Changes in quantity and timing of foliar and reproductive phenology of tropical dry-forest trees under a warming and drying climate

Abstract

1. Plant phenology directly drives population dynamics and forest productivity; it is also impacted by shifting environmental cues under climate change such as more prevalent drought. It is imperative to better understand how species and community phenology respond to climate change in leaf turnover and reproduction, both of which are required to integrate phenological shifts into full life-cycle assessments.
2. Many studies to date, however, disproportionately favoured reproductive over foliar phenology and examined the quantity and timing of phenology separately. We demonstrate that the simultaneous assessment of phenological quantity and timing across multiple organs reveals more nuanced and holistic insights into the consequences of climate change.
3. Extending a regression approach based on Fourier series, we decomposed the long-term (2004–2020) monthly leaf shedding, leaf flush, flowering and fruiting of 617 trees across 94 taxa at a Nigerian seasonally dry tropical forest into three periodic components—mean intensity, amplitude and phase—which respectively represents the total quantity, pulse concentration and peak timing of phenology. We then related each periodic component to shifts in minimum temperature and wet-season rainfall.
4. We found that climate, especially wet-season rainfall, explained more variation in phenological amplitudes compared to mean intensity and timing. In drier years, more species shed leaves in more concentrated pulses by increasing amplitude, rather than in greater

total amount by increasing mean intensity. This combined with the decreased mean intensity of leaf flush imply a lower primary productivity as trees deployed fewer leaves for a shorter period. Species produced more flowers but fewer fruits in total, potentially due to a shortened flowering period that limited pollination. At the community level, the production of leaves, flowers and fruits became more synchronous, potentially creating periods of scarcity for consumers.

Synthesis: Our findings highlights several contrasting yet complementary phenology–climate insights across organs and periodic components, indicating that assessments of forests' climate resilience necessitate multiple aspects of phenology rather than a single performance indicator. The decline of primary productivity in litterfall and fruiting, as well as the temporal mismatches in leaf turnover and reproduction, will have cascading impacts on trophic interactions and nutrient cycling.

Keywords: Afromontane forest, amplitude, climate change, cosinor rhythmometry, Fourier series, litterfall, phase, primary productivity

Introduction

The phenology of tropical forest describes the temporal patterns of primary productivity and reproduction (Sakai, 2001), which have direct consequences on ecosystem processes such as nutrient cycling, multitrophic interaction, and species coexistence (Cleland & Wolkovich, 2024; Tang et al., 2016). However, the stability of these ecosystem processes are impacted by climate change as plants react by shifting the quantity and timing of reproduction and biomass turnover (Cleland et al., 2007; Iler et al., 2021). For example, more prevalent leaf shedding under the warmer and drier conditions in Amazonian forests has reduced trees' ability to sequestrate carbon in living biomass (Janssen et al., 2021). Climate-induced changes in flowering and fruiting intensities across tropical forests have also impacted tree recruitment and consumer populations (Bush et al., 2020; Butt et al., 2015; Numata et al., 2022). As increasing drought and aridity weakens the role of tropical forests as carbon sinks (Corlett, 2016), it is imperative that we

study phenological shifts as indicators of species' and communities' demographic responses to climate change (Hacket-Pain et al., 2024; Iler et al., 2021).

Across tropical forests, there is accumulating evidence of temperature and rainfall as key determinants of tree phenology (Sakai & Kitajima, 2019; Van Schaik et al., 1993). Water stress due to declining rainfall and rising temperature have been associated with greater quantity of leaf shedding (Janssen et al., 2021), as well as reduced leaf flush (Nomura et al., 2003), flowering (Butt et al., 2015; Lasky et al., 2016; Numata et al., 2022) and fruiting (Bush et al., 2020; C. A. Chapman et al., 2018); though the opposite or weaker relationships have also been found (Babweteera et al., 2018; C. A. Chapman et al., 2018; Pau et al., 2013; Wright & Calderón, 2006). However, many previous studies and even the largest open-data initiative of global phenology (Hacket-Pain et al., 2022) analysed phenology as time-implicit total quantities (e.g., the weight of litterfall or abundance of individuals in flower summed or averaged over a period — usually a year) despite the temporal fluctuation of phenology *within* an annual cycle. These studies quantified how climate influences the annual *intensity* of organ production and turnover, which is not directly comparable to studies that explicitly quantified the effects of environmental conditions on the *timing* of phenology (e.g., Borchert, 1983; Chang-Yang et al., 2024; Chen et al., 2018; Ho et al., 2024; Ouédraogo et al., 2020; Reich & Borchert, 1984).

Extending on Newstrom et al. (1994), Sakai (2001) and Mendoza et al. (2018), we argue that it is important to examine both the quantity and timing of phenology, as they reveal different but complementary insights on the impacts of climate change. Furthermore, we highlight the informative value in decomposing phenological quantity into mean intensity and *amplitude*. There are many ways to model a time series; here we focus on a regression approach that combines advances in Fourier analysis (Bush et al., 2017) and circular statistics (Davis et al., 2022) for tropical phenology with the flexibility of generalised hierarchical regressions to directly include climate predictors and estimate species-specific responses. We reserve details to the *Methods* section but in brief, a periodic time series of phenology can be represented as a (series of) cosine function(s) with three components (Fig. 1): mean intensity, amplitude and phase (timing of peak) (Fidino & Magle, 2017; Nelson et al., 1979). Each periodic component could be influenced by climate in separate ways, leading to different consequences on the ecosystem.

For example, an increase in the mean intensity of annual leaf shedding recycles foliar nutrients at a higher total amount per year to the forest floor, whereas an increase in phase delays litterfall and could decouple it from other processes such as decomposition or seed germination. More nuanced is the implication of increased amplitude, which can be interpreted as a more concentrated phenology within a shorter duration (this also implies that amplitude encompasses both quantity and timing, as in timespan). An increase in amplitude leads to a more sudden pulse of leaf shedding *without changing its mean intensity*, therefore the *same total quantity* of leaves are shed within a narrower window of time, potentially outpacing decomposition or leading to more transient ecosystem functioning (Sayer et al., 2024).

In addition a simultaneous examination of phenological quantity and timing, a pan-tropical synthesis of the effects of climate change on plant phenology also requires more complete data across organs. While there has been tremendous progress in reproductive phenology (e.g., Hacket-Pain et al., 2022), foliar phenology remains poorly documented (Abernethy et al., 2018). This impedes the integration of phenological shifts into full life-cycle assessments, which are crucial to forecast population dynamics under climate change (Iler et al., 2021). This knowledge gap could be especially problematic for seasonally dry tropical forests (SDTFs), where leaf turnover is tightly regulated by strong rainfall and temperature seasonality (Murphy & Lugo, 1986; Van Schaik et al., 1993). SDTFs account for about 40% of the world's tropical forests (Siyum, 2020) and may be more vulnerable to climate change due to their reliance on water availability (Aguirre-Gutiérrez et al., 2020). Nonetheless, a considerable phenological diversity exists among species in SDTFs (Lasky et al., 2016; Meir & Pennington, 2011; Singh & Kushwaha, 2016), providing a promising premise to learn the wide range of plant life-history strategies against past and future droughts.

From a pilot analysis of 47-year climate data in a Nigerian SDTF, we found that minimum temperature has risen by 0.8°C while rainfall has become more erratic, with wet-season monthly rainfall decreased by about 10%; these changes were congruent to broader trends across tropical Africa (Bennett et al., 2021). To address the aforementioned knowledge gaps, we analysed 17 years of monthly foliar and reproductive phenology—leaf shedding, leaf flush, flowering and fruiting—of 617 trees across 94 taxa and quantified how multiple

periodic components—intensity, amplitude and timing—of individual-species phenology responded to rainfall and temperature. Given the phenological diversity and wide range of drought adaptations among SDTF species (K. Allen et al., 2017), we expected and found high interspecific variation in phenology–climate relationships across organs and periodic components. We show that the different responses of each periodic component provide a finer interpretation on how climate influences phenology, and that a more consistent pattern may still emerge at the community level when phenological synchrony is calculated from apparently idiosyncratic changes in species-specific timings.

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. S1). Within the reserve, Ngel Nyaki forest is a 5.2-km^2 stand of submontane forest on the steep slopes (1,600-m elevation) of an ancient volcano (J. D. Chapman & Chapman, 2001). 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 (J. D. 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.

Ngel Nyaki forest is relatively diverse for the Afromontane with at least 105 tree species from 47 families and 87 genera (Abiem et al., 2020). Forest species comprise a mix of Afromontane specialists (J. D. Chapman & Chapman, 2001), 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 grassland species (Abiem et al., 2020).

Phenology data

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). Tagged trees were chosen to ensure a representative sample of the forest composition including taxonomy, dispersal modes and flower types. During the monthly phenology monitoring from 2004 to 2020, trees are observed close-up, with binoculars when necessary. As an indicator of monthly leaf shedding, leaf flush, flowering and fruiting, the proportion of whole 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. (1996).

Exploratory analyses of climate data

To provide context for climate-change impacts on phenology, we used a 47-year monthly time series from 1976–2022 from weather model-reanalysis data and in-situ observations. Rainfall was gathered from the Gembu State Government weather station (6° 41′ 13.08 N; 11° 17′ 33.48 E) 40 km from our study site. For ambient temperature, we used the 2-m air temperature product from the NASA ERA5-Land hourly data reanalysis dataset (Muñoz Sabater, 2019) with a $0.1° \times 0.1°$ horizontal resolution. Hourly values were converted to monthly means of daily minimum temperature.

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). Additionally, we performed trend analysis using all months to examine overall changes. These exploratory analyses revealed significant increase and decline in all-month minimum temperature (hereafter “minimum temperature”) and wet-season

rainfall, respectively. Therefore, we modelled monthly phenology as a function of minimum temperature and wet-season rainfall in the main regression as follows.

Modelling framework for periodic phenology

To quantify the effects of climate change on the periodic components of tree phenology, we turn to a statistical approach known as cosine-vector or "cosinor" rhythmometry (Nelson et al., 1979). Cosinor is commonly used to model periodic time series that display regular cycles, and is generally defined nonlinearly as:

$$\eta_\tau = \alpha + A\cos(2\pi\tau/P + \phi)\,, \tag{1}$$

where a variable such as phenology, η_τ, that varies over time τ is described by its midline α (mean intensity about which oscillation occurs), amplitude A (magnitude of fluctuation, or *concentration* of intensity as interpreted in this study) and phase ϕ (timing or starting point of the time series) for a given period P (e.g., a period of 12 months means that the time series has an annual cycle; see Fig. 1). It is possible to incorporate the potential effects of external factors, X, such as temperature on phenology by allowing them to influence the midline, amplitude and phase, for instance:

$$\eta_\tau = (\alpha_0 + \alpha_X X) + (A_0 + A_X X)\cos[2\pi\tau/P + (\phi_0 + \phi_X X)]\,, \tag{2}$$

where α_X, A_X and ϕ_X denote the effect of temperature on the midline, amplitude and phase, respectively. For example, positive values of A_X and ϕ_X would mean that warming temperature increases the amplitude and delays (right-shifts) the timing of phenology (Fig. 1).

In practice, however, fitting a statistical model based on Equation 2 could be challenging because of parameter non-identifiability, i.e., the parameters are often correlated causing model non-convergence. A solution lies in the rewriting of Equation 1 using the trigonometric identity $\cos(u+v) = \cos(u)\cos(v) - \sin(u)\sin(v)$, which is a common practice in cosinor modelling to

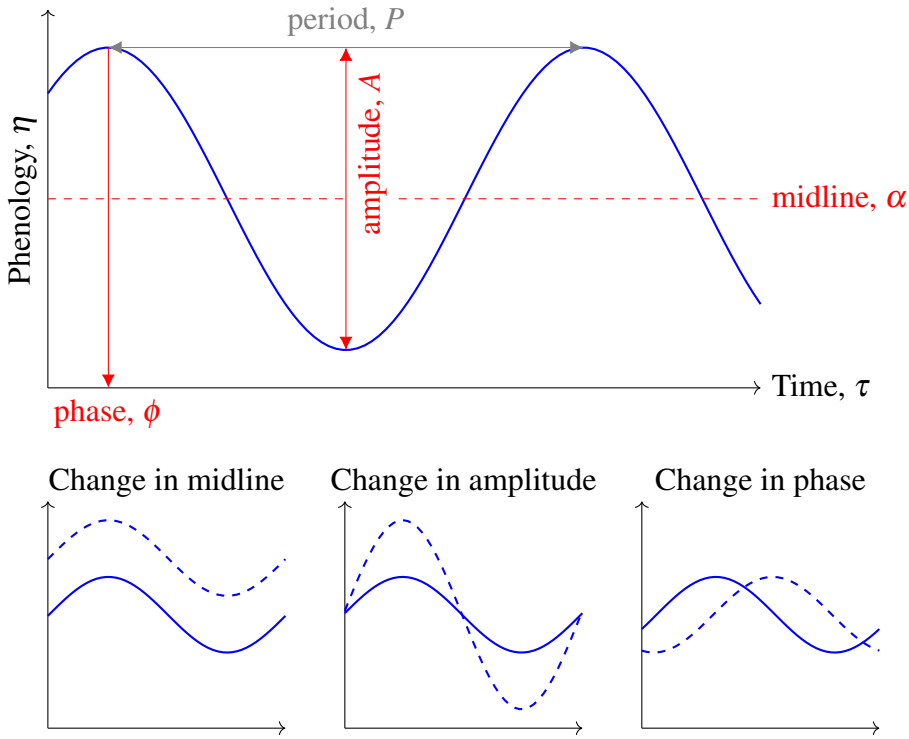

Figure 1: **(Top panel)** An example cosinor plot showing the basic components that correspond to Equation 1. Parameters in red are components that could be moderated by climate factors in this study. **(Bottom panels)** Examples illustrating how each cosinor components could be altered by climate factors.

ease computation (Fidino & Magle, 2017):

$$\eta_\tau = \alpha + \beta C + \gamma S, \tag{3}$$

where $C = \cos(2\pi\tau/P)$, $S = \sin(2\pi\tau/P)$, $\beta = A\cos(\phi)$ and $\gamma = -A\sin(\phi)$. The reparameterised Equation 3 can then be fitted as a linear regression with intercept α and slopes β and γ, after which the original parameters can be recovered as $A = \sqrt{\beta^2 + \gamma^2}$ and $\phi = \tan^{-1}(-\gamma/\beta)$ (Nelson et al., 1979; Shumway & Stoffer, 2010). See Bingham et al. (1982) for additional sign correction for ϕ.

We could further include climate covariates into Equation 3:

$$\begin{aligned}\eta_\tau &= (\alpha_0 + \alpha_X X) + (\beta_0 + \beta_X X)C + (\gamma_0 + \gamma_X X)S \\ &= \alpha_0 + \alpha_X X + \beta_0 C + \beta_X XC + \gamma_0 S + \gamma_X XS, \end{aligned} \tag{4}$$

where α_0 now serves as the intercept (midline); α_X as the main effect of climate (on midline); β_0 and γ_0 are the cosinor parameters under average climate condition (after centering the climate variable X); while β_X and γ_X are interactions between the cosinor and climate terms, i.e., the moderating effects of climate on amplitude and phase.

However, the computational efficiency of Equation 4 comes with a trade-off: we do not specify the relationship between climate, amplitude and phase directly. Instead, amplitude is now a function of climate as $A = \sqrt{(\beta_0 + \beta_X X)^2 + (\gamma_0 + \gamma_X X)^2}$, which when expanded contains the quadratic term X^2 and hence introduces unintended nonlinearity between amplitude and climate. The same unintended nonlinearity also applies to the phase–climate relationship as $\phi = \tan^{-1}[-(\gamma_0 + \gamma_X X)/(\beta_0 + \beta_X X)]$. In a pilot analysis, we fitted the direct parameterisation (Equation 2) but were unable to achieve model convergence, therefore we opted for the reparameterisation (Equation 4) and circumvented the unintended nonlinear climate effect using counterfactual comparisons (Arel-Bundock et al., in press). Specifically, we calculated amplitude or phase under the minimum and maximum climate conditions (i.e., $X_{\min}$ and $X_{\max}$), then took the difference (i.e., A or ϕ under $X_{\max}$ minus that of $X_{\min}$) to represent the effect of climate of amplitude or phase.

Model fitting

To apply the cosinor Equation 4 to our data, we fitted the ordinal scores Y_{pijnmt} of leaf shedding, leaf flush, flowering and fruiting of individual tree i of species j in transect n, month m and year t in a multivariate generalised linear mixed-effects model (GLMM) as cumulative processes with logit link:

$$Y_{pijnmt} \sim \text{Cumulative-logit}(\kappa_{pk},\ \eta_{pijnmt})$$

$$\eta_{pijnmt} = \alpha_{pjt} + \textstyle\sum_{d=1}^{2} \left(\beta_{pjtd} C_{md} + \gamma_{pjtd} S_{md}\right) + \varepsilon_{pn} + \varepsilon_{pi} \tag{5}$$

$$\alpha_{pjt} = \alpha_{0,pj} + \alpha_{1,pj} R_{\text{wet},t} + \alpha_{2,pj} R_{\text{wet},t-1} + \alpha_{3,pj} T_{\min,t} + \alpha_{4,pj} T_{\min,t-1} + \varepsilon_{\alpha,pt} \tag{6}$$

$$\beta_{pjtd} = \beta_{0,pjd} + \beta_{1,pj} R_{\text{wet},t} + \beta_{2,pj} R_{\text{wet},t-1} + \beta_{3,pj} T_{\min,t} + \beta_{4,pj} T_{\min,t-1} + \varepsilon_{\beta,ptd} \tag{7}$$

$$\gamma_{pjtd} = \gamma_{0,pjd} + \gamma_{1,pj} R_{\text{wet},t} + \gamma_{2,pj} R_{\text{wet},t-1} + \gamma_{3,pj} T_{\min,t} + \gamma_{4,pj} T_{\min,t-1} + \varepsilon_{\gamma,ptd}\,, \tag{8}$$

where subscript p denotes phenology of leaf shedding, leaf flush, flowering or fruiting. For each phenology, the model estimates an underlying latent, *continuous* variable η from which the five possible discrete ordinal scores $Y \in \{0, 1, ..., 4\}$ were categorised and partitioned from four cutpoints, κ_k, where $k = 1, 2, ..., 4$ (Bürkner & Vuorre, 2019, see Fig. S2 for an illustrated explanation). In other words, the model reflects that phenology is an underlying continuous quantity that was discretised by the field observers for logistical feasibility.

In the continuous linear predictor η (Equation 5), we began by including species-specific random intercepts, α_{pj}, which model the midline for each species. Then we included the periodic terms $C_{md} = \cos(2\pi m/P_d)$ and $S_{md} = \sin(2\pi m/P_d)$, as well as the corresponding species-specific slopes β_{pjtd} and γ_{pjtd} to model species' phenological amplitudes and phases. Note that we included two sets of periodic terms (hence the summation up to $d = 2$) to estimate the relative signals in annual ($P_{d=1} = 12$) and sub-annual ($P_{d=2} = 6$) cycles for each species. This is essentially a Fourier transformation to break down monthly phenologies into two dominant cycles (Fidino & Magle, 2017), and we chose the 12- and 6-month cycles based on Bush et al. (2017) from the same biome.

Next, we inferred the effects of annual climate factors—wet-season rainfall R_{wet} and minimum temperature T_{min}—on phenology. We included both current- and previous-year climate (denoted with subscript t and $t-1$, respectively) for two reasons: (1) there might be a lag effect and we opted to at least consider a lag of one year; (2) species with phenologies that peak in earlier months would respond more to previous- than to current-year climate. For the second reason, a better approach would be to iteratively estimate the phenological phase and then compute the climate variable 12 months prior to the phase, but this would be computationally too demanding for our modelling approach (but see Chang-Yang et al., 2024). We therefore fitted both current- and previous-year climate effects and then compare their effect sizes for each species to determine their relative importance.

In the midline submodel (Equation 6), $\alpha_{0,pj}$ denotes the species-specific midline under the average climate condition (after centering $R_{\text{wet},t}$, $T_{\text{min},t}$, $R_{\text{wet},t-1}$ and $T_{\text{min},t-1}$), while $\alpha_{1,pj}$ and $\alpha_{3,pj}$ are the effects of current-year wet-season rainfall and minimum temperature on species' midlines, respectively. Similarly, $\alpha_{2,pj}$ and $\alpha_{4,pj}$ are the effects of previous-year wet-season

rainfall and minimum temperature on species' midlines, respectively. We further included the year-specific random error $\varepsilon_{\alpha,pt}$ to account for residual variation in species' midlines unexplained by climate. We also specified similar submodels for the other two cosinor parameters, β_{pjtd} and γ_{pjtd}, to infer the effects of climate on species' annual and sub-annual amplitudes and phases (Equations 7 and 8). It is important to note that the annual climate covariates (as well as the year-specific random errors $\varepsilon_{\alpha,pt}$, $\varepsilon_{\beta,pt}$, and $\varepsilon_{\gamma,pt}$) address our study goal by accounting for potential non-stationary in the time series, i.e., by allowing each year to have different phenological midline, amplitude and phase (note the t subscript in the year-varying α, β and γ terms). Lastly, we included transect- and individual- random intercepts, ε_{pn} and ε_{pi}, to account for spatial and among-tree non-independence (Equation 5).

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 117,964 observations from 617 trees across 94 taxa, 17 transects and 17 years. The climate variables were centred and scaled to unit standard deviation to promote model convergence.

The model was fitted with the `brms` package v2.18.3 (Bürkner, 2017) in `R` v4.2.1 (R Core Team, 2022). Four chains of Hamiltonian Monte Carlo (HMC) iterations were run, 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 $\hat{R} < 1.05$.

Community synchrony

To examine how climate-induced shifts in species' phenological timing lead to changes in community synchrony, we calculated the circular standard deviation (SD) of the estimated values of phases ϕ across climate gradients of R_{wet} and T_{min} following Bush et al. (2017) using the `R` package `circular` (Agostinelli & Lund, 2024). The SD was inverted to precision so that higher values indicate greater synchrony.

Results

Overall temporal trends in climate and phenology

From 1976 to 2022, there was no clear annual rainfall trend in the Mambilla plateau where our forest is situated (Fig. S3). When broken down into seasons, however, the dry and wet seasons had become significantly wetter by 16 mm per month and significantly drier by 55 mm per month, respectively (Fig. 2a). During the same period, minimum temperature had increased significantly by 0.017°C per year, or 0.8°C in total (Figs 2a and S4).

Within this warming and drying period, we recorded monthly foliar and reproductive phenologies from 2004 to 2020 (Fig. 2b). Averaged across the years, we found that fruiting phases varied by species but their timings were regularly spaced throughout a year (Fig. S5d). In contrast, there was a gap in flowering towards the end of wet season (Fig. S5c), a gap in leaf shedding between the end of dry season and the beginning of wet season (Fig. S5a), as well as a slight gap in leaf flush in the middle of wet season (Fig. S5b). Almost all species exhibited annual cycles in leaf shedding, flowering and fruiting, while relatively more species exhibited sub-annual cycles in leaf flush (Fig. S6). Current- and previous-year climate were important to roughly the same number of species for phenologies except leaf shedding, in which more species were more strongly influenced by current-year climate (Fig. S7). In the following sections, we discuss results based on the dominant cycle (annual or sub-annual) and lag (current- or previous-year climate) of each species.

Climate effects on aspects of phenology

Over time, we found that leaf shedding was the most variable from year to year, whereas flowering was the most synchronised across species (Fig. 2b). Over time, leaf shedding had overall increased, whereas leaf flush and fruiting had overall decreased slightly across species (Fig. 2b). We modelled phenology as a function of wet-season rainfall (R_{wet}) and minimum temperature (T_{min}) and found that, across periodic components, climate explained the greatest amount of temporal variation in amplitudes (38–76%), followed by phases (16–35%) and then midlines (14–21%; Fig. S8). Across organs, climate explained the most temporal variation

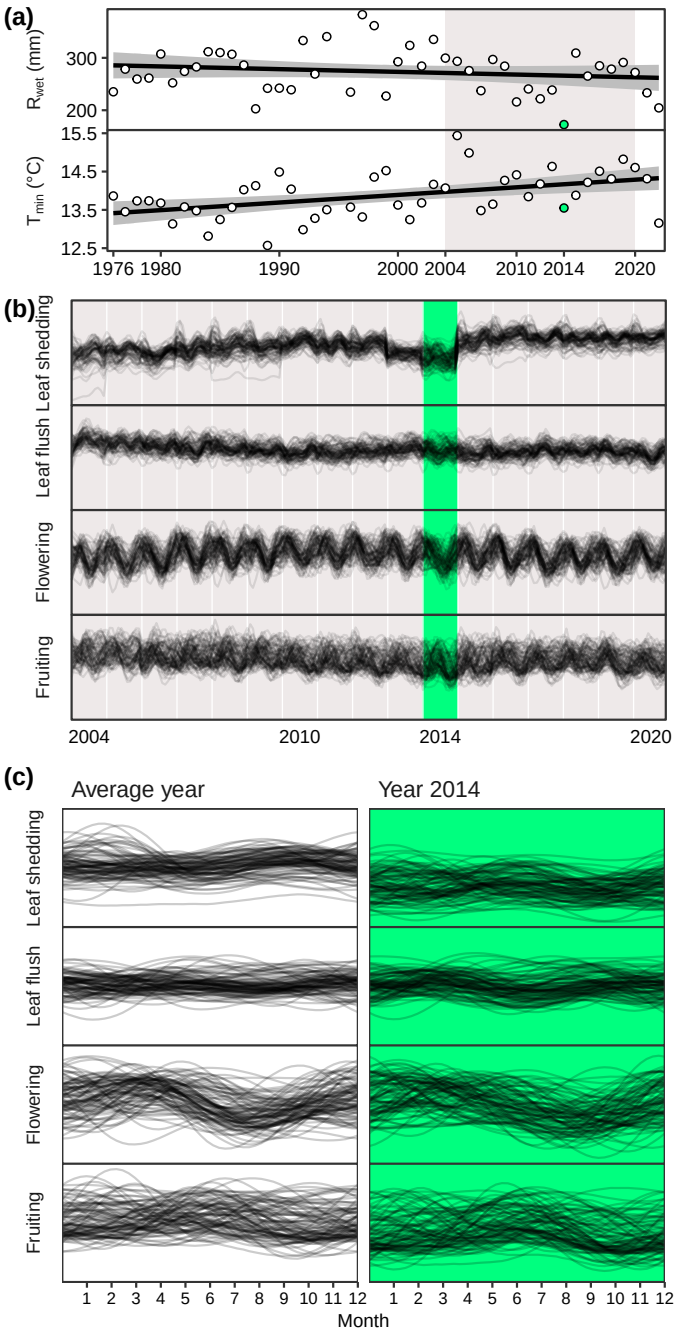

Figure 2: Temporal trends in climate and phenology. **(a)** Annual changes in wet-season rainfall (R_{wet}) and minimum temperature (T_{min}) in the Mambilla plateau over nearly half a century. Thick black lines and grey shaded regions are fitted trends and 90% confidence intervals, respectively. Grey box highlights the period in which we collected phenological data. **(b)** Model-fitted values of species-specific monthly phenology from 2004 to 2020 (thin black lines). Green dot in **(a)** and green box in **(b)** highlights the driest year with the lowest R_{wet} within the study period. **(c)** Comparing the average model-fitted species-specific monthly phenology to that of the driest year, 2014.

in fruiting and the least in leaf flush. As an example, the year 2014 experienced the driest wet season during our study, which corresponded to less intense but earlier leaf shedding, less intense fruiting, and varied amplitudes in all phenologies across species (Fig. 2c).

Specifically, the effect of climate on midlines had a more consistent direction than the effects on amplitudes and phases. The midline of leaf shedding, leaf flush and fruiting of most species decreased with drying R_{wet}, while the midline of flowering decreased with warming T_{min} (left column of Fig. 3 and Figs S9–S10). The phenological amplitudes of many species were more strongly influenced by climate, but the huge interspecific variation and mixed signs in climate effects resulted in an overall more neutral change at the community level (middle column of Fig. 3 and Figs S11–S12). There were also some species-specific changes in the phases or timing of phenology with climate, but they tended to have much greater uncertainties (right column of Fig. 3 and Figs S13–S14).

Climate effects on community synchrony

Although R_{wet} and T_{min} had disparate effects on species' phenologies, the climate variables had a more consistent effect on the community-level synchrony of phenology. With decreasing current- and/or previous-year R_{wet}, the bi-directional and uncertain change in the phases of species emerged as a clearer decrease in the community synchrony of leaf shedding, while other phenologies became more synchronous (Fig. 4). These synchrony changes were particularly obvious when comparing the driest year 2014 to the long-term average climate condition. On the other hand, increasing current-year T_{min} was associated with increased reproductive synchrony, whereas increasing previous-year T_{min} was associated with increased foliar synchrony.

Discussion

Over 17 years in a seasonally dry tropical forest (SDTF) in Nigeria, we observed the foliar and reproductive phenology of 94 tree taxa, which mostly exhibited annual cycles in leaf shedding, flowering, and fruiting. This corroborates with previous studies in African forests (Adamescu et al., 2018; Bush et al., 2017; Ouédraogo et al., 2020), where periodic phenology evolved under

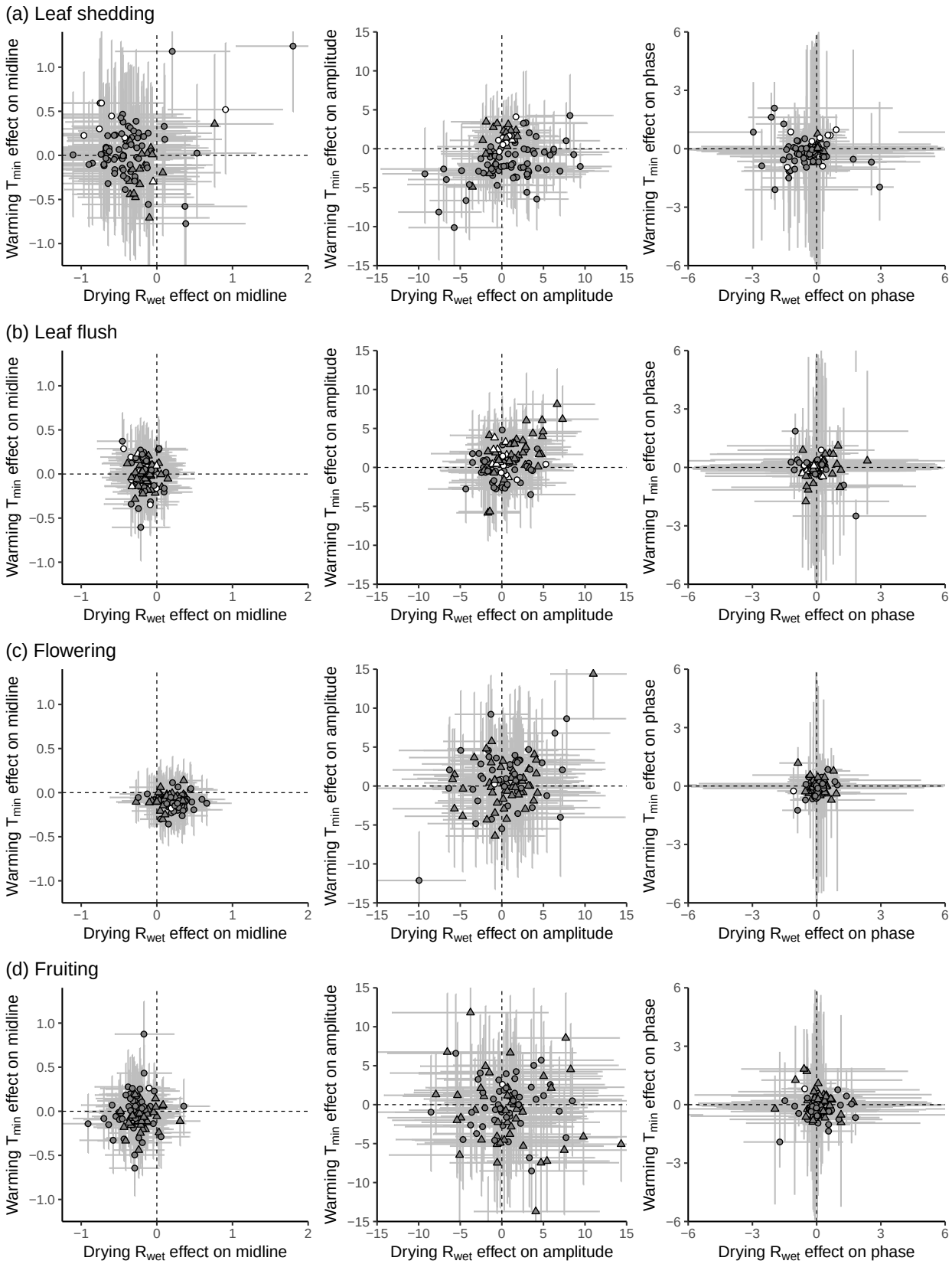

Figure 3: The effects of decreasing annual wet-season rainfall (X-axes, R_{wet}) and increasing minimum temperature (Y-axes, T_{min}) on the three aspects of phenology—midline (1st column), amplitude (2nd column), and phase (3rd column)—for leaf shedding **(a)**, leaf flush **(b)**, flowering **(c)**, and fruiting **(d)**. Symbols denote the posterior median of species, while error bars are the 89% credible intervals of posterior distribution. Grey and white circles represent species with predominantly annual and subannual phenology, respectively. Circles and triangles represent species that were more influenced by current- and previous-year climate variables, respectively.

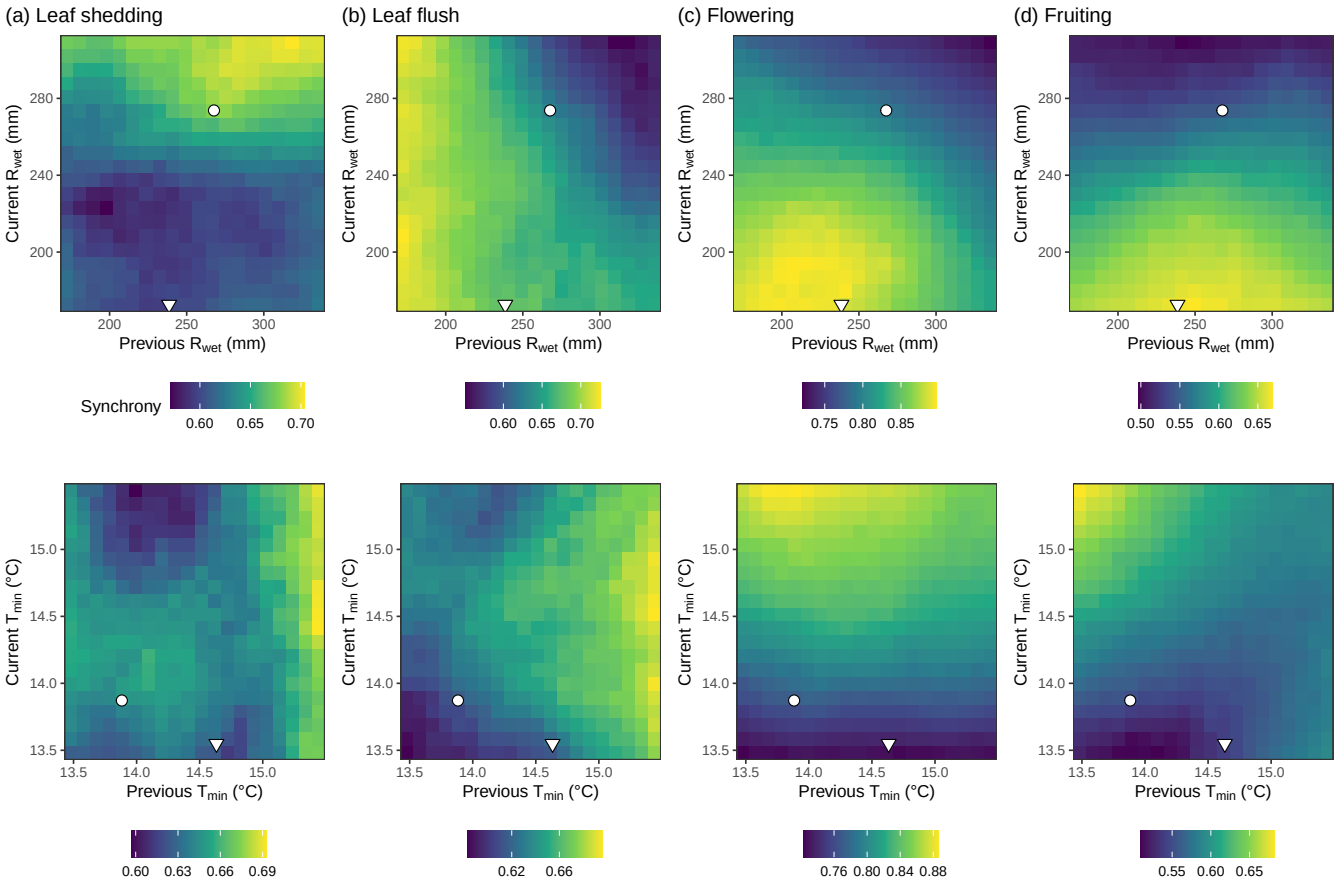

Figure 4: Community synchrony of phenology (calculated as the standard deviation on phases across species following Bush et al., 2017) along gradients of wet-season rainfall, R_{wet} **(top panels)** and minimum temperature, T_{min} **(bottom panels)**. X- and Y-axes are previous- and current-year climate values, respectively. Yellow and blue colours represent high and low synchrony, respectively. In each panel, the white dot denotes the long-term (47-year) average climate condition, while the white-downward triangle denotes the climate in 2014.

strong environmental cues across distinct wet–dry seasons (Borchert 1983; van Schaik, 1993; Sakai, 2001; Daïnou 2012). Leaf flush, however, displayed sub-annual cycles in more species and indicates an adaptive strategy to capitalise intermittent rainfall events that characterise our dry season (Lieberman and Lieberman, 1984). As observed in other African forests (Chapman et al 1999; Adamescu, 2018), our species varied considerably in the quantity and timing of foliar and reproductive phenologies, reflecting their survival strategies to seasonal abiotic and biotic cues (Daïnou et al 2012; Singh and Kushwaha 2005; Williams et al 2008; Lensky 2016) and roles in providing food supply for frugivores and pollinators spread across the year (Chapman et al 2018). More importantly, we detected huge interspecific and among-organ variations in the phenological timing and quantity (which we decomposed into mean intensity and amplitude) in response to decreasing wet-season rainfall (R_{wet}) and increasing minimum temperature (T_{min}). Consequently, the driest year of our study (2014) displayed less intense and earlier leaf shedding, less intense fruiting and varied amplitudes in all phenologies across species.

Phenological amplitude reveal more nuanced insights than intensity or timing alone

One of the emergent patterns from the phenology–climate relationships was changing deciduousness. Whereas previous tropical studies have demonstrated increased deciduousness with leaf-shedding intensity and timing under drier conditions (Borchert et al., 2002; Condit et al., 2002; Edwards et al., 2018; Janssen et al., 2021; Wu et al., 2021), we show that increased deciduousness could also result from increased amplitude. In our study, amplitude was more sensitive to climate change than timing and intensity. Twenty-one percent of species in total showed strong increases in deciduousness with drying R_{wet} but in different periodic components: 2% shedded more leaves due to increased mean intensity, 9% shedded leaves earlier due to advanced timing, 6% had more concentrated leaf shedding due to increased amplitude, while 4% had more concentrated and earlier leaf shedding due to changes in both timing and amplitude. Therefore, most of our species with increased deciduousness did not shed more leaves in total under drier conditions, instead they tended to shed the same amount of leaves in a more concentrated pulse within a shorter window of time. This phenomenon could be due to reduced

leaf flush in a previously dry year (this study and Ho et al., 2024), so that there was less foliar biomass to begin with, highlighting the importance of considering the lag and cumulative effects of consecutive droughts (Wunderling et al., 2022). The combination of reduced leaf flush followed by more abrupt and earlier leaf shedding implies that trees hold onto fewer leaves for a shorter period; if droughts continue to exacerbate such a feedback there could be cascading forest die-off (C. D. Allen et al., 2015).

Including amplitude in the analysis also helped reconcile an apparent conflict between the results of flowering and fruiting. For example, *Anthonotha noldeae* is a widespread tree species in our forest with increased mean flowering intensity, but decreased mean fruiting intensity, in drier years. A possible explanation for the mismatch between flower and fruit quantities is the increased flowering amplitude of *A. noldeae* in drier years; this indicates that the species flowered for a shorter duration, thus providing less opportunity for bird pollinators that are already rare to visit the flowers even when they pulsed in higher numbers (Beavon & Chapman, 2011). When the phenology of a widespread species that produces hyperabundant floral and fruit resources is affected by climate change, there could be cascading effects across the food web (Renner & Zohner, 2018). The fruiting of another common species, *Carapa oreophila*, not only had reduced mean intensity but also increased amplitude in drier years; this meant fewer fruits in total and for a shorter period. Such a compounding decline in fruit availability may drastically shift the behavior of being a key seed disperser—the African giant pouched rat (*Cricetomys* sp.)—from a scatterhoarding mutualist to a seed predator (Yadok et al., 2019), which would then feedback to a population decline of the primary producer.

Phenological mean intensity had more consistent climate responses

Compared to amplitude, the mean intensity of phenology had a more unidirectional response to climate, especially R_{wet}. In drier years, mean intensities tended to decrease for most species in all phenologies except flowering. As most species produce less litter, fewer leaves and fewer fruits in total, this indicates a lower primary productivity overall in drier conditions as previous studies suggested (Castro et al., 2018; Laan-Luijkx et al., 2015; Xu et al., 2019). Although the reduced leaf shedding during drought may suggest that trees were holding onto their leaves as

a form of drought tolerance, there might be alternative mechanisms at play, such as the dust-laden harmattan winds of the dry season (Jenik & Hall, 1966) or aerial particulates from fires that could reduce irradiation to a point where evapotranspiration is less exacerbated by drought (Wright & Cornejo, 1990). The decreased mean fruiting intensities in drier years despite the opposite trend in flowering suggests poorer floral quality (Kuppler & Kotowska, 2021), resulting in higher rates of fruit abortion (Bawa & Webb, 1984). Surplus flower production may also be a strategy to satiate predispersal fruit and seed predators in harsher environments (Stephenson, 1981), but support for this hypothesis remains weak (Jeffs et al., 2018). In drier years, 35 of our species had strong decline in mean fruiting intensity with increasing or no change in mean flowering intensity; this could be due to pollination mismatch by shortened flowering duration (increased amplitudes) in two species (*A. noldeae* and *Diospyros monbuttensis*) or delayed flowering in one species (*Isolona deightonii*). For the remaining species, more research is urgently needed to explain such a decoupling between total flower and fruit production under drought conditions, especially when five species (including *I. deightonii*) are important fruit providers for the endangered Nigeria–Cameroon chimpanzee (*Pan troglodytes ellioti*).

Phenological phase had uncertain climate responses but led to consistent synchrony

There was high uncertainties around the effects of climate on the timing of species-level phenology but they lined up to more consistent trends in community synchrony, which was more strongly associated with R_{wet} than T_{min}. Community leaf shedding were less synchronous in drier years due to strong bidirectional changes in the timing of leaf shedding among species. Such a more evenly distributed leaf-litter deposition throughout the year could alter the rate of nutrient cycling, primary productivity and window for seed germination (Sayer, 2006; Wood et al., 2009). In contrast, the production of leaves, flowers and fruits were more synchronous in drier years, indicating a tighter schedule around the onset of wet season for trees to perform photosynthesis and reproduction. A more synchronous primary production could also create periods of scarcity for herbivores, pollinators and frugivores (Renner & Zohner, 2018), thereby increasing competition among consumers due to behavioural changes or fewer opportunities

to temporally partition resources (Ovaskainen et al., 2013). On the other hand, a more synchronous leaf flush during drought might avoid prolonged damage by herbivorous insects, but this requires further testing (Lieberman & Lieberman, 1984).

Conclusions

Using a long-term community dataset of multi-organ phenology, we show that examining both the quantity and timing of phenology contributed to a more nuanced and complete understanding about the consequences of climate change on ecosystem functioning. There was a high diversity of phenology–climate relationships across the 94 taxa, yet a few general patterns emerged: interspecific phenological responses to climate change were more consistent in terms of total quantity and less consistent in terms of timing (but more consistent when viewed as synchrony at the community level). Furthermore, the duration or concentration of phenology potentially reconciles some of the phenological inconsistencies among organs. Lastly, the modelling framework applied here could be vastly improved by the inclusion of life-history traits (Lasky et al., 2016) and phylogeny (Davis et al., 2022) towards a more generalised and mechanistic understanding.

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