

RESEARCH ARTICLE

Leveraging natural history collections to understand the impacts of global change

Herbarium records provide reliable phenology estimates in the understudied tropics

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Abstract

1. Plant phenology has been shifting dramatically in response to climate change, a shift that may have significant and widespread ecological consequences. Of particular concern are tropical biomes, which represent the most biodiverse and imperilled regions of the world. However, compared to temperate floras, we know little about phenological responses of tropical plants because long-term observational datasets from the tropics are sparse.
2. Herbarium specimens have greatly increased our phenological knowledge in temperate regions, but similar data have been underutilized in the tropics and their suitability for this purpose has not been broadly validated. Here, we compare phenological estimates derived from field observational data (i.e. plot surveys) and herbarium specimens at various spatial and taxonomic scales to determine whether specimens can provide accurate estimations of reproductive timing and its spatial variation.
3. Here, we demonstrate that phenological estimates from field observations and herbarium specimens coincide well. Fewer than 5% of the species exhibited significant differences between flowering periods inferred from field observations versus specimens regardless of spatial aggregation. In contrast to studies based on field records, herbarium specimens sampled much larger geographic and climatic ranges, as has been documented previously for temperate plants, and effectively captured phenological responses across varied environments.

Daniel S. Park and Goia M. Lyra contributed equally to this work.

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4. *Synthesis*. Herbarium specimens are verified to be a vital resource for closing the gap in our phenological knowledge of tropical systems. Tropical plant reproductive phenology inferred from herbarium records is widely congruent with field observations, suggesting that they can and should be used to investigate phenological variation and their associated environmental cues more broadly across tropical biomes.

KEYWORDS

Brazil, citizen science, climate, field survey, herbaria, natural history collections, neotropics, phenology

1 | INTRODUCTION

Shifts in plant phenology—the timing of life-history events—are among the most iconic biological responses to climatic change and have widespread consequences for individual taxa and critical ecosystem processes (Keenan et al., 2014; Polgar & Primack, 2011; Richardson et al., 2013; Willis et al., 2008). Of particular concern are tropical biomes, which represent the most biodiverse and imperilled regions of the world (Jenkins et al., 2013; Kreft & Jetz, 2007; Mora et al., 2013; Raven et al., 2020). However, there is comparatively little information on the phenological responses of tropical plants to climate (Abernethy et al., 2018; Cook et al., 2012; Davis & Ellison, 2018; Davis, Lyra, Park, Asprino, et al., 2022; Pau et al., 2011). Along these lines, most of our knowledge regarding the patterns, cues and mechanisms of plant phenology derives from temperate biomes in North America, western Europe and northeast Asia (Davis, Lyra, Park, Asprino, et al., 2022; Wolkovich et al., 2014). Our understanding of tropical plant phenology has been especially limited by the overall paucity of long-term observational data and the overwhelming diversity of tropical species and their varied phenological behaviours (Abernethy et al., 2018; Davis & Ellison, 2018; Davis, Lyra, Park, Asprino, et al., 2022). Tropical systems comprise diverse climates, from aseasonal rainforests to seasonally dry forests and grasslands. Moreover, various reproductive phenological strategies coexist in the tropics, including near complete synchrony and total asynchrony; sub- and supra-annual flowering; and short bursts of activity as well as continuous reproduction (Augspurger, 1983; Bronstein & Patel, 1992; Frankie et al., 1974; Galetto et al., 2000; Medway, 1972; Newstrom et al., 1994; Sakai, 2002; Van Schaik et al., 1993). Although these strategies may differ among and within species, tropical biomes as a whole do not exhibit a regular marked and reliable annual resting season in terms of plant reproductive activity as is common in temperate systems (Borchert, 1996; Boulter et al., 2006; Davis & Ellison, 2018; Davis, Lyra, Park, Asprino, et al., 2022; Mendoza et al., 2017; Morellato et al., 2013; Staggemeier et al., 2020; Zalamea et al., 2011). This has contributed to a ‘temperate phenological paradigm’, which we recently argued has been a major obstacle for understanding tropical phenology (Davis, Lyra, Park, Asprino, et al., 2022). To better understand such patterns in

the tropics, we require more and better long-term records with greater spatiotemporal and taxonomic sampling.

Herbarium collections comprise large geographical, temporal and taxonomic depth and have been used to great effect in temperate zone investigations of phenology (Davis et al., 2015; Gallinat et al., 2018; Park et al., 2019; Park, Breckheimer, et al., 2021; Willis, Ellwood, et al., 2017; Willis, Law, et al., 2017; Zohner & Renner, 2014). Herbarium specimens also have shown promise in studies of tropical plant phenology but have seen comparatively little use and have yet to be applied broadly (Borchert, 1996; Boulter et al., 2006; Davis & Ellison, 2018; Davis, Lyra, Park, Asprino, et al., 2022; Fava et al., 2019; Lima et al., 2021; Zalamea et al., 2011). On this front, Davis, Lyra, Park, Asprino, et al., (2022) recently demonstrated the likely utility of applying massive herbarium data for resolving tropical phenology, especially in Brazil. Several promising findings were identified in this effort, namely, that (i) phenological variation is great across the tropics, (ii) certain biomes are much more sampled than others (e.g. Caatinga, Cerrado, Amazonia and Atlantic Forest), herbarium-based phenological observations are most abundant after only 1960 and that (iii) precipitation is a likely crucial factor for phenological cueing. In addition, the ongoing digitization and online mobilization of herbarium specimens have made them more widely available than ever before, and the onset of Digitization 2.0 *sensu* Hedrick et al. (2020)—the analysis solely of digitized collections—has enabled the efficient extraction of phenological information from specimens at a massive scale (Davis et al., 2020; Hedrick et al., 2020; Park et al., 2019; Willis, Law, et al., 2017).

Here, we harness a recently published dataset (Davis, Lyra, Park, Asprino, et al., 2022; Davis, Lyra, Park, Zhang, et al., 2022) of high-resolution phenological data scored from open access, digitized specimens from Brazil and contrast these with direct field observation records from the literature to examine the phenological patterns of 24 phylogenetically diverse species across four major tropical Brazilian biomes. To determine if herbarium specimens adequately represent flowering times in the tropics, we explicitly test whether phenological data inferred from herbarium specimens differ from data collected from field surveys. In summary, we demonstrate that herbarium specimens provide reliable information in the tropics across a broad range of taxa, thus expanding their utility for

the assessment of this key climate response trait where biodiversity risk is greatest.

2 | MATERIALS AND METHODS

We searched the literature and collected field observational phenological data for 24 species spanning diverse angiosperm clades (Bignoniaceae, Chrysobalanaceae, Fabaceae and Malpighiaceae; Table S1). These species were chosen for their broad representation in the neotropics and availability of digitized images of herbarium specimens. After discarding studies with missing data (i.e. gaps in phenological observations), we were left with observational data from nine studies (23 species) across Brazil. Phenological observations were available as presence/absence information of flowering/fruiting events per month/species. These field observations spanned four diverse biomes: Amazonia, Atlantic Forest, Caatinga and Cerrado. Amazonia comprises the largest tropical rainforest in the world, with factors such as altitude, vegetation cover and inundation patterns driving the formation of diverse communities therein (Ferreira-Ferreira et al., 2015). The Atlantic Forest comprises dense, mixed and seasonally deciduous and semi-deciduous forests as well as mangroves and restinga vegetation (Duarte et al., 2014). The seasonally dry tropical forests in Caatinga and the neotropical savanna of Cerrado can experience up to 10 months of drought a year (Terra et al., 2018) and are included among the most endangered biomes on the planet (Hoekstra et al., 2004). However, Cerrado benefits from the presence of the headwaters of the three largest hydrographic basins in South America (Amazonian, São Francisco and Prata). Cerrado vegetation is also characterized by the marked presence of adaptations to fire (Terra et al., 2018).

We simultaneously gathered digitized specimen images and associated metadata for 4638 specimens across these 23 species from a variety of online aggregators, including REFLORA (Forzza et al., 2016), SpeciesLink (<http://splink.cria.org.br/>), iDigBio (<https://www.idigbio.org/>) and Tropicos (<https://www.tropicos.org/>). Each species was represented by at least 100 unique herbarium specimens. Citizen-scientists hired through Amazon's Mechanical Turk service (MTurk; <https://www.mturk.com/>) counted the number of buds, flowers and fruits to assess peak flowering time using the CrowdCurio interface following Willis, Law, et al. (2017). Further methods on data collection are presented by Davis, Lyra, Park, Zhang, et al., 2022 and summarized in Davis, Lyra, Park, Asprino, et al., 2022.

In summary, crowdworkers were required to discern and quantify the different organs present on a test specimen with at least 80% accuracy across three trials before they could participate in the actual tasks. To provide an estimate of reliability, each image set scored by a single crowdworker included a single duplicate image randomly selected from the others (Williams et al., 2017). Species with reproductive organs that were difficult to discern were further examined by experts (i.e. the authors of this study). We estimated the consistency score for each participant based on

the data for each image set by dividing the absolute difference in counts for each organ by the total count of that specimen across the two duplicate specimens and subtracting this value from 1 ($1 - (|\text{count1} - \text{count2}| / (\text{count1} + \text{count2}))$) (Park et al., 2019; Williams et al., 2017). Consistency scores range from zero (unreliable/inconsistent) to one (reliable/consistent). Participants who reported no organs on one sheet and a non-zero number of the same organ on the duplicate sheet were assigned a reliability score of zero for that organ (i.e. the lowest reliability score). Each specimen was examined by at least three people and we weighted their counts of each organ by their consistency scores and averaged them to obtain a single set of quantifications per specimen. These quantifications were used to separately infer the start, end and length of flowering and fruiting periods at the municipality, state, biome and country level using the data collected therein. Flowering and fruiting periods were defined as the span of time between the earliest and latest observations of flowering and fruiting individuals, respectively. Although tropical systems comprise both seasonal and aseasonal climates, plant reproductive activity occurs year-round (Mendoza et al., 2017; Morellato et al., 2013). Given the non-resting nature of tropical systems, we determined the start and end of flowering and fruiting periods from a circular distribution of collection dates (Davis, Lyra, Park, Asprino, et al., 2022; Morellato et al., 2010; Staggemeier et al., 2020) of specimens with at least a single flower or fruit present (≥ 1) using the `CIRCULAR` package (Agostinelli & Lund, 2022) in R v3.6.3 (R Core Team, 2017). Likewise, we determined the start, end and length of flowering and fruiting periods from a circular distribution of field observation dates.

To determine whether phenological inference from specimen data differed from field surveys, we compared the phenological period of each species as observed in the field with the circular 95% highest posterior density interval of flowering/fruiting periods inferred from herbarium collection dates within the same spatial category (i.e. municipality, state, biome and country). Where there was no overlap between the 95% highest posterior density interval of the specimen collection dates of a species and the field observed phenological period in the same spatial category, we concluded that the two were significantly different at $p < 0.05$. The circular 95% highest posterior density interval of specimen collection dates was calculated using the `hpd_est_circ` function in the R package `BPNREG` (Cremers, 2018). We also applied linear mixed models to examine the effects of these two methods of phenological inference on the inferred length of flowering/fruiting periods at each spatial scale. Data source (herbarium specimen or field observation) was also included as a fixed effect, and species identity entered the models as random effects. Analyses were conducted using the `LME4` package (Bates et al., 2015) in R v3.6.3 (R Core Team, 2017). In total, comparisons of field survey and specimen derived phenological information were made across 23 species spanning four biomes, six states and five municipalities in Brazil (Figure S1). On average, municipalities were $2839 \pm 4791 \text{ km}^2$, states $532,276 \pm 612,210 \text{ km}^2$, biomes $2,042,371 \pm 1,526,713 \text{ km}^2$ in size, and the area of Brazil is approximately $8,515,767 \text{ km}^2$.

Climate data, including maximum air temperature and total precipitation, were downloaded from CHELSA (<https://chelsa-climate.org/>) at 30 arc second resolution and resampled at the municipality level for each year (Karger et al., 2017). These data were used to compare the sampling of climate space between the two data categories—field versus herbarium observations of phenology—and to demonstrate how herbarium specimens may be used to investigate the environmental drivers of tropical phenology.

3 | RESULTS

Herbarium specimens represented a much broader sampling across geographic and climatic space than field observational data (Figure 1). No observational studies were outside the geographic and climatic range represented by herbarium collections of the same species. Most flowering herbarium specimens were collected in the same specific months (Figure 2a) and temporal period (i.e. the span of time between the earliest and latest flowering observations across all field surveys of the same species; Figure 2b) in which flowering was observed in monthly field surveys, especially when specimens were collected in the same municipality as the observations. The degree of overlap between flowering periods estimated from field surveys and specimens varied across species and spatial scale (Appendix S1). However, less than 5% of the species in our dataset exhibited significant differences between flowering periods inferred from observations or specimens, regardless of spatial aggregation ($p < 0.05$). Flowering periods inferred from herbarium specimens did not differ from those inferred from field observations in the same

municipality. The proportion of species with significant differences between flowering periods inferred from field versus herbarium observations within the same state, biome and country were 4.8%, 4.2% and 4.5% respectively.

The duration of flowering period inferred from specimens was positively correlated with field observations, especially at smaller spatial scales (Figure 3). Fruiting durations inferred from herbarium specimens were not significantly correlated with field observed durations, regardless of spatial scale (Figure S2). There was no significant difference in the length of flowering and fruiting periods inferred from field observations and herbarium specimens at the municipality and state levels (Table S2). However, flowering and fruiting periods inferred from herbarium specimens were significantly longer at the biome and country scales. Along these lines, species could exhibit phenological variation across their ranges not captured by the more narrow geographic focus of the field observations. For instance, our crowdsourcing results suggested *Chamaecrista desvauxii* (Collad.) Killip flowering phenology may differ substantially among Amazonia, Caatinga, Cerrado and Mata Atlântica (Figure 4). Overall similar patterns were observed for fruiting phenology, but the discrepancies between estimates derived from herbarium specimens and field observations tended to be larger (Appendix S1).

4 | DISCUSSION

Tropical biomes are simultaneously the most biodiverse and most threatened by anthropogenic change (Raven et al., 2020). To understand the effects and consequences of global change on processes

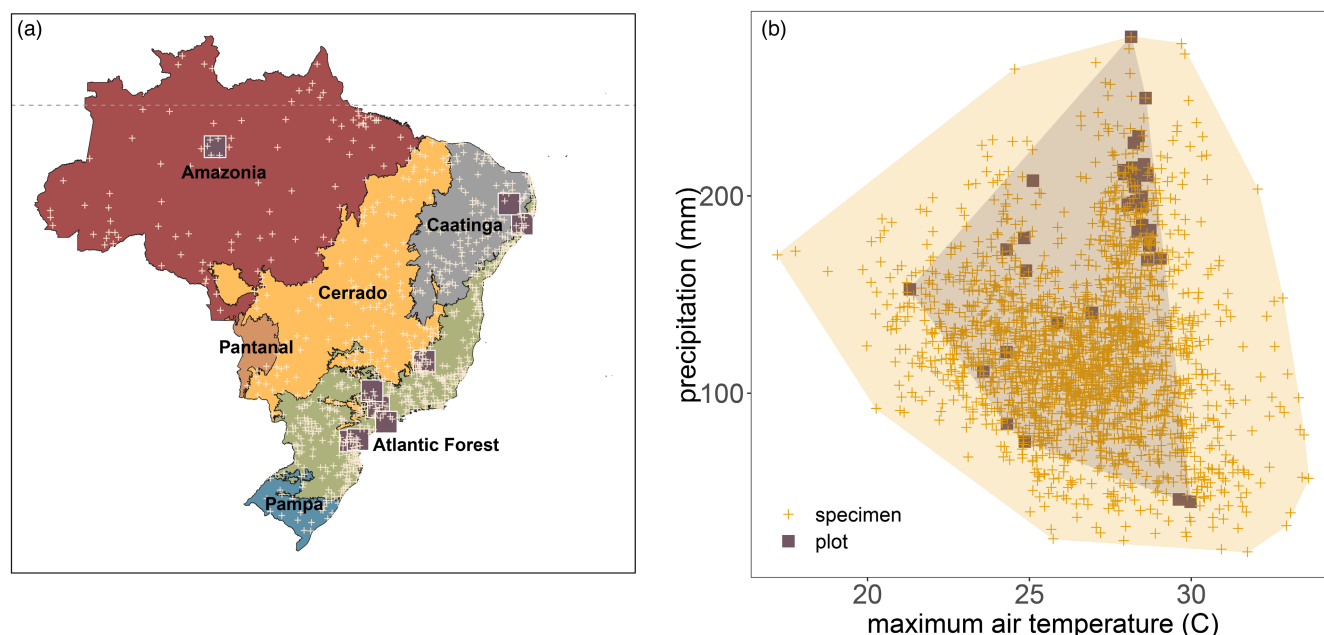


FIGURE 1 Distribution of field versus herbarium observations of phenology. Field observations of plant phenology (purple squares) and herbarium specimen collection locations (yellow crosses) in geographic (a) and climatic space (b). Each biome is depicted in a different colour on panel (a). Shaded polygons in panel (b) are convex hulls encompassing all data points from each source, and the x and y axes refer to average monthly maximum air temperature and precipitation of the year/location of collection/observation respectively.

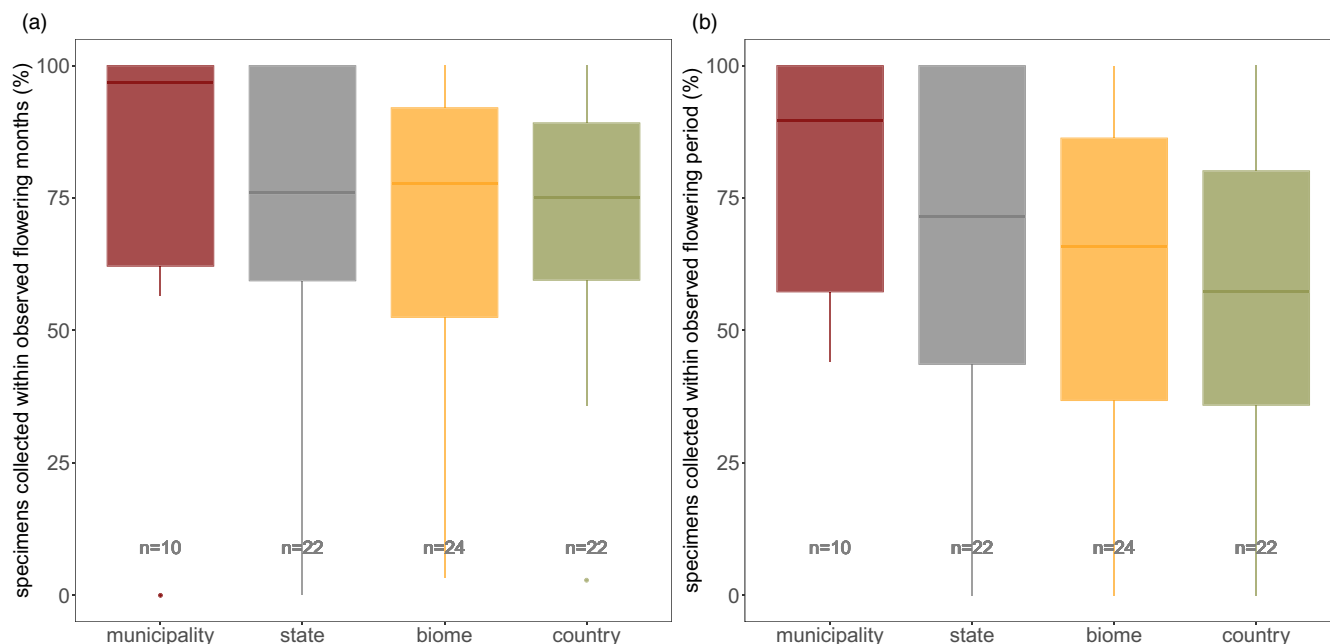


FIGURE 2 Proportion of herbarium specimens with flowers collected within the same months (a) and periods (b) during which flowering of the same species was observed in field surveys from the same municipality, state, biome and country. Flowering period was inferred from a circular distribution of field observation dates of each species in each spatial category. The number of data points at each spatial scale are listed beneath each box and whisker plot. These species were compared across five municipalities, six states, four biomes and the entire country of Brazil.

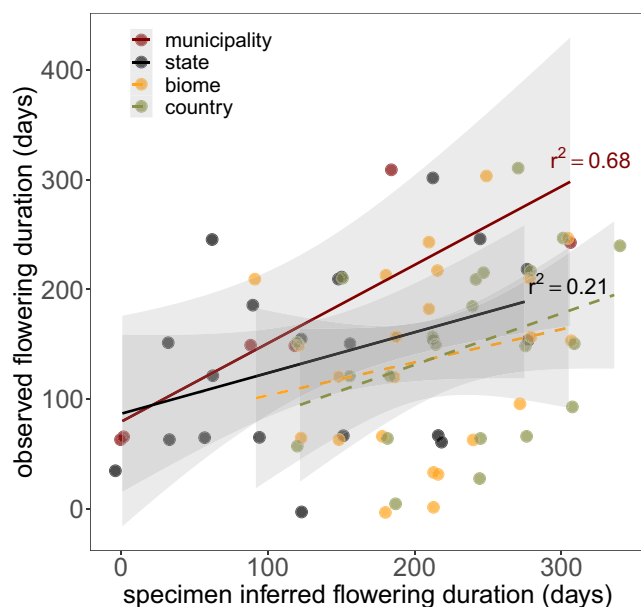


FIGURE 3 Comparison of flowering period inferred from field versus herbarium observations at varying spatial scales. R^2 values are depicted only for significant correlations indicated by solid lines ($p < 0.05$). Dashed lines indicate non-significant relationships.

that shape tropical ecosystems, such as plant reproductive phenology, we require data that span vast spatial, temporal and taxonomic scales. Yet direct field observations of tropical phenology are rare (Abernethy et al., 2018; Davis & Ellison, 2018; Davis, Lyra, Park, Asprino, et al., 2022). The utility of herbarium specimens to bridge

this impasse to investigate tropical phenology has not been assessed broadly. Although such assessments have been attempted for temperate biomes, temporal and environmental cues for phenological states are likely to differ between temperate and tropical regions (Borchert et al., 2005; Davis, Lyra, Park, Asprino, et al., 2022). Our results indicate that herbarium specimens are indeed informative for phenological research in the tropics, yet need to be explored cautiously.

4.1 | Herbarium specimens provide reliable estimates of tropical phenology

Leaf phenology is by far the most common subject of investigations examining the effects of climate change on plant phenology, especially at large scales (Park, Newman, et al., 2021). However, flowering and fruiting phenologies are key to the fitness and survival of plant species, and shifts therein can potentially lead to cascading trophic changes within ecosystems (Butt et al., 2015; Mendoza et al., 2017; Morellato et al., 2016; Polansky & Boesch, 2013; Ting et al., 2008; Willis et al., 2008). Our results demonstrate high congruence between reproductive phenology inferred from field observations and digitized herbarium specimens at every scale we analysed. Despite the potential spatial biases of herbarium collections (Daru et al., 2018), both the geographic and climatic ranges represented by herbarium collections were substantially larger than those covered by field observations and fully encompassed the range of observational data. As in temperate regions, herbarium

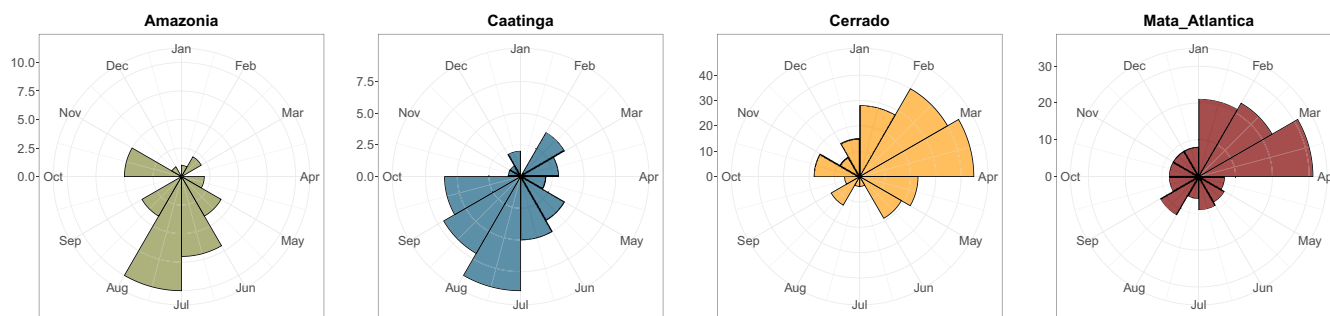


FIGURE 4 Histogram of *Chamaecrista desvauxii* flowering specimens collected in four biomes. Circular diagrams depict the time of collection in angles.

specimens represent phenological observations across a much wider spatial extent and variety of tropical biomes and environments than do direct field surveys (Davis et al., 2015). Furthermore, the herbarium specimens in our dataset comprised phenological information spanning more than 60 years, demonstrating that these specimens can help address the paucity of historic and long-term observational datasets in the tropics (see also Davis, Lyra, Park, Asprino, et al., 2022). Indeed, most of the field observations we reviewed were relatively recent (1988–2008), whereas many specimens were collected before the onset of what we now recognize as substantial global warming. We note that although specimens span greater temporal scales than most field observations, they do not necessarily comprise regular, repeated sampling of the same location through time. Thus, while we may infer coarse temporal trends from specimens and complement the results from field observations, they do not replace the need for regularly censused, long-term observational investigations.

As with flowering, estimates of fruiting phenology were generally congruent between specimens and field observations, but to a lesser degree. We suggest four reasons for the weaker congruence of fruiting estimates. First, most herbarium specimens tend to be of plants in flower, resulting in fewer fruiting specimens from which to infer phenology. The comparative lack of specimens with fruit may result in greater uncertainty and stochasticity in specimen-derived estimates of fruiting phenology. Second, fruits in some tropical species may persist on the parental plant well beyond maturation, across months or even years. Thus, it can be difficult to determine how old a fruit is from a digitized specimen, which can greatly complicate the interpretation of these scores. Third, smaller fruits may be confused with leaf/or flower buds during scoring (Figure 5), reducing the accuracy of fruiting phenology estimates (see also Willis, Law, et al., 2017 and Davis et al., 2020 for variation across the scores of different phenophases).

4.2 | The promise of herbarium specimens for determining phenological cues in the tropics

Numerous studies have documented phenological patterns in the tropical regions of the world, and factors such as precipitation,

insolation and photoperiod have been suggested to influence these events (Borchert, 1996; Borchert et al., 2005, 2015; Calle et al., 2010). However, most of these did not attempt to test the environmental or physiological drivers of these patterns (Abernethy et al., 2018). Herbarium specimens have been used to investigate the drivers of plant phenology in temperate regions, and similar approaches could potentially be applied to tropical systems (Davis & Ellison, 2018; Davis, Lyra, Park, Asprino, et al., 2022). For example, data from herbarium specimens of the monkey's comb, *Amphilophium crucigerum* (L.) L.G. Lohmann (Bignoniaceae) suggest the same climate–flowering phenology relationships as data from field observations (Figure 6). *A. crucigerum* tends to flower earlier in wetter (and slightly cooler) climates in both field surveys and herbarium specimens. Although the general lack of observational data prevents us from making more concrete inferences, this demonstrates the promise of using herbarium specimens to investigate environmental drivers of tropical phenology.

The phenological timing of species and their responses to climate have been demonstrated to vary substantially across latitude, both within and among species (Park et al., 2019; Park, Newman, et al., 2021; Xie et al., 2022). Although these studies focused on temperate floras, we expect similar responses exist in the tropics, as the ranges of numerous taxa span multiple tropical biomes (Lucrecia et al., 2021). For instance, *Banisteriopsis pubipetala* (A. Juss.) Cuatrec. (Malpighiaceae) has been independently observed to flower from July to December in Cerrado (Batalha & Mantovani, 2000), while flowering appears to be restricted to October in Mata Atlântica (Morellato & Leitao-Filho, 1996). However, it is difficult to assess phenological variation across their ranges from existing, geographically restricted field observations. As in temperate regions, herbarium specimens collected from across species' ranges can be used effectively to explore how their phenological responses vary across space and time. Indeed, our results captured substantial variation in flowering time across the four different biomes that constitute the range of *Chamaecrista desvauxii* (Figure 4). Along these lines, the decrease in congruence we observe between phenological timing inferred from field observations and herbarium specimens at larger spatial scales (e.g. country) may reflect the presence of widespread phenological variation across species' ranges in the tropics.



FIGURE 5 Specimens of *Couepia grandiflora* (a) and *Leandra quinquedentata* (b), illustrating overlap and similarity among reproductive organs. Images are from the Re flora virtual herbarium under CC BY-SA 4.0.

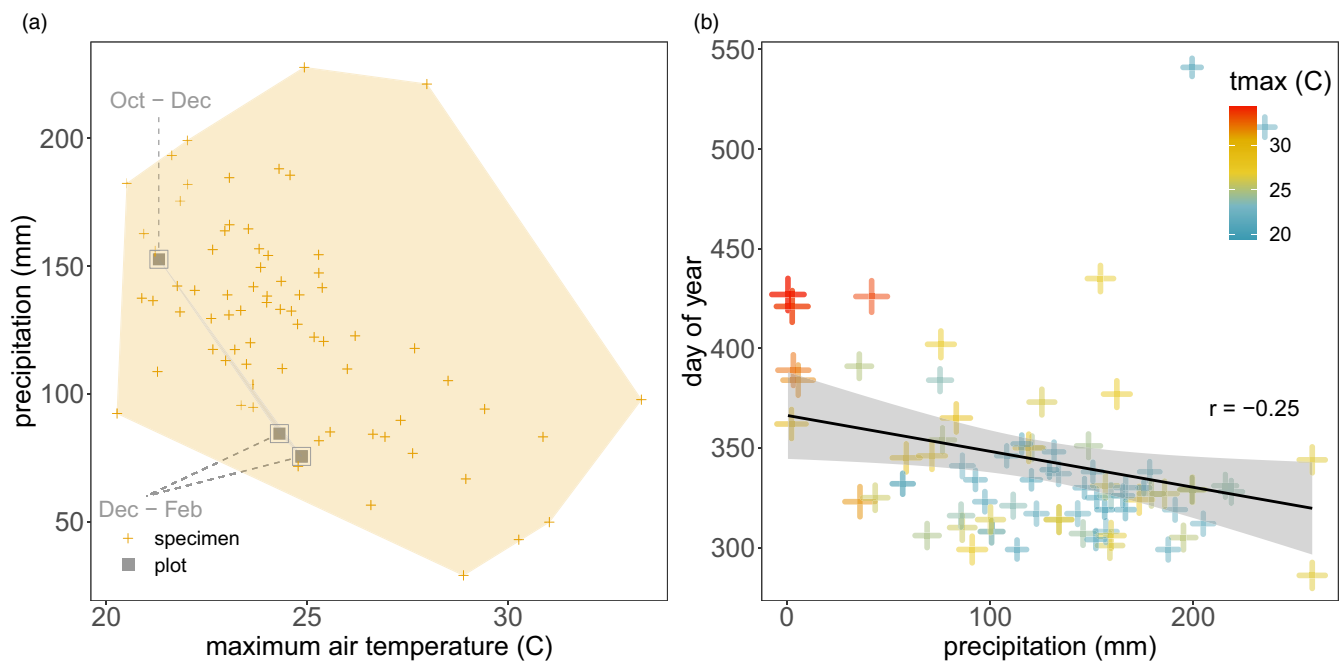


FIGURE 6 *Amphilophium crucigerum* phenology and its relationship with climate. (a) Flowering phenology field observations (grey squares) versus herbarium specimens (yellow crosses) are depicted in climate space. Maximum air temperature and precipitation represent monthly averages of the year/location of collection/observation, respectively. Crosses represent specimens and grey squares represent surveyed plots. Grey text insets indicate the flowering periods of this species as surveyed in each plot. (b) The relationship between day of year flowering and mean September–October precipitation inferred from herbarium specimens. Both field observation data and specimen data indicated that *A. crucigerum* flowering begins in October and persists into the following year.

4.3 | Limitations, caveats and ways forward

Herbarium specimens represent a non-random, non-comprehensive sampling of phenological events (Davis et al., 2015; Willis, Ellwood, et al., 2017) because they are rarely collected for phenological studies and reflect gaps and biases related to collector behaviour. Taxonomic challenges, including misidentified specimens and species complexes, can mislead results of phenological investigations, but especially those based on digital specimen images and particularly for tropical plants, which are notoriously misidentified (Goodwin et al., 2015). For instance, we found disparities in phenological information inferred from specimens and field observations in *Banisteriopsis variabilis* B. Gates (Malpighiaceae) and *Licania heteromorpha* Benth (Chrysobalanaceae) (Appendix S1; see also Davis, Lyra, Park, Asprino, et al., 2022). As their specific epithets suggest, both taxa are morphologically variable and may constitute species complexes (Prance, 1972). However, taxonomic difficulty can affect field-based studies as well, and collection-based studies have increasingly found ways to detect and account for such biases (Belitz et al., 2020; Park et al., 2019). Moreover, these instances potentially represent opportunities to explore cryptic species that may be delimited by phenology.

Inferring phenophases from digital images can be difficult for certain taxa. For instance, most species of *Miconia* and *Leandra* (Melastomataceae) and most species of Chrysobalanaceae possess tiny buds and flowers, often clumped and/or overlapping in specimens (Figure 5). Fruits may be harder to recognize in several species, as they can be confused with flower or leaf buds. Quantifying reproductive organs and assessing the phenological stage of such taxa can be difficult when the physical specimens are not available for direct examination. Thus, digital specimen-based investigations of phenology may not be appropriate for all taxa. Still, although time consuming, expert botanists are able to discern and quantify different reproductive organs of these taxa from high-resolution digital images as we demonstrate here. Furthermore, advances in machine-learning applications for phenological research are making the automatic extraction of data from digitized specimens with equal or better accuracy than non-expert humans increasingly feasible even if heuristics are applied to identify whether a specimen is mostly in fruit vs mostly in flower (Davis et al., 2020; Goëau et al., 2020; Lorieul et al., 2019).

Inferring phenological phenomena from herbarium specimens faces additional challenges in tropical biomes. Some species can reproduce multiple times during a single year, while others may reproduce supra-annually (Bawa et al., 2003; Engel & Martins, 2005; Rojas-Robles & Stiles, 2009). For example, *Licania octandra* var. *pallida* Prance (Chrysobalanaceae) flowered four times in 25 years of field observations in the Reserva Ducke (Amazon Rainforest) from 1970 to 1994 (Ruiz & Alencar, 1999). Although the density of flowering specimen collections suggest that several species may exhibit multiple flowering peaks throughout the year (e.g. *Tabebuia aurea* (Bignoniaceae), *Hirtella racemosa* (Chrysobalanaceae), *Byrsonima crassifolia* (Malpighiaceae) and *Mimosa somnians* (Fabaceae);

Appendix S2), such patterns cannot always be reliably inferred from herbarium specimens, especially for taxa and phenological stages that have not been well collected. Indeed, the discrepancies between herbarium specimen versus field observational records derived phenological estimates tended to be larger for fruits (Table S2; Appendix S1). Finally, herbarium specimens often comprise only part of a larger plant, and thus may not always reflect the general phenological stage of an entire individual. This issue may be exacerbated in tropical ecosystems due to the comparative abundance of tree species, although reproductive materials are often prioritized for collection.

Nonetheless, our study shows that tropical plant reproductive phenology inferred from herbarium records are widely congruent with field observations and demonstrates that herbarium specimens can be effectively used to assess patterns and mechanisms of plant phenological responses in the tropics. In particular, with theoretical and methodological advances that have made collections-based phenological studies increasingly efficient, herbarium specimens are positioned to be a vital resource for closing the gap in our phenological knowledge in tropical biomes (Davis & Ellison, 2018; Davis, Lyra, Park, Asprino, et al., 2022). Such efforts will be critical to enhance our ability to predict how plant assemblages in the tropics will respond to an increasingly changing climate and implement mitigation strategies.

AUTHOR CONTRIBUTIONS

Charles C. Davis conceived the initial idea for the project which was refined with discussions with the entire author group; Charles C. Davis supervised the study; Charles C. Davis, Daniel S. Park, Goia M. Lyra, Débora dos Reis Torquato, Renata C. Asprino and Rogério Katsuhito Barbosa Maruyama collected data; Aaron M. Ellison and Daniel S. Park analysed the data; Daniel S. Park and Goia M. Lyra drafted the first version of the manuscript, and all authors contributed significantly to subsequent revisions.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and (permanent links to) imagery are available from the Environmental Data Initiative (EDI) Data Portal: <https://doi.org/10.6073/pasta/7f004957c6cc224d84e61bf1f4bb76a4> (Davis, 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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