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Cascading effects of climate change: new advances in drivers and shifts of tropical reproductive phenology

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Abstract
Tropical forests were long viewed as relatively stable systems, with little biologically important variation in climate. However, in recent years, accumulating evidence has suggested that tropical forests vary widely both in climate and phenology, that climate and phenology are inextricably linked, and that tropical forests increasingly display the effects of climate change. It is critically important to understand these climate-phenology interactions to be able to predict the cascading impacts on resource availability that will affect wildlife. There are many important and unanswered questions regarding how the mechanistic drivers and proximate cues of tropical forest reproductive phenology will vary in response to environmental change. Addressing these questions remains a huge challenge due to a paucity of long-term comparable data that hampers our ability to connect observed phenology patterns with fundamental theory. In this review, we highlight ten focal papers that have advanced our ability to identify phenological patterns, improved our understanding of the drivers of flowering and fruiting, and have innovatively linked fruiting patterns with impacts on wildlife diet, reproduction, and survival. We end with a call for increased collaboration among forest and wildlife ecologists, theoretical ecologists, meteorologists, and decision-makers to advance and apply phenological research in the tropics and reduce the negative impact of climate change on vital ecological functions, and services, of tropical forest ecosystems.

Keywords Tropical forests · Phenology · Climate change · Forest function · Cue · Driver

Introduction

Tropical forests are global centers of biodiversity and carbon storage (Sullivan et al. 2017) and are home to over half of the earth's vertebrate species (Pillay et al. 2022), many of which are frugivores. Understanding how these tropical ecosystems will respond to current and future climatic changes is a major challenge in ecology (Malhi et al. 2020). In response to changing environmental conditions, tropical plants may either shift the allocation of resources away from reproduction and toward growth or alter the timing of life cycle events, both of which may have cascading impacts on other species. For example, the timing of leaf production, flowering, and fruiting in trees (i.e. the phenology or the timing of major life cycle events) can affect food availability for consumers, which can lead to changes in the distribution, behavior, and survival of wildlife species relying on tree resources (van Schaik et al. 1993). Such shifts may be particularly consequential for biodiversity and ecosystem function if they occur out of sync with the environmental variables that are particularly important to consumers. Yet, we know relatively little about potential phenological responses to climate change because it is challenging both to identify phenological patterns in the tropics, and to determine the environmental cues and drivers that drive

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these patterns. Thus, it is difficult to predict the impacts that climate change-driven phenological shifts will have on fruit availability and tropical frugivores.

Much of the difficulty in identifying phenology patterns and their drivers is because the concept of tropical forests as aseasonal ecosystems with abundant unconstrained resources is prevalent when viewed through the lens of temperate phenology. Tropical forests have a great diversity of reproductive phenological patterns (Sakai 2001). In comparison with temperate areas, the tropical growing season is less constrained, because there is no freezing winter, thus temperature and solar irradiance remain relatively high throughout the year. Reproductive events can therefore occur at many and various times of the year, as trees potentially have access to the resources needed for fruiting and flowering. This wider "phenological space" may allow for more and different types of abiotic and biotic relationships to affect phenology in the tropics (Newstrom et al. 1994; Sakai 2001; Abernethy et al. 2018; Sakai and Kitajima 2019), and for a diversity of trophic interactions to exist in tropical ecosystems (Terborgh 2015).

The temperate phenology perspective has also contributed to a lack of comparable data across sites quantifying the particular kinds of environmental variation that constrain resource availability and phenology for tropical plant species (Abernethy et al. 2018). For example, many tropical forests do experience seasonal variation in climate-resource constraints. These constraints could take the form of a dry season (Allen et al. 2017), analogous to freezing winter temperatures that limit water uptake in temperate plants, or variation in insolation that results from cloud cover limiting light availability during the rainy season. There are only a handful of medium -to long-term climate and phenology datasets, from very few key sites. For example, a review of Neotropical fruiting phenology found that only 10 out of 218 phenology studies conducted monitoring for 10 years or more, and that phenology studies across the region were spatially clustered around two main areas: the state of São Paulo, Brazil, and Costa Rica (Mendoza et al. 2017). These existing long-term datasets are highly valuable for beginning to understand patterns in tropical phenology. But we need more of these datasets to characterize and explain phenological patterns of plants in tropical forests at various spatial, temporal, and phylogenetic scales.

Many important proximate cues and mechanistic drivers of flowering and fruiting have been identified across the tropics. For example, flowering and fruiting can be determined by temperature (Tutin and Fernandez 1993 in Gabon, Numata et al. 2022 in Malaysia), rainfall (Chen 2018 in Malaysia, Wright and Calderón 2018 in Panama), or solar radiation (Wright & van Schaik 1994 in Panama, Zimmerman et al. 2007 in Puerto Rico and Panama, Borchert et al. 2015 in Costa Rica, Wright and Calderón 2018 in Panama, Chapman et al. 2018, in Uganda). Overall, cues and drivers of phenology are variable, within and across sites and over different time scales and seasonal and climate cycles.

Climate change may affect many of the cues and drivers of reproductive phenology that have been identified to be important in tropical forests. Understanding these impacts can help us to determine which sites, species, and trophic interactions may be more vulnerable to, or better able to resist, climate change. Flower production (Wright and Calderón, 2006) and seed fall (Detto et al. 2018) increased in seasonal moist Neotropical forests in response to ENSO events that alter some of these cues and drivers in El Nino or La Nina years. These natural climate variations are more extreme than normal seasonal climate variation, and thus might give us clues as to how human-caused warming and drying may impact phenology patterns. Climate change-driven environmental shifts will likely result in a variety of phenological responses with ecological effects that are difficult to predict (Chapman et al. 2005) and may have unforeseen impacts on frugivores that rely on available fruit throughout the year (Staggemeier et al. 2017).

Consequently, we urgently need studies that link climate, phenology, and trophic interactions, and to prioritize the maintenance of long-term monitoring in key sites using similar methods and producing comparable tropical phenology datasets. In this paper, we focus on studies that outline recent advances in the study of reproductive phenology in tropical forests, concentrating on ten focal papers (Table 1) that (i) explore the diversity of patterns in tropical reproductive phenology, (ii) outline how environmental drivers and cues determine phenology patterns, and (iii) link phenological patterns that determine fruit availability to trophic interactions that impact wildlife. Uniting these research themes will help us to better identify and predict the cascading impacts of climate change on forests and wildlife in tropical ecosystems.

Section 1. Defining reproductive phenology patterns: insights into methods for tropical ecosystems

Identifying phenology patterns has been a challenge in tropical ecology (Abernethy et al. 2018). A better understanding of both the site- and taxonomic-level variation in phenological patterns is a key factor in being able to identify and understand the ecological and evolutionary drivers of tree reproduction. Together, this information can be used to understand the differences in phenology patterns across sites and species. Additionally, identifying flowering and fruiting patterns can help determine food availability in tropical forests and help identify important trophic interactions between fruiting trees and wildlife species (Butt et al. 2015).

Table 1 Ten focal papers on diversity (group 1), cues & drivers (group 2), and impacts on resources (group 3) of reproductive phenology in tropical forests, highlighting their critical contributions to the field

	Reference	Section	Key contribution	Research agenda item	Methodological improvements
1	Adamescu et al. 2018	Diversity	Explores within-community diversity of phenological patterns	Tropical phenological patterns are often irregular and highly variable. Even if climate seasonality is similar across sites, phenological responses may be different across sites	• Collect standardized phenology data to facilitate cross-site comparisons • Compare sites with similar species compositions to understand phenological variation across space
2	Zalamea et al. 2011	Diversity	Explores species-level phenological patterns using herbarium specimens	Using herbarium specimens to compare phenological patterns of taxonomic groups across sites can help identify large scale drivers, but lack of site-specific environmental data makes it difficult to identify cues	• Collect standardized data on environmental drivers to identify differences between both climate and phenological patterns across space
3	Norden et al. 2007	Diversity	Provides evidence that mast fruiting is a common strategy	Irregular fruiting patterns require long-term data to identify, and may be simultaneously driven by ENSO-related shifts	• Prioritize the continuation of long-term data collection to better understand how longer-timescale climate cycles impact phenology
4	Garwood et al. 2023	Cues & drivers	Explores irradiance and precipitation as drivers of phenology patterns in an ‘aseasonal’ forest	Light and precipitation may simultaneously be important drivers of phenology patterns	• Collect standardized measurements for top-of-canopy light in addition to information on other abiotic drivers
5	Pau et al. 2013	Cues & drivers	Establishes light and temperature as important drivers of flowering phenology	Cloud cover may have variable effects on phenology depending on the local context	• Collect standardized measurements of cloud cover to disentangle the impact of clouds and environmental variables
6	Chen et al. 2018	Cues & drivers	Shows that cool temperatures and low rainfall are flowering cues that trigger flowering	Considering drought and minimum temperature simultaneously may better predict flowering than considering environmental variables alone	• Include multiple environmental variables that could act as cues in models predicting flowering or fruiting timing
7	Wright and Calderón 2018	Cues & drivers	Shows that individual species flower after a heavy rain during the dry-season period	Considering timing of cues may help to predict flowering timing	• Include timing of environmental cues in models predicting flowering or fruiting timing
8	Matthews et al. 2019	Impacts on resources	Explores how fluctuations in fruiting phenology influence chimpanzee feeding behavior	Reduced fruit availability of keystone species during the dry season may change movement and behavior patterns in frugivores	• Identify reductions in keystone fruiting species and link to implications for wildlife
9	Campos et al. 2020	Impacts on resources	Explores the consequences of severe drought on fruiting and flowering phenology and the survival of infant primates	Extreme climate events like drought can have long-term impacts to resources that impact wildlife	• Prioritize study of sites & species to those that may be least resilient to climate events
10	Bush et al. 2020	Impacts on resources	Shows how shifts in fruiting phenology affect elephant body condition	When environmental cues shift incrementally in the long-term, fruit availability may be impacted	• Prioritize predicting changes in fruit availability with cues models (e.g. focal papers 6 & 7), alongside cascading impacts on wildlife

Long-term field studies and advances in Fourier analyses identify tropical phenology patterns

Advances in the methods and models used to identify phenology patterns have been developed over the past few decades. Phenology data is circular by nature (Milton et al. 1982; Davies et al. 1998), because the growing season repeats year after year and a phenological event that happens on 31 Dec in year *t* is much more closely related to 1 Jan in year *t + 1* than to 1 Dec in year *t*. Even so, choosing a starting point for data from the tropics can be more arbitrary than in temperate phenology where there are clearer start and end points to the growing season (Morellato et al. 2010; Staggemeier et al. 2020). Thus, phenological patterns in the tropics can be more irregular and variable than those in the temperate zone and may require techniques such as Moran's Eigenvector Maps (MEMs, Dray et al. 2006) and spectral analysis using Fourier and wavelet transformations (Bloomfield 2000) or Fourier and confidence intervals (Bush et al. 2017) to improve detection of patterns at multiple frequencies and time scales. We must first be able to identify phenology patterns accurately and precisely in order to detect shifts in these patterns over time. Identifying both phenology patterns and shifts is critically important for understanding temporal variability in resource availability for wildlife and identifying keystone fruiting species at specific sites and for specific wildlife species.

Adamescu et al. (2018) compared the flowering and fruiting phenology of tropical trees across Africa by combining several observational field studies across 12 sites. Following Bush et al. (2017), they identified dominant cycles of reproductive phenology and time of year that individual trees bloom and the relationship to local seasonality, documenting a high diversity of reproductive patterns. Climate seasonality was bimodal at most sites, with two wet and two dry seasons each year. Annual cycles of flowering and fruiting were the most common (42% of individuals), followed by sub-annual (35%) and supra-annual (23%) patterns. Traditional circular statistics can mask the detection of non-annual cyclical patterns, and the Bush et al. (2017) method of Fourier analysis helped to uncover diverse phenology patterns and identify the particular timing of flowering and fruiting. The application of this method across the dataset used in Adamescu et al. (2018) emphasizes the need for both innovative analytical methods and long-durations of observational data to be able to detect patterns at different scale and across sites.

Herbaria extend our understanding of phenology data across time, space, and species

Field studies are incredibly valuable, but they have historically been limited by sample size, number of individuals, species ranges, geographic area, frequency of observations, and length of study (Mendoza et al. 2017). Another, more immediate, source of data is to extract phenological information from herbarium specimens that have been collected and preserved, providing information on much longer timescales than is available from observational datasets (see Ouédraogo et al. 2020 for timber species in tropical Africa).

Zalamea et al. (2011) used a continental-scale dataset of herbarium specimens to explore the diversity of species-level phenology patterns within the emblematic Neotropical pioneer tree genus *Cecropia*. The herbarium data covered a wide geographic scale, allowing their analyses to identify phenological variation among sites for species with wide distributions across a range of climates, which is not possible in most observational studies that are geographically limited to one or a few sites. They found that 41% of the 35 studied species (30% of all the 61 species in the genus) had annual flowering phenology, and that sites with annual patterns of precipitation and mean temperature tended to have annual patterns in species phenology. For example, *Cecropia sciadophylla* from regions with annual climate patterns had annual reproduction patterns. However, the relationship between climate and phenology was weaker when looking at *C. sciadophylla's* entire distribution range at different sites with varying climate across the continent. These findings shed light on the variation in within-species variation in phenology–climate relationships at different spatial and temporal scales, and help to explain why the patterns and findings from geographically limited observational studies have not been as similar as expected when exploring phenology patterns and the relationships between phenology and climate using large-scale geographic data.

Despite these advantages, there are several limitations of herbarium-based studies. For example, we can link herbarium specimens that were collected on a specific date and place to the general climate in that time period and location but not to specific weather conditions or cues. This linkage makes it possible to understand some of the drivers of phenology at site-to-continental scales and identify relationships between climate and seasonality that may vary on those scales. However, the use of herbarium specimens restricts analyses of fine-scale patterns of cues, where data on local temperatures or precipitation may be unavailable. Additionally, sterile herbarium specimens are rarely collected, so phenology studies using herbarium data contain few observed zeroes (i.e. observations of the absence of flowers or fruit). As such, all dates that do not have flowering or fruiting specimens collected are usually assumed to be zeroes by default in the analyses. Nonetheless, herbarium datasets can be a valuable complement to phenological field data from tropical sites, allowing us to expand the geographic and temporal scope, especially for taxonomic groups that are limited by the lack of observational field data (Willis et al. 2017).

Community-wide studies highlight within-site differences in phenology patterns and the importance of non-annual phenology patterns in the tropics

Even though annual fruiting patterns are most common in both direct observation studies (Adamescu et al. 2018) and herbarium studies (Zalamea et al. 2011), non-annual patterns, such as mast fruiting and even continuous patterns of reproduction, are often observed across the tropics. Thus, it is necessary to use community-wide studies in a geographically limited area that is subject to the same climate conditions to better understand what drives the diversity of phenology patterns.

Norden et al. (2007) used community-wide seed fall data to show that mast fruiting is a common strategy in a tropical forest in French Guiana. This strategy was initially found in 23% of species, but with the addition of five more years of data, up to 40% of species showed evidence of masting behavior (Mendoza et al. 2018). Mast fruiting has been found at other sites, but in fewer species: for example, < 10% of species observed for four years in the Philippines (Hamann 2004), and < 9% of species observed for twelve years in Costa Rica (Newstrom et al. 1994). Fruiting patterns also vary within species across sites. For example, *Jacaranda copaia* is reported as a masting species in French Guiana (ter Steege and Persaud 1991; Ratiarison 2003), but not in Panama (Croat 1978, p. 956; Jones et al. 2005). This variation in fruiting phenology suggests that species-specific cues and drivers may be dependent on specific climatological factors that vary among local environments.

The El Niño Southern Oscillation (ENSO) appears to affect mast fruiting in many tropical forests (Ashton et al. 1988, Chechina and Hamann 2019 for Asian dipterocarp forests, Wright et al. 1999, Wright and Calderón 2006 for Panamanian forests, and Norden et al. 2007, Henkel et al. 2005, Henkel and Mayor 2019 for Guiana Shield forests), and could explain some of the variation in fruiting patterns within species across sites, because the ENSO effect is likely geographically variable. However, ENSO is only one of a suite of factors that can determine irregular phenology patterns, because examples of mast fruiting in Sumatra and elsewhere in Malaysia do not coincide or link to ENSO cycles (Wich and Van Schaik 2000; Hamann 2004). Further, to detect such phenological patterns often requires longer time series of data, because climate phenomena such as ENSO occur on multi-year cycles (Wright and Calderón 2006). For example, ten years of phenology data did not show any link between mast fruiting and ENSO in the Guiana Shield (Mendoza et al. 2018). Masting phenology may also reflect other selective pressures that affect reproductive success. For mast fruiting, synchronous large fruiting events may satiate seed predators, overwhelming the predator community with more food than they can consume and allowing some seeds to escape uneaten (Silvertown 1980; Zwolak et al. 2022). Alternatively, the high number of canopy trees that die because of ENSO droughts may reduce competition for light and water, conferring an advantage to seeds that germinate and establish as seedlings at the end of the drought (Williamson and Ickes 2002). Since some mast fruiting occurs concurrently with ENSO events, it is likely that these multi-year climate fluctuations play an important role in driving mast-fruiting. However, ENSO-related light availability, seed predator satiation, and ENSO-related seedling release all likely confer an advantage to trees that have mast-fruiting patterns.

Overall, community-wide studies that focus on the presence of irregular phenology patterns that do not line up with seasonal or annual climate patterns call attention to the fact that these patterns are observed across many sites in the tropics. These irregular fruiting patterns may be more difficult to detect with the limited time-scales of phenology data that is currently available. Additionally, these studies indicate that the cues and drivers of these irregular patterns may not be universal across all sites, may be more challenging to identify, and require more site-specific data on longer timescales than is currently available at many sites.

Section 2: Environmental factors as drivers and cues of reproductive phenology

Understanding which factors contribute to the diversity of phenological patterns in the tropics remains a challenge in observational, herbarium, and community-wide studies. These patterns come about because of environmental cues and drivers, which are often difficult to differentiate. Climate change is affecting some of these environmental factors, but not others. Ultimately, these climate shifts may have cascading impacts on flowering and fruiting patterns of trees, and food availability for different wildlife species (Butt et al. 2015). To predict which sites, tree species, and wildlife species might be most affected by or resilient to climate change (Willis et al. 2017; Harris et al. 2022; Park et al. 2023), we need to improve our understanding of the cues and drivers that shape phenology patterns and how climate change-driven shifts will result in changes to both phenological patterns and trophic interactions in tropical forests.

The lack of distinction between cues and drivers in the tropical phenology literature impedes our understanding of cross-site variation in phenological patterns and highlights the importance of including local context in cross-site comparisons. The proximate cues that are tracked by individual plants as triggers for synchronous reproduction within populations (e.g. temperature dips, drought followed by rain, peaks in irradiance, and photoperiod; Wright and Schaik

1994; Borchert et al. 2015; Wright & Calderón, 2018) may or may not be the same as the mechanistic drivers of plant reproduction (e.g. limiting resources such as light and water). Nevertheless, both proximate cues and mechanistic drivers are critical in determining the frequency and regularity with which reproduction occurs in tropical plant species (Newstrom et al. 1994).

Experimental approaches that test which environmental factors affect flowering and fruiting are logistically challenging and often infeasible at the community level (but, see Augspurger 1981; Graham et al. 2003). Observational phenology studies often track different climate variables between sites, and a lack of comparable climate information between sites makes comparison challenging (Mendoza et al. 2017). Additionally, important covarying factors such as light and water availability are often difficult to disentangle at tropical latitudes (Adamescu et al. 2018). And a dearth of information on long-term cycles such as ENSO climate phenomenon and masting phenology patterns hinder our understanding of the cues and drivers of irregular flowering and fruiting patterns that occur across many tropical sites without clear links to the annual or seasonal climate patterns (Williamson and Ickes 2002). To improve future observational phenology studies, consistent climate and phenology data collected from various long-term monitoring sites across gradients of geography and climate is needed.

Drivers

The availability of light and water ultimately enforces physiological limits on tropical plant phenology. Garwood et al. (2023) explored potential limitations of light and water as driving resources in an ever-wet lowland tropical forest in the Ecuadorian Amazon. Because these equatorial forests are typically described as having an aseasonal climate (i.e. no biologically important variation in water availability), and because day length varies only by a few minutes over the year, it has long been thought that phenology here should also be aseasonal. However, over 90% of the species had seasonal flowering and fruiting over 18 years. Furthermore, both top-of-canopy light availability and rainfall were highly seasonal, even though there is no regular dry season. In their study, annual variation in irradiance was the biggest driver, with a community peak of flowering coinciding with the single annual peak in irradiance.

A key aspect of this paper supports top-of-canopy light availability as an important driver of tropical canopy tree phenology (Graham et al. 2003; Huete et al. 2006; Wu et al. 2017). Extensive cloud cover can substantially curtail incoming irradiance, reducing the light that reaches the forest canopy (top-of-canopy). The Garwood et al. (2023) site should experience two peaks in irradiance based on its location and solar angle, but the second insolation peak is dampened at the forest canopy by cloud cover. Additionally, in an innovative experiment in Panama, Graham et al. (2003) installed stadium lights to illuminate canopy trees during periods of cloud cover, proving that even completely exposed canopy and emergent trees can be limited by light availability during cloudy periods.

Complicating the matter further, drought and light are often assumed to be correlated, with fewer clouds and more light available in the dry season. However, in contrast to the temperate zone—where photoperiod is correlated with winter and water is limited by freezing temperatures—this is not the case in many tropical forests. For example, in Gabon and other areas of western Central Africa, a low-level cloud layer is persistent during the dry season (Philippon et al. 2019). Here, the cloudy dry season may facilitate the existence of evergreen forests, because the strong cloud cover reduces the water demands on trees and provides more photosynthetically useful diffuse light (Dommo et al. 2018).

Light is one important example of how climatic drivers can have different effects on tropical forest phenology depending on other co-occurring factors. Pau et al. (2013) considered the simultaneous effects of temperature, light, and precipitation on flower production in two tropical forest sites: a seasonally dry forest on Barro Colorado Island, Panama, and an ever-wet forest in Luquillo, Puerto Rico. Temperature was broadly important and had a positive impact on flower production. However, the effect of light varied: in the seasonally dry forest (BCI), thicker cloud cover limited flower production, whereas in the wet forest (Luquillo), a longer day length and thinner cloud cover were associated with greater flower production. Similar to the recent studies from Ecuador and Gabon, thicker clouds effectively block solar radiation, whereas thinner clouds allow for more diffuse scattered light to reach the canopy.

More light available to trees allows them to allocate more resources to flower and fruit production (Williamson & Ickes 2002; Henkel et al. 2005). However, light can also increase temperature and cause water stress in trees. Other studies find variable effects of light and cloud cover on co-occurring climate variables that impact phenology. In some tropical and sub-tropical forests, clouds can provide important services (García-Santos et al. 2004 in Canary Islands, Spain, Del-Val et al. 2006 in Chile, Bush et al. 2020 in Gabon), because they suppress temperatures and can provide a source of water (Schreel & Steppe 2020). Cloud cover indirectly affects water availability by limiting evapotranspiration, and therefore a light-deficient dry season may be less stressful (Philippon et al. 2019). Cloud cover can also limit carbon dioxide uptake and growth during the rainy season because of reduced irradiance for photosynthesis (Graham et al. 2003). Additionally, ENSO events can reduce cloud cover leading to reduced precipitation, shifts in temperature, and higher light levels. These studies emphasize the need to measure additional relevant climate variables that are not often measured (e.g. light/irradiance) and analyze multiple climate predictors (light, temperature, precipitation) simultaneously across long time-scales. Pau (2013) determined that temperature strongly and positively impacted flowering, and that the impact of light availability was contingent on clouds and other co-occurring climate conditions. In the absence of comprehensive data on light availability (Mendoza et al. 2017) we can easily miss the effect of cloud cover, and therefore light, as a main driver of phenology.

Crucially, a single environmental driver will likely not be the only factor that explains variation in phenology patterns. It is rather a suite of pressures or simultaneous constraints and physiological responses that determine phenology patterns. Assumptions about the patterns and drivers of phenology based on observations from temperate systems have limited this understanding in tropical forests. The importance of disentangling light, water, temperature, and day length in tropical forests with limited seasonality is critical for understanding the links between climate and phenology. Additionally, these focal papers highlight how climate change-driven shifts in the environmental drivers may result in augmentation or reduction of available fruit in tropical forests, which will have cascading impacts on wildlife (Butt et al. 2015). Understanding how environmental factors determine fruit availability is vitally important for wildlife populations and can improve wildlife management strategies.

Cues

Across tropical forests, a variety of proximate cues synchronize reproductive activity with temporal variation in resources, and these cues can vary among species within the same forest (Chen 2018). Potential proximate cues include temperature dips, seasonally sufficient moisture availability, drought followed by rain, solar irradiance, and photoperiod (Wright & Calderón, 2018). Cues in the tropics can be more difficult to identify than in the temperate zone, because at northern and southern latitudes, photoperiod, temperature, and water availability are often geographically and temporally correlated, and because these cues can vary based on ENSO climate cycles on longer-than-annual timescales. In the tropics, the growing season is less well defined and may not even be annual (Knoben et al. 2019). An understanding of the condition (or combination of conditions) that occurs before flowering is needed to identify cues in the tropics that may be temporally decoupled from resource availability (Yeang 2007; Calle et al. 2010; Borchert et al. 2015).

To address this knowledge gap, Chen et al. (2018) developed a model to identify species-specific flowering cues in *Shorea* species using 13 years of weekly flowering records and daily precipitation and temperature records from a Malaysian tropical forest. Minimum temperature and length of drought were hypothesized to be important, but those factors alone did not explain flowering. However, a model which considered the thirty-day running mean values of minimum temperatures and length of drought simultaneously was much better at predicting the timing of flowering initiation. Therefore, this study points to the importance of considering the synergistic effects of multiple climate factors and the sequential order in which these factors occur.

In addition to less covariation in climate, patterns of flowering in the tropics are also often more complex than in the temperate zone. We can predict first-flowering dates with good accuracy for non-tropical plant populations that flower once each year (Chuine and Régnière 2017). However, in tropical forests, species may flower multiple times a year (Zimmerman et al. 2007) during the less-defined growing season, rendering predictions of first-flowering dates more complex. Thus, predicting first-flowering dates for tropical tree species requires both phenological and meteorological data at high temporal resolution and frequency. Wright et al. (2019) were able to identify cues and create a model that predicts flowering, using 29 years of very fine resolution data: daily climate and weekly flowering records for two species (*Hybanthus prunifolius*, Violaceae, and *Handroanthus guayacan*, Bignoniaceae) on Barro Colorado Island, Panama. These models were able to capture a temporal sequence of environmental cues that occurred before flowering: a period of an unfavorable environmental condition (e.g. drought), followed by a break of the unfavorable condition (e.g. rainfall), and finally the lag time between the shift in environmental conditions and first-flowering. Their models also predicted the proportion of individuals flowering in each census, rather than first-flowering dates, information that is more relevant for the type of phenology data collected via weekly seed trap censuses.

Overall, considering combinations of climate factors and their order and synchrony to determine the cues that trigger flowering allows us to predict when flower initiation will occur. The prediction of the timing of flowering and fruiting is especially critical for keystone fruiting species that wildlife rely on during times of the year where the forest is otherwise depauperate of calorie- or nutrient-rich food sources (Messeder et al. 2020). Being able to identify and predict climate change shifts in the timing of fruiting can inform wildlife management strategies, because animal movement, behavior, and survival and mortality may shift if fruits are not available at critical times. These analyses require both long-term and high-resolution climate and phenological data as the only way to identify cues.

Section 3: Effects of seasonality and climate change on phenology: trophic cascades

Climate change is affecting many of the cues and drivers of reproductive phenology in tropical forests: duration and intensity of rainfall (Feng et al. 2013), frequency and intensity of droughts (Corlett 2016), and duration and thickness of cloud cover that mediates top-of-canopy irradiance (Garwood et al. 2023). These changes have already altered the species and functional composition of some tropical forests (Fauset et al. 2012; Aguirre-Gutiérrez et al. 2020) and have been documented to impact phenology in several tropical sites. Cues and drivers of phenology are variable within and across sites, which is likely to result in a variety of phenological responses with unforeseen ecological effects (Chapman et al. 2005), especially on the frugivores that rely on available fruit throughout the year (Staggemeier et al. 2017).

The impacts of climate change on phenology are likely to have profound effects on community composition, structure, and function, as well as on other organisms that depend on plant communities. Evidence of phenological mismatch between plants and their pollinators or dispersers is clear in temperate and arctic ecosystems (Renner and Zohner 2018) and is likely in the tropics. Since tropical phenology is more complex and less well understood, it is still unclear exactly how these biotic interactions will respond to climate change. Some cross-site studies have prompted a re-evaluation of existing hypotheses and assumptions about the underlying drivers of trophic interactions. For example, Federman et al. (2017) found that a Malagasy forest had similar fruit availability and climate predictability as a mainland African forest, contradicting the energy frugality hypothesis which suggests that Madagascar has an unpredictable climate, unreliable fruiting patterns, and thus few obligate seed dispersers because fruit resources are not always available (Wright 1999). Additionally, Butt et al. (2015) predicted that in the tropics food availability will be less temporally and spatially consistent, and that animals will need to travel further to obtain sufficient food, than in temperate forests. The authors recommended a robust investment in research to better understand how climate change will affect phenological activity, biotic interactions, and trophic cascades.

Seasonality/interannual climate variation and reproductive resource allocation

Climate change and subsequent impacts on the seasonality of reproductive phenology may have stark implications for the availability of food resources that underlie many trophic interactions. A shift in the allocation of resources by trees away from reproduction can affect the availability of food in tropical forests and have cascading effects on the animals that depend on flowers, fruits, or seeds. Matthews et al. (2019) observed chimpanzees feeding in Nyungwe National Park, Rwanda, and found that fruit, especially figs, were abundant in chimpanzees' diets during the dry season, indicating the importance of dry-season fruits as a key resource for these primates during a period of otherwise low resource availability. In contrast, other plant parts (leaves, bark, and twigs, and terrestrial herbaceous plants) and flowers were observed to be eaten throughout the year. If the timing or abundance of fruiting in key tree species is affected by climate change, animals that depend on those fruits to survive during the dry season may be impacted.

Changes to animal behaviors can occur when nutritious and energy-dense preferred foods such as fruits become limited. For example, animals may switch to foraging on alternate foods, such as seeds and vegetative plant parts to compensate for the lack of fruit, or restrict traveling to reduce energy demands from foraging (Nagy-Reis and Setz 2017). Additionally, reduced fruit production may have population-level effects on animal reproduction for species that exhibit risk-averse breeding strategies and strategically time their own reproductive phenology (e.g. copulation and conception events) with habitat-wide increases in available fruit (Ellis et al. 2021). Seasonality is therefore an important factor shaping the relationships between climate, fruit production, and animal foraging, movement, and reproduction. Future work should examine how the effects of climate change on tropical plant phenology may alter these trophic interactions.

Climate shifts: drought and long-term warming and drying

In addition to shifts in seasonality, extreme events such as drought can reduce resource availability in forests. Campos (2020) illustrated the consequences of severe drought on fruiting and flowering phenology and how this effect ultimately determines the survival of Neotropical primates. They found that infant capuchin monkeys had very high mortality rates during intense droughts but not during moderate droughts, indicating that there is a threshold of drought tolerance that these infants are able to endure. Similarly, spider monkeys stopped reproducing during severe drought, and infant mortality peaked during periods of low fruit abundance when fruit trees died due to drought. The death of a fruiting tree could have long-term implications for local populations of seed dispersers, in particular for less mobile dispersers or dispersers that have fewer alternative food sources.

This study underscores the importance of species-specific responses and interactions. Tree species have specific responses to climate change based on the drivers and cues of their phenology patterns. Additionally, animal species have specific foraging strategies, range distributions, movement patterns and habitat use, copulation and reproduction phenology, and strategies for infant care. How each animal species adapt to intense climate stress events, and what tolerance thresholds they exhibit in response to climate change and the cascading effects on flowering and fruiting phenology and resource availability will vary between animal species and the tree species they depend on for food, across sites and regions.

Long-term climate shifts can also have powerful consequences on trophic interactions in tropical ecosystems. Bush et al. (2020) showed that over 32 years (1986–2018) fruit production in a rainforest in central Gabon declined by 81%, coincident with a 10-year decline in the body condition of forest elephants (2008–2018). This occurred simultaneously with a period of long-term drying and warming (Bush et al. 2020). The decline in fruit production suggests that some trees rely on a minimum temperature threshold as a cue to start fruiting (the minimum temperature hypothesis, Tutin and Fernandez 1993), although the decline might also be explained by trees suffering water stress.

This study reflects the importance of studying climate over the long term and illustrates the impacts that shifts in climate may have on ecosystem structure and function. If fruit availability drops in such a way that animals do not have enough food to maintain their populations, individuals will suffer and population reductions or local extinctions are a risk. Animals affect seed dispersal, habitat structure, and carbon stocks in forests, and also compete with humans for food. Declining fruit availability in forests where megafauna exist might not only change forests, but also exacerbate food security and human–wildlife conflict (Ngama et al. 2019). Future studies should leverage long-term phenology and meteorological data to better understand long-term drying, loss of minimum temperature cues, and other slow-occurring climate impacts. Predicting the sites and species that will be most strongly affected by these shifts in trophic interactions is vital to prioritize conservation and management policies and resources.

Conclusion and recommendations

Several key ideas emerged from our review of the drivers and cues of tropical reproductive phenology patterns and how they will be affected by climate change. First, we recognize both the value and challenges of studying tropical phenology. To understand these phenological patterns, researchers in this discipline have been using observational field datasets (crown observations or traps) and data from herbaria in order to compare relationships between phenology and seasonal climate variation across species and sites. Moving forward, researchers will have to fill gaps in phenology and climate data, prioritizing long-term and cross-site phenology data, to better explain the diversity and complexity of reproductive phenology across the tropics. Additionally, longer-term climate variation (e.g. ENSO) and other ecological and evolutionary factors (e.g. biotic interactions) acting concurrently or sequentially are also likely to shape tropical phenology. More research into how these phenomena interact with seasonal climate drivers of phenological patterns will further improve our understanding.

Next, ensuring that both the climate and the phenology data are equivalent across sites is paramount. In the absence of comparable data, we are unable to identify how resource availability drives phenology patterns or how cues trigger reproductive timing. This comparable data is needed on a variety of scales. Small-scale weather variation is particularly needed to identify cues that can be site-specific, even within taxa. One challenge here is that cues are not always easily identifiable by observation alone, perhaps because they occur sequentially rather than simultaneously. Both long-term and site-specific comparable phenology and climate data are needed to develop models that can identify these cues.

Finally, the cascading impacts on trophic interactions with animals will be very diverse and specific. Animals vary widely in their behaviors such as foraging, range, habitat use, copulation, reproduction, and infant care. In worst case scenarios, when climate change leads to reduced fruit availability and shifts in animal behavior, we may see reductions in wildlife population sizes, and possibly local extinctions. Clearly, research that combines both plant and animal responses to climate change is needed. These data can inform conservation and management strategies and help better predict and understand where reduced fruit availability may cause threats to animal populations and identify where management resources are most needed.

Our review represents a timely attempt to link climate, phenology, and impacts on wildlife. The research from these focal papers has improved our understanding of the complexity of climate–phenology interactions. But, more empirical work is needed to understand the overall impact that shifts in climate will have on tropical phenology and the cascading impacts on wildlife. A unified research agenda would help drive research forward, address knowledge gaps, and foster cross-disciplinary links among scientists. This research agenda should focus on (i) uniting the current long-term phenology sites to facilitate cross-site comparisons and identify large-scale environmental drivers of tropical phenology, (ii) standardizing the collection of both phenology and environmental data across sites, and prioritize adding data on top-of-canopy light availability and cloud cover to models of phenology, (iii) using predictive models to identify environmental cues using information about drought, minimum temperatures, and the timing of these factors between different sites, and (iv) using information about environmental cues and shifts in climate to identify potential forest-wide collapse in fruit production, and to disentangle the highly specific and variable interactions of climate, phenology, and trophic cascades. With this information, we could answer questions such as: how do top-of-canopy light and cloud cover impact tropical phenology across sites? How does the timing of simultaneous and/or sequential environmental shifts explain flowering? Which sites may be at risk of reduced fruit availability based on their environmental cues and predicted climate shifts? Which animals are most at risk from reductions in fruit availability? This research agenda requires climate, phenology, and wildlife scientists to work together to maintain long-term monitoring of key phenological and climate variables in key sites around the globe.

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Declarations

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