high-frequency data acquisition capability of phenocams allows for the detection of rapid phenological shifts as the precise timing of budbreak and the assessment of leaf age that may not be captured by other methodologies (Alberton *et al* 2017, Katal *et al* 2022). Long-term datasets are particularly important to establish the dynamics of the ecosystem and to understand vegetation responses and climate change (Piao *et al* 2019a). Despite the large temporal coverage of data, the spatial distribution of studies using near-surface phenology is highly uneven. The datasets are concentrated in specific regions, with studies using phenocams to monitoring and validation of phenology in the South America (Alberton *et al* 2017, 2019, 2023, Paloschi *et al* 2021, Ramos *et al* 2023) and North America (Guzmán *et al* 2019). This trend is probably due to the facilitation of research linked to the use of repeated digital photographs or phenocameras to monitor leaf phenology and the implementation of the *e-phenology* phenocamera network (www.ephenology.br), which currently spans more than ten sites across vegetation types in SDTFs, including the Caatinga (Morellato *et al* 2014, Alberton *et al* 2017). However, we emphasize that continuous phenological monitoring in other regions could further benefit our ability to understand how seasonal patterns vary across different SDTF ecosystems (Schwartz 2024).

Seasonal tropical communities time series often exhibit a 'rainy green' pattern, which is linked to rainfall events and makes the series noisy and more difficult to characterize temporally (Beurs and Henebry 2010). Nevertheless, the use of metrics derived from daily phenocamera images, such as the green chromatic coordinate (GCC), has allowed the quantification of seasonal variations in vegetation greenness, offering insights into growing seasons, productivity and water use strategies of tropical forests trees (Alberton *et al* 2019, 2023, Ramos *et al* 2023) and also validate a tool to detect the phenology (Rankine *et al* 2017, Guzmán *et al* 2019). Recent studies have used phenocam data to calibrate remote sensing time series from satellites in SDTFs in an aridity gradient (Ramos *et al* 2023). Moreover, phenocam-derived vegetation indices (e.g. GCC), have proven to be reliable proxies for quantifying gross primary productivity in the Caatinga community (Alberton *et al* 2023). Despite advances in the use of spectral indices to characterize tropical phenology, there is still great potential to deepen the understanding of the correspondence between phenological transition dates derived from these indices and direct field observations, although few studies have benefited from direct field validations (Alberton *et al* 2014, 2019). Furthermore, the processing and interpretation of large volumes of image data are computationally intensive and time-consuming. In this context, the use of deep learning techniques in the analysis of phenological data is still in its early stages (but see Almeida *et al* 2014, 2016, Almeida *et al* 2015). Especially compared to other applications such as automated species identification from images (Almeida *et al* 2014), these techniques represent a promising path to increase the efficiency and accuracy in the treatment of these large datasets (Katal *et al* 2022).

3.2.4. Phenological metrics

Seasonal phenological cycles in TDFs encompass several phenological stages, the timing details of

Table 1. Phenological variables most used in each observation method. The metrics include start (SOS), end (EOS), peak (POS) and length (LOS) of season.

Method	Phenological variable	Methodological references
Direct human observation	Individual phenophase (start, end, peak)	(Lopezaraiza-Mikel *et al* 2013, Machado *et al* 1997)
Land surface phenology (satellite)	Growing season (SOS, EOS, LOS)	(Medeiros *et al* 2022, Ramos *et al* 2023)
Near-surface phenocam	Growing season (SOS, POS, EOS, LOS)	(Alberton *et al* 2019, Paloschi *et al* 2021, Alberton *et al* 2023)

which vary depending on the scale and method of observation (table 1). Direct human observations often allow us to characterize individual phenological patterns as to onset, peak, and the end and variation during the duration of the phenophase. Satellite imaging traditionally assesses landscape patterns, focusing on the start (or green-up) and end (or green-down) of the season. Recent long-term series also allow for more accurate estimates of growing season length (LOS) (Zeng *et al* 2019, Medeiros *et al* 2022). Phenocameras allow the segmentation of plants or focal communities that correspond to regions of interest for the analysis of phenological patterns (Alberton *et al* 2017). Therefore, phenocamera derived time series often integrate all phenological metrics, including start, end, peak, and duration, which offers a more detailed understanding of phenological patterns and a fine definition of environmental drivers influencing and triggering the phenological transition dates. It is important to note that there is variability in the terms used to characterize same events within the same methods. For instance, leaf flushing is sometimes referred to as start of season (SOS) or budding in various studies employing direct observations and phenocameras (e.g. Costa *et al* 2021), whereas leaf expansion is associated with changes in overall greenness patterns SOS captured by satellites (Medeiros *et al* 2022). Similarly, leaf abscission, also known as end of the growing season (EOS) is often linked to leaf fall, demonstrating greater consistency in terminology across both methods (Paloschi *et al* 2021, Ramos *et al* 2023).

3.3. Mechanisms and environmental drivers of phenology in the Caatinga

In the Caatinga, the climate is marked by the high seasonality of rainfall events, ranging from 250 to 1200 mm annually, which results in a prolonged dry season lasting at least five to six months (Murphy and Lugo 1986, Alvalá *et al* 2019). The harsh conditions of climate restrict the leaf exchange patterns of Caatinga plants and most species are deciduous, losing all the leaves during the dry season (June–November) and flushing rapidly on the onset rainy season (December–May) (Machado *et al* 1997). Despite this, the heterogeneity of patterns in coexisting functional groups (e.g. deciduous, semi-deciduous, and evergreen), suggest an interdependence of environmental cues, mechanisms and functional strategies of the species, though this is understudied (Fagundes *et al* 2022). Therefore, in this section, we concentrate in the key environmental drivers that regulate phenology in the Caatinga, and discuss briefly how ecological traits help understand the underlying mechanisms of phenological responses to the dry conditions typical of SDTF.

3.3.1. Environmental triggers of phenology

Although this review focused on leafing patterns, several studies have also extensively investigated environmental drivers of reproductive phenology in SDTFs (Silveira *et al* 2013, Lima and Bruno 2018, Costa *et al* 2022). Figure 3 illustrates the interactions between climatic and non-climatic factors and both vegetative (leaf flushing and leaf fall) and reproductive (flowering and fruiting) phenological patterns, highlighting significant correlations found in studies in Caatinga. As expected, water availability is the primary driver of leaf exchange in many species (Alberton *et al* 2019, 2023), closely linked to precipitation and soil moisture dynamics (figure 3). While precipitation largely controls phenology, some species exhibit asynchronous patterns related to the timing of rainfall events during the dry-to-wet season transition. For example, Amorim *et al* (2009) and, more recently, Oliveira *et al* (2020) demonstrated that some plants produce new leaves as a rapid metabolic response to sporadic rainfall during the dry season, while others remain dormant, showing their flushing with the onset of rainy season. In addition, Lima *et al* (2012, 2021), studies suggest that the interplay between rainfall seasonality and internal water storage mechanisms explain these responses of Caatinga vegetation. The authors observed that deciduous species with high wood density respond rapidly to rainfall, producing leaves, flowers and fruits during wet season. In contrast, softwood species initiate leafing and flowering at the end of the dry season, triggered initially by increasing photoperiod, but synchronize their peak activity (and fruiting) with the rainy season (Lima *et al* 2021, 2012, figure 3).

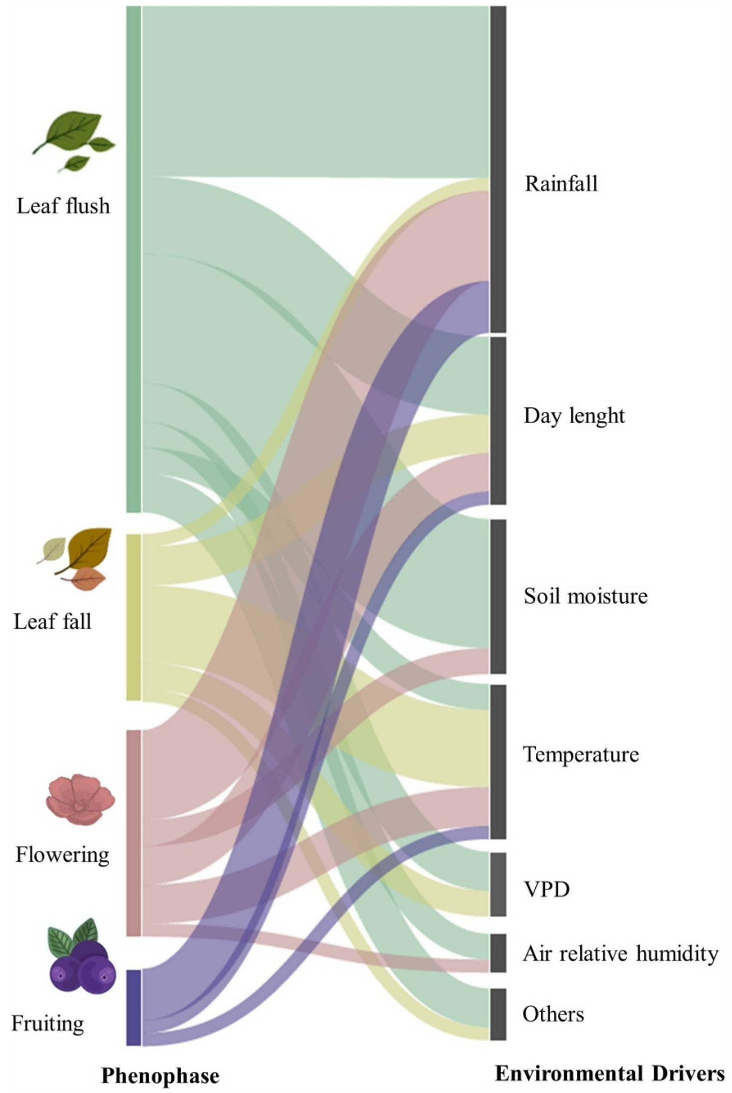

Figure 3. Diagram showing interrelationships of climatic and non-climatic drivers to phenological patterns positively related to Caatinga seasonally dry forest. The length of the nodes implies the number of times the phenology variable (left) was evaluated in the studies and the amplitude of the lines shows the magnitude of the relationships of potential drivers of phenological events (right). VPD is the vapor pressure deficit.

Besides the rainfall influence, air temperature and vapor pressure deficit (VPD) further modulate phenophase transitions, influencing plant water status and evapotranspiration rates. For instance, increased temperatures and high VPD during the dry season can accelerate leaf shedding as a drought-avoidance strategy, while moderate temperatures in the rainy season facilitate leaf expansion (figure 3). da Silva e Teodoro *et al* (2022) found that deciduous and semi-deciduous species are strongly dependent on precipitation and temperature, whereas evergreen species exhibit a greater dependence on VPD as a trigger for leafing patterns. Furthermore, at the community level, the amount of rainfall during the dry season plays a critical role in determining flowering dynamics (Neves *et al* 2017). These findings highlight the contrasting climatic controls on phenology in the Caatinga, reinforcing the role of climatic variability in shaping phenological patterns in these ecosystems.

3.3.2. Ecological traits related to phenological strategies

Plant functional traits provide critical insights into the mechanisms driving species' responses to environmental variability (Fagundes *et al* 2022). In the Caatinga, where seasonality is pronounced, traits related to water use efficiency, carbon assimilation, and hydraulic conductivity play a key role in determining phenological strategies. The figure 4 illustrates the ecological traits (leaf and wood) reported in phenological studies and the relationship between the Caatinga community's main functional groups and phenological strategies. To discuss the importance of these functional traits in shaping plant phenological strategies, we identify three main functional groups based on their deciduousness strategy and

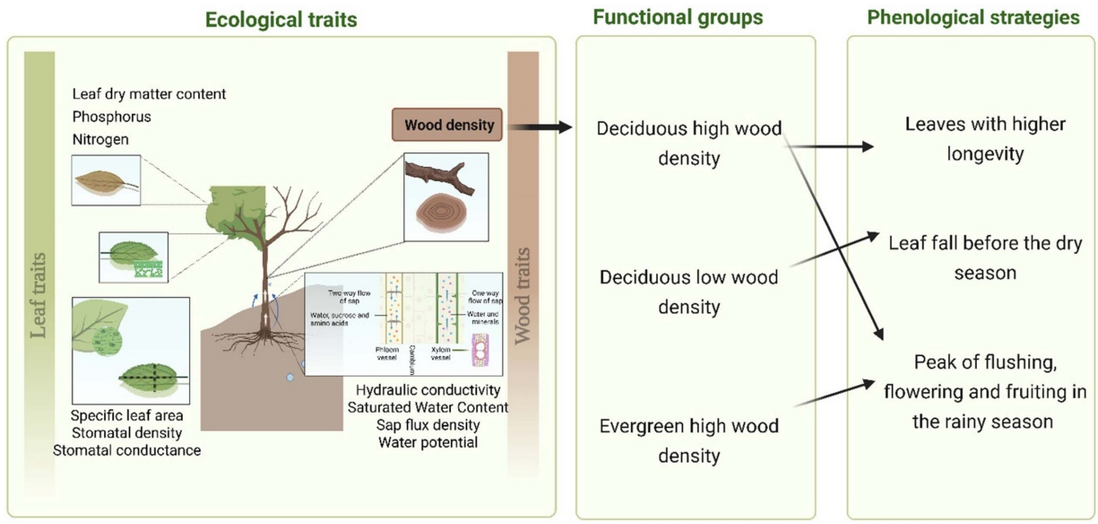

Figure 4. Ecological traits (leaf and wood) recorded in phenological studies within the Caatinga, and the relation between main functional groups based on deciduousness, wood density, and their phenological strategies.

wood density: (i) deciduous species with low wood density (DLWD), (ii) deciduous species with high wood density (DHWD), and (iii) evergreen species with high wood density (EVHWD). These groups represent distinct adaptive strategies in response to seasonal water availability, balancing water storage capacity, leaf longevity, and physiological performance under drought conditions (Medeiros *et al* 2024, Brito *et al* 2022, Lima *et al* 2021, figure 4).

Deciduous behavior in seasonal dry ecosystems is primarily driven by water limitation; however, it also results from the combined action of morpho-physiological, anatomical, and hydraulic traits that shape plant water-use strategies (Borchert 1994, Lima and Rodal 2010, Brito *et al* 2022, da Silva e Teodoro *et al* 2022). Among these, wood density plays a key role in determining phenological patterns, as it influences stem water storage capacity and drought response strategies (Borchert 1994, Luna-Nieves *et al* 2022, figure 4). Low wood density deciduous (DLWD) species typically shed their leaves before the dry season due to limited water storage, adopting a drought-avoidance strategy that prioritizes rapid resource acquisition during the wet season. In contrast, high wood density deciduous (DHWD) species maintain leaves longer and synchronize leaf production with rainfall, employing a more conservative water-use strategy (Lima and Rodal 2010, Lima *et al* 2012, 2021, Oliveira *et al* 2015). Souza *et al* (2020) further demonstrated that DHWD species experience greater seasonal declines in xylem water potential, reinforcing their reliance on stored water and structural adaptations to withstand prolonged drought.

Beyond wood traits, leaf characteristics also play a critical role in phenological strategies (figure 4). Deciduous species tend to have higher specific leaf area and lower leaf dry matter content, facilitating efficient carbon assimilation in favorable conditions. In contrast, evergreen species exhibit lower specific leaf area and higher leaf dry matter content, enhancing drought resistance through resource conservation (da Silva e Teodoro *et al* 2022). Brito *et al* (2022) further highlighted that DLWD species exhibit higher stomatal conductance and greater vulnerability to hydraulic failure, whereas DHWD species possess reinforced vascular structures that improve hydraulic safety. The complexity of plant functional attributes underscores the significance of wood and leaf traits in elucidating phenological strategies, thereby enriching our understanding of drought adaptation mechanisms in arid ecosystems.

4. Conclusions

Our systematic review provides a comprehensive overview of the phenology research of Neotropical seasonally dry forests, highlighting significant progress in understanding patterns, key environmental triggers, and functional strategies related to phenology. Despite an increase in research efforts, especially in South America, our synthesis reveals critical geographic and temporal biases that limit broader generalizations about the phenological responses across SDTF ecosystems. Long-term phenological datasets remain scarce, although are essential to investigate intra- and interannual changes, as well as the impacts of climate change and extreme weather events on the phenological responses of TDFs. Nevertheless, the integration of new monitoring tools, such as phenocameras, has significantly expanded the capacity for high-resolution and large-scale data acquisition, providing a valuable foundation for future research. In addition, as the connections between phenology and the environmental drivers are being clarified, it is possible to advance the development of predictive models to forecast future changes in dry ecosystems. Multidisciplinary approaches that combine phenological observations, plant functional traits, and climate data will be further crucial for refining our understanding of adaptive mechanisms and improving forecasts of vegetation responses in dry forests.

Data availability statement

The dataset supporting this study is publicly available on Zenodo (https://doi.org/10.5281/zenodo.15660934) (Santos et al 2025).

Acknowledgments

The present study was benefited by grants from the Coordination for the Improvement of Higher Education Personnel-CAPES (Finance code 001); the São Paulo Research Foundation-FAPESP (#2021/10639-5, #2022/02323-0, #2022/07735-5); Pernambuco Science and Technology Foundation (FACEPE) (Process: APQ-1159-1.07/14). MMPS received fellowships from FACEPE (IBPG Scholarship-0140-5.01/20); CAPES (88887.817587/2023-00) and FAPESP (#2024/06113-6). AMRFJ receives Fellowship from FAPESP (#2023/05323-4), LPCM and TGFS receive a research productivity fellowship from CNPq (grants #306562/2022-3 and #305980/2025-4).

Author contributions

Maria Maraíza Pereira Dos Santos
0000-0001-8139-0888
Conceptualization (equal), Data curation (equal), Formal analysis (equal), Investigation (equal), Methodology (equal), Writing – original draft (equal), Writing – review & editing (equal)

Leonor Patrícia Cerdeira Morellato
0000-0001-5265-8988
Conceptualization (equal), Funding acquisition (equal), Investigation (equal), Methodology (equal), Supervision (equal), Writing – original draft (equal), Writing – review & editing (equal)

Thieres George Freire da Silva
0000-0002-8355-4935
Conceptualization (equal), Funding acquisition (equal), Investigation (equal), Methodology (equal), Supervision (equal), Writing – original draft (equal), Writing – review & editing (equal)

Alexandre Maniçoba da Rosa Ferraz Jardim
0000-0001-7094-3635
Writing – original draft (equal), Writing – review & editing (equal)

Carlos André Alves de Souza
0000-0003-1946-0421
Writing – original draft (equal), Writing – review & editing (equal)

Wilma Roberta Dos Santos
Writing – original draft (equal), Writing – review & editing (equal)

Luciana Sandra Bastos de Souza
0000-0001-8870-0295
Conceptualization (equal), Funding acquisition (equal), Investigation (equal), Methodology (equal), Supervision (equal), Writing – original draft (equal), Writing – review & editing (equal)

References

Abernethy K, Bush E R, Forget P M, Mendoza I and Morellato L P C 2018 Current issues in tropical phenology: a synthesis *Biotropica* **50** 477–82

Adole T, Dash J and Atkinson P M 2016 A systematic review of vegetation phenology in Africa *Ecol. Inform.* **34** 117–28

Aguiar B A, Lopes C G, de Sousa G M, e Medeiros M J, da Silva K A and Araújo E de 2024 Effect of simulated extreme rainfall on the vegetative phenology of perennial and annual herbaceous plants from a Brazilian dry forest *Plant Biol. J.* **26** 868–77

Alberton B, Almeida J, Helm R, Torres R D S, Menzel A and Morellato L P C 2014 Using phenological cameras to track the green up in a cerrado savanna and its on-the-ground validation *Ecol. Inform.* **19** 62–70

Alberton B, Martin T C M, Da Rocha H R, Richardson A D, Moura M S B, Torres R S and Morellato L P C 2023 Relationship between tropical leaf phenology and ecosystem productivity using phenocameras *Front. Environ. Sci.* **11** 1223219

Alberton B, Torres R D S, Cancian L F, Borges B D, Almeida J, Mariano G C, Dos Santos J and Morellato L P C 2017 Introducing digital cameras to monitor plant phenology in the tropics: applications for conservation *Perspect. Ecol. Conserv.* **15** 82–90

Alberton B, Torres S, Sanna T, Silva F, Rocha H R, Moura M S B, Patricia L and Morellato C 2019 Leafing patterns and drivers across seasonally dry tropical communities *Remote Sens.* **11** 1–21

Almeida J, Dos Santos J A, Alberton B, Morellato L P C and Torres R D S 2016 Phenological visual rhythms: compact representations for fine-grained plant species identification *Pattern Recognit. Lett.* **81** 90–100

Almeida J, Dos Santos J A, Alberton B, Torres R D S and Morellato L P C 2014 Applying machine learning based on multiscale classifiers to detect remote phenology patterns in Cerrado savanna trees *Ecol. Inform.* **23** 49–61

Almeida T I R, Penatti N C, Ferreira L G, Arantes A E and Do Amaral C H 2015 Principal component analysis applied to a time series of MODIS images: the spatio-temporal variability of the Pantanal wetland, Brazil *Wetland Ecol. Manage.* **23** 737–48

Alvalá R C D S, Cunha A P M A, Brito S S B, Seluchi M E, Marengo J A, Moraes O L L and Carvalho M A 2019 Drought monitoring in the Brazilian semiarid region *An. Acad. Bras. Cienc.* **91** 1–15

Amorim I L D, Sampaio E V D S B and Araújo E D L 2009 Phenology of wood species in the Caatinga of Seridó, RN, Brazil *Rev. Árvore* **33** 491–9

Banda K R *et al* 2016 Plant diversity patterns in neotropical dry forests and their conservation implications *Science* **353** 1383–87
Bebber D P *et al* 2010 Herbaria are a major frontier for species discovery *Proc. Natl Acad. Sci. USA* **107** 22169–71
Beurs K M and Henebry G M 2010 Spatio-temporal statistical methods for modelling land surface phenology *Phenological Research: Methods for Environmental and Climate Change Analysis* ed I Hudson and M Keatley (Springer) pp 177–205
Borchert R 1994 Soil and stem water storage determine phenology and distribution of tropical dry forest trees *Ecology* **75** 1437–49
Borchert R and Rivera G 2001 Photoperiodic control of seasonal development and dormancy in tropical stem-succulent trees *Tree Physiol.* **21** 213–21
Brito N D S *et al* 2022 Drought response strategies for deciduous species in the semiarid Caatinga derived from the interdependence of anatomical, phenological and bio-hydraulic attributes *Flora* **288** 152009
Brown T B *et al* 2016 Using phenocams to monitor our changing earth: toward a global phenocam network *Front. Ecol. Environ.* **14** 84–93
Browning D, Karl J, Morin D, Richardson A and Tweedie C 2017 Phenocams bridge the gap between field and satellite observations in an arid grassland ecosystem *Remote Sens.* **9** 1071
Butz P, Hölscher D, Cueva E and Graefe S 2018 Tree water use patterns as influenced by phenology in a dry forest of southern ecuador *Front. Plant Sci.* **9** 945
Cardenas-Henao M, Londoño-Lemos V, Llano-Almario M, González-Colorado Á M, Rivera-Hernández K L, Vargas-Figueroa J A, Duque-Palacio O L, Torres-González A M, Jiménez-Taquinas Á C and Moreno-Cavazos M P 2017 Fenología de cuatro especies arbóreas de bosque seco tropical en el Jardín Botánico Universitario, Universidad del Valle (Cali), Colombia *Actual. Biol.* **37** 121–30
Castro S M, Sanchez-Azofeifa G A and Sato H 2018 Effect of drought on productivity in a Costa Rican tropical dry forest *Environ. Res. Lett.* **13** 045001
Chaves Ó M and Avalos G 2006 Is the inverse leafing phenology of the dry forest understory shrub Jacquinia nervosa (Theophrastaceae) a strategy to escape herbivory? *Rev. Biol. Trop.* **54** 951–63
Cleland E E, Chuine I, Menzel A, Mooney H A and Schwartz M D 2007 Shifting plant phenology in response to global change *Trends Ecol. Evol.* **22** 357–65
Costa G B *et al* 2022 Seasonal ecosystem productivity in a seasonally dry tropical forest (Caatinga) using flux tower measurements and remote sensing data *Remote Sens.* **14** 3955
Costa T M, Santos M G M, Neves S P S, Miranda L đAfonsêca P and Funch L S 2021 Phenological dynamics of Croton heliotropiifolius populations in a savanna/caatinga gradient, Chapada Diamantina, Brazil *Rodriguésia* **72**
Costa T L N, Lucas F M F, da Silva B R F, das Chagas K P T, Freire A D S M, Ucella-Filho J G M, da Silva Santana J A and Costa M D P 2022 How do meteorological factors alter the phenology of a neotropical tree species? *CERNE* **28** e103098
Daru B H *et al* 2018 Widespread sampling biases in herbaria revealed from large-scale digitization *New Phytol.* **217** 939–55
Davis C C, Willis C G, Connolly B, Kelly C and Ellison A M 2015 Herbarium records are reliable sources of phenological change driven by climate and provide novel insights into species' phenological cueing mechanisms *Am. J. Bot.* **102** 1599–609
da Silva e Teodoro É D M *et al* 2022 Functional traits determine the vegetative phenology of woody species in riparian forest in semi-arid Brazil *Plant Ecol.* **223** 1137–53
D'Eça-Neves F F and Morellato L P C 2004 Métodos de amostragem e avaliação utilizados em estudos fenológicos de florestas tropicais *Acta Bot. Bras.* **18** 99–108
de Freitas G V, Da Cunha M and Vitória A P 2024 A systematic review of leaf and wood traits in the neotropics: environmental gradients and functionality *Trees* **38** 551–72
de Jesus J B, Kuplich T M, de Carvalho Barreto Í D, da Rosa C N and Hillebrand F L 2021 Temporal and phenological profiles of open and dense Caatinga using remote sensing: response to precipitation and its irregularities *J. For. Res.* **32** 1067–76
Díaz M and Granadillo E 2005 The significance of episodic rains for reproductive phenology and productivity of trees in semiarid regions of northwestern Venezuela *Trees* **19** 336–48
Fagundes M V, Souza A F, Oliveira R S and Ganade G 2022 Functional traits above and below ground allow species with distinct ecological strategies to coexist in the largest seasonally dry tropical forest in the Americas *Front. For. Glob. Change* **5** 207
Fitchett J M, Grab S W and Thompson D I 2015 Plant phenology and climate change *Prog. Phys. Geogr. Earth Environ.* **39** 460–82
Fournier L A 1974 Un método cuantitativo para la medición de características fenológicas en árboles *Turrialba* **24** 422–3
Guedes J J M, Moura M R, Jardim L, Alexandre J and Diniz-Filho F 2025 Global patterns of taxonomic uncertainty and its impacts on biodiversity research *Syst. Biol.* syaf010
Gutiérrez A P A, Engle N L, De Nys E, Molejón C and Martins E S 2014 Drought preparedness in Brazil *Weather Clim. Extremes* **3** 95–106
Gutiérrez-Soto M V, Pacheco A and Holbrook N M 2008 Leaf age and the timing of leaf abscission in two tropical dry forest trees *Trees* **22** 393–401
Guzmán Q J A, Sanchez-Azofeifa G A and Espírito-Santo M M 2019 MODIS and PROBA-V NDVI products differ when compared with observations from phenological towers at four tropical dry forests in the Americas *Remote Sens.* **11** 2316
Hassan T, Gulzar R, Hamid M, Ahmad R, Waza S A and Khuroo A A 2024 Plant phenology shifts under climate warming: a systematic review of recent scientific literature *Environ. Monit. Assess.* **196** 36
Hayden B, Greene D F and Quesada M 2010 A field experiment to determine the effect of dry-season precipitation on annual ring formation and leaf phenology in a seasonally dry tropical forest *J. Trop. Ecol.* **26** 237–42
Huang C Y, Durán S M, Hu K T, Li H J, Swenson N G and Enquist B J 2021 Remotely sensed assessment of increasing chronic and episodic drought effects on a Costa Rican tropical dry forest *Ecosphere* **12** e03824
Hudson I L and Keatley M R 2010 *Phenological Research: Methods for Environmental and Climate Change Analysis* (Springer) pp 15–521
Inouye D W 2022 Climate change and phenology *Wiley Interdiscip. Rev. Clim. Change* **13** e764
Jardim A M D R F, *et al* 2023 A systematic review of energy and mass fluxes, and biogeochemical processes in seasonally dry tropical forests and cactus ecosystems *J. South Am. Earth Sci.* **126** 104330
Jin C, Zha T, Bourque C P A, Jia X, Tian Y, Liu P, Li X, Xu M, Guo Z and Hu Z 2024 Ecosystem-scale carbon dynamics in desert Shrublands: unraveling the complex interplay among leaf functional and physiological traits and environment *Agric. For. Meteorol.* **355** 110133
Katal N, Rzanny M, Mäder P and Wäldchen J 2022 Deep learning in plant phenological research: a systematic literature review *Front. Plant Sci.* **13** 649
Kushwaha C P, Tripathi S K, Tripathi B D and Singh K P 2011 Patterns of tree phenological diversity in dry tropics *Acta Ecol. Sin.* **31** 179–85
Lima A L and Rodal M J N 2010 Phenology and wood density of plants growing in the semi-arid region of northeastern Brazil *J. Arid Environ.* **74** 1363–73
Lima C R and Bruno R L A 2018 Phenology of Poincianella pyramidalis (TUL.) L. P QUEIROZ and its relationship with

the temporal distribuition of rainfall in the brazilian semiarid region *Cienc. Florest* **28** 1035–48
Lima A L A *et al* 2021 Phenology of high- and low-density wood deciduous species responds differently to water supply in tropical semiarid regions *J. Arid Environ.* **193** 104594
Lima A L A, de Sá Barretto Sampaio E V, de Castro C C, Rodal M J N, Antonino A C D and de Melo A L 2012 Do the phenology and functional stem attributes of woody species allow for the identification of functional groups in the semiarid region of Brazil? *Trees* **26** 1605–16
Linares-Palomino R, Oliveira-Filho A T and Pennington R T 2011 Neotropical seasonally dry forests: diversity, endemism, and biogeography of woody plants *Seasonally Dry Tropical Forests: Ecology and Conservation* ed R Dirzo, H S Young, HA Mooney and G Ceballos (Island Press) pp 3–21
Lopezaraiza-Mikel M, Quesada M, Yolotl Alvarez-Añorve M, Daniel L and Cabadilla A 2013 Phenological patterns of tropical dry forest along latitudinal and successional gradients in the Neotropics *Tropical Dry Forests in the Americas: Ecology, Conservation, and Management* 1st edn, ed A Sanchez-Azofeifa, J S Powers, G W Fernandes and M Quesada (CRC Press, Taylor & Francis Group) pp 101–28
Luna-Nieves A L, González E J, Cortés-Flores J, Ibarra-Manríquez G, Maldonado-Romo A and Meave J A 2022 Interplay of environmental cues and wood density in the vegetative and reproductive phenology of seasonally dry tropical forest trees *Biotropica* **54** 500–14
Machado I C S, Barros L M and Sampaio E V S B 1997 Phenology of caatinga species at Serra Talhada, PE, Northeastern Brazil *Biotropica* **29** 57–68
Mas J F and de Araújo F S 2021 Assessing landsat images availability and its effects on phenological metrics *Forests* **12** 574
Medeiros M, Wright C L, de Lima A L A, da Silva Brito N D, Souza R, Silva J R I and Souza E 2024 Divergent hydraulic strategies of two deciduous tree species to deal with drought in the Brazilian semi-arid region *Trees* **38** 1–14
Medeiros R, Andrade J, Ramos D, Moura M, Pérez-Marin A M, Dos Santos C A C, da Silva B B and Cunha J 2022 Remote sensing phenology of the Brazilian Caatinga and its environmental drivers *Remote Sens.* **14** 2637
Mendoza I, Peres C A and Morellato L P C 2017 Continental-scale patterns and climatic drivers of fruiting phenology: a quantitative neotropical review *Glob. Planet. Change* **148** 227–41
Morellato L P C *et al* 2016 Linking plant phenology to conservation biology *Biol. Conserv.* **195** 60–72
Morellato L P C, Altomare M and Gressler E 2024 A review of reproductive plant phenology in South and Central America: new perspectives *Phenology: An Integrative Environmental Science* ed M Schwartz (Springer) pp 107–38
Morellato L P C, Camargo M G G and Gressler E 2013 A review of plant phenology in South and Central America *Phenology: An Integrative Environmental Science* ed M Schwartz (Springer) pp 91–113
Morellato P, Alberton B, Almeida J, Jefersson A, Greice M and Torres R 2014. *e-Phenology: Monitoring Leaf Phenology and Tracking Climate Changes in the Tropics EGU General Assembly Conference Abstracts* vol 16 (available at: https://ui.adsabs.harvard.edu/abs/2014EGUGA.1612020M/abstract)
Murphy P G and Lugo A E 1986 Ecology of tropical dry forest *Annu. Rev. Ecol. Syst.* **17** 67–88
Neto E M F L, Almeida A L S, Peroni N, Castro C C and Albuquerque U P 2013 Phenology of Spondias tuberosa Arruda (Anacardiaceae) under different landscape management regimes and a proposal for a rapid phenological diagnosis using local knowledge *J. Ethnobiol. Ethnomed.* **9** 1–13
Neves D M, Dexter K G, Pennington R T, Bueno M L and Oliveira Filho A T 2015 Environmental and historical controls of floristic composition across the South American Dry Diagonal *J. Biogeogr.* **42** 1566–76
Neves S P S, de Miranda L D A P, Rossatto D R and Funch L S 2017 The roles of rainfall, soil properties, and species traits in flowering phenology along a savanna-seasonally dry tropical forest gradient *Rev. Bras. Bot.* **40** 665–79
Neves S P S, Mendes Dos Santos M G, Vitória A P, Rossatto D R, de Miranda L D A P and Funch L S 2022 The roles of functional traits in canopy maintenance along a savanna/seasonally dry tropical forest gradient in northeastern Brazil *Flora* **292** 152090
Ocón J P, Ibanez T, Franklin J, Pau S, Keppel G, Rivas-Torres G, Edward M and Gillespie T W 2021 Global tropical dry forest extent and cover: a comparative study of bioclimatic definitions using two climatic data sets *PLoS One* **16** e0252063
Oliveira A C P, Nunes A, Rodrigues R G and Branquinho C 2020 The response of plant functional traits to aridity in a tropical dry forest *Sci. Total Environ.* **747** 141177
Oliveira C C, Zandavalli R B, de Lima A L A and Rodal M J N 2015 Functional groups of woody species in semi-arid regions at low latitudes *Austral Ecol.* **40** 40–49
Orellana J T, Nascimento J O V, Grilo J, Neves S P S, de Miranda L D A P and Funch L S 2020 Seasonality and the relationships between reproductive and leaf phenophases in myrtaceae using field and herbarium data *Floresta e Ambiente* **28** e20200035
Page M J *et al* 2021 PRISMA 2020 explanation and elaboration : updated guidance and exemplars for reporting systematic reviews *BMJ* **372** n160
Paloschi R A *et al* 2021 Environmental drivers of water use for caatinga woody plant species: combining remote sensing phenology and sap flow measurements *Remote Sens.* **13** 75
Parente H N, de Andrade A P, da Silva D S, Santos E M, Araujo K D and Parente M O M 2012 Phenology of four caatinga species under continuous grazing *Rev. Arvore* **36** 411–21
Park D S, Lyra G M, Ellison A M, Maruyama R K B, Dos Reis Torquato D, Asprino R C, Cook B I and Davis C C 2023 Herbarium records provide reliable phenology estimates in the understudied tropics *J. Ecol.* **111** 327–37
Parker G, Martínez-Yrízar A, Álvarez-Yépiz J C, Maass M and Araiza S 2018 Effects of hurricane disturbance on a tropical dry forest canopy in western Mexico *For. Ecol. Manage.* **426** 39–52
Pau S, Okin G S and Gillespie T W 2010 Asynchronous response of tropical forest leaf phenology to seasonal and el niño-driven drought *PLoS One* **5** e11325
Piao S, Liu Q, Chen A, Janssens I A, Fu Y, Dai J, Liu L, Lian X, Shen M and Zhu X 2019a Plant phenology and global climate change: current progresses and challenges *Glob. Change Biol.* **25** 1922–40
Piao S *et al* 2019b Characteristics, drivers and feedbacks of global greening *Nature Rev. Earth Envron.* **1** 14–27
Portillo-Quintero C A and Sánchez-Azofeifa G A 2010 Extent and conservation of tropical dry forests in the Americas *Biol. Conserv.* **143** 144–55
Prado D 2003 As caatingas da América do Sul *Ecologia e Biogeografia da Caatinga* vol 2, ed I Leal, M Tabarelli and J M C Silva (Universidade Federal de Pernambuco) pp 3–74
Primack R B, Gallinat A S, Ellwood E R, Crimmins T M, Schwartz M D, Staudinger M D and Miller-Rushing A J 2023 Ten best practices for effective phenological research *Int. J. Biometeorol.* **67** 1509–22
Rafferty N E and Nabity P D 2017 A global test for phylogenetic signal in shifts in flowering time under climate change *J. Ecol.* **105** 627–33
Ramos D M *et al* 2023 Multiscale phenology of seasonally dry tropical forests in an aridity gradient *Front. Environ. Sci.* **11** 1275844
Rankine C, Sánchez-Azofeifa G A, Guzmán J A, Espirito-Santo M M and Sharp I 2017 Comparing MODIS and near-surface vegetation indexes for monitoring tropical dry forest phenology along a successional gradient using optical phenology towers *Environ. Res. Lett.* **12** 105007

Rosenzweig C *et al* 2008 Attributing physical and biological impacts to anthropogenic climate change *Nature* **453** 353–7
Sakai S and Kitajima K 2019 Tropical phenology: recent advances and perspectives *Ecol. Res.* **34** 50–54
Sánchez O, Quesada M, Dirzo R and Schlichting C D 2020 A field experiment to determine the effect of dry-season irrigation on vegetative and reproductive traits in the wet-deciduous tree Bonellia nervosa *J. Trop. Ecol.* **36** 29–35
Sanchez-Azofeifa A, Sharp I and Stan K 2024 MODIS fPAR products do not reflect *in-situ* conditions in a tropical dry forest based on wavelet and cross-wavelet transforms *Remote Sens. Appl. Soc. Environ.* **36** 101298
Sánchez-Azofeifa G A *et al* 2005 Research priorities for neotropical dry forests *Biotropica* **37** 477–85
Santos M M P, Morellato L P C, Silva T G F, Jardim A M R F, Santos W R and Souza L S B 2025 Phenological research in Neotropical seasonally dry forests: a systematic review dataset (1984–2024) *Zenodo* (https://doi.org/10.5281/zenodo.15660935)
Santos W R *et al* 2024 Can changes in land use in a semi-arid region of Brazil cause seasonal variation in energy partitioning and evapotranspiration? *J. Environ. Manage.* **367** 121959
Schwartz M D 2024 *Phenology: An Integrative Environmental Science* (Springer) (available at: https://link.springer.com/chapter/10.1007/978-3-031-75027-4_1)
Schwartz M D 2003 *Phenology: An Integrative Environmental Science* vol 39, ed M D Schwartz (Springer)
Seneviratne S I *et al* 2021 Weather and climate extreme events in a changing climate *The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* pp 1513–766
Sheldon K S 2019 Climate change in the tropics: ecological and evolutionary responses at low latitudes *Annu. Rev. Ecol. Evol. Syst.* **50** 303–33
Silva C R, Machado S L D, Araújo A A D and Abreu Junior C A M D 2018 Analysis of the phenology dynamics of Brazilian caatinga species with NDVI time series *CERNE* **24** 48–58
Silva J M C, Barbosa L C F, Leal I R and Tabarelli M 2017 The Caatinga: undestanding the challenges *Caatinga: The Largest Tropical Dry Forest Region in South America* ed J M C Silva, I R Leal and M Tabarelli (Springer) pp 3–23
Silva J O, Espírito-Santo M M, Santos J C and Rodrigues P M S 2020 Does leaf flushing in the dry season affect leaf traits and herbivory in a tropical dry forest? *Sci. Nat.* **107** 1–10
Silva Filho R D, Vasconcelos R S, Galvão C D O, Rufino I A A and Cunha J E D B L 2020 Mathematical modelling of the intra-annual behaviour of NDVI in the Caatinga Biome, Brazil *Ciênc. Florest* **30** 473–88
Silveira A P, Martins F R and Araújo F S 2013 Do vegetative and reproductive phenophases of deciduous tropical species respond similarly to rainfall pulses? *J. For. Res.* **24** 643–51
Singh J S and Chaturvedi R K 2018 Vegetation attributes *Tropical Dry Deciduous Forest: Research Trends and Emerging Features* (Springer) pp 31–65
Sloan S A, Zimmerman J K and Sabat A M 2007 Phenology of plumeria alba and its herbivores in a tropical dry forest *Biotropica* **39** 195–201
Song G *et al* 2024 Scale matters: spatial resolution impacts tropical leaf phenology characterized by multi-source satellite remote sensing with an ecological-constrained deep learning model *Remote Sens. Environ.* **304** 114027
Souza B C, Carvalho E C D, Oliveira R S, de Araujo F S, de Lima A L A and Rodal M J N 2020 Drought response strategies of deciduous and evergreen woody species in a seasonally dry neotropical forest *Oecologia* **194** 221–36
Staggemeier V G, Camargo M G G, Diniz-Filho J A F, Freckleton R, Jardim L and Morellato L P C 2020 The circular nature of recurrent life cycle events: a test comparing tropical and temperate phenology *J. Ecol.* **108** 393–404
Stan K and Sanchez-Azofeifa A 2019 Tropical dry forest diversity, climatic response, and resilience in a changing climate *Forests* **10** 1–19
Tang J, Körner C, Muraoka H, Piao S, Shen M, Thackeray S J and Yang X 2016 Emerging opportunities and challenges in phenology: a review *Ecosphere* **7** e01436
Toby Pennington R, Prado D E and Pendry C A 2000 Neotropical seasonally dry forests and quaternary vegetation changes *J. Biogeogr.* **27** 261–73
Valdez-Hernández M, Andrade J L, Jackson P C and Rebolledo-Vieyra M 2010 Phenology of five tree species of a tropical dry forest in Yucatan, Mexico: effects of environmental and physiological factors *Plant Soil* **329** 155–71
Vico G *et al* 2015 Climatic, ecophysiological, and phenological controls on plant ecohydrological strategies in seasonally dry ecosystems *Ecohydrology* **8** 660–81
Villalobos S D C *et al* 2013 Interspecific and interannual variation in foliar phenological patterns in a successional mosaic of a dry forest in the central llanos of Venezuela *Tropical Dry Forests in the Americas: Ecology, Conservation, and Management* ed A Sánchez-Azofeifa, J S Powers, G Fernandes and M Quesada (CRC Press, Taylor & Francis Group) pp 301–24
Walther G R, Post E, Convey P, Menzel A, Parmesan C, Beebee T J C, Fromentin J M, Hoegh-Guldberg O and Bairlein F 2002 Ecological responses to recent climate change *Nature* **416** 389–95
Wang J *et al* 2023 An ecologically-constrained deep learning model for tropical leaf phenology monitoring using PlanetScope satellites *Remote Sens. Environ.* **286** 113429
Willis C G *et al* 2017 Old plants, new tricks: phenological research using herbarium specimens *Trends Ecol. Evol.* **32** 531–46
Worbes M, Blanchart S and Fichtler E 2013 Relations between water balance, wood traits and phenological behavior of tree species from a tropical dry forest in Costa Rica—A multifactorial study *Tree Physiol.* **33** 527–36
Zeng L, Wardlow B D, Xiang D, Hu S and Li D 2019 A review of vegetation phenological metrics extraction using time-series, multispectral satellite data *Remote Sens. Environ.* **237** 111511
Zettlemoyer M A and DeMarche M L 2022 Dissecting impacts of phenological shifts for performance across biological scales *Trends Ecol. Evol.* **37** 147–57
Zhao M, Peng C, Xiang W, Deng X, Tian D, Zhou X, Yu G, He H and Zhao Z 2013 Plant phenological modeling and its application in global climate change research: overview and future challenges *Environ. Rev.* **21** 1–14
Zhu K and Song Y 2023 Harnessing herbaria to advance plant phenology research under global change *New Phytol.* **239** 2057–9