Discordant changes in foliar and reproductive phenology of tropical dry-forest trees under increasing temperature and decreasing wet-season rainfall

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Summary

- Plant phenology drives population demography and ecosystem functioning. We urgently need to better understand whether species and communities can cope with changing environmental cues of phenology, especially in tropical dry forests that may experience more droughts.
- We analysed long-term monthly foliar and reproductive phenology (2003–2021) of 623 trees across 94 taxa in a seasonally-dry Afromontane forest in Nigeria and related them to climate trends (1976–2023).
- We found decreasing trends in leaf flush and fruit production, but leaf shedding has increased. Community synchrony decreased markedly for leaf shedding but increased for fruiting.
- These phenological trends corresponded to signs of increased aridity. Minimum temperature has increased, with greater warming in the dry and intermediate seasons than the wet season. Rainfall fluctuated, but the dry season has become significantly wetter and the wet season drier.
- Our study highlights the discordant trends in foliar and reproductive phenologies. Fewer fruits and increasing leaf shedding indicate reduced productivity that will impact frugivores and nutrient cycling. More asynchronous leaf shedding suggests a decoupling from leaf flush and reproduction, potentially disrupting ecosystem regimes. Interspecific variation in response to climate change implies forest composition may shift towards the dominance of deciduous species.

Keywords: Cameroon highlands, climate change, cosinor rhythmometry, Fourier series, Ngel Nyaki forest reserve, Nigeria, resilience

Introduction

Climate change, such as increasing drought and aridity, is expected to severely weaken the role of tropical forests as carbon sinks (Corlett, 2016). Tropical dry-forest assemblages, despite their long evolutionary history under water deficit, are also not exempt from diversity loss (Siyum, 2020; Moura *et al.*, 2023). These seasonally dry forests, characterised by alternating wet and dry seasons that last between four to seven months (Allen *et al.*, 2017), are widespread across sub-Saharan Africa where they are central to biodiversity conservation and people's livelihoods (Siyum, 2020). For example, the seasonally dry montane forests of the Cameroon highlands are some of the most diverse and threatened plant communities in Africa (Cheek *et al.*, 2000), and being montane they may be especially vulnerable to climate change (Salinas *et al.*, 2021; Mata-Guel *et al.*, 2023). These forests provide essential ecosystem services including carbon storage (Cuni-Sanchez *et al.*, 2021), freshwater provision, flood mitigation (Abiem *et* *al.*, 2023), pollinators and pest control agents of crops (Tela *et al.*, 2021), but are additionally threatened by land use change, overgrazing, fire and bush meat hunting (Cheek *et al.*, 2000; Chapman *et al.*, 2004; Cheek *et al.*, 2021). It is thus imperative that we understand the resilience of these forests to climate change.

While the impact of climate change on forest tree demography (e.g., mortality and growth) is relatively well studied (Corlett, 2016), we are only beginning to understand how climate change influences phenology, i.e., the timing of life-cycle events (Sakai & Kitajima, 2019). Shifts in the phenology of photosynthetic and reproductive organs provide finer insights into the underlying mechanisms that drive demographic changes under climate change (Iler *et al.*, 2021). In seasonally dry forests, for example, the timing of leaf shedding (deciduousness or senescence) and leaf flush are especially important because they strongly reflect tree water status (Borchert, 1994; Kushwaha & Singh, 2005; Pires *et al.*, 2018; Kaewthongrach *et al.*, 2020). Moreover, plant phenology provides a more direct link to ecosystem functioning (Chapman *et al.*, 2005; Zhao *et al.*, 2013; Gray & Ewers, 2021; Hacket-Pain & Bogdziewicz, 2021), affecting processes such as carbon sequestration, multitrophic networks, and species coexistence (Tang *et al.*, 2016). Consequently, the sensitivity of species phenology to climate change holds critical information for ecosystem resilience, contingent upon the responses of both individual species and the entire community (Sullivan *et al.*, 2023).

Individual species vary in their phenology or “temporal niche” (Sakai, 2001), which has evolved in response to both abiotic and biotic selection pressures (Pau *et al.*, 2011). Key climate-related cues include temperature, precipitation, solar irradiance (Van Schaik *et al.*, 1993; Butt *et al.*, 2015; Chapman *et al.*, 2018; Numata *et al.*, 2022) and climate anomalies such as the El Niño–Southern Oscillations and in Africa, the Inter-Tropical Convergence Zone (Igboabuchi *et al.*, 2018). Biotic cues include pollinators, seed dispersers, herbivores, and predators (Bawa, 1990; Chapman *et al.*, 1999). Cues are not mutually exclusive and interact to drive complex plant phenologies (Van Schaik *et al.*, 1993). For instance, while the stressful conditions brought about by wet or dry seasons may promote community synchrony (Van Schaik *et al.*, 1993; Lasky *et al.*, 2016), biotic factors can lead to either synchronous or asynchronous phenologies (Lasky *et al.*, 2016). As climate change modifies environmental cues, species may adjust their phenology accordingly (Thébault & Fontaine, 2010; Clark *et al.*, 2013; Butt *et al.*, 2015; Deb *et al.*, 2018; Flores *et al.*, 2023). Given the diverse responses of different species to these changes (Rafferty *et al.*, 2015; León-Sánchez *et al.*, 2018; Samplonius *et al.*, 2021; Flores *et al.*, 2023), phenological mismatches may, for example, arise between the timing of leaf flush and flowering and their associated herbivores or mutualists, potentially disrupting community synchrony (Ovaskainen *et al.*, 2013; Renner & Zohner, 2018). The impact of species-specific phenological shifts on overall community synchrony remains uncertain however (Lima *et al.*, 2021; Chen *et al.*, 2023), partly because responses are often subjected to multiple climatic cues (Chang-Yang *et al.*, 2016).

Given that periods of drought define seasonally dry forests (Feng *et al.*, 2013) and that

Afromontane forests have expanded and contracted with climatic fluctuations since the Pleistocene (Meadows & Linder, 1993; Lézine *et al.*, 2019), a reasonable hypothesis would be that they are relatively resilient to climate change. Afromontane forests comprise a diverse array of species that have migrated from a wide range of habitats (White, 1983); they have a broad ecological tolerance and adaptive strategies. This is also evident in the wide range of species-specific responses we found to changes in rainfall, and especially temperature in this study. Pollen records suggest that in the Cameroon highlands submontane forests such as Ngel Nyaki, which include species from lowland forest and grassland or forest edge, have been compositionally stable over the past 90,000 years (Lézine *et al.*, 2019). Alternatively, Afromontane forests might be especially sensitive to changes in rainfall patterns (Allen *et al.*, 2017) such as extended drought into historically wet periods of the year, if most Afromontane species are already at the limit of their climate range (Bennett *et al.*, 2021).

In this study, we analysed 19 years of phenological data for leaf shedding, leaf flush, flowering and fruiting from the observations of 623 trees across 94 taxa in a submontane dry forest in northeast Nigeria. This dataset contributes to the long-term phenological data that remain rare from African tropical forests relative to other regions (Abernethy *et al.*, 2018; Adole *et al.*, 2018; Hacket-Pain & Bogdziewicz, 2021; Flores *et al.*, 2023). Even among the limited long-term data from African forests, the majority are from humid or moist tropical lowland or montane forests (Adamescu *et al.*, 2018), representing non-random subsets of tree communities, often selected to include species with fleshy fruits important for frugivores or valuable timber trees (Abernethy *et al.*, 2018; Adamescu *et al.*, 2018). Furthermore, most of these studies focus solely on flowering and fruiting, neglecting leaf phenologies as they are deemed less important for wildlife (Abernethy *et al.*, 2018). We combined the 19-year phenology data with concurrent monthly weather data and 48 years of historical rainfall and temperature climate data to answer the following questions:

1. What are the overall species-level patterns in leaf shedding, leaf flush, flowering and fruiting?
2. What are the community-level phenological patterns including peak phenology and community synchrony?
3. How does weather influence phenology?
4. How is the climate changing on the Mambilla Plateau and how might this influence forest phenology in the long term?
5. How resilient is the forest to climate change?

Materials and Methods

Study system

The study was carried out in the 46-km^2 Ngel Nyaki Forest Reserve (7.06°N, 11.1°E) on the south west escarpment of the Mambilla Plateau in Taraba State, Nigeria (Fig 1). Within the reserve, Ngel Nyaki forest is a 5.2-km^2 stand of submontane forest on the steep slopes of an ancient volcano, which offer protection from fire and grazing (Chapman & Chapman, 2001; Abiem *et al.*, 2020). The mean annual rainfall is approximately 1,800 mm, with most of the rain falling between April and October, followed by a six-month dry season. During the wet season, the forest can be covered in mist or fog for weeks on end, severely reducing irradiation (Chapman & Chapman, 2001). The mean annual temperature is 19°C and the monthly mean maximum and minimum temperatures for the wet and dry seasons are 25.6 and 15.4°C, and 28.1 and 15.5°C, respectively (Nigerian Montane Forest Project weather data). The soil in Ngel Nyaki forest is clay-loam with pH of 5.8–4.7 (Chapman & Chapman, 2001).

Ngel Nyaki forest is relatively diverse for the Afromontane with approximately 105 tree species from 47 families and 87 genera (Abiem *et al.*, 2020). Rubiaceae is the most diverse family with nine species. Abundant tree species include *Garcinia smeathmannii*, *Deinbollia pinnata* and *Pleiocarpa pycnantha*. The three principle emergent species are *Pouteria altissima*, *Entandrophragma angolense* and *Newtonoia buchanannii*, which reach to 36–46 m in height (Chapman & Chapman, 2001). A middle canopy layer sensu Richards (1952) between 15–30-m tall comprises species such as *Cordia millenii*, *Chrysophyllum albidum*, *Leptalus zenkeri* and *Drypetes gossweileri*. Forest species comprise a mix of Afromontane endemics or near-endemics (White, 1983), lowland forest and forest edge/grassland species. There is a gradient in species composition from forest core to edge, with edge species comprising more drought tolerant, often grassland species (Abiem *et al.*, 2020). The forest is a Birdlife International Important Bird Area and rich in primate species including the endangered Nigeria–Cameroon chimpanzee (*Pan troglodytes* ssp. *ellioti*). While the forest is a State Forest Reserve and therefore theoretically protected from hunting and grazing, in practice there is very little protection. Forest edges have been farmed on the lower slopes of the forest and cattle have damaged a substantial proportion of the reserve.

Data collection

Approximately 10 km^2 of phenology transects were established in 2004. Under a systematic design, the transects are 500 m apart (Beck & Chapman, 2008), running east to west to criss-cross the forest and obtain a good representation of the community composition. Along the transects, 800 trees $>$ 10 cm in diameter-at-breast-height (DBH), comprising 95 species were tagged, numbered and DBH measured. The number of trees per species ranged from 1 to 36 (median = 18.5). Voucher specimens are deposited in the Nigerian Montane Forest Project

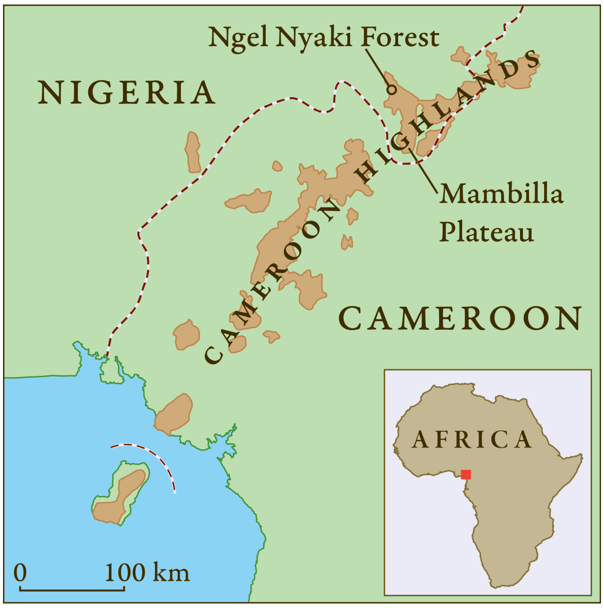

Figure 1: Map of the Cameroon Highlands showing the Mambilla Plateau and the location of Ngel Nyaki forest reserve. Modified from Thia (2014).

herbarium. Samples were sent to the Royal Botanical Gardens Kew for identification and other were confirmed through the ForestGeo DNA fingerprinting protocol (Kenfack *et al.*, 2022). Tagged trees were chosen to ensure a representative sample of the forest composition including taxonomy, dispersal modes and flower types. Since then, the transects have been walked every month for tree phenology monitoring. Trees are observed close-up, with binoculars when necessary, to observe flowers and fruits. As an indicator of monthly leaf shedding, leaf flush, flowering and fruiting, the proportion of crown occupied by each phenological variable in a given tree is given an ordinal score between zero and four (0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, 4 = 76–100%) following Sun *et al.* (2009). To test the influence of concurrent monthly weather on phenology, we then matched monthly field observations with local monthly weather data of temperature and rainfall obtained remotely from NASA's Prediction of Worldwide Energy and Resources portal (https://power.larc.nasa.gov/).

To quantify changes in longer-term climate and provide context for climate change impacts on phenology, we used a 48-year monthly time series from 1976–2023 from weather model-reanalysis data and in-situ observations. In-situ measurements of rainfall were gathered from the Gembu State Government weather station in the Sardauna Province ($6^\circ\ 41'\ 13.08$ N; $11^\circ\ 17'\ 33.48$ E), which is 40 km from our study site. Records of rainfall were corrected for annotation errors, but missing values were not filled. The minimum and maximum temperatures recorded at the Gembu station showed a long-term cooling, likely caused by tree planting in the vicinity of the weather station and thus reflecting the micro-meteorology surrounding the weather station. Therefore, we instead used the 2-m air temperature product from the ERA5-Land hourly data reanalysis dataset (Muñoz Sabater, 2019). The ERA5 hourly land product has a $0.1^\circ \times 0.1^\circ$ horizontal resolution. To match the Gembu time series, we also used data from 1976–2023. Hourly values were converted to monthly means of daily minimum temperature (hereafter simply as "minimum temperature"), using `Python` v3.11.5 including packages `numpy` v1.24.3, `pandas` v2.0.3, and `scipy` v1.11.1.

Statistical analyses

To quantify temporal trends in phenology, we modelled the ordinal canopy scores ($k = 1, 2, ..., 5$) of leaf shedding, leaf flush, flowering and fruiting of individual tree i of species j in transect n, month m and year t as in a multivariate generalised linear mixed model (GLMM) as cumulative processes with logit link:

$$\begin{aligned} Y_{pijnmt} &\sim \text{Cumulative-logit}(\kappa_{pk},\ \eta_{pijnmt}) \\ \eta_{pijnmt} &= \alpha_{pj} + f_{pjt}(m) + g_{pj}(R_{mt},\ T_{mt}) + \varepsilon_{pt} + \varepsilon_{pn} + \varepsilon_{pi} \\ f_{pjt}(m) &= \textstyle\sum_{d=1}^{2} \left(\beta_{1pjt,d} C_{m,d} + \beta_{2pjt,d} S_{m,d}\right) \\ g_{pj}(R_{mt},\ T_{mt}) &= \rho_{pj} R_{mt} + \tau_{pj} T_{mt}\,, \end{aligned}$$

where subscript p denote phenology of leaf shedding, leaf flush, flowering or fruiting. For each phenology, the cumulative-logit model estimates an underlying latent, continuous variable η from which the k ordinal scores were categorised and partitioned from $k-1$ cutpoints, κ (Bürkner & Vuorre, 2019).

In the linear predictor η, we began by including species-specific random intercepts α_j that model the average intensities of phenology for each species. We then included two predictor components to the model. First, $f_{pjt}(m)$ denotes the Fourier decomposition (Fidino & Magle, 2017) of calendar months ($m = 1, 2, ..., 12$) into the first two dominant components with periodicity of 12 and 6 months (based on Bush *et al.*, 2017) in the time series. Each periodic component consists of two Fourier terms, C and S, and the respective coefficients, β_1 and β_2. In Appendix S1, we provide the mathematical details of these Fourier terms and coefficients, as well as how to derive the amplitude of both periodicities to define whether annual (12 months) or subannual (6 months) is the predominant cycle. This decomposition, also known as 'cosinor' (Nelson *et al.*, 1979), allowed us to model the periodic cycles in phenology. The same technique has been used to quantify leaf phenology (e.g., Williams *et al.*, 2008 who coined 'circular statistics') but not expanded into GLMM as here. We allowed the Fourier coefficients β_1 and β_2 to vary by species and year to accommodate interspecific and interannual (nonstationary) variations in phenological periods.

In the second component $g_{pj}(R,\ T)$, we included two monthly-average weather variables, precipitation R and temperature T, and their effects, ρ and τ, on phenology, which varied by species to capture interspecific variations in weather responses. Between the Fourier component $f_{pjt}(m)$ and the weather component $g_{pj}(R,\ T)$, we will interpret the former as the longer-term variation in phenology responding to climate regimes, and the latter as shorterterm variation in phenology responding to monthly weathers.

Lastly, we included transect-, individual- and year-specific random intercepts (ε_n, ε_i and ε_t) to account for spatial, among-tree, and temporal non-independence, respectively. Importantly, the year random intercepts also accounted for potential nonstationary in the time series, by allowing each year to have different mean intensity in phenology.

Prior to modelling, we selected living tree individuals with at least 10 years of records and which had no observation gap for > 3 months, were not too tall for reliable measurement, and did not have constant phenology during the study period. We also grouped all *Ficus* spp. into a single taxonomic unit. This resulted in a total of 121,340 observations from 623 trees across 94 taxa, 17 transects and 19 years. The climate variables were centred and scaled to unit standard deviation to promote model convergence; as a consequence, the intercepts are interpretable as the overall phenology under the average climate condition within the study period.

The model was fitted in Stan (Stan Development Team, 2022), implemented with the `brms` package v2.18.3 (Bürkner, 2017) in `R` v4.2.1 (R Core Team, 2022). Bayesian inference was performed in four chains of Hamiltonian Monte Carlo (HMC) iterations, each with 2,000 iterations and the first 1,000 samples as warmup. We used the default weakly informative priors for all parameters in `brms`. Chain convergence was assessed visually using trace plots and the Gelman–Rubin diagnostic $\hat{R} < 1.05$.

Long-term climate trends in rainfall and minimum temperature were estimated the using linear regression, performed in `Python` v3.11.5 using the package `Seaborn` v0.12.2. Trends were fitted for individual months, as well as grouped months for dry (December, January and February), wet (June, July, August and September) and intermediate seasons (March, April, May, October and November). In addition, we performed trend analysis of all months to look at overall changes in the climate data.

Calculating community-level phenology

To understand what species-level phenology means at the community level, we leverage on the hierarchical nature of GLMM to extract community-mean patterns. This is done by using the fixed effects in the GLMM and marginalising over random species effects when predicting community-mean phenology. While the community-mean predictions are not exactly what is called "community-weight mean" in trait ecology, they can be interpreted similarly because they are both conceptually the expected value of a randomly drawn individual from an assemblage.

Next, we extracted the community-mean magnitude of peak intensity for each phenology in each year, as well as the month in which the peak occurred. We acknowledge that amplitudes and phase shifts can be analytically derived from the Fourier coefficients (Nelson *et al.*, 1979; Shumway & Stoffer, 2010, see also Supplementary Information), but they are calculated for each Fourier components and hence may not reflect the overall shape of the cycles. We therefore opted to numerically calculate peaks to obtain the total magnitudes across all Fourier components, i.e., by computing fitted values from the model and then locate the highest peaks. For every year, we also calculated community synchrony in phenology as the mean pairwise Spearman's ranked correlation in the fitted values between individuals (Loreau & De Mazancourt, 2008). Finally, we quantified the prediction accuracy of whole-community phenology in every year using the continuously ranked probability score (CRPS, which indicates how well the predicted ordinal values match the observed, Gneiting & Raftery, 2007) using the loo package v2.6.0 (Vehtari *et al.*, 2017). Assessing prediction accuracy allows us to understand whether some phenologies are less deterministic than others, and if phenology has become more unpredictable under climate disruptions.

Results

Species-level phenology

Our model explained 49%, 39%, 61% and 58% of variation in leaf shedding, leaf flush, flowering and fruiting, respectively. Of the explained variation, most were captured by the fourier decomposition of monthly trends followed by interspecific variation, with the exception of very high interannual variation in leaf shedding (Fig. 2). Interspecific variation was greater than intraspecific variation. Monthly temperature and precipitation did not capture a lot of variation in phenology, and there was very little variation among transects. Almost all species exhibited annual patterns in leaf shedding, flowering and fruiting, while relatively more species exhibited some degree of sub-annual cycles in leaf flush (Figs S1–S2).

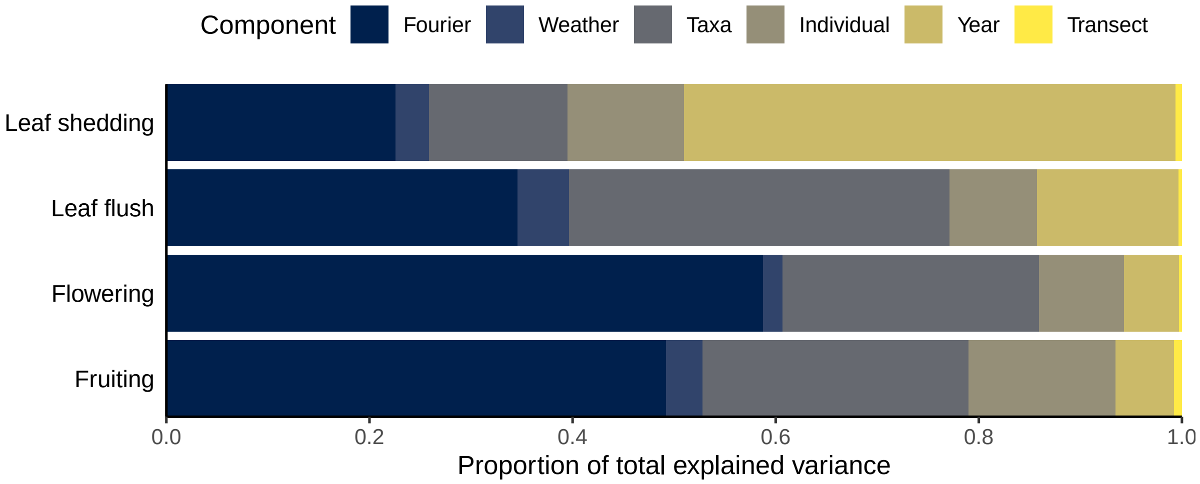

Figure 2: Variance partitioning of each phenology variable. Key to the variance components: Fourier = the fourier component f in the main text, Climate = the climate component g, Taxa = taxon-specific random intercept α_j, Individual = tree-specific random intercept ε_i, Year = year-specific random intercept ε_t, Transect = transect-specific random intercept ε_n.

Forty-eight species (51%) showed seasonal deciduousness whereby at least half of the crown was bare for 1–2 months (Fig. 3). Of the deciduous species, 29 shed their leaves during the height of the dry season, while the remaining 20 species shed leaves during the mid-late wet season. All other species lost varying amounts of leaves across the year. There were fewer species that shed leaves at the beginning of the wet season (Fig. S3A). Seven of the 94 species (7%) showed strong seasonal leaf flush, whereby over half of the crown had fresh leaves at any one month (Fig. 3). Of these, 2 species flushed in the dry season and 5 in the wet season. The remaining 77 species had small amounts of leaf flush throughout the year. Species with signals of sub-annual cycles seemed to produce leaves around the beginning and end of the wet season (Fig. S3B).

Compared to foliar phenology, reproduction had stronger seasonality and a greater proportion of variations explained by the Fourier components (Fig. S1). Almost all species showed strong annual seasonality in flowering (Fig. 3), with most of these showing peak flowering either throughout the dry season or towards the end and into the beginning of the rains (Fig. S3C). Very few species had peak flowering towards the end of the wet season. Fruiting varied strongly among species (Fig. 3). Species of *Anthocleista*, *Leea*, *Pavetta*, *Rothmania*, *Trema* and *Vitex* are among those that produced abundant fruit all year round (up to 6–11 months annually). Compared to other phenologies, interspecific peak fruiting seems to be the most evenly distributed phenology throughout the year (Fig. S3D).

Community-level phenology

At the community-level, the timing of peak foliar phenologies varied inconsistently across years. Peak leaf flushing was mostly in the mid-dry season (January or February), but in some years was earlier or later (Fig. 4A). In 2017 it was in the middle of the rains. Leaf shedding used to peak towards the end of wet season, but more recently has shown signs of delay into the dry season. Peak flowering was consistently towards the end of the dry season in March or April, followed by fruiting between March and July. Intensity of community peaks showed trends over time in all phenologies except flowering: leaf shedding has increased, coupled with less intense leaf flush and a slight decline in fruit production.

Community synchrony was inconsistent across years for leaf flush and shedding, varying between 0.5 (highly synchronised) and 0.1 (asynchronous). Flowering was more consistently synchronous between 0.2–0.4. Fruiting showed a clear trend of increased synchrony over time (Fig. 4B). Community synchrony did not always translate to greater whole-community predictive accuracy. Although leaf shedding, flowering and fruiting seemed to be most predictable when the community was most synchronous, the prediction accuracy of leafing seemed to be decoupled from its community synchrony (Fig. 4C).

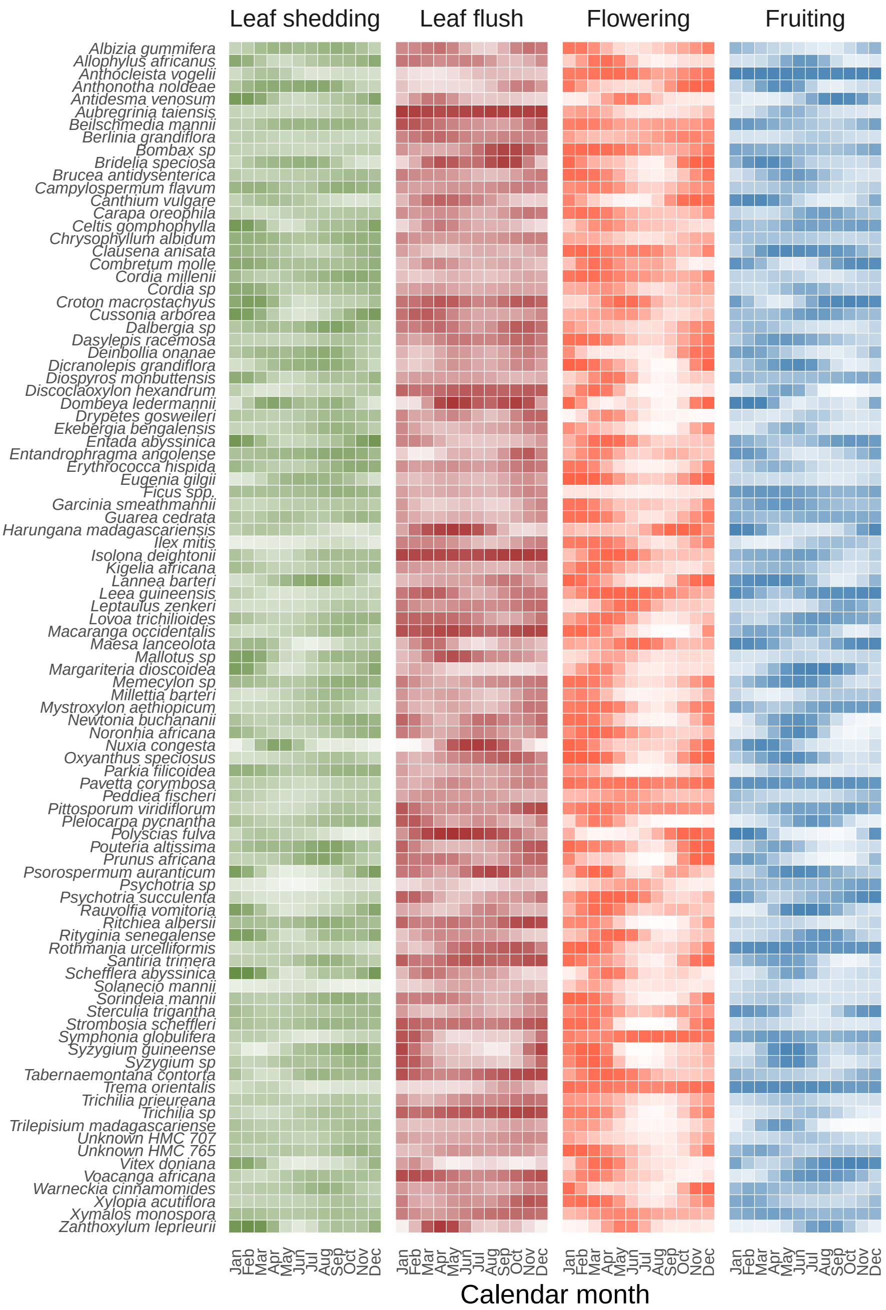

Figure 3: Overall phenological calendar for each species. Darker colours indicate more intense phenology (posterior median of of η_j). Predictions are made under the average climate conditions in this study and are marginalised across all other random effects.

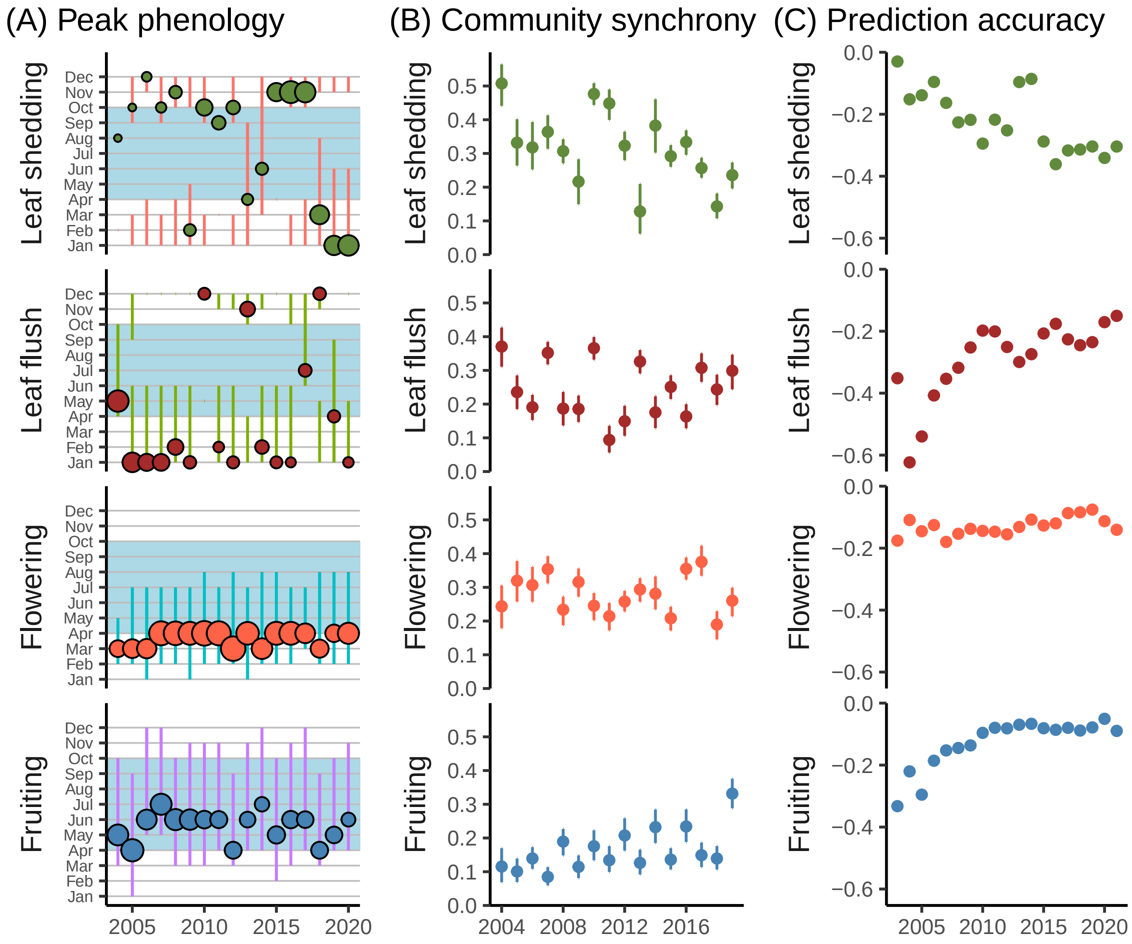

Figure 4: Community-level phenology across years. **(A)** Calendar month when the community is predicted to reach peak phenology. Points and error bars are circular median and interquartile range, respectively. Larger point size indicates higher peak intensity. Light-blue shaded regions denote the historical wet season. **(B)** Yearly change in synchrony of phenology across species within the community, calculated as the mean pairwise Spearman correlation in temporal trends. Solid points and vertical bars are posterior median and 89% credible intervals, respectively. **(C)** Yearly change in the model's prediction accuracy measured as mean continuously ranked probability score (CRPS) within year. Higher values indicate greater prediction accuracy.

Weather influence on phenology

Although local weather variables explained relatively little of the variation in species phenologies, our model revealed that species varied more in their responses to monthly temperature than monthly precipitation, especially in terms of leaf shedding and flowering (Fig. 5). For most species, leaf shedding and flowering was more intense under high precipitation. The weather responses of leafing were more varied: there were different species that leafed more intensely under all four factorial combinations of cool–warm and dry–wet conditions (Fig. 5). The weather responses of fruiting were similarly variable among species, except that there were no species that fruited more intensely under cool–dry conditions.

Climate trends

Using the Gembu weather station rainfall data and the ERA5-Land temperature data, our study site had a long-term (i.e., 1976–2023) average minimum temperature of 19.9°C and an annual rainfall of 1,848 mm. The dry-season (December, January and February) mean temperature was 20.8°C with a mean rainfall of 14 mm per month (Fig. S4). The intermediate-season (March, April, May, October and November) mean minimum temperature was 20.4°C with a mean rainfall of 150 mm per month, while the wet season (June, July, August and September) was cooler with a mean minimum temperature of 18.6°C and a mean rainfall of 271 mm per month.

Minimum temperature had a highly significant increasing trend of 0.017°C per year, or 0.8°C over the 48-year observation period (Fig. S5). The increase during the intermediate season was greatest at 0.020°C per year, or 1.0°C over 48 years; similarly the dry season increased for 0.019°C per year, or 0.9°C over 48 years, but less during the wet season at 0.012°C per year or 0.6°C over 48 years. All seasons and all individual months (except January) showed significant increases in minimum temperature; February and March showed the greatest increases in minimum temperature at 1.8 and 1.9°C over 48 years. Rainfall did not show a significant trend overall. When broken down into seasons, however, the dry season was significantly wetter by 16 mm per month by the end of 48 year observation period. Conversely, the wet season was significantly drier by 55 mm per month by the end of the 48 year observation period.

Discussion

We described the foliar and reproductive phenological trends over 19 years of 623 trees across 94 taxa in a seasonally dry submontane forest in the Cameroon highlands, Nigeria. We found that annual cycles were by far the most common periodicity across all four phenologies, agreeing with findings for flowering and fruiting phenologies from other West African forests (Bush *et al.*, 2017; Adamescu *et al.*, 2018). We also detected discordant trends in the intensity of

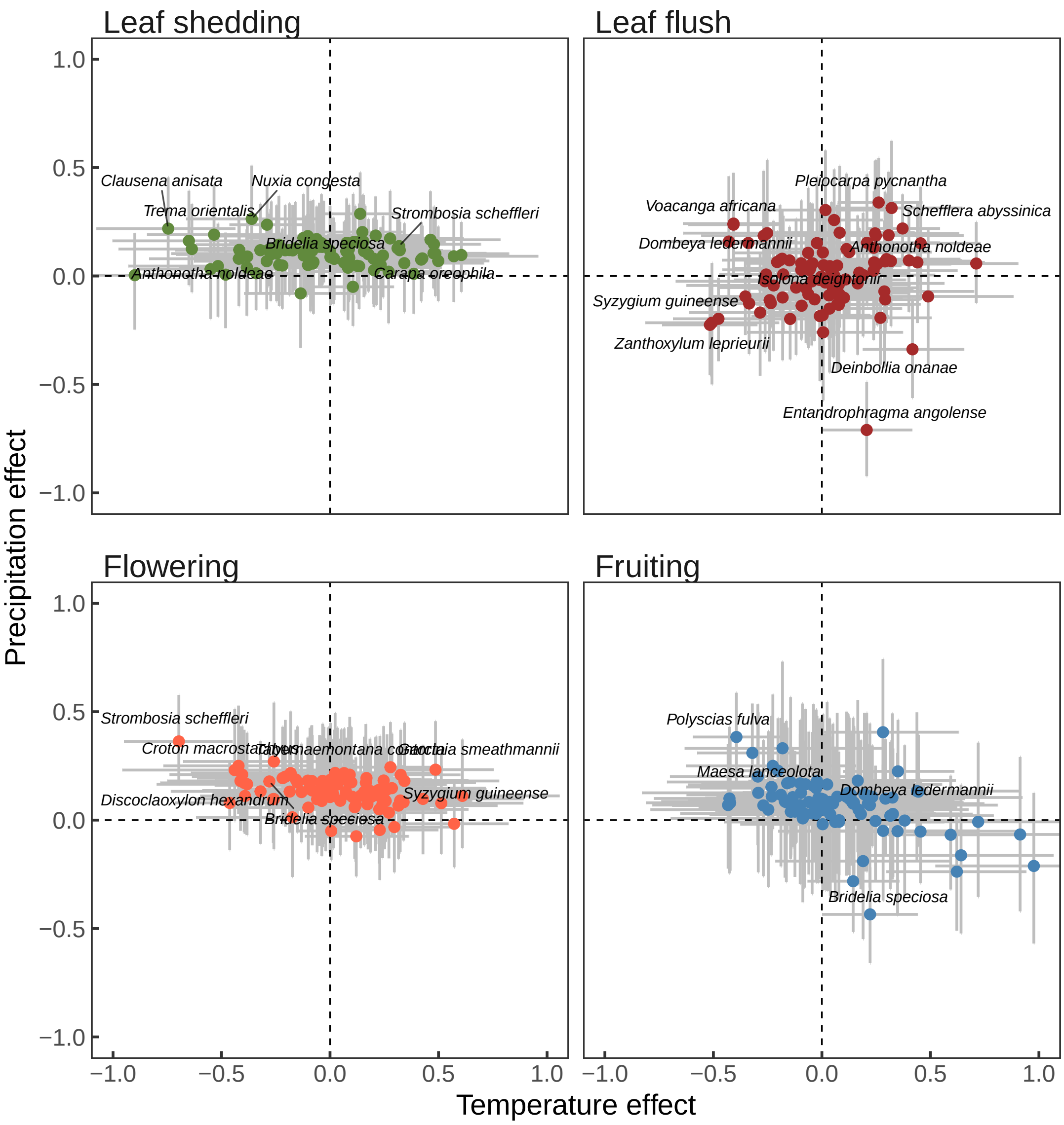

Figure 5: Species-specific phenological responses to total monthly precipitation and mean monthly temperature. Solid points and error bars are posterior median and 89% credible intervals, respectively. Each point corresponds to a focal species. Higher values lead to more intense phenology with increasing weather values and vice versa. Name labels denote species with strong responses to both monthly temperature and precipitation (do not overlap with zero on both axes).

leaf shedding, leaf flush and fruit production; leaf flush and fruit production have reduced in intensity while leaf shedding has increased. Community synchrony decreased markedly for leaf shedding and increased for fruiting. The climate at nearby Gembu township has changed over the past 48 years; minimum temperature has increased by 0.8°C on average, but more so in the dry and intermediate seasons. Total rainfall has not changed, but there is a trend for the dry season becoming significantly wetter and the wet season drier.

Species and community level patterns, peak phenology and synchrony

Leaf shedding

Over half the species (~51%) in our study were fully or semi-deciduous. Qualitatively, we found no obvious common phylogeny or ecological niche explaining deciduousness. While most deciduous species lost their leaves during the dry season as a common adaptation to avoid water stress in seasonally dry forests (Wright & Cornejo, 1990; Reich, 1995; Yang *et al.*, 2021), a suite of species shed their leaves during the wet season instead. Among forest edge species (e.g., *Psorospermum aurantiacum*, *Scheffleria abysinica*, *Cussonia arborea* and *Nuxia congesta*), leaf shedding during the rains may be an adaptation to low nitrogen (February & Higgins, 2016); tropical montane forests have low nitrogen availability relative to lowland forests (Ostertag *et al.*, 2022). In the forest core, another explanation may be an adaptive strategy to low light during the rains (Cornforth, 1970; Yang *et al.*, 2021) caused by cloud cover and fog (Chapman & Chapman, 2001).

At the community level, we found a noticeable trend towards peak leaf shedding now aligning more closely with the dry season. This shift corresponds with increasing temperatures and decreasing wet-season rainfall, leading to heightened drought conditions. An additional factor contributing to this trend may be the intensification of the desiccating desert Harmattan wind during the dry season (November–March), which also brings in more dust than previously, negatively impacting irradiation (Jenik & Hall, 1966; Balarabe, 2018). The most significant escalation in peak leaf shedding occurred concurrently with the onset of the 2015–16 El Niño phenomenon, mirroring the findings of Detto *et al.* (2018), Kaewthongrach *et al.* (2020) and Janssen *et al.* (2021). Since then, not only has leaf shedding become more pronounced, it is also less synchronous among species. The underlying explanations for these changes are likely multifaceted, intricate and encompass a mix of diverse physiological and ecological strategies among species to warming and drying (Janssen *et al.*, 2021), along with shifts in biological interactions (Renner & Zohner, 2018). Additionally, the absence of evident parallel shifts in the peak timing of other phenological events suggests a potential discordance between leaf shedding and the broader community phenology.

Leaf flush

Most species showed year-round leaf production, indicating adaption to a persistent environmental stressor such as dry-season drought and low wet-season irradiance (Nomura *et al.*, 2003). However, a suite of species comprising both understory and canopy trees showed distinct seasonal patterns in leaf flushing, mostly during the dry season. Despite the expectation of reduced flushing during drought (Aide, 1993; Van Schaik *et al.*, 1993), some studies have observed prevalent dry-season leaf flush like ours (Williams *et al.*, 1997; Rivera *et al.*, 2002; Williams *et al.*, 2008; Janssen *et al.*, 2021). Dry-season leaf flush may be an adaptation to reduce insect herbivory during the dry season (Kasenene & Roininen, 1999) and is perhaps tolerated in the understorey because species are relatively protected from drought by shade from taller trees. Furthermore, dry-season leaf flush among forest edge species that experience more drought (Abiem *et al.*, 2020) may be an adaptation to limited nitrogen availability (February & Higgins, 2016). It is also possible that subsoil water reserves allowed these species to produce new leaves weeks before the first rain for a competitive edge (Rivera *et al.*, 2002; Williams *et al.*, 2008).

At the community level, leaf flush also tended to peak in the height of the dry season (around January), but its peaks were less distinct compared to flowering and fruiting (Fig. S1). We therefore caution against over-interpreting the precise timing of peak community leaf flush. Nevertheless, community-level leaf flush peak intensity has shown a gradual yet consistent decline across the study period, though the community synchrony of leaf flush did not change directionally. The combined trends in leaf shedding and leaf flush suggest a biomass shift from living to dead components of the ecosystem, and thus may have negative consequences for herbivory (Meineke *et al.*, 2021), nutrient cycling (Sayer *et al.*, 2024) and carbon sequestration (Clark *et al.*, 2013) as has been evidenced in the Amazon (Laan-Luijkx *et al.*, 2015; Janssen *et al.*, 2021) and southeast Asia (Kaewthongrach *et al.*, 2020).

Flowering and fruiting

In contrast to the foliar phenology, the timing of flowering and fruiting were noticeably more regular. The majority of species consistently co-flowered towards the end of the dry season, around the timing of the first rain. This fairly constant community synchrony in flowering over the years has led to a community-level flowering that peaked around March. Flowering towards the end of the dry season is a common pattern in tropical dry forests (Van Schaik *et al.*, 1993) and may allow for fleshy fruits to later develop during peak rains (Chapman *et al.*, 1999), though there were forest edge or grassland species (e.g., *Antidesma venosum*, *Croton macrostachyus* and *Maesa lanceolata*) that did not reach peak flowering until later in the wet season. After flowering, community-level fruiting peaked during early to mid-wet season (April–June). Therefore, fruits were more abundant in the wet than in the dry season, but the considerable interspecific variation meant there was always something in fruit, as evidenced by Dutton & Chapman (2015) who in the same study site found equivalent amounts of seeds in chimpanzee faeces across the year, but from different seed species. Similar patterns of fruit production have been noted elsewhere in Africa (Chapman *et al.*, 2005; Adamescu *et al.*, 2018; Potts *et al.*, 2020).

The community peak and synchrony of flowering have not changed over the 19 years of our study, while community fruiting has decreased slightly in peak intensity and became more synchronous. It is difficult to tell where our results sit among previous findings, which show disparate trends of increased (Pau *et al.*, 2013; Polansky & Boesch, 2013; Dunham *et al.*, 2018; Flores *et al.*, 2023), decreased (Bush *et al.*, 2020; Numata *et al.*, 2022), or varying (Chapman *et al.*, 2005; Potts *et al.*, 2020) reproductive intensity or synchrony. The stable flowering phenology at Ngel Nyaki may indicate strong internal physiological inertia (Stevenson *et al.*, 2008) or that cues for flowering have not changed over the study period. However, the driver of fruit production at Ngel Nyaki remains in question as declining fruit production has decoupled from the stable flower production. Irradiation could be important (Chapman *et al.*, 2018) and this may be changing with either fog duration or more intense Harmattan (Jenik & Hall, 1966; Balarabe, 2018). Another explanation could be increased frugivory; while Ngel Nyaki has fewer chimpanzees and other primates than in the past (Chapman *et al.*, 2004), these individuals are now confined to within the forest boundaries due to extreme habitat fragmentation and edge encroachment (Knight *et al.*, 2016). We have not yet studied the pollinator communities within the forest but they could also influence fruiting intensity and synchrony (Wheelwright, 1985; Bawa, 1990). Of note is that while collecting seeds for forest restoration, we have recorded an apparent decline in fruit production in areas of the forest that field assistants visit regularly, but not in more remote parts of the forest. A possible explanation is that our presence has reduced bush meat hunting around the phenology transects, thus making the area less threatening to frugivores.

Weather, climate change and forest resilience

Analyses of the 48 years of ERA5-reanalysis climate for our study site shows that between 1976 and 2023 minimum temperatures are rising. This is in agreement with other reports of increasing minimum temperatures across much of West Africa (Bush *et al.*, 2020; Bedair *et al.*, 2023 and citations therein). For example, Bush *et al.* (2020) found minimum daily temperatures at Lopé, Gabon have increased at a rate of $+0.25$°C per decade since 1984. Total annual rainfall on the Mambilla Plateau showed no significant trend, and no evidence of prolonged droughts, which is in contrast to large parts of West Africa which are experiencing markedly reduced rainfall (Malhi & Wright, 2004; Polansky & Boesch, 2013; Bush *et al.*, 2020). However, the Plateau is experiencing increased variability in the magnitude, timing, and duration of rainfall. For example, we found a significant decrease in wet season rainfall, which may lead to rainfall shortages during times of the year that were historically wetter, which Allen *et al.* (2017) define as droughts. These subtle rainfall changes could affect phenology, as Valdez-Hernández *et al.* (2010) found that it was rainfall timing, rather than amount that influences phenology for a dry forest in Mexico. In addition, Ho *et al.* (in review) showed that leaf flush could be related to increased seasonality in rainfall.

Although species varied in their responses to weather, the monthly weather variables did not contribute much to the total variance in phenology. However, this should not be interpreted as environmental cues being unimportant or as a sign of the community's resilience to climate change. There were significant variations, especially in reproduction, as elucidated by the Fourier components, which indicates that reproductive phenology responds to whole climate regimes such as day length, cumulative rainfall and seasonal temperature across months (Chapman *et al.*, 2005, 2018; Pau *et al.*, 2013; Pires *et al.*, 2018), rather than the concurrent weather of any particular month. The disproportionately high amount of variance in leaf shedding explained by year is also noteworthy; it indicates that leaf shedding may be more sensitive to interannual environmental irregularities outside of the Fourier cycles, such as El Niño (Chapman *et al.*, 2018; Zhu *et al.*, 2022). Overall, this highlights that long-term shifts in climate regime or lag effects are more important than short-term weather fluctuations when studying phenology, as well as the importance of long-term monitoring data (Bush *et al.*, 2018).

To what extent the phenological trends of species and community we found are adaptive and might confer resilience to climate change is unclear. African tropical forests may be resilience to drought because many species are pre-adapted to dry conditions (Bennett *et al.*, 2021). The survival of trees against future drought, however, does not guarantee the stability of ecosystem functions. If droughts do become more frequent and aseasonal, more deciduous species will possibly gain a competitive advantage over evergreens in the long term (Vico *et al.*, 2017). Such a compositional shift, coupled with the increasing leaf shedding from our results, suggests a lower leaf biomass during extended periods of droughts, potentially undermining the role of these forests as carbon sinks (Reichstein *et al.*, 2013; Kaewthongrach *et al.*, 2020; Bennett *et al.*, 2021; Janssen *et al.*, 2021). Similarly, the stable flowering phenology does not guarantee long-term resilience because of its mismatch with leaf flush, which has decreased in peak intensity over the years. The reduced leaf production and hence photosynthetic resources may led to poorer flower and fruit qualities, even if their quantities do not change (Singh & Kushwaha, 2006). Such nuances may be missed from phenology studies that only focus on reproductive, but not foliar, organs.

Ultimately, management actions depend not only on good understandings but also accurate predictions of phenology. Leaf shedding was the only phenology that declined in prediction accuracy over the years, possibly related to it becoming more asynchronous among trees. The decreasing prediction accuracy also indicates nonstationaries due to some missing year-specific factor that influenced leaf shedding, for instance species-by-year interactions whereby some species were more sensitive to certain interannual anomalies (e.g., deciduous species to El Niño). Unfortunately, we were unable to include the species-by-year random effect in our model because of the limited replications of several species, but this could be tested by future studies with a more even sampling. Other phenologies had stable or increasing prediction accuracies, but they are not necessarily good news; leaf flush may become more predictable because most trees produced new leaves consistently at very low intensities, while fruiting may become more predictable because it is more synchronous in the wet season but less available in the dry season. Further studies could consider functional traits (e.g., leaf physiology, rooting depth and the ability to store water in the trunk) to improve the prediction and generalisation of phenological responses to drought (Van Schaik *et al.*, 1993; Corlett, 2016; Radford Smith *et al.*, 2024). Tree size could also strongly moderate performance under drought (Bennett *et al.*, 2015). Our monthly phenology survey did not include repeated measures of tree size due to logistic constraints, but we recommend future studies to include tree size as a covariate of phenology.

Whether the studied forest is resilient to climate change as a whole remains an open question without more information. The drivers and consequences of tree phenology do not solely involve the plants, but also their interactions with other trophic levels (Ovaskainen *et al.*, 2013; CaraDonna *et al.*, 2014; Visser & Gienapp, 2019) as well as the environment (Sayer *et al.*, 2024). Importantly, the discordant changes in foliar and reproductive phenology in our data suggest that assessments of forest resilience should rely on multiple aspects of phenology rather than a single performance indicator. That concurrent weather explains very little compared to long-term climatic cycles suggests that tree species may be resilient to short-term weather irregularities, but they may not be able to withstand prolonged shifts in the climate regime.

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Competing interests

The authors declared no competing interest.

Author contributions

HRL and HMC conceived the idea and led the writing. HRL analysed the phenology data. TM facilitated the collection and analyses of the climate data. SS maintained the weather data from weather stations. HMC set up the phenology transects and facilitated data collection. All authors contributed to the final draft and approved the final submission.

Data availability

The data and code that support the findings of this study will be openly available in Zenodo upon acceptance.

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