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SPECIAL FEATURE

Phenology in the tropics: Ultimate causes and physiological controls revealed by long-term monitoring and predictive models

Tropical phenology: Recent advances and perspectives

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Tropical phenology is characterized by its high diversity. Lacking a cool season that restricts growth, phenological cycles vary from species that reproduce multiple times per year to those that reproduce only once in several years even within a community. As such, environmental cues of phenological events are more diverse among species and communities of tropical organisms compared with those in higher latitudes. Community-wide phenological patterns differ among regions that differ in climate patterns and biogeographical backgrounds. These patterns are increasingly revealed as long-term phenology data accumulate especially for tree species at long-term monitoring sites. Advances in analytical methods applied to sufficiently long-term data sets generate novel insights. Long-term data are also critically important for understanding how climate changes affect phenological patterns and consequently species interactions and biological diversity. Particularly important is to understand how changes in drought regimes, both in terms of frequency and intensity, may affect plant phenology, and consequently have cascading impacts on tropical forest communities. To effectively link phenology studies and management of tropical forests and their ecosystem services in future studies, we should not only continue observation at existing sites, but also expand monitoring sites across regions, including ecosystems modified by human activities.

KEYWORDS
climate change, drought, long-term monitoring, time-series data, tropical phenology

1 | PHENOLOGY IN TROPICS: RESEARCH HISTORY AND KEY CHARACTERISTICS

Phenology, that is, the temporal patterns of biological activities in response to annual and multi-year fluctuations of environmental factors, has been studied by people throughout history, as it indicates timing for hunting, gathering and agricultural activities (Demarée & Rutishauser, 2009). Scientists, predominantly researchers of temperate ecosystems, have documented seasonal activities of individual organisms and communities. They have studied both proximate cues (environmental factors, such as changes in day length, temperature and rainfall that cue specific biological activities by affecting gene expressions) and ultimate causes (evolutionary advantages and disadvantages associated with a particular phenology pattern). It is commonly believed that each population of animals and plants exhibits seasonal patterns of growth and reproduction in a manner adaptive to its current environment. As such, the relevance of phenology as a scientific topic is as significant as ever in the context of understanding climate change impacts on ecosystems (IPCC, 2014).

How and why plants and animals behave under continual warmth and moisture has been the most fundamental question in tropical phenology, as evident in the edited volume by Leigh, Rand, and Windsor (1985) "The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes." At higher latitudes where unfavorable seasons for growth, such as winter or a long dry season, occur annually, a clear one-year cycle is observed, and we rarely question why this is. In the tropics without winter, should they continuously grow and reproduce throughout the year or have annual cycles? The answer depends on the level of organization at which phenology is observed, species and locations (Newstrom, Frankie, & Baker, 1994; Sakai, 2001). Even if all individuals regularly flower once a year, flowering at the population level can be continuous without a clear peak if individuals flower asynchronously and sequentially (Newstrom, Frankie, Baker, & Colwell, 1994). Within a tropical forest, species differ in phenological patterns, and phenological patterns at the community level differ among regions (Sakai, 2001). Thus, we need sufficiently long records across multiple levels of organization to cover diversity of phenological patterns in the tropics.

Given the high diversity of phenological patterns and small annual changes in day length and temperature in the tropics, tropical ecologists searched for proximate factors that may explain phenological changes (van Schaik, Terborgh, & Wright, 1993). In higher latitudes, changes in temperature and day length are the cues for phenological events, while in the tropics, drought, rain and high solar insolation are more likely candidates for the proximate cues (van Schaik et al., 1993).

2 | ACCUMULATION OF LONG-TERM DATA

The first hurdle of phenology research is to maintain observations or sampling over a sufficiently long duration with regular intervals, preferably along with monitoring of meteorological factors. Global recognition of the importance of long-term ecological research has helped generate such data during the last three decades in several key research sites, despite the challenge of securing continuous funding and human resources. El Nino Southern Oscillation (ENSO), which involves supra-annual fluctuations of sea surface temperature and atmospheric pressure over the Pacific Ocean, affects temperature, precipitation, solar radiation and phenology in many tropical forests (Ashton, Givnish, & Appanah, 1988; Detto, Wright, Calderón, & Muller-Landau, 2018; Morellato, Camargo, & Gressler, 2013; Sakai, 2002; Wright, Carrasco, Calderon, & Paton, 1999). While the majority of empirical studies on supra-annual patterns of phenology associated with ENSO come from America and Asia, tropical forests in Africa also show significant influence of ENSO (Adamescu et al., 2018; Chapman, Valenta, Bonnell, Brown, & Chapman, 2018). Given the strong influence of ENSO cycles on supra-annual phenological events, observations that encompass multiple ENSO cycles (e.g., >10 years) are necessary. Analyzing flowering cycles in Gabon, Bush et al. (2017) report that at least 6 years of data are needed to confident detection of the least noisy species, and >20 years for the most noisy species.

Most long-term phenology datasets are those of plant communities monitored by direct observation of individual plants (e.g., Sakai et al., 2006) or by litter traps (e.g., long-term data analyzed for Asian forests by Nakagawa, Ushio, Kume, & Nakashizuka, 2019; Niiyama et al., 2019; Chen et al., 2017; Kitayama, Ushio, & Aiba, 2018). In contrast, similarly long studies of insects and other animals are comparatively rare (e.g., Kishimoto-Yamada et al., 2009; Wolda, 1992 for light-trap monitoring of insects). The duration covered by a phenology dataset is crucial. But, long-term datasets of more than 10 years are still exceptions. Mendoza, Peres, and Morellato (2017) in their review of 218 phenology datasets from the Neotropics report that only 10 sites have studies that lasted for more than 10 years. But, long-term studies are increasing, along with studies using automated monitoring systems, such as satellites or fixed-point cameras (Adole, Dash, & Atkinson, 2016; Alberton et al., 2014; Moore, Beringer, Evans, Hutley, & Tapper, 2017). It is still challenging to apply remote-sensing technologies to evergreen forest canopies with little variations in color spectra, compared to similar efforts to analyze temperate grasslands and deciduous forests, but newly developed methodologies have improved monitoring techniques (Alberton et al., 2017; Albrecht, Riesen, & Schmid, 2010; Nagai et al., 2016; Wu et al., 2018). Such approaches are expected to reduce the logistical costs of monitoring and extend the spatial dimensions of observation.

3 | NEW TOOLS TO ANALYZE PHENOLOGY DATA

Recent advances in analytical methods have started to overcome challenges of describing diverse phenological patterns, as well as associations between phenological events and environmental variables (Abernethy, Bush, Forget, Mendoza, & Morellato, 2018). The most straightforward way to deal with the phenological diversity is to categorize patterns based on frequencies and other criteria (e.g., Gentry, 1974; Newstrom, Frankie, & Baker, 1994). These criteria often differ among studies; however, comparison of the patterns observed by different authors may be possible if the criteria are clearly described (Sakai, 2002). More sophisticated methods include circular analysis, although it must assume the cycle of one year (Morellato, Alberti, & Hudson, 2010). It is frequently used to measure the degree of synchronization among individuals, predictability and timing of the event on a calendar date. If one wants to detect the periodicity, which may not necessarily be annual in the tropics, Fourier analysis is useful (Bush et al., 2017, 2018). This analysis enables us to quantify the periodicity of different lengths in phenological patterns and statistically evaluates their significance (e.g., Chapman et al., 2018; Kitayama et al., 2018; Nakagawa et al., 2019). Fourier analysis does not directly show frequency or timing in relation to the calendar dates, so circular analysis and Fourier analysis are complementary rather than alternative methods. One has to choose the most appropriate method depending on the purpose and the data characteristics.

Associations of phenological patterns with climate variables have been the focus of many tropical phenology studies (van Schaik et al., 1993). Time-series data including periodically recorded phenology and climate data typically violate the assumption that all ordinate values on the *y*-axis should be mutually independent, as there is usually a high positive autocorrelation between consecutive observations. Therefore, a simple correlation test should not be used. Without proper statistical techniques or modeling framework, potential triggers have sometimes been suspected on the basis of the visual inspection of the temporal patterns of flowering events and climate variable changes (Sakai et al., 2006).

With new modeling frameworks to test alternative hypotheses, it is possible not only to evaluate the individual cues, but also to examine multiple cues that may work sequentially. In order to investigate climate conditions that trigger flowering, Satake, Chen, and Kosugi (2019) and Wright, Calderón, and Muller-Landau (2019) construct models to investigate associations between flowering events and climatic conditions. Chen et al. (2017) and Satake et al. (2019) report that drought and cool temperature variations within a 2–3-month period synergetically trigger flowering of emergent trees in genus *Shorea* in a SE Asian rainforest. Wright et al. (2019) conclude that precipitation > 5 mm per day for a few days after a period (~40 day) of dryness triggers flowering of two woody species in a seasonal Neotropical forest. The good correspondence between the predictions by their models to data demonstrates that they are promising approaches.

Application of molecular tools is becoming increasingly popular in ecological studies, including phenological investigations of wild plants (Aikawa, Kobayashi, Satake, Shimizu, & Kudoh, 2010; Kobayashi et al., 2013; Kudoh, 2016; Yeoh et al., 2017). There is always a long time lag between flower induction by the climatic cue and recognizable flower development in the field. Such time lag obscures the association between the cue and response. Gene expression analysis, however, allows immediate detection of plant responses. Identities of genes that respond first to the trigger give further clues about what environmental factors are likely cues. Molecular approach may also enable analyses of regional variations in the molecular basis in threshold involved (e.g., temperature threshold difference between warm and cold climate zones), and reconstruction of evolutionary trajectory of phenology patterns at the macroevolutionary level (Kudoh, 2016).

4 | EFFECTS OF CLIMATE CHANGES

How global, regional and local climate changes affect phenology and ecosystem functions, is an urgent research question recognized by many. In mid to high latitudes, phenological shifts are already evident, especially in terms of growing season lengths (IPCC, 2014). Species differ in their responses to temperature regime shifts, and such differences may lead to mismatches of phenological events among interacting species and seriously impact their reproduction and survival (Kudo & Ida, 2013; Ovaskainen et al., 2013). On the other hand, limited information suggests that temporal mismatches between plants and animals rarely have had serious cascading effects, at least in aseasonal tropical forests, because population dynamics are stochastic (Kishimoto-Yamada et al., 2009) and interactions between plants and animals are diffused and not sufficiently specific (Kishimoto-Yamada et al., 2013).

While the degree of climate warming in the tropics may not be as much as in higher latitudes, we should pay close attention to the effects of climate changes in the tropics. The tropics are projected to experience climatic conditions that have not existed for tens of millions of years into the past (Garcia, Cabeza, Rahbek, & Araújo, 2014). Pau et al. (2013) have suggested that tropical plant phenology may respond to even slight temperature increases, but there may be large regional variations. In the Neotropics, plants produce more flowers in warmer (and sunnier) years (Wright et al., 1999). In contrast, rising temperatures may reduce the frequencies of supraannual general flowering in SE Asian dipterocarps, because a temperature drop together with a dry spell is a likely trigger of flowering (Chen et al., 2017). If phenology is also controlled by the physical conditions of the plant, such as accumulation of limiting resources over multiple years (Ichie & Nakagawa, 2013; Kitayama, Tsujii, & Aoyagi, 2015), phenological changes in response to climate changes may be more complicated. To elucidate how plants plastically respond to climate changes, comparing phenology patterns of the same or closely related species across sites with different climatic conditions would be useful (Kurten, Bunyavejchewin, & Davies, 2018), considering that it is usually very difficult to experimentally control potential flowering triggers for large tropical trees.

In tropical and subtropical regions, changes in the range (maximum and minimum) and frequency of temperatures and precipitation extremes, rather than the averages, might have strong effects on tropical phenology (Butt et al., 2015; Garcia et al., 2014). Climate models predict that in the tropics ENSO will remain to be a dominant mode of interannual variability in the future, and ENSO-induced rainfall variability is considered to be intensifying (IPCC, 2014). In particular, droughts may be further intensified by landcover changes, as deforestation and forest degradation cause reduction in evapotranspiration, and lead to a decrease in precipitation in forests (Malhi et al., 2008; Takahashi, Kumagai, Kanamori, Fujinami, & Hiyama, 2017).

We have already witnessed cascading impacts of extreme droughts (Butt et al., 2015); in Borneo, a prolonged drought associated with El Niño in 1998 caused a substantial break in the production of inflorescences in dioecious figs. Their fig-wasp pollinators have very short adult lives and hence are dependent on the near-continuous production of inflorescences at the population level. The break led to local extinction of the pollinators and continuous failure of fruit production by the figs (Harrison, 2000). On the other hand, after the drought, an explosion of the moth population was observed; plants, which could not renew leaves during the drought produced new leaves all at once, and this leaf flush resulted in a rapid increase of lepidopteran larvae that fed on new leaves (Itioka & Yamauti, 2004). In Panama, the year of low fruit production (during the La Niña phase) that followed a dry El Niño year with a bonanza crop starved fruigovorous mammals (Wright et al., 1999). Other anthropogenic effects, such as fragmentation of the forest, may delay or hinder re-colonization of locally extinct animals and plants from outside of the forest, which are needed for recovery of the community from the extreme events.

5 | CONCLUSION

Tropical forests provide diverse ecosystem services to local and global communities, but they are critically threatened by deforestation, forest degradation and forest fragmentation (Gibbs et al., 2010; Lewis, Edwards, & Galbraith, 2015). For sustainable management of the tropical forests and their ecosystem services, better understanding of proximate and ultimate causes of the phenological patterns of forest regeneration, interspecific interactions and material cycling is essential. Long-term datasets, produced by immense investments of time and effort by scientists in several key long-term research forests, are still rare, but are increasingly reported from Neotropical and African forests (e.g., Chapman et al., 2018; Wright & Calderón, 2018), and some such data sets from SE Asian forests are reported for the first time in this special issue (Nakagawa et al., 2019; Niiyama et al., 2019). We now have improved analytical tools to handle big data on phenology. To effectively link these phenology studies and management of tropical forests and their ecosystem services, we should not only continue observations at each site, but also extend monitoring areas, so as to encompass natural forests under different climatic conditions, disturbed forests, and heavily modified ecosystems such as plantation forests. Multi-pronged research efforts are necessary in order to achieve such ambitious networks of phenological observations. Some key attributes of successful phenology monitoring network include data exchange and collaboration among researchers, and development of common and inexpensive monitoring methods, as well as capacity building within tropical countries.

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