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Current Issues in Tropical Phenology: a synthesis

Katharine Abernethy*, Biological and Environmental Sciences, University of Stirling, UK and Institut de Recherches en Ecologie Tropicale, CENAREST, Libreville, Gabon.

Emma R. Bush, Biological and Environmental Sciences, University of Stirling, UK

Pierre-Michel Forget, Museum National d'Histoire Naturelle, Département Adaptations du Vivant, UMR MECADEV 7179 CNRS-MNHN, Brunoy, France

Irene Mendoza, Universidade Estadual Paulista UNESP, Instituto de Biociências, Departamento de Botânica, Laboratório de Fenologia, Rio Claro, São Paulo, Brasil

Leonor Patricia C. Morellato, Universidade Estadual Paulista UNESP, Instituto de Biociências, Departamento de Botânica, Laboratório de Fenologia, Rio Claro, São Paulo, Brasil

*corresponding author, k.a.abernethy@stir.ac.uk

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PHENOLOGY, OR THE TIMING OF RECURRENT BIOLOGICAL EVENTS and the causes of their occurrence (Lieth 1974), is such as obvious part of the way in which ecosystems function around us that it was barely considered as a scientific discipline until the beginning of the past century (Fig. 1). People inherently knew (to a degree of accuracy they deemed sufficient) when grass would rise or harvests should be gathered. Only exceptionally, and rather as a pastime, did anyone empirically monitor these recurrent cycles, or suspect them not to be regular and reliable (Aono & Kazui 2008, Sparks & Carey 1995). However, phenology has gained significance for the global research community this century as we endeavor to provide explanations for, and to understand the consequences of, the ecosystem changes taking place in response to a changing climate (e.g. Butt *et al.* 2015, Harrington *et al*. 1999, IPCC 2015, Rosenzweig *et al.* 2007).

Our recent awareness of global change has not only inspired ecologists to quantify shifts over time in ecosystem processes, but has also led climate scientists to investigate the ways by which the natural environment mechanistically effects climate, developing an Earth System approach (Steffen *et al*. 2004). Vegetation changes that alter surface albedo or canopy roughness affect local weather (Makarieva *et al*. 2014) providing feedback to the rate and spatial pattern of climate changes (Richardson *et al*. 2013). Modifications in atmospheric CO_2 arise through variations in the carbon cycle, in which biomes with large carbon stocks per unit area over large areas, such as the tropical forests, are highly significant (Fisher *et al*., 2013, Lewis 2006, Mao *et al*. 2015, Pan *et al.* 2011). Recurrent phenological events that modify the properties of whole biomes, such as the leaf exchange patterns defining the growth season, have of course attracted attention, as both indicators of climate change and causal processes (Peñuelas *et al*. 2009). The Intergovernmental Panel on Climate Change (IPCC) noted in its fourth Assessment Report that phenology “is perhaps the simplest process in which to track changes in the ecology of species in response to climate change" (Rosenzweig *et al.* 2007). In this synthesis we review the development of tropical phenology, collate significant recent advances in the discipline and comment on perspectives for the future.

The climate-change line of enquiry in phenology concentrated first on long-term species-level studies (Fitter *et al*. 1995, Menzel *et al*. 2006), but now focusses on landscape-level proxies for leaf phenology, derived from satellite remote sensing (e.g. Myneni *et al*. 2007, Yu *et al*. 2015). Research in this arena recognizes large-scale processes as both drivers of and responses to climate change, asking how the phenology of large areas of vegetation influences local weather, carbon cycling, and water cycles (Makarieva *et al*. 2014, Richardson *et al.* 2013), as well as how reproduction or leafing responds to local climate (Krishnaswamy *et al*. 2014, Myneni *et al*. 2007, Streher *et al*. 2017, Zhou *et al*. 2014). New remote-sensing and digital technologies allow for large-scale results which bear more effectively on our most pressing questions of ecosystem change. They enable us to monitor more sites, more remote places, larger areas, and to improve standardization between sites (Alberton *et al.* 2017, Richardson *et al.* 2013). New data are now coming from studies designed to understand biome-level responses to climate change, rather than the responses of individual plants (Adole *et al.* 2016, Alberton *et al.* 2014, Moore *et al.* 2017, Streher *et al.* 2017, Wu *et al.* 2016). In 2013, Pereira and colleagues included remotely–sensed land-surface leaf phenology as one of the six Essential Biodiversity Variables recommended to monitor global change (Pereira *et al.* 2013).

Tropical environments were considered nearly aseasonal for a long time, and thus phenology studies were few. In contrast to temperate regions, tropical phenology data are very rare before 1950 (Fig. 1). Some herbaria hold records of tropical phenological observations (Couralet *et al.* 2013), but few hold such extensive collections that patterns can be derived from them (ter Steege & Persaud 1991; http://junglerhythms.org). Widespread tropical phenology field research began only around 70 years ago, and was often driven by ecologists studying foods available for primates or birds (Borchert 1983) or the descriptive studies of early naturalists (Morellato *et al.* 2013 and references therein). This has resulted, pan-tropically, in an empirical databank in which many of the oldest and longest studies are biased towards the observation of flowers or zoochorous fruits, rather than a representative sample of plants, recording all their phenophases. The early scholarly record in the tropics contains many anecdotal or non-systematic studies, and, contrary to today, least information on leaf phenology, perhaps because it is not an easily observed cyclical phenophase in semi-evergreen or evergreen forests (Alberton *et al.* 2017) or is of less importance to large wildlife, the foci of early studies.

Directly observed phenology studies proliferated in the tropics through the 1990's (Chambers *et al*. 2013, Morellato *et al.* 2013) and by then it was becoming clear that climate change was effecting rapid and considerable shifts in phenology in temperate ecosystems (Fitter *et al.* 1995, Harrington *et al*. 1999, Sparks & Carey 1995, Schwartz 1998). This encouraged ecologists to look for indicators of change in the tropics, but to measure change long term studies are required. Given the relative lack of resources allocated to scientific endeavor in many tropical countries there is considerable difficulty in sustaining scientific programs. There are also challenges in correctly identifying species, successfully marking individuals and preserving records for the long term. Thus, robust empirical datasets spanning more than a decade or reaching back beyond the 1980's are rare (see Chambers *et al*. 2013, Mendoza *et al*. 2017, for a summary). The longest datasets in the tropics are often those originally conceived for the study of the abundance of food resources (Fig.1) but in our race to grasp the consequences of climate change, the use of these data to investigate vegetation responses to climate is tempting. A few long term tropical phenology datasets, originally collected for other research questions, have since been analyzed to search for effects of climatic drivers or climate change (Chapman *et al*. 2005, Dunham *et al*. 2018, this issue, Polansky & Boesch 2013, Tutin & Fernandez 1993, Zimmerman *et al*. 2007). This has been done in temperate regions too (Menzel *et al.* 2006) and of course, presents many challenges for data analysis (Kelly, 2010; Morellato *et al.*, 2010). However, the period of time documented is of such enormous value in the data-poor tropics, that in this phase of potentially rapid shifts in climatic cues and plant responses, the analytical innovations required seem worthwhile (Bush *et al.* 2017, Hudson & Keatley 2010, Polansky & Robbins 2013).

Although leaf phenology is a prime choice for future study of climate change effects at the ecosystem or biome level, nevertheless, fruit and flower phenologies remain key to understanding the range of individual responses and the potential for climate changes to initiate cascading trophic changes within ecosystems (Butt *et al.*, 2015; Mendoza *et al.*, 2017; Morellato *et al.*, 2016; Polansky & Boesch, 2013; Ting *et al*., 2008). Detecting change in any phenophase requires first establishing a mean behavior, from which deviations can be quantified, demanding datasets covering several cycles. The three-decade community-level dataset from Barro Colorado Island, Panama has been successfully analyzed to show climatic drivers of flowering phenology for some species (Wright 1991, Wright *et al.* 1999, Wright & Calderón 2018). Yet in a 30-year flowering dataset from individual trees in Lopé, Gabon, although Bush *et al*. (2017) could detect regular cycles for 93% of the species they studied, they still failed to find any regular cyclical behavior in 40% of the 856 individuals monitored for >20 years. This demonstrates huge intra-specific as well as inter-annual variation in behavior. Long-term datasets on individual tree phenology are critical to understanding how the trees’ recurrent cycles vary within a population and change through a tree's lifetime. The emerging analyses of individual performance through time will greatly improve explanatory models of tree behavior based on direct observations (Babweteera & Plumptre 2018, Ouédraogo *et al*. 2018).

Many available tropical phenology studies did not set out to understand or sample the environmental context or physiology of the plant, key issues for disentangling drivers of phenology. The lack of contextual data considerably hampers our efforts to understand the drivers of responses – and we can never go back in time to collect that precious information. We can however improve research design for the future and expand our analytical approaches. Figure 2 shows the tropical sites with published long-term phenological records from ground, direct observation or litter trap phenology data. Although still scant compared to temperate regions (the German national phenology network has 474 sites with >50 years data; Kaspar *et al.* 2015), more empirical information on tropical phenology is available for each continent than has yet been analyzed. Comparing these diverse datasets is a significant challenge and harnessing the latent information will require considerable analytical skill and innovation (Morellato *et al.* 2010, Schaber *et al.* 2010). In the Neotropics, Asia and Australia such innovative analytical approaches are beginning to yield continental patterns for fruiting and flowering (Chambers *et al.* 2013, Mendoza *et al.* 2017, Mo *et al*. 2017, Moore *et al*. 2016, Morellato *et al.* 2013) in analyses which also extend beyond the forest biome (Camargo *et al.* 2018, Moore *et al*. 2017). Across Africa, however, differences in field methods and particularly the dire paucity of site-specific weather data have so far prevented any clear continental patterns being brought to light (Adamescu *et al.* 2018, Plumptre *et al.* 2012). Nonetheless, some site-specific links to climate now emerging (Chapman *et al*. 2018, Dunham *et al.* 2018) and the next few years are likely to bring significant advances.

The poor quality or inexistence of data such as temperature, rainfall or insolation, let alone more technically demanding measures, such as nutrient concentrations, pollutant presence or genotype, render detailed and robust analyses of phenophase triggers very difficult. For the future, multidisciplinary research teams and better integration between all plant science disciplines is essential for the identification and measurement of key drivers of change and uptake of phenology data for conservation planning (Morellato *et al*. 2016, Pau *et al*. 2011). Field ecologists may advise which taxa could make good indicators for a particular biome or vegetation type and which sampling methods may be best adapted to monitoring them (Bush *et al.* 2018, Morellato *et al.* 2010). Climate scientists can best advise which locations could be most informative for different questions; which are likely to be under the most predictable, directional climate change, or the most unpredictable (Wang *et al*. 2014, Maidment *et al.* 2015, IPCC 2013). Collaboration with modelers on research design and analytical tools will permit the inclusion of new explanatory parameters in phenology research, such as the ‘phenospecies’ concept (Proença *et al.* 2012) or indicator species for the behavior of larger groups (Siddig *et al.* 2016).

Much higher priority must be given to data collection on the environment surrounding the studied plants and improving standardization of sampling protocols to resolve the challenges of inter-site, continental and global comparisons. The research agenda should encourage the standardization of the best methods for each research question and must seek to identify and mitigate sources of noisy data in these inherently complex systems (Bush *et al*. 2018). The inclusion of better biometric expertise in research teams will allow the field to progress in dealing with the imperfect empirical datasets common in large, long term endeavors (Bush *et al*. 2017, Hudson & Keatley 2010, Mendoza *et al.* 2018).

Governmental agencies as well as international and regional organizations have invested considerable resources in monitoring climate and land cover change over time using satellites with sophisticated technologies (e.g. Bustamante *et al.* 2016). Yet, far less has been invested in monitoring ecosystems on the ground, particularly across tropical Africa, leaving us sometimes trusting in models to predict the future without sufficient raw data from the field (Abernethy *et al.* 2016, Maidment *et al*. 2015). Although Brazil and Mexico have made impressive advances in ecosystem monitoring, in many tropical countries the data we have describing change over time in ecosystem processes are still the result of local initiative and the perseverance of local scientists, rather than strategic investment from the State. Assessing the health of the biomes via direct observation of their reproductive phenophases (Morellato *et al*. 2016) and remote sensing of their leaf production (Pereira *et al.* 2013) should become integral to national environmental monitoring programs in the tropics, including citizen science - as they now are in temperate zones (see Fig.1).

Tropical phenology encompasses two broad areas of research: the study of plant resource production and related trophic interactions within ecosystems, and the study of climatic effects on vegetation phenophases and their feedback loops to climate from the state of the vegetation cover of the earth. These two research areas are parts of the same system, are complementary, and should strive to share insights and data wherever possible, even though research designs and field methodologies may often need to differ. Bringing tropical phenology closer to the top of the international research agenda will surely help society in its quest to understand and survive global environmental change.

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FIGURE LEGENDS.

FIGURE 1. Timeline of the development of tropical and temperate phenology research over the past 200 years.

FIGURE 2. Sites from which long-term directly-observed tropical phenology data have been published (blue dots) and the long-term observation sites included in this special section (red dots). Sources of site locations and minimum available dataset lengths: Adamescu *et al*. 2018, Babweteera & Plumptre 2018, Brearley *et al.* 2007, Chen *et al.* 2017, Chang-Yang *et al*. 2016, Dunham *et al*. 2018, Kurten *et al.* 2017, Mendoza *et al.* 2017, Plumptre *et al.* 2012, Sakai *et al.* 2006.