Opinion

New directions in tropical phenology

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Highlights

Climatic change is disrupting phenology worldwide, but understanding and responding to these disruptions is constrained by a century-old, geo- graphically biased 'temperate phe- nological paradigm'.

Statistical models applied to data with circular distributions, including circular representations of phenology, are robust analytical methods that eliminate geo- graphical bias. They are especially useful for analyzing phenological data from biomes that are not characterized by annual climates or life histories.

Museum specimens provide a 'window on the past' and reflect distribution, abundance, and phenology of many organisms. Digitized and mobilized herbarium data are revolutionizing our understanding of phenological re- sponses to climate and climatic change in temperate climates but have been sparsely applied to tropical plants.

Finally, as more inclusive and reliable phylogenies become available, incorpo- rating phylogenetic data into phenolog- ical investigations will provide novel and robust insights into all species' responses to ongoing climatic change.

Earth's most speciose biomes are in the tropics, yet tropical plant phenology remains poorly understood. Tropical phenological data are comparatively scarce and viewed through the lens of a 'temperate phenological paradigm' expecting phenological traits to respond to strong, predictably annual shifts in climate (e.g., between subfreezing and frost-free periods). Digitized herbarium data greatly expand existing phenological data for tropical plants; and circular data, statistics, and models are more appropriate for analyzing tropical (and temper- ate) phenological datasets. Phylogenetic information, which remains seldom ap- plied in phenological investigations, provides new insights into phenological responses of large groups of related species to climate. Consistent combined use of herbarium data, circular statistical distributions, and robust phylogenies will rapidly advance our understanding of tropical – and temperate – phenology.

Phenology research has a temperate zone bias

Phenology – the timing of key events in an organism's development or life history [1] – strongly affects individual fitness; interactions among individuals, populations, and species; the generation and maintenance of species boundaries; and how populations and species are managed [2,3]. Perhaps because of its origins in northern Europe [4,5], the study of phenology has for more than 150 years emphasized annually recurring seasonal or cyclic life-history phenomena [6]. Common objects of phenological investigation include the onset of flowering of individual plant species, the return to temperate (northern or southern) nesting grounds of seasonally migratory birds, and peak colors of foliage as the leaves of temperate deciduous trees senesce. The primary environmental drivers of phenology in the temperate zone are the predictably large, seasonal changes in daylength, precipitation, and especially the shift from below- to above-freezing temper- atures [1,6]. We refer to the emphasis on large seasonal phenological drivers that occur predictably on annual cycles as the 'temperate phenological paradigm'. We suggest that this temperate phenological paradigm has constrained how evolutionary ecologists – especially those of us who live and work in temperate zones – think about and model phenology in the tropics. We argue herein that the uncritical application of the temperate phenological paradigm to tropical species and communities is unwarranted and poses an obstacle to a more detailed and nuanced assess- ment of the patterns of, and processes that influence, tropical phenology.

A broader and more flexible understanding of phenology is especially important because accel- erating anthropogenically caused climatic change is disrupting phenology worldwide [7]. Even though these disruptions are global, researchers investigating phenological responses to climatic change have focused overwhelmingly on terrestrial and aquatic organisms and ecosystems in northern (Asia, Europe, North America) [8–14], and southern [15–18] temperate zones. By contrast, phenological responses of tropical species to climatic change are woefully understudied [19–21]. Moreover, uncritical applications of the temperate phenological paradigm to tropical systems can lead to unreliable or incorrect forecasts of phenological responses to climatic change in the tropics [22]. Although temperature is increasing rapidly in high-latitude environments, with

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predictable effects on phenology, tropical species may be phenologically more sensitive to subtle changes in patterns of rainfall or cloud cover associated with comparatively small increases in temperature [23]. Within- and between-year – for example, El Niño–Southern Oscillation (ENSO) events – changes in temperature, precipitation, and solar irradiation may also interact to trigger bursts of flowering or fruiting [24–27]. Identifying key biotic and abiotic drivers of phenology in the tropics and its sensitivity to a range of changing climatic variables requires much more data than are currently available from small-scale field studies or remote-sensing platforms. In this regard, herbarium data represent an important and underutilized source of data [28,29].

It is clear that the traditional approaches applied to temperate regions may be unsuitable for analyses of tropical phenology. Here, we argue for a new direction that combines (i) circular statistical models, (ii) herbarium data, and (iii) phylogenetic conservatism. While these tools have been used extensively in phenological research independently, we believe that combining them offers significant benefits for rapidly advancing and unifying our understanding of temperate and tropical phenology (Figure 1).

The temperate phenology paradigm hinders our interpretation and understanding of tropical phenology

Applying phenological approaches and techniques from temperate regions to predicting phenology in tropical species is inadequate because in the tropics the fundamental phenological drivers are

Trends in Ecology & Evolution Figure 1. Conceptual figure illustrating new approaches to gathering and analyzing tropical phenology data and harmonizing them with data from temperate regions.

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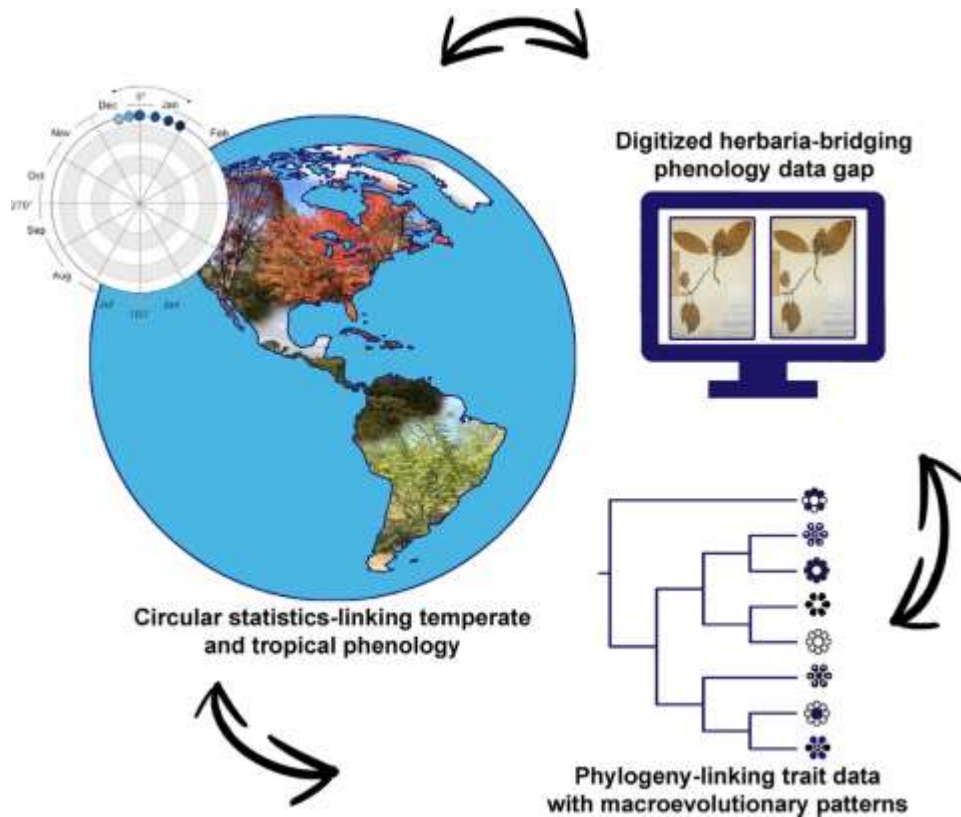
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Digitized herbaria-bridging phenology data gap

Circular statistics-linking temperate and tropical phenology

Phylogeny-linking trait data with macroevolutionary patterns

different and poorly understood; seasonal climate cues often are subtler, and species, functional, and phylogenetic diversity are much greater. In the temperate zone, cold temperatures and low insolation during winter define a marked resting season, and the phenology of key life-history events is typically triggered by increasing day length and sustained temperatures above 0°C (Figure 2A) [22]. Therefore, models combining daylength with chilling and heat accumulations, based on well understood and constrained physiological mechanisms, work well for a broad diversity of temperate-zone ecosystems and species [30].

However, for most tropical species we still lack data on their phenological patterns and the different endogenous (e.g., upregulated hormonal triggers) and exogenous (e.g., environmental) cues that regulate their phenologies [20]. In the frostless tropics, there is no transition from subfreezing 'winter' to above-freezing 'spring'. Rather, growing seasons span the entire year, intra- and interannual pulses or cycles of rainfall may be key regulators of phenology (Figure 2B) [31,32], and the uncritical use of 'temperate-centric' models based on resting seasons and dramatic temperature changes to explain patterns and processes in tropical phenology can be problematic [22]. Although large temperature changes do play a central role in regulating phenology of both temperate and tropical plants [33], small changes or subtle variations in daylength, temperature, and precipitation in the tropics can also have unexpectedly dramatic effects on flowering and leafing phenology of tropical species [23,26,34–36]. Furthermore, phenology in tropical species and ecosystems with ostensibly similar life histories or climatic regimes may have drastically different cues. The first challenge to understanding phenology and forecasting phenological change in the tropics is to use more informative ways of describing and analyzing phenological patterns.

## Circular statistics are better for tropical and temperate phenological data

Phenology in the temperate zone has abrupt, temperature-driven transitions that can be readily illustrated and modeled using data from truncated distributions whose endpoints are approxi- mated by the onsets of meteorological spring and fall (i.e., the growing season or frost-free period of the year) (Figure 2A). Because these phenological data have distinct upper and lower bounds, it is often reasonable to model them assuming that the data have a continuous univariate distribution on a fixed interval (Figure 2C).

By contrast, phenological events in the tropics can cross a calendar year – that is, ranging from 0 (January 1) to 364 (December 31) (Figure 2B) – but the difference between day 364 and day 0 is only a single day, not 365 days. Such data are considered 'circular' (or, more generally, 'direc- tional'); common probability distributions of circular variables include the von Mises circular distri- bution and the wrapped normal distribution (Figure 2D) [37,38].

Despite showing apparent phenological events spanning adjacent years, many tropical pheno- logical data have been plotted on bounded (calendar-year) scales and modeled assuming bounded univariate distributions (Figure 2C) [22,35,39–41]. (See the references in the supple- mental material online for examples of studies applying circular statistics to tropical plant data sets.) Such data would be coded more accurately using a continuous circular scale (in radians 0–2π) and then analyzed assuming circular distributions that allow for continuous transitions without artificial boundaries imposed by human calendars (Figure 2D,E). Indeed, results can differ greatly between analyses of key phenological events coded from 0 to 364 (as a bounded calen- dar year) or continuously in radians (circularly from 0 to 2π) [22]. For example, if the data are as- sumed to be drawn from a bounded univariate distribution, a plant that flowered on December 31 (day 365) and January 2 (day 2) would have an expected peak flowering day of July 1 [day 183 = (2 + 365)/2]. By contrast, the corresponding expected peak flowering day from a circular distribu- tion would be estimated correctly as January 1 (0 radians).

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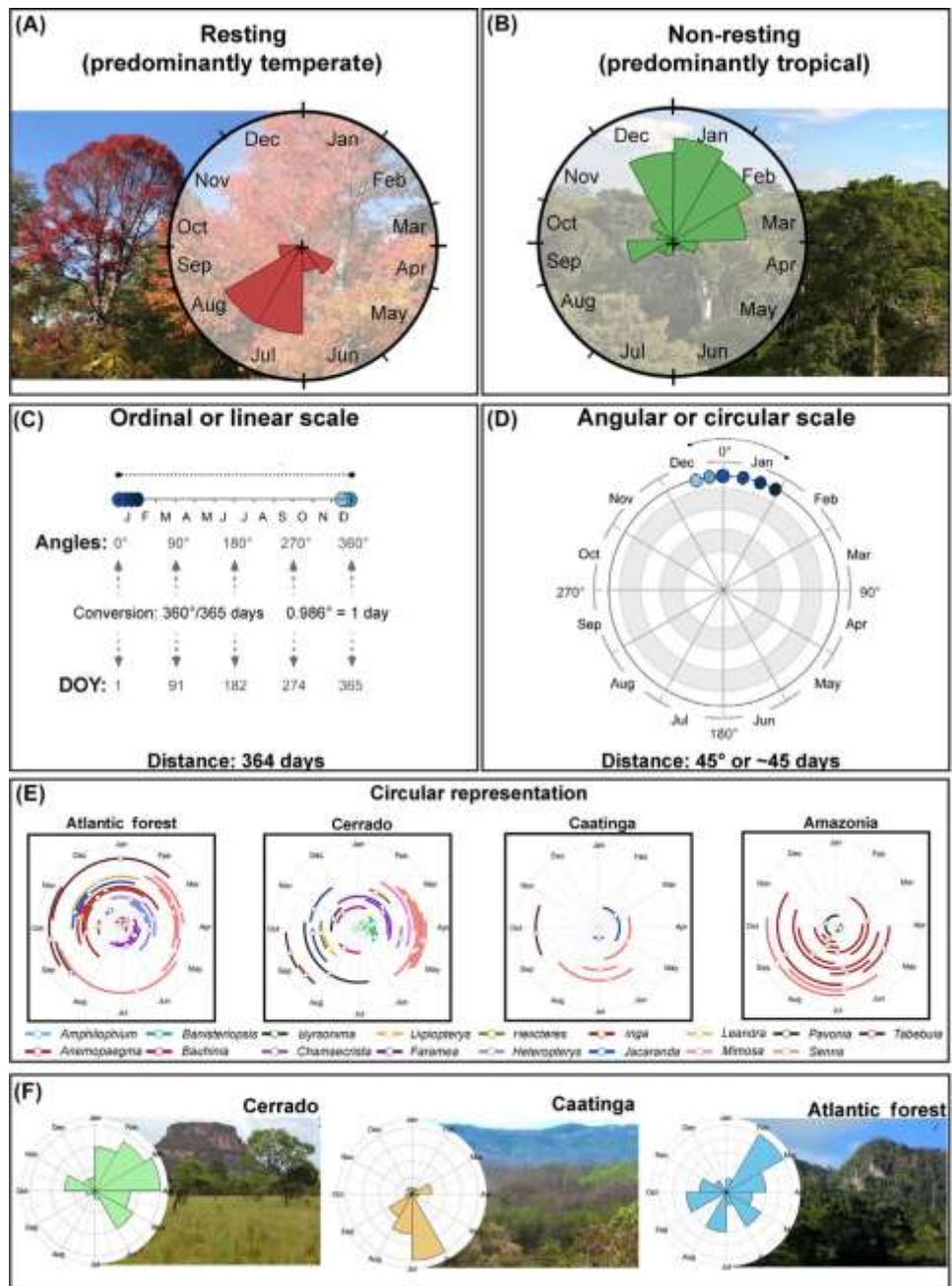
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Figure 2. Phenology in the tropics. In contrast to that in temperate regions (A, red circular histogram), plant phenology in the tropics often does not have distinct resting periods and can span calendar years (B, circular histogram). Thus, an ordered and bounded linear assessment of phenological events can result in erroneous estimations of their start, duration, and end (C). Circular distributions avoid such errors (D). The temporal ranges of peak flowering across 66 species in 17 genera and six families of plants common in four neotropical biomes illustrate the variation and prevalence of phenological periods that cross the December–January calendar boundary (E) (see also Figure I B in Box 1 in the main text); white circles indicate median dates and colored lines span the first and third quantiles of peak flowering dates. Species that span more than one biome may exhibit large variation in their periodicity of flowering (F). For example, Chamaecrista desvauxii (Collad.)

(Figure legend continued at the bottom of the next page.)

Such estimations matter. Use of bounded univariate distributions has been shown to lead to incorrect inferences about associations between climatic variables and simulated [22] or empirical [30] phenological data. This is a particular problem when the patterns or the climatic variables have irregular or supra-annual cycles characteristic of many tropical plant species and biomes (Figure 2E), and because there can be large variation in phenology within species across biomes (Figure 2F). Because circular distributions can be applied to any periodic data [38], including those from temperate systems with predictable winter dormancy or resting periods [22], we suggest that, moving forward, all phenological data – whether from tropical or temperate climates – should be plotted in radians and analyzed using statistical methods for circular (directional) data. We note that supra-annual phenological data could also be analyzed using standard time-series methods for periodic data; these methods have also been rarely used for modeling phenological data and their association with environmental change. Perhaps equally important, using either approach achieves our ability to better harmonize tropical and temperate data in a single analytical framework, which is greatly needed (Figures 1 and 2).

We also note that circular plots and statistical models can highlight more clearly the diversity of phenological functional groupings in the tropics. These can range from regular sub-annual or annual reproductive episodes, through continuous reproduction, to irregular supra-annual and infrequent, massively synchronized mast events (Figure 2E) [28]. Like the diversity of tropical species, the diversity of phenological patterns in the tropics far outstrips the diversity found amongst temperate-zone species. We also see distinct phenological variation within species across biomes (Figure 2F).

Herbarium data greatly expand phenological datasets

Elucidating and modeling the interplay between endogenous and exogenous cues that trigger and sustain developmental shifts are required to accurately forecast the phenological responses of individuals, populations, and species to ongoing local, regional, and global climatic change. However, we lack the baseline data required to assess directions, magnitudes, and mechanisms of phenological responses to climate and climatic change for most tropical species. Not only are these data lacking for individual species at a single place and time, but there are few long-term spatially or temporally extensive phenological data from any tropical location. On average, there is only one phenological monitoring station in the tropics per 80 000 km^2; no site includes observations before 1950 or accounts for more than 100 species, and few sites have more 10 ten years of data [20,42]. By comparison, the temperate-zone USA National Phenology Network alone has one phenological monitoring station per 655 km^2 and >23M records for >1400 species [43]. Even if the spatiotemporal data density we have now for temperate-zone sites were available for the tropics, it would still not provide sufficient replication to cover the extraordinary size and diversity of tropical forests. For example, a single hectare of Amazonian rainforest can include more than 450 tree species, which is more tree species than in all of Canada and the USA combined [44].

Herbarium specimens are helping to break this impasse and offer compelling snapshots of phenological events (e.g., flowering and fruiting) at specific places and in specific times and climates (see Figure IA,B in Box 1). Herbarium specimens have greatly expanded the temporal, spatial, and taxonomic depth of phenological data in the temperate zone [14,45–49] while faith- fully reflecting directly observed phenological sensitivity to local climate and climatic change [50].

Killip (Fabaceae) demonstrates highly divergent flowering responses between Cerrado (flowering October–May), Caatinga (March–September), and Atlantic rainforest (year-round). All metrics were circularly derived. Data from panels A, B, E, and F from Davis et al. [82]. Panels A–D reproduced from Staggemeier et al. [22] with permission.

Box 1. Phenological data from Brazilian herbarium specimens

Herbarium samples appear to be densest from the early 1960s onward (Figure IA) across four large Brazilian biomes spanning diverse temperature and precipitation gradients (Figure IB). These data are in striking contrast to historical collecting efforts in the USA, for which abundant herbarium specimens have been accumulated from the mid-1800s to mid-1900s [51]. In parallel, historical climatic records in the temperate zone date to the mid- to late-1800s [80], but most long-term tropical climatic records do not extend earlier than the 1950s [81].

To explore the utility of herbarium specimens for extracting valid phenological data for tropical plants, we identified two species in the Malpighiaceae for which long-term field observations of flowering phenology and numerous digitized herbarium specimens are available (Figure IC). Flowering times estimated from field observations and digitized herbarium data were similar for Banisteriopsis laevifolia (A. Juss.) B. Gates but were quite dissimilar for Banisteriopsis variabilis B. Gates (Figure IC). Moving forward, more and larger comparative analyses of phenological data collected in the field and derived from herbarium specimens will help to better determine the validity of using tropical herbarium specimens for phenological research.

Similar validation analyses have yet to be performed for tropical plants, but preliminary assess- ments (see Figure IC in Box 1) suggest that herbarium specimens of tropical plants should also be useful for these kinds of analyses. Early investigations of the utility of herbarium species for inferring tropical plant phenology also appear promising [28,29]. However, some key confounding factors common to tropical plants could complicate inferences drawn from herbarium specimens. The first may be the sparsity of individuals across vast areas in the tropics. The consequent small sample sizes for any given species or population will reduce the statistical power to reliably detect phenological responses to climatic change. Second, variation in phenological onset, duration, and periodicity of tropical plants is very large (Figure 2E,F). It will be difficult to identify this variation if collecting intensity (specimens collected $\cdot$ area^{-1} $\cdot$ time^{-1}) is biased by collection activity (i.e., when specimens are actually collected) [51]. This is a particular problem for species with very short flowering or very long flowering durations, or those that flower supra-annually or sporadically.

Using herbarium specimens to assess and forecast phenological change

As herbarium specimens have been digitized and the associated data have been mobilized online, researchers around the world are increasingly using them to assess long-term phenological changes in hundreds of species [14,45,46,49], to document variation in phenological responses across species ranges now [14] and in the future [49], and to identify their plausible mechanistic responses to climatic and geographic factors [14]. But like observational and experimental data, herbarium data have largely been applied to assess phenological responses to climatic change primarily in temperate regions [23,45,46,50,52–55], not tropical ones.

Digitization also dramatically increases access to herbarium specimens and their associated metadata [48]. An interesting consequence of this broader access is the expansion of herbarium-based scholarship into new domains. For example, methods to automate digitization pipelines and apply machine learning to analyze the associated massive datasets at

large spatio- temporal scales are maturing, with promising results [48,56]. Crowd-sourcing has proven useful for acquiring the phenological data necessary to train more sophisticated machine-learning models and automate data-gathering from herbarium sheets [57–60]. These efforts remain in their infancy, and far more data are required to broadly assess phenological responses to abiotic and biotic drivers of phenological sensitivity in the tropics.

Nevertheless, inferences derived from herbarium data about how climate and climatic change affect phenology should be used cautiously. For example, long-term monitoring datasets span- ning multiple years of data at single sites are ideal for investigating how intra- and inter-annual climate variability affects phenology. Such observational data are often collected using clearly defined and stringent protocols designed to minimize observer and sampling errors. Herbarium datasets, however, are typically composed of spatially distributed data points collected over

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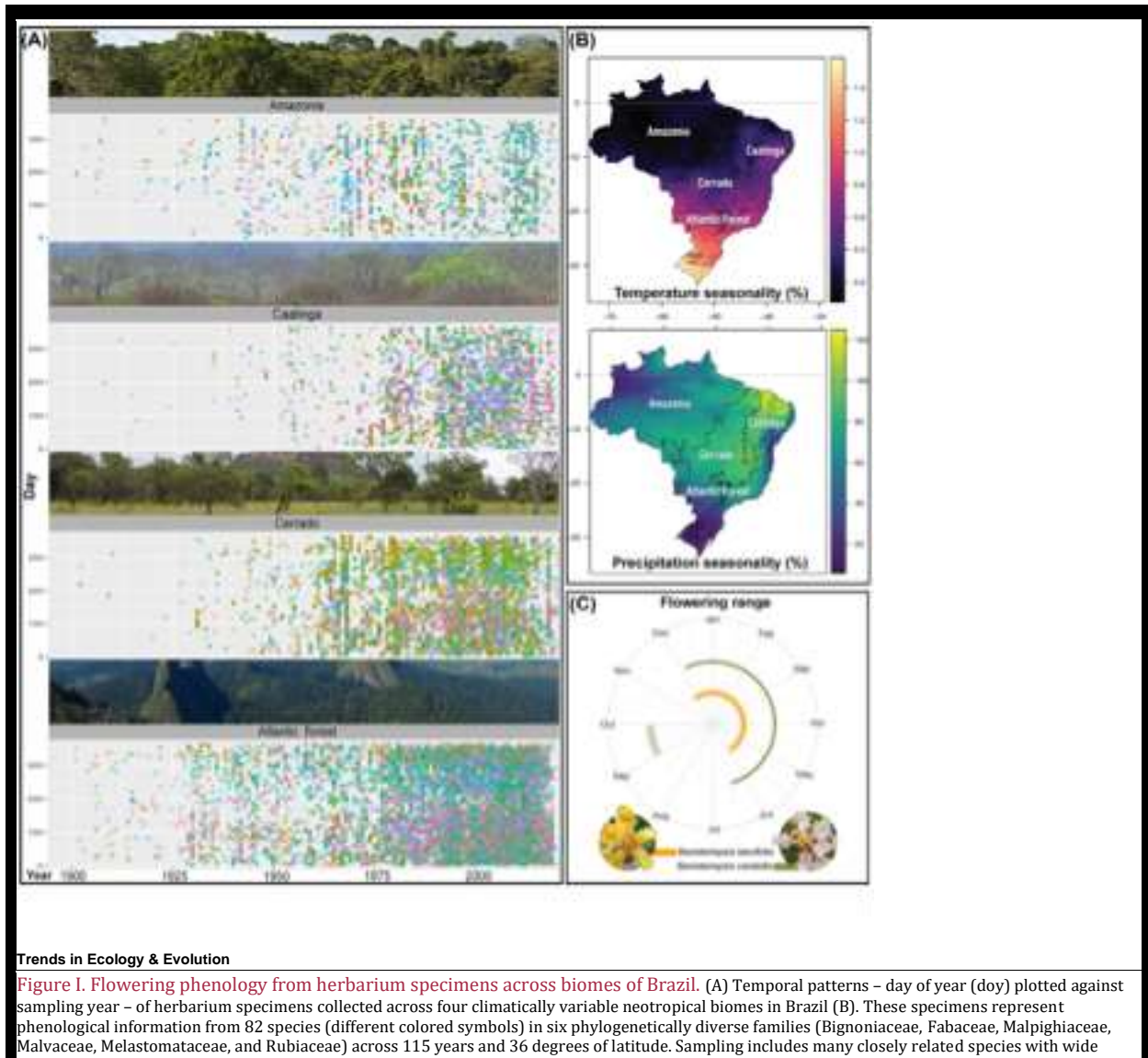
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Figure I. Flowering phenology from herbarium specimens across biomes of Brazil. (A) Temporal patterns – day of year (doy) plotted against sampling year – of herbarium specimens collected across four climatically variable neotropical biomes in Brazil (B). These specimens represent phenological information from 82 species (different colored symbols) in six phylogenetically diverse families (Bignoniaceae, Fabaceae, Malpighiaceae, Malvaceae, Melastomataceae, and Rubiaceae) across 115 years and 36 degrees of latitude. Sampling includes many closely related species with wide

large regions and many years, often with few or no single locations sampled in multiple years. Thus, inferences about changes in phenology over time from herbarium data depend heavily on analyses using space-for-time substitutions, which can be problematic or misleading [61].

Such assessments could be substantially improved if the variety of data types – including herbar- ium data, forest inventories, and near-Earth remote sensing – were harmonized in individual, biome, and continental-scale models, and forecasts of phenological responses to climate and cli- matic change.

The relevance of phylogeny to phenological investigation

Groups with similar phenological patterns may share a common phylogenetic history [62], but this has seldom been explored in tropical plants [63,64]. Conversely, phylogenetic relationships can provide important information regarding species' phenological responses to climate (Figure 3) [62,65], and suggest phenological patterns and traits for species whose phenologies have not yet been studied. However, existing community-wide phenological datasets and associated analyses used to demonstrate long-term phenological responses to climatic change commonly lack phylogenetic frameworks.

Results have differed among the few studies in which phylogenetic information was included in phenological analyses. For example, members of less phenologically responsive clades in the New England (USA) flora have declined significantly in abundance as the climate has warmed [62,66,67]. Park et al. 2022 [49] found evidence of a phylogenetic signal in peak flowering time and its sensitivity to spring temperatures, but not precipitation, among species in the eastern USA. By contrast, CaraDonna and Inouye [68] found no association between phenological responsiveness, abiotic correlates, and the phylogenetic distribution of these traits in an alpine system in Colorado (USA). Bock et al. [69] also identified relatively few pheno- logical differences attributable to major clades of angiosperms in the UK flora. In the tropics, Staggemeier et al. [64] suggested phylogenetic conservation of flowering and fruiting time and a potential increase in sensitivity for tropical members of Myrtaceae in the Atlantic Forest of Brazil.

There are several important barriers to using phylogeny to enhance our understanding of pheno- logical pattern and process in the tropics. First, many ecologists uncritically use turn-key phylog- enies generated by, for example, Phylocom [70] that are often from super-trees with limited

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Figure 3. Flowering phenology as derived from Davis et al. [82] reflects both climate (precipitation) and phylogenetic relationships in Banisteriopsis (Malpighiaceae). Points depict median peak flowering dates, lines show quantiles of these focal clades inferred from phenological trait data, and the gray shaded area indicates average precipitation. Banisteriopsis species tend to flower towards the end of the rainy season. An exception is Banisteriopsis anisandra, which flowers during the beginning of the rainy season and is phylogenetically distinct from the other taxa in the clade.

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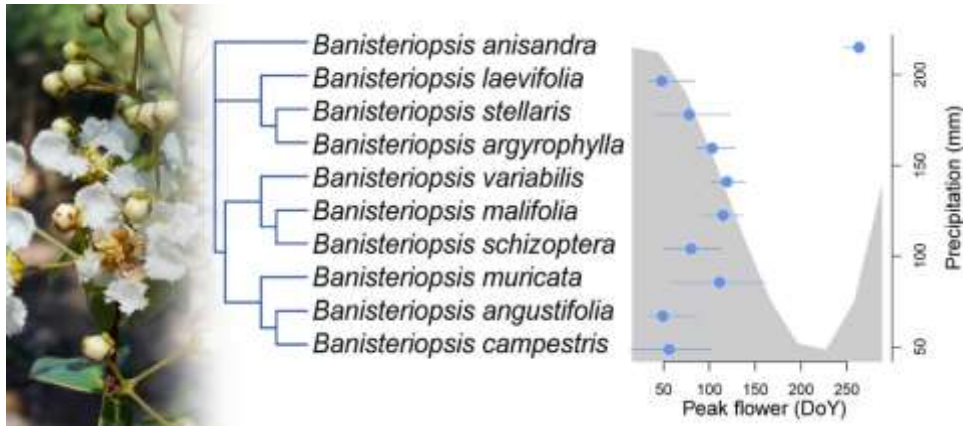
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Outstanding questions

How do patterns and drivers of plant phenological events differ between temperate and tropical regions?

What are the strengths and weaknesses of herbarium-derived phenology data compared with long-term ecological monitoring datasets?

How do we best implement crowd- sourcing methods to gather data that can be used to train machine-learning models for fully automating and accelerating data acquisition from herbarium specimens?

How do we best harmonize the range of phenological data types – including herbarium data, forest inventories, and near-Earth remotely-sensed imagery – to yield a more complete picture of phenological response?

Are phenological events and their responses to climatic change phylogenetically conserved, and what is the range of variation in phylogenetic conservation across space and taxa?

generic or species-level resolution and limited taxon sampling [62,66,67,71]. Ecologically impor- tant taxa in the tropics have in many cases radiated rapidly, and their evolutionary histories can be difficult to infer [72]. When applied to ecological studies, trees with low phylogenetic resolution may mask significant patterns by reducing statistical power [73,74] or even suggest significant phylogenetic patterns that do not exist [75]. Moreover, there is greater phylogenetic diversity in the tropics, which may be strongly associated with the diversity of phenological strategies observed there. Furthermore, even more robust phylogenies may still include hundreds to thousands of species for which there are minimal or missing trait data, phenological or otherwise [76]. This is a particular problem for tropical taxa, for which there are far fewer phenological trait data even for species whose evolutionary history has been identified.

In sum, at regional and larger geographic scales in both the temperate zone and the tropics, the importance of phylogenetic conservation in phenological responses remains an open hypothesis to be tested, yet is a crucially overlooked covariate in the analysis of these data. Only expanded sampling to achieve broad phylogenetic richness at shallow and deep timescales will yield the data required to determine the relevance of phylogeny and phenology in large clades of tropical plants. High-throughput sequencing of DNA from herbaria will greatly expand the current scarcity of tropical samples [77–79]. Finally, we emphasize that testing predictions from pheno- phylogenetic studies based on herbarium data will require field observations and experiments. Such observations and experiments will also help to identify the genetic and developmental bases of phenology in tropical plants. For example, better characterization of periodicity, develop- mental transitions, and phenological duration applying our proposed framework (Figure 1) can help guide when genomic sampling should proceed (e.g., RNA sampling) to inform on the nature and degree of regulatory changes that take shape at the genomic level. These data will in turn help to test whether phenotypic plasticity or evolution contributes most to short-term phenological responses to climatic change.

Concluding remarks

New tools and directions promise breakthroughs in our understanding of patterns of tropical plant phenology and the processes driving them. A key to bridging this longstanding im- passe is to break free of the temperate phenological paradigm that has been applied uncrit- ically to diverse tropical systems. While none of the tools or approaches we describe are new to the field of phenological research, we believe that, when used together, they offer strong potential for advancing our understanding of tropical phenology (see also Outstanding questions).

Newer circular statistical models help to better visualize and understand drivers of phenological events, but they still need to be applied more broadly and uniformly to advance studies of phenol- ogy in tropical and temperate systems. Furthermore, digitized herbarium species can massively expand the data available to more comprehensively assess phenological responses to climate and climatic change in the tropics. These efforts will continue to improve as collections become more available online and phenological data gathering is automated via machine learning trained by crowd-sourced data. Finally, phylogenetic data remain underutilized, but are crucial to more accurately assess and interpret phenological patterns and processes, and to better forecast future change.

Acknowledgments

Declaration of interests

No interests are declared.

Supplementary information

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