

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

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25 Summary

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

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

48 Introduction

49 Climate change, such as increasing drought and aridity, is expected to severely weaken the role
50 of tropical forests as carbon sinks (Corlett, 2016). Tropical dry-forest assemblages, despite
51 their long evolutionary history under water deficit, are also not exempt from diversity loss
52 (Siyum, 2020; Moura *et al.*, 2023). These seasonally dry forests, characterised by alternating
53 wet and dry seasons that last between four to seven months (Allen *et al.*, 2017), are widespread
54 across sub-Saharan Africa where they are central to biodiversity conservation and people's
55 livelihoods (Siyum, 2020). For example, the seasonally dry montane forests of the Cameroon
56 highlands are some of the most diverse and threatened plant communities in Africa (Cheek *et*
57 *al.*, 2000), and being montane they may be especially vulnerable to climate change (Salinas *et*
58 *al.*, 2021; Mata-Guel *et al.*, 2023). These forests provide essential ecosystem services including
59 carbon storage (Cuni-Sanchez *et al.*, 2021), freshwater provision, flood mitigation (Abiem *et*

60 *al.*, 2023), pollinators and pest control agents of crops (Tela *et al.*, 2021), but are additionally
61 threatened by land use change, overgrazing, fire and bush meat hunting (Cheek *et al.*, 2000;
62 Chapman *et al.*, 2004; Cheek *et al.*, 2021). It is thus imperative that we understand the resilience
63 of these forests to climate change.

64 While the impact of climate change on forest tree demography (e.g., mortality and growth)
65 is relatively well studied (Corlett, 2016), we are only beginning to understand how climate
66 change influences phenology, i.e., the timing of life-cycle events (Sakai & Kitajima, 2019).
67 Shifts in the phenology of photosynthetic and reproductive organs provide finer insights into
68 the underlying mechanisms that drive demographic changes under climate change (Iler *et al.*,
69 2021). In seasonally dry forests, for example, the timing of leaf shedding (deciduousness or
70 senescence) and leaf flush are especially important because they strongly reflect tree water sta-
71 tus (Borchert, 1994; Kushwaha & Singh, 2005; Pires *et al.*, 2018; Kaewthongrach *et al.*, 2020).
72 Moreover, plant phenology provides a more direct link to ecosystem functioning (Chapman *et*
73 *al.*, 2005; Zhao *et al.*, 2013; Gray & Ewers, 2021; Hackett-Pain & Bogdziewicz, 2021), af-
74 fecting processes such as carbon sequestration, multitrophic networks, and species coexistence
75 (Tang *et al.*, 2016). Consequently, the sensitivity of species phenology to climate change holds
76 critical information for ecosystem resilience, contingent upon the responses of both individual
77 species and the entire community (Sullivan *et al.*, 2023).

78 Individual species vary in their phenology or “temporal niche” (Sakai, 2001), which has
79 evolved in response to both abiotic and biotic selection pressures (Pau *et al.*, 2011). Key
80 climate-related cues include temperature, precipitation, solar irradiance (Van Schaik *et al.*,
81 1993; Butt *et al.*, 2015; Chapman *et al.*, 2018; Numata *et al.*, 2022) and climate anomalies
82 such as the El Niño–Southern Oscillations and in Africa, the Inter-Tropical Convergence Zone
83 (Igboabuchi *et al.*, 2018). Biotic cues include pollinators, seed dispersers, herbivores, and
84 predators (Bawa, 1990; Chapman *et al.*, 1999). Cues are not mutually exclusive and interact to
85 drive complex plant phenologies (Van Schaik *et al.*, 1993). For instance, while the stressful con-
86 ditions brought about by wet or dry seasons may promote community synchrony (Van Schaik
87 *et al.*, 1993; Lasky *et al.*, 2016), biotic factors can lead to either synchronous or asynchronous
88 phenologies (Lasky *et al.*, 2016). As climate change modifies environmental cues, species may
89 adjust their phenology accordingly (Thébault & Fontaine, 2010; Clark *et al.*, 2013; Butt *et al.*,
90 2015; Deb *et al.*, 2018; Flores *et al.*, 2023). Given the diverse responses of different species to
91 these changes (Rafferty *et al.*, 2015; León-Sánchez *et al.*, 2018; Samplonius *et al.*, 2021; Flores
92 *et al.*, 2023), phenological mismatches may, for example, arise between the timing of leaf flush
93 and flowering and their associated herbivores or mutualists, potentially disrupting community
94 synchrony (Ovaskainen *et al.*, 2013; Renner & Zohner, 2018). The impact of species-specific
95 phenological shifts on overall community synchrony remains uncertain however (Lima *et al.*,
96 2021; Chen *et al.*, 2023), partly because responses are often subjected to multiple climatic cues
97 (Chang-Yang *et al.*, 2016).

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

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

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

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

132 **Materials and Methods**

133 **Study system**

134 The study was carried out in the 46-km² Ngel Nyaki Forest Reserve (7.06°N, 11.1°E) on the
135 south west escarpment of the Mambilla Plateau in Taraba State, Nigeria (Fig 1). Within the
136 reserve, Ngel Nyaki forest is a 5.2-km² stand of submontane forest on the steep slopes of an
137 ancient volcano, which offer protection from fire and grazing (Chapman & Chapman, 2001;
138 Abiem *et al.*, 2020). The mean annual rainfall is approximately 1,800 mm, with most of the
139 rain falling between April and October, followed by a six-month dry season. During the wet
140 season, the forest can be covered in mist or fog for weeks on end, severely reducing irradiation
141 (Chapman & Chapman, 2001). The mean annual temperature is 19°C and the monthly mean
142 maximum and minimum temperatures for the wet and dry seasons are 25.6 and 15.4°C, and
143 28.1 and 15.5°C, respectively (Nigerian Montane Forest Project weather data). The soil in
144 Ngel Nyaki forest is clay-loam with pH of 5.8–4.7 (Chapman & Chapman, 2001).

145 Ngel Nyaki forest is relatively diverse for the Afromontane with approximately 105 tree
146 species from 47 families and 87 genera (Abiem *et al.*, 2020). Rubiaceae is the most diverse fam-
147 ily with nine species. Abundant tree species include *Garcinia smeathmannii*, *Deinbollia pin-*
148 *nata* and *Pleiocarpa pycnantha*. The three principle emergent species are *Pouteria altissima*,
149 *Entandrophragma angolense* and *Newtonia buchananii*, which reach to 36–46 m in height
150 (Chapman & Chapman, 2001). A middle canopy layer sensu Richards (1952) between 15–
151 30-m tall comprises species such as *Cordia millenii*, *Chrysophyllum albidum*, *Leptalus zenkeri*
152 and *Drypetes gossweileri*. Forest species comprise a mix of Afromontane endemics or near-
153 endemics (White, 1983), lowland forest and forest edge/grassland species. There is a gradient
154 in species composition from forest core to edge, with edge species comprising more drought
155 tolerant, often grassland species (Abiem *et al.*, 2020). The forest is a Birdlife International
156 Important Bird Area and rich in primate species including the endangered Nigeria–Cameroon
157 chimpanzee (*Pan troglodytes* ssp. *elliotti*). While the forest is a State Forest Reserve and there-
158 fore theoretically protected from hunting and grazing, in practice there is very little protection.
159 Forest edges have been farmed on the lower slopes of the forest and cattle have damaged a
160 substantial proportion of the reserve.

161 **Data collection**

162 Approximately 10 km² of phenology transects were established in 2004. Under a systematic
163 design, the transects are 500 m apart (Beck & Chapman, 2008), running east to west to criss-
164 cross the forest and obtain a good representation of the community composition. Along the
165 transects, 800 trees > 10 cm in diameter-at-breast-height (DBH), comprising 95 species were
166 tagged, numbered and DBH measured. The number of trees per species ranged from 1 to 36
167 (median = 18.5). Voucher specimens are deposited in the Nigerian Montane Forest Project

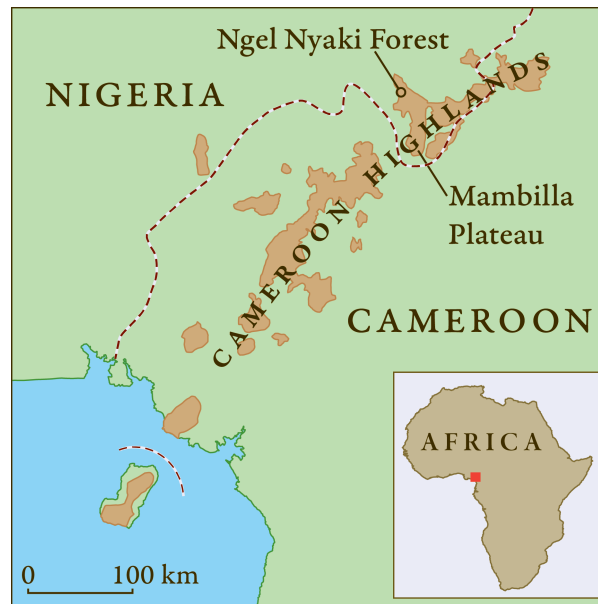


Figure 1: Map of the Cameroon Highlands showing the Mambilla Plateau and the location of Ngel Nyaki forest reserve. Modified from Thia (2014).

168 herbarium. Samples were sent to the Royal Botanical Gardens Kew for identification and other
169 were confirmed through the ForestGeo DNA fingerprinting protocol (Kenfack *et al.*, 2022).
170 Tagged trees were chosen to ensure a representative sample of the forest composition including
171 taxonomy, dispersal modes and flower types. Since then, the transects have been walked ev-
172 ery month for tree phenology monitoring. Trees are observed close-up, with binoculars when
173 necessary, to observe flowers and fruits. As an indicator of monthly leaf shedding, leaf flush,
174 flowering and fruiting, the proportion of crown occupied by each phenological variable in a
175 given tree is given an ordinal score between zero and four (0 = 0%, 1 = 1–25%, 2 = 26–50%,
176 3 = 51–75%, 4 = 76–100%) following Sun *et al.* (2009). To test the influence of concur-
177 rent monthly weather on phenology, we then matched monthly field observations with local
178 monthly weather data of temperature and rainfall obtained remotely from NASA’s Prediction
179 of Worldwide Energy and Resources portal (<https://power.larc.nasa.gov/>).

180 To quantify changes in longer-term climate and provide context for climate change im-
181 pacts on phenology, we used a 48-year monthly time series from 1976–2023 from weather
182 model-reanalysis data and in-situ observations. In-situ measurements of rainfall were gathered
183 from the Gembu State Government weather station in the Sardauna Province (6° 41' 13.08 N;
184 11° 17' 33.48 E), which is 40 km from our study site. Records of rainfall were corrected for
185 annotation errors, but missing values were not filled. The minimum and maximum tempera-
186 tures recorded at the Gembu station showed a long-term cooling, likely caused by tree planting
187 in the vicinity of the weather station and thus reflecting the micro-meteorology surrounding the
188 weather station. Therefore, we instead used the 2-m air temperature product from the ERA5-
189 Land hourly data reanalysis dataset (Muñoz Sabater, 2019). The ERA5 hourly land product
190 has a 0.1° × 0.1° horizontal resolution. To match the Gembu time series, we also used data

191 from 1976–2023. Hourly values were converted to monthly means of daily minimum temper-
192 ature (hereafter simply as “minimum temperature”), using Python v3.11.5 including packages
193 numpy v1.24.3, pandas v2.0.3, and scipy v1.11.1.

194 Statistical analyses

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

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

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

203 In the linear predictor η , we began by including species-specific random intercepts α_j that
204 model the average intensities of phenology for each species. We then included two predictor
205 components to the model. First, $f_{pjt}(m)$ denotes the Fourier decomposition (Fidino & Magle,
206 2017) of calendar months ($m = 1, 2, \dots, 12$) into the first two dominant components with pe-
207 riodicity of 12 and 6 months (based on Bush *et al.*, 2017) in the time series. Each periodic
208 component consists of two Fourier terms, C and S , and the respective coefficients, β_1 and β_2 .
209 In Appendix S1, we provide the mathematical details of these Fourier terms and coefficients, as
210 well as how to derive the amplitude of both periodicities to define whether annual (12 months)
211 or subannual (6 months) is the predominant cycle. This decomposition, also known as ‘cosinor’
212 (Nelson *et al.*, 1979), allowed us to model the periodic cycles in phenology. The same tech-
213 nique has been used to quantify leaf phenology (e.g., Williams *et al.*, 2008 who coined ‘circular
214 statistics’) but not expanded into GLMM as here. We allowed the Fourier coefficients β_1 and
215 β_2 to vary by species and year to accommodate interspecific and interannual (nonstationary)
216 variations in phenological periods.

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

222 term variation in phenology responding to monthly weathers.

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

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

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

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

246 **Calculating community-level phenology**

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

254 Next, we extracted the community-mean magnitude of peak intensity for each phenology
255 in each year, as well as the month in which the peak occurred. We acknowledge that ampli-
256 tudes and phase shifts can be analytically derived from the Fourier coefficients (Nelson *et al.*,
257 1979; Shumway & Stoffer, 2010, see also Supplementary Information), but they are calculated
258 for each Fourier components and hence may not reflect the overall shape of the cycles. We

259 therefore opted to numerically calculate peaks to obtain the total magnitudes across all Fourier
260 components, i.e., by computing fitted values from the model and then locate the highest peaks.
261 For every year, we also calculated community synchrony in phenology as the mean pairwise
262 Spearman's ranked correlation in the fitted values between individuals (Loreau & De Mazan-
263 court, 2008). Finally, we quantified the prediction accuracy of whole-community phenology
264 in every year using the continuously ranked probability score (CRPS, which indicates how
265 well the predicted ordinal values match the observed, Gneiting & Raftery, 2007) using the loo
266 package v2.6.0 (Vehtari *et al.*, 2017). Assessing prediction accuracy allows us to understand
267 whether some phenologies are less deterministic than others, and if phenology has become
268 more unpredictable under climate disruptions.

269 Results

270 Species-level phenology

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

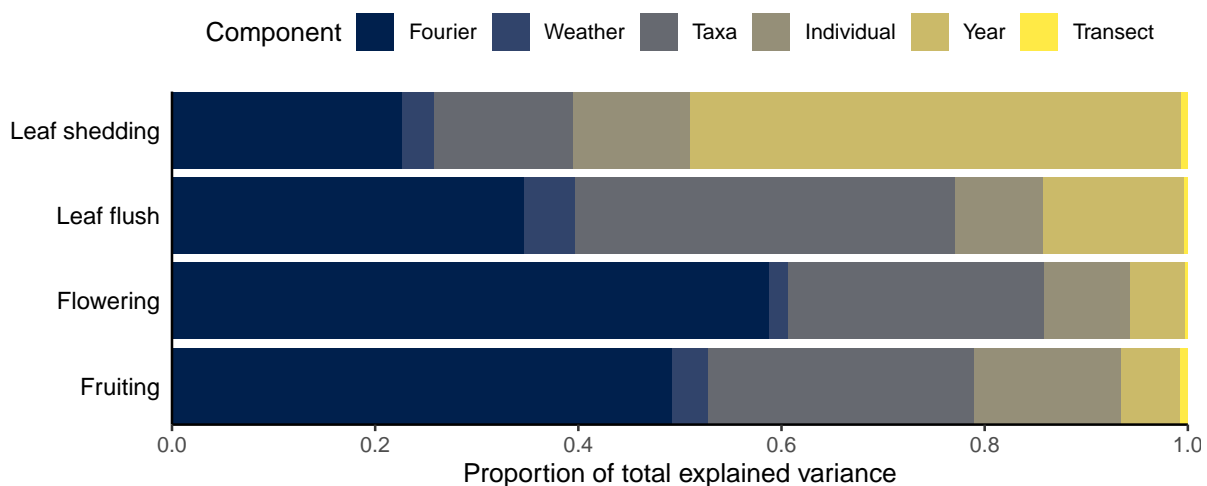


Figure 2: Variance partitioning of each phenology variable. Key to the variance components: Fourier = the fourier component f in the main text, Climate = the climate component g , Taxa = taxon-specific random intercept α_j , Individual = tree-specific random intercept ϵ_i , Year = year-specific random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

279 Forty-eight species (51%) showed seasonal deciduousness whereby at least half of the
280 crown was bare for 1–2 months (Fig. 3). Of the deciduous species, 29 shed their leaves during
281 the height of the dry season, while the remaining 20 species shed leaves during the mid-late
282 wet season. All other species lost varying amounts of leaves across the year. There were fewer
283 species that shed leaves at the beginning of the wet season (Fig. S3A). Seven of the 94 species
284 (7%) showed strong seasonal leaf flush, whereby over half of the crown had fresh leaves at any
285 one month (Fig. 3). Of these, 2 species flushed in the dry season and 5 in the wet season. The
286 remaining 77 species had small amounts of leaf flush throughout the year. Species with signals
287 of sub-annual cycles seemed to produce leaves around the beginning and end of the wet season
288 (Fig. S3B).

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

298 **Community-level phenology**

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

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

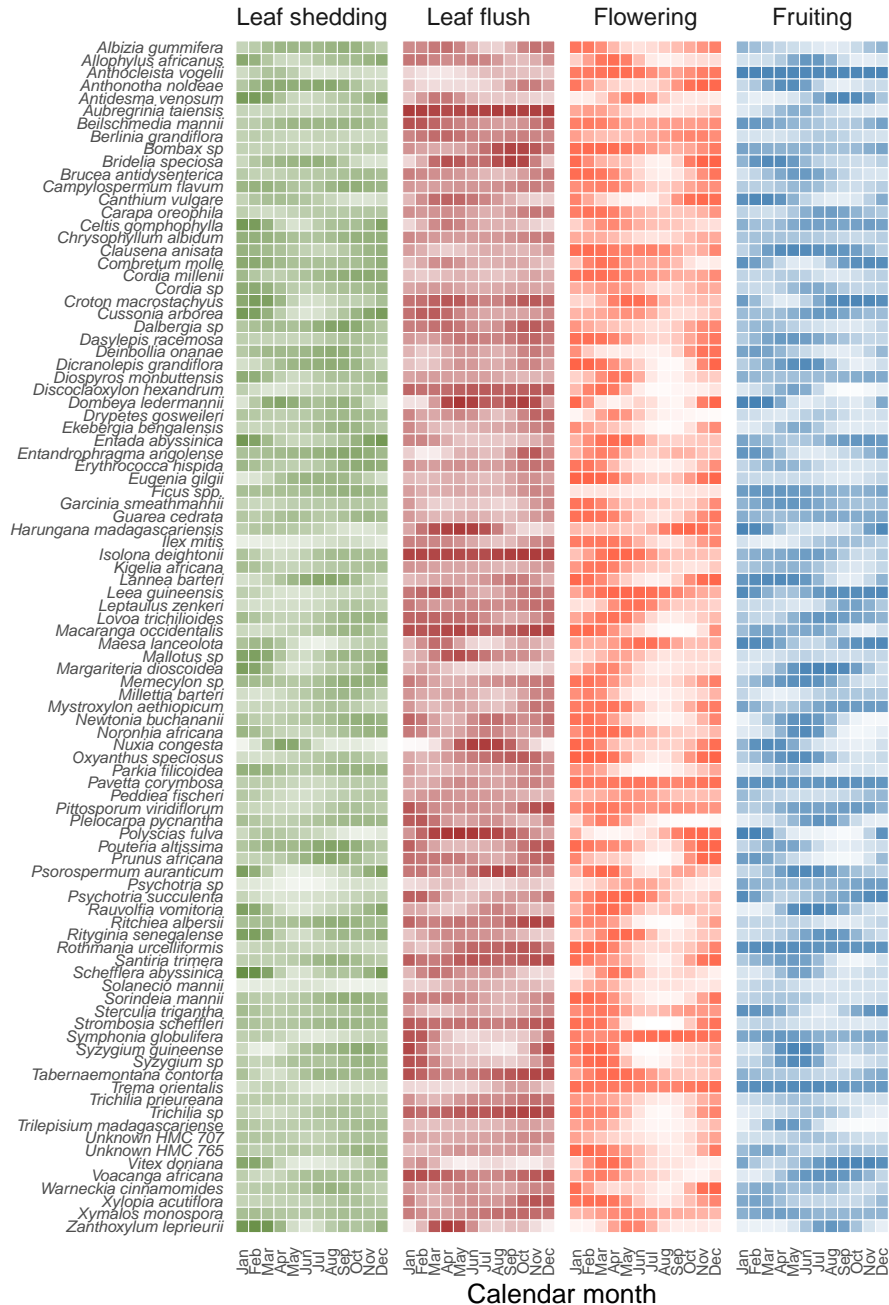


Figure 3: Overall phenological calendar for each species. Darker colours indicate more intense phenology (posterior median of η_j). Predictions are made under the average climate conditions in this study and are marginalised across all other random effects.

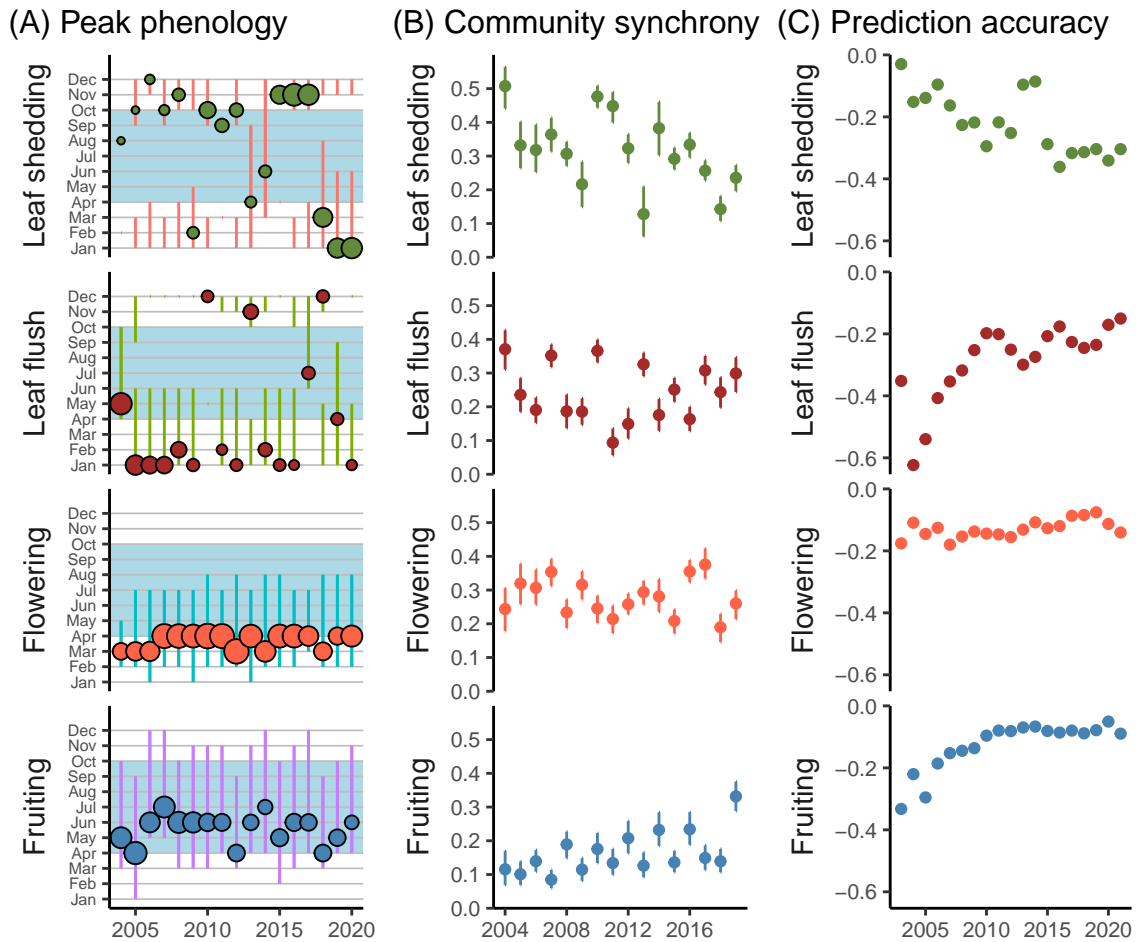


Figure 4: Community-level phenology across years. **(A)** Calendar month when the community is predicted to reach peak phenology. Points and error bars are circular median and interquartile range, respectively. Larger point size indicates higher peak intensity. Light-blue shaded regions denote the historical 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.

314 **Weather influence on phenology**

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

323 **Climate trends**

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

332 Minimum temperature had a highly significant increasing trend of 0.017°C per year, or
333 0.8°C over the 48-year observation period (Fig. S5). The increase during the intermediate sea-
334 son was greatest at 0.020°C per year, or 1.0°C over 48 years; similarly the dry season increased
335 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
336 or 0.6°C over 48 years. All seasons and all individual months (except January) showed signifi-
337 cant increases in minimum temperature; February and March showed the greatest increases in
338 minimum temperature at 1.8 and 1.9°C over 48 years. Rainfall did not show a significant trend
339 overall. When broken down into seasons, however, the dry season was significantly wetter by
340 16 mm per month by the end of 48 year observation period. Conversely, the wet season was
341 significantly drier by 55 mm per month by the end of the 48 year observation period.

342 **Discussion**

343 We described the foliar and reproductive phenological trends over 19 years of 623 trees across
344 94 taxa in a seasonally dry submontane forest in the Cameroon highlands, Nigeria. We found
345 that annual cycles were by far the most common periodicity across all four phenologies, agree-
346 ing with findings for flowering and fruiting phenologies from other West African forests (Bush
347 *et al.*, 2017; Adamescu *et al.*, 2018). We also detected discordant trends in the intensity of

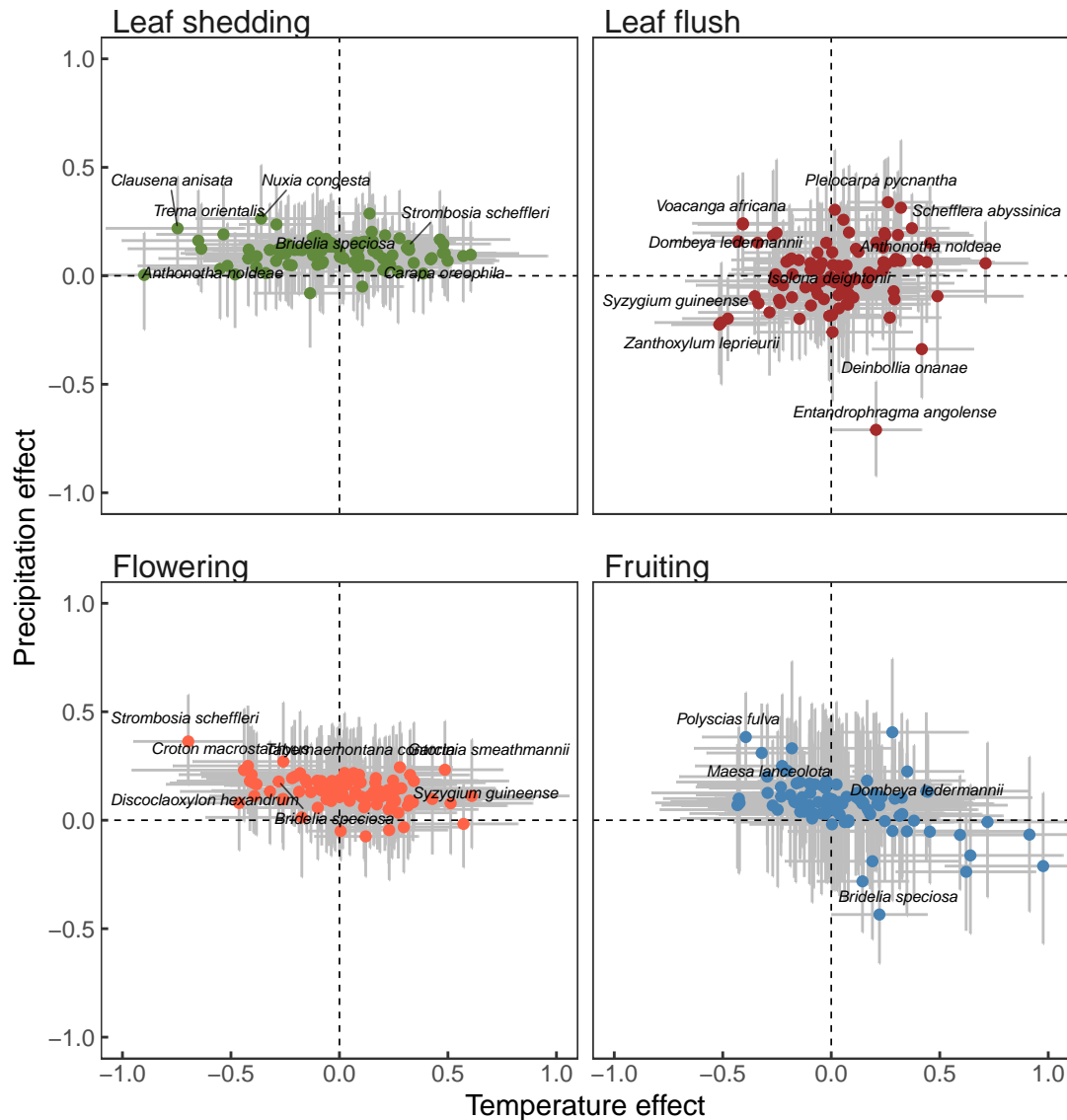


Figure 5: Species-specific phenological responses to total monthly precipitation and mean monthly temperature. Solid points and error bars are posterior median and 89% credible intervals, respectively. Each point corresponds to a focal species. Higher values lead to more intense phenology with increasing 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).

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

354 **Species and community level patterns, peak phenology and synchrony**

355 **Leaf shedding**

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

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

382 **Leaf flush**

383 Most species showed year-round leaf production, indicating adaptation to a persistent environ-
384 mental stressor such as dry-season drought and low wet-season irradiance (Nomura *et al.*,
385 2003). However, a suite of species comprising both understory and canopy trees showed dis-
386 tinct seasonal patterns in leaf flushing, mostly during the dry season. Despite the expectation
387 of reduced flushing during drought (Aide, 1993; Van Schaik *et al.*, 1993), some studies have
388 observed prevalent dry-season leaf flush like ours (Williams *et al.*, 1997; Rivera *et al.*, 2002;
389 Williams *et al.*, 2008; Janssen *et al.*, 2021). Dry-season leaf flush may be an adaptation to
390 reduce insect herbivory during the dry season (Kasenene & Roininen, 1999) and is perhaps tol-
391 erated in the understory because species are relatively protected from drought by shade from
392 taller trees. Furthermore, dry-season leaf flush among forest edge species that experience more
393 drought (Abiem *et al.*, 2020) may be an adaptation to limited nitrogen availability (February &
394 Higgins, 2016). It is also possible that subsoil water reserves allowed these species to produce
395 new leaves weeks before the first rain for a competitive edge (Rivera *et al.*, 2002; Williams *et*
396 *al.*, 2008).

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

407 **Flowering and fruiting**

408 In contrast to the foliar phenology, the timing of flowering and fruiting were noticeably more
409 regular. The majority of species consistently co-flowered towards the end of the dry season,
410 around the timing of the first rain. This fairly constant community synchrony in flowering
411 over the years has led to a community-level flowering that peaked around March. Flowering
412 towards the end of the dry season is a common pattern in tropical dry forests (Van Schaik
413 *et al.*, 1993) and may allow for fleshy fruits to later develop during peak rains (Chapman *et*
414 *al.*, 1999), though there were forest edge or grassland species (e.g., *Antidesma venosum*, *Cro-*
415 *ton macrostachyus* and *Maesa lanceolata*) that did not reach peak flowering until later in the
416 wet season. After flowering, community-level fruiting peaked during early to mid-wet season
417 (April–June). Therefore, fruits were more abundant in the wet than in the dry season, but the
418 considerable interspecific variation meant there was always something in fruit, as evidenced

419 by Dutton & Chapman (2015) who in the same study site found equivalent amounts of seeds
420 in chimpanzee faeces across the year, but from different seed species. Similar patterns of fruit
421 production have been noted elsewhere in Africa (Chapman *et al.*, 2005; Adamescu *et al.*, 2018;
422 Potts *et al.*, 2020).

423 The community peak and synchrony of flowering have not changed over the 19 years of
424 our study, while community fruiting has decreased slightly in peak intensity and became more
425 synchronous. It is difficult to tell where our results sit among previous findings, which show
426 disparate trends of increased (Pau *et al.*, 2013; Polansky & Boesch, 2013; Dunham *et al.*, 2018;
427 Flores *et al.*, 2023), decreased (Bush *et al.*, 2020; Numata *et al.*, 2022), or varying (Chapman *et*
428 *al.*, 2005; Potts *et al.*, 2020) reproductive intensity or synchrony. The stable flowering phenol-
429 ogy at Ngel Nyaki may indicate strong internal physiological inertia (Stevenson *et al.*, 2008) or
430 that cues for flowering have not changed over the study period. However, the driver of fruit pro-
431 duction at Ngel Nyaki remains in question as declining fruit production has decoupled from the
432 stable flower production. Irradiation could be important (Chapman *et al.*, 2018) and this may
433 be changing with either fog duration or more intense Harmattan (Jenik & Hall, 1966; Balarabe,
434 2018). Another explanation could be increased frugivory; while Ngel Nyaki has fewer chim-
435 panzees and other primates than in the past (Chapman *et al.*, 2004), these individuals are now
436 confined to within the forest boundaries due to extreme habitat fragmentation and edge en-
437 croachment (Knight *et al.*, 2016). We have not yet studied the pollinator communities within
438 the forest but they could also influence fruiting intensity and synchrony (Wheelwright, 1985;
439 Bawa, 1990). Of note is that while collecting seeds for forest restoration, we have recorded an
440 apparent decline in fruit production in areas of the forest that field assistants visit regularly, but
441 not in more remote parts of the forest. A possible explanation is that our presence has reduced
442 bush meat hunting around the phenology transects, thus making the area less threatening to
443 frugivores.

444 **Weather, climate change and forest resilience**

445 Analyses of the 48 years of ERA5-reanalysis climate for our study site shows that between
446 1976 and 2023 minimum temperatures are rising. This is in agreement with other reports of
447 increasing minimum temperatures across much of West Africa (Bush *et al.*, 2020; Bedair *et al.*,
448 2023 and citations therein). For example, Bush *et al.* (2020) found minimum daily temperatures
449 at Lopé, Gabon have increased at a rate of +0.25°C per decade since 1984. Total annual rainfall
450 on the Mambilla Plateau showed no significant trend, and no evidence of prolonged droughts,
451 which is in contrast to large parts of West Africa which are experiencing markedly reduced
452 rainfall (Malhi & Wright, 2004; Polansky & Boesch, 2013; Bush *et al.*, 2020). However, the
453 Plateau is experiencing increased variability in the magnitude, timing, and duration of rainfall.
454 For example, we found a significant decrease in wet season rainfall, which may lead to rainfall
455 shortages during times of the year that were historically wetter, which Allen *et al.* (2017) define

456 as droughts. These subtle rainfall changes could affect phenology, as Valdez-Hernández *et al.*
457 (2010) found that it was rainfall timing, rather than amount that influences phenology for a dry
458 forest in Mexico. In addition, Ho *et al.* (in review) showed that leaf flush could be related to
459 increased seasonality in rainfall.

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

473 To what extent the phenological trends of species and community we found are adaptive
474 and might confer resilience to climate change is unclear. African tropical forests may be re-
475 siliance to drought because many species are pre-adapted to dry conditions (Bennett *et al.*,
476 2021). The survival of trees against future drought, however, does not guarantee the stability
477 of ecosystem functions. If droughts do become more frequent and aseasonal, more deciduous
478 species will possibly gain a competitive advantage over evergreens in the long term (Vico *et al.*,
479 2017). Such a compositional shift, coupled with the increasing leaf shedding from our results,
480 suggests a lower leaf biomass during extended periods of droughts, potentially undermining
481 the role of these forests as carbon sinks (Reichstein *et al.*, 2013; Kaewthongrach *et al.*, 2020;
482 Bennett *et al.*, 2021; Janssen *et al.*, 2021). Similarly, the stable flowering phenology does not
483 guarantee long-term resilience because of its mismatch with leaf flush, which has decreased in
484 peak intensity over the years. The reduced leaf production and hence photosynthetic resources
485 may led to poorer flower and fruit qualities, even if their quantities do not change (Singh &
486 Kushwaha, 2006). Such nuances may be missed from phenology studies that only focus on
487 reproductive, but not foliar, organs.

488 Ultimately, management actions depend not only on good understandings but also accurate
489 predictions of phenology. Leaf shedding was the only phenology that declined in prediction
490 accuracy over the years, possibly related to it becoming more asynchronous among trees. The
491 decreasing prediction accuracy also indicates nonstationaries due to some missing year-specific
492 factor that influenced leaf shedding, for instance species-by-year interactions whereby some
493 species were more sensitive to certain interannual anomalies (e.g., deciduous species to El
494 Niño). Unfortunately, we were unable to include the species-by-year random effect in our

495 model because of the limited replications of several species, but this could be tested by future
496 studies with a more even sampling. Other phenologies had stable or increasing prediction
497 accuracies, but they are not necessarily good news; leaf flush may become more predictable
498 because most trees produced new leaves consistently at very low intensities, while fruiting may
499 become more predictable because it is more synchronous in the wet season but less available
500 in the dry season. Further studies could consider functional traits (e.g., leaf physiology, rooting
501 depth and the ability to store water in the trunk) to improve the prediction and generalisation
502 of phenological responses to drought (Van Schaik *et al.*, 1993; Corlett, 2016; Radford Smith
503 *et al.*, 2024). Tree size could also strongly moderate performance under drought (Bennett *et*
504 *al.*, 2015). Our monthly phenology survey did not include repeated measures of tree size due
505 to logistic constraints, but we recommend future studies to include tree size as a covariate of
506 phenology.

507 Whether the studied forest is resilient to climate change as a whole remains an open ques-
508 tion without more information. The drivers and consequences of tree phenology do not solely
509 involve the plants, but also their interactions with other trophic levels (Ovaskainen *et al.*, 2013;
510 CaraDonna *et al.*, 2014; Visser & Gienapp, 2019) as well as the environment (Sayer *et al.*,
511 2024). Importantly, the discordant changes in foliar and reproductive phenology in our data
512 suggest that assessments of forest resilience should rely on multiple aspects of phenology rather
513 than a single performance indicator. That concurrent weather explains very little compared to
514 long-term climatic cycles suggests that tree species may be resilient to short-term weather ir-
515 regularities, but they may not be able to withstand prolonged shifts in the climate regime.

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525 **Competing interests**

526 The authors declared no competing interest.

527 **Author contributions**

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

532 **Data availability**

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

535 **References**

- 536 **Abernethy K, Bush ER, Forget PM, Mendoza I, Morellato LPC. 2018.** [Current issues in](#)
537 [tropical phenology: a synthesis](#). *Biotropica* **50**: 477–482.
- 538 **Abiem I, Arellano G, Kenfack D, Chapman H. 2020.** [Afromontane Forest Diversity and the](#)
539 [Role of Species Distribution](#). *Diversity* **12**: 1–19.
- 540 **Abiem I, Kenfack D, Chapman HM. 2023.** [Assessing the impact of abiotic and biotic factors](#)
541 [on seedling survival in an African montane forest](#). *Frontiers in Forests and Global Change* **6**:
542 1–11.
- 543 **Adamescu GS, Plumptre AJ, Abernethy KA, Polansky L, Bush ER, Chapman CA, Shoo**
544 **LP, Fayolle A, Janmaat KRL, Robbins MM, et al. 2018.** [Annual cycles are the most common](#)
545 [reproductive strategy in African tropical tree communities](#). *Biotropica* **50**: 418–430.
- 546 **Adole T, Dash J, Atkinson PM. 2018.** [Characterising the land surface phenology of Africa](#)
547 [using 500 m MODIS EVI](#). *Applied Geography* **90**: 187–199.
- 548 **Aide TM. 1993.** [Patterns of leaf development and herbivory in a tropical understory commu-](#)
549 [nity](#). *Ecology* **74**: 455–466.
- 550 **Allen K, Dupuy JM, Gei MG, Hulshof C, Medvigy D, Pizano C, Salgado-Negret B, Smith**
551 **CM, Trierweiler A, Van Bloem SJ, et al. 2017.** [Will seasonally dry tropical forests be sensi-](#)
552 [tive or resistant to future changes in rainfall regimes?](#) *Environmental Research Letters* **12**.
- 553 **Balarabe M. 2018.** [Analysis of Trend and Variability of Summer Season Visibility and Tem-](#)
554 [perature in Sahel Zone of Nigeria](#). *Phys. Memoir 1* **15**: 15–21.
- 555 **Bawa KS. 1990.** [Plant-pollinator interactions in tropical rain forests](#). *Annual Review of Ecology*
556 *and Systematics* **21**: 399–422.
- 557 **Beck J, Chapman H. 2008.** [A population estimate of the Endangered chimpanzee Pan](#)
558 [troglodytes vellerosus in a Nigerian montane forest: Implications for conservation](#). *Oryx* **42**:
559 448–451.

- 560 **Bedair H, Alghariani MS, Omar E, Anibaba QA, Remon M, Bornman C, Kiboi SK, Rady**
561 **HA, Salifu AMA, Ghosh S, et al. 2023.** [Global Warming Status in the African Continent:](#)
562 [Sources, Challenges, Policies, and Future Direction.](#) *International Journal of Environmental*
563 *Research* **17**: 1–23.
- 564 **Bennett AC, Dargie GC, Cuni-Sanchez A, Mukendi JT, Hubau W, Mukinzi JM, Phillips**
565 **OL, Malhi Y, Sullivan MJP, Cooper DLM, et al. 2021.** [Resistance of African tropical forests](#)
566 [to an extreme climate anomaly.](#) *Proceedings of the National Academy of Sciences of the United*
567 *States of America* **118**: 1–12.
- 568 **Bennett AC, Mcdowell NG, Allen CD, Anderson-Teixeira KJ. 2015.** [Larger trees suffer](#)
569 [most during drought in forests worldwide.](#) *Nature Plants* **1**: 1–5.
- 570 **Borchert R. 1994.** Soil and Stem Water Storage Determine Phenology and Dis-
571 tribution of Tropical Dry Forest Trees Author (s): Rolf Borchert Stable URL :
572 <http://www.jstor.org/stable/1937467> REFERENCES Linked references are available on
573 JSTOR for this article : You may need. *Ecology* **75**: 1437–1449.
- 574 **Bürkner PC. 2017.** [brms: An R package for Bayesian multilevel models using Stan.](#) *Journal*
575 *of Statistical Software* **80**: 1–28.
- 576 **Bürkner PC, Vuorre M. 2019.** [Ordinal Regression Models in Psychology: A Tutorial.](#) *Ad-*
577 *vances in Methods and Practices in Psychological Science* **2**: 77–101.
- 578 **Bush ER, Abernethy KA, Jeffery K, Tutin C, White L, Dimoto E, Dikangadissi JT, Jump**
579 **AS, Bunnefeld N. 2017.** [Fourier analysis to detect phenological cycles using long-term tropical](#)
580 [field data and simulations.](#) *Methods in Ecology and Evolution* **8**: 530–540.
- 581 **Bush ER, Bunnefeld N, Dimoto E, Dikangadissi JT, Jeffery K, Tutin C, White L, Aber-**
582 **nethy KA. 2018.** [Towards effective monitoring of tropical phenology: maximizing returns and](#)
583 [reducing uncertainty in long-term studies.](#) *Biotropica* **50**: 455–464.
- 584 **Bush ER, Jeffery K, Bunnefeld N, Tutin C, Musgrave R, Moussavou G, Mihindou V,**
585 **Malhi Y, Lehmann D, Ndong JE, et al. 2020.** [Rare ground data confirm significant warming](#)
586 [and drying in western equatorial Africa.](#) *PeerJ* **2020**: 1–29.
- 587 **Butt N, Seabrook L, Maron M, Law BS, Dawson TP, Syktus J, Mcalpine CA. 2015.** [Cas-](#)
588 [cading effects of climate extremes on vertebrate fauna through changes to low-latitude tree](#)
589 [flowering and fruiting phenology.](#) *Global Change Biology* **21**: 3267–3277.
- 590 **CaraDonna PJ, Iler AM, Inouye DW. 2014.** [Shifts in flowering phenology reshape a sub-](#)
591 [alpine plant community.](#) *Proceedings of the National Academy of Sciences of the United States*
592 *of America* **111**: 4916–4921.
- 593 **Chang-Yang CH, Sun IF, Tsai CH, Lu CL, Hsieh CF. 2016.** [ENSO and frost codetermine](#)
594 [decade-long temporal variation in flower and seed production in a subtropical rain forest.](#) *Jour-*
595 *nal of Ecology* **104**: 44–54.
- 596 **Chapman JD, Chapman HM. 2001.** *The Forests of Taraba and Adamawa States, Nigeria. An*
597 *Ecological Account and Plant Species Checklist.* Christchurch: University of Canterbury.
- 598 **Chapman CA, Chapman LJ, Struhsaker TT, Zanne AE, Clark CJ, Poulsen JR. 2005.** [A](#)

- 599 long-term evaluation of fruiting phenology: Importance of climate change. *Journal of Tropical*
600 *Ecology* **21**: 31–45.
- 601 **Chapman HM, Olson SM, Trumm D. 2004.** An assessment of changes in the montane forests
602 of Taraba State, Nigeria, over the past 30 years. *Oryx* **38**: 282–290.
- 603 **Chapman CA, Valenta K, Bonnell TR, Brown KA, Chapman LJ. 2018.** Solar radiation
604 and ENSO predict fruiting phenology patterns in a 15-year record from Kibale National Park,
605 Uganda. *Biotropica* **50**: 384–395.
- 606 **Chapman CA, Wrangham RW, Chapman LJ, Kennard DK, Zanne AE. 1999.** Fruit and
607 flower phenology at two sites in Kibale National Park, Uganda. *Journal of Tropical Ecology*
608 **15**: 189–211.
- 609 **Cheek M, Onana JM, Chapman HM. 2021.** The montane trees of the Cameroon Highlands,
610 West-Central Africa, with *Deinbollia onanae* sp. Nov. (Sapindaceae), a new primate-dispersed,
611 Endangered species. *PeerJ* **9**.
- 612 **Cheek M, Onana J, Pollard B. 2000.** *The Plants of Mount Oku and the Ijim Ridge, Cameroon:*
613 *A Conservation Checklist*. Kew: Royal Botanic Gardens.
- 614 **Chen Y, Collins SL, Zhao Y, Zhang T, Yang X, An H, Hu G, Xin C, Zhou J, Sheng X, et**
615 **al. 2023.** Warming reduced flowering synchrony and extended community flowering season in
616 an alpine meadow on the Tibetan Plateau. *Ecology* **104**: 1–13.
- 617 **Clark DA, Clark DB, Oberbauer SF. 2013.** Field-quantified responses of tropical rainfor-
618 est aboveground productivity to increasing CO₂ and climatic stress, 1997–2009. *Journal of*
619 *Geophysical Research: Biogeosciences* **118**: 783–794.
- 620 **Corlett RT. 2016.** The Impacts of Droughts in Tropical Forests. *Trends in Plant Science* **21**:
621 584–593.
- 622 **Cornforth IS. 1970.** Leaf-Fall in a Tropical Rain Forest. *The Journal of Applied Ecology* **7**:
623 603.
- 624 **Cuni-Sanchez A, Sullivan MJP, Platts PJ, Lewis SL, Marchant R, Imani G, Hubau W,**
625 **Abiem I, Adhikari H, Albrecht T, et al. 2021.** High aboveground carbon stock of African
626 tropical montane forests. *Nature* **596**: 536–542.
- 627 **Deb JC, Phinn S, Butt N, McAlpine CA. 2018.** Climate change impacts on tropical forests:
628 Identifying risks for tropical Asia. *Journal of Tropical Forest Science* **30**: 182–194.
- 629 **Detto M, Wright SJ, Calderón O, Muller-Landau HC. 2018.** Resource acquisition and re-
630 productive strategies of tropical forest in response to the El Niño–Southern Oscillation. *Nature*
631 *Communications* **9**: 1–8.
- 632 **Dunham AE, Razafindratsima OH, Rakotonirina P, Wright PC. 2018.** Fruiting phenology
633 is linked to rainfall variability in a tropical rain forest. *Biotropica* **50**: 396–404.
- 634 **Dutton P, Chapman H. 2015.** Dietary preferences of a submontane population of the rare
635 Nigerian-Cameroon chimpanzee (*Pan troglodytes ellioti*) in Ngel Nyaki Forest Reserve, Nige-
636 ria. *American Journal of Primatology* **77**: 86–97.
- 637 **February EC, Higgins SI. 2016.** Rapid leaf deployment strategies in a deciduous savanna.

638 *PLoS ONE* **11**.

639 **Feng X, Porporato A, Rodriguez-Iturbe I. 2013.** Changes in rainfall seasonality in the trop-
640 ics. *Nature Climate Change* **3**: 811–815.

641 **Fidino M, Magle SB. 2017.** Using Fourier series to estimate periodic patterns in dynamic
642 occupancy models. *Ecosphere* **8**.

643 **Flores S, Forister ML, Sulbaran H, Díaz R, Dyer LA. 2023.** Extreme drought disrupts plant
644 phenology: Insights from 35 years of cloud forest data in Venezuela. *Ecology* **104**: 1–11.

645 **Gneiting T, Raftery AE. 2007.** Strictly proper scoring rules, prediction, and estimation. *Jour-
646 nal of the American Statistical Association* **102**: 359–378.

647 **Gray REJ, Ewers RM. 2021.** Monitoring forest phenology in a changing world. *Forests* **12**.

648 **Hacket-Pain A, Bogdziewicz M. 2021.** Climate change and plant reproduction: Trends and
649 drivers of mast seeding change. *Philosophical Transactions of the Royal Society B: Biological
650 Sciences* **376**.

651 **Ho B-C, Chia EJJ, Chong KY, Tan JSY, Tan WX, Lai S, Choo TYS, Tan PY, Er KBH. in
652 review.** Shortening of leafing intervals with changes in rainfall patterns over a 90-year period
653 in a tropical botanical garden. *In review*.

654 **Igboabuchi NA, Echereme CB, Ekwealor KU. 2018.** Phenology in Plants: Concepts and
655 Uses. *International Journal Of Science And Research Methodology* **11**: 8–24.

656 **Iler AM, Caradonna PJ, Forrest JRK, Post E. 2021.** Demographic Consequences of Phe-
657 nological Shifts in Response to Climate Change. *Annual Review of Ecology, Evolution, and
658 Systematics* **52**: 221–245.

659 **Janssen T, Van Der Velde Y, Hofhansl F, Luysaert S, Naudts K, Driessen B, Fleischer K,
660 Dolman H. 2021.** Drought effects on leaf fall, leaf flushing and stem growth in the Amazon
661 forest: Reconciling remote sensing data and field observations. *Biogeosciences* **18**: 4445–4472.

662 **Jenik J, Hall JB. 1966.** The Ecological Effects of the Harmattan Wind in the Djebobo Massif
663 (Togo Mountains, Ghana). *The Journal of Ecology* **54**: 767.

664 **Kaewthongrach R, Chidthaisong A, Charuchittipan D, Vitasse Y, Sanwangsri M, Var-
665 nakovida P, Diloksumpun S, Panuthai S, Pakoktom T, Suepa T, et al. 2020.** Impacts of
666 a strong El Niño event on leaf phenology and carbon dioxide exchange in a secondary dry
667 dipterocarp forest. *Agricultural and Forest Meteorology* **287**: 107945.

668 **Kasenene JM, Roininen H. 1999.** Seasonality of insect herbivory on the leaves of *Neobouto-
669 nia macrocalyx* in the Kibale National Park, Uganda. *African Journal of Ecology* **37**: 61–68.

670 **Kenfack D, Abiem I, Chapman H. 2022.** The Efficiency of DNA Barcoding in the Identifica-
671 tion of Afromontane Forest Tree Species. *Diversity* **14**: 1–10.

672 **Knight A, Chapman HM, Hale M. 2016.** Habitat fragmentation and its implications for
673 Endangered chimpanzee *Pan troglodytes* conservation. *Oryx* **50**: 533–536.

674 **Kushwaha CP, Singh KP. 2005.** Diversity of leaf phenology in a tropical deciduous forest in
675 India. *Journal of Tropical Ecology* **21**: 47–56.

676 **Laan-Luijckx IT van der, Velde IR van der, Krol MC, Gatti LV, Domingues LG, Correia**

- 677 **CSC, Miller JB, Gloor M, Leeuwen TT van, Kaiser JW, et al. 2015.** Response of the Ama-
678 zon carbon balance to the 2010 drought derived with CarbonTracker South America. *Global*
679 *biogeochemical cycles* **29**: 1092–1108.
- 680 **Lasky JR, Uriarte M, Muscarella R. 2016.** Synchrony, compensatory dynamics, and the
681 functional trait basis of phenological diversity in a tropical dry forest tree community: Effects
682 of rainfall seasonality. *Environmental Research Letters* **11**.
- 683 **León-Sánchez L, Nicolás E, Goberna M, Prieto I, Maestre FT, Querejeta JI. 2018.** Poor
684 plant performance under simulated climate change is linked to mycorrhizal responses in a semi-
685 arid shrubland. *Journal of Ecology* **106**: 960–976.
- 686 **Lézine AM, Izumi K, Kageyama M, Achoundong G. 2019.** A 90,000-year record of
687 Afromontane forest responses to climate change. *Science* **363**: 177–181.
- 688 **Lima DF, Mello JHF, Lopes IT, Forzza RC, Goldenberg R, Freitas L. 2021.** Phenological
689 responses to climate change based on a hundred years of herbarium collections of tropical
690 Melastomataceae. *PLoS ONE* **16**: 1–19.
- 691 **Loreau M, De Mazancourt C. 2008.** Species synchrony and its drivers: Neutral and nonneu-
692 tral community dynamics in fluctuating environments. *American Naturalist* **172**.
- 693 **Malhi Y, Wright J. 2004.** Spatial patterns and recent trends in the climate of tropical rainforest
694 regions. *Philosophical Transactions of the Royal Society B: Biological Sciences* **359**: 311–329.
- 695 **Mata-Guel EO, Soh MCK, Butler CW, Morris RJ, Razgour O, Peh KSH. 2023.** Impacts
696 of anthropogenic climate change on tropical montane forests: an appraisal of the evidence.
697 *Biological Reviews* **98**: 1200–1224.
- 698 **Meadows ME, Linder HP. 1993.** Special Paper: A Palaeoecological Perspective on the Origin
699 of Afromontane Grasslands. *Journal of Biogeography* **20**: 345.
- 700 **Meineke EK, Davis CC, Davies TJ. 2021.** Phenological sensitivity to temperature mediates
701 herbivory. *Global Change Biology* **27**: 2315–2327.
- 702 **Moura MR, Nascimento FAO do, Paolucci LN, Silva DP, Santos BA. 2023.** Pervasive
703 impacts of climate change on the woodiness and ecological generalism of dry forest plant as-
704 semblages. *Journal of Ecology* **111**: 1762–1776.
- 705 **Muñoz Sabater J. 2019.** ERA5-Land hourly data from 1950 to present.
- 706 **Nelson W, Tong YL, Lee JK, Halberg F. 1979.** Methods for cosinor-rhythmometry. *Chrono-*
707 *biologia* **6**: 305–323.
- 708 **Nomura N, Kikuzawa K, Kitayama K. 2003.** Leaf Flushing Phenology of Tropical Montane
709 Rain Forests: Relationship to Soil Moisture and Nutrients. *Tropics* **12**: 261–276.
- 710 **Numata S, Yamaguchi K, Shimizu M, Sakurai G, Morimoto A, Alias N, Noor Azman NZ,**
711 **Hosaka T, Satake A. 2022.** Impacts of climate change on reproductive phenology in tropical
712 rainforests of Southeast Asia. *Communications Biology* **5**.
- 713 **Ostertag R, Restrepo C, Dalling JW, Martin PH, Abiem I, Aiba S ichiro, Alvarez-Dávila**
714 **E, Aragón R, Ataroff M, Chapman H, et al. 2022.** Litter decomposition rates across tropical
715 montane and lowland forests are controlled foremost by climate. *Biotropica* **54**: 309–326.

- 716 **Ovaskainen O, Skorokhodova S, Yakovleva M, Sukhov A, Kutenkov A, Kutenkova N,**
717 **Shcherbakov A, Meyke E, Del Mar Delgado M. 2013. Community-level phenological re-**
718 **sponse to climate change. *Proceedings of the National Academy of Sciences of the United***
719 ***States of America* 110: 13434–13439.**
- 720 **Pau S, Wolkovich EM, Cook BI, Davies TJ, Kraft NJB, Bolmgren K, Betancourt JL,**
721 **Cleland EE. 2011. Predicting phenology by integrating ecology, evolution and climate science.**
722 ***Global Change Biology* 17: 3633–3643.**
- 723 **Pau S, Wolkovich EM, Cook BI, Nytech CJ, Regetz J, Zimmerman JK, Joseph Wright S.**
724 **2013. Clouds and temperature drive dynamic changes in tropical flower production. *Nature***
725 ***Climate Change* 3: 838–842.**
- 726 **Pires JPA, Marino NAC, Silva AG, Rodrigues PJFP, Freitas L. 2018. Tree community**
727 **phenodynamics and its relationship with climatic conditions in a lowland tropical rainforest.**
728 ***Forests* 9.**
- 729 **Polansky L, Boesch C. 2013. Long-term Changes in Fruit Phenology in a West African Low-**
730 **land Tropical Rain Forest are Not Explained by Rainfall. *Biotropica* 45: 434–440.**
- 731 **Potts KB, Watts DP, Langergraber KE, Mitani JC. 2020. Long-term trends in fruit produc-**
732 **tion in a tropical forest at Ngogo, Kibale National Park, Uganda. *Biotropica* 52: 521–532.**
- 733 **R Core Team. 2022. *R: A language and environment for statistical computing.* Vienna,**
734 **Austria: R Foundation for Statistical Computing.**
- 735 **Radford Smith J, Cathcart-van Weeren E, Lai HR, Dwyer J. 2024. An ecophysiological**
736 **basis for the assembly of Australian rainforest tree communities. *In review.***
- 737 **Rafferty NE, Caradonna PJ, Bronstein JL. 2015. Phenological shifts and the fate of mutu-**
738 **alisms. *Oikos* 124: 14–21.**
- 739 **Reich PB. 1995. Phenology of tropical forests: patterns, causes, and consequences. *Canadian***
740 ***Journal of Botany* 73: 164–174.**
- 741 **Reichstein M, Bahn M, Ciais P, Frank D, Mahecha MD, Seneviratne SI, Zscheischler J,**
742 **Beer C, Buchmann N, Frank DC, et al. 2013. Climate extremes and the carbon cycle. *Nature***
743 **500: 287–295.**
- 744 **Renner SS, Zohner CM. 2018. Climate change and phenological mismatch in trophic in-**
745 **teractions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and***
746 ***Systematics* 49: 165–182.**
- 747 **Richards PW. 1952. *The Tropical Rain Forest.* Cambridge: Cambridge University Press.**
- 748 **Rivera G, Elliott S, Caldas LS, Nicolossi G, Coradin VT, Borchert R. 2002. Increasing**
749 **day-length induces spring flushing of tropical dry forest trees in the absence of rain. *Trees -***
750 ***Structure and Function* 16: 445–456.**
- 751 **Sakai S. 2001. Phenological diversity in tropical forests. *Population Ecology* 43: 77–86.**
- 752 **Sakai S, Kitajima K. 2019. Tropical phenology: Recent advances and perspectives. *Ecologi-***
753 ***cal Research* 34: 50–54.**
- 754 **Salinas N, Cosio EG, Silman M, Meir P, Nottingham AT, Roman-Cuesta RM, Malhi Y.**

- 755 **2021.** Editorial: Tropical Montane Forests in a Changing Environment. *Frontiers in Plant*
756 *Science* **12**: 1–5.
- 757 **Samplonius JM, Atkinson A, Hassall C, Keogan K, Thackeray SJ, Assmann JJ, Burgess**
758 **MD, Johansson J, Macphie KH, Pearce-Higgins JW, et al. 2021.** Strengthening the evidence
759 base for temperature-mediated phenological asynchrony and its impacts. *Nature Ecology and*
760 *Evolution* **5**: 155–164.
- 761 **Sayer EJ, Leitman SF, Wright SJ, Rodtassana C, Vincent AG, Bréchet LM, Castro B,**
762 **Lopez O, Wallwork A, Tanner EVJ. 2024.** Tropical forest above-ground productivity is
763 maintained by nutrients cycled in litter. *Journal of Ecology*: 1–11.
- 764 **Shumway RH, Stoffer DS. 2010.** *Time series analysis and its applications: with R examples.*
765 New York: Springerlink.
- 766 **Singh KP, Kushwaha CP. 2006.** Diversity of flowering and fruiting phenology of trees in a
767 tropical deciduous forest in India. *Annals of Botany* **97**: 265–276.
- 768 **Siyum ZG. 2020.** Tropical dry forest dynamics in the context of climate change: syntheses of
769 drivers, gaps, and management perspectives. *Ecological Processes* **9**.
- 770 **Stan Development Team. 2022.** RStan: The R interface to Stan.
- 771 **Stevenson PR, Castellanos MC, Cortés AI, Link A. 2008.** Flowering patterns in a seasonal
772 tropical lowland forest in western Amazonia. *Biotropica* **40**: 559–567.
- 773 **Sullivan MK, Fayolle A, Bush E, Ofosu-Bamfo B, Vleminckx J, Metz MR, Queenborough**
774 **SA. 2023.** Cascading effects of climate change: new advances in drivers and shifts of tropical
775 reproductive phenology. *Plant Ecology*.
- 776 **Sun C, Kaplin BA, Kristensen KA, Munyaligoga V. 2009.** Tree Phenology in a Tropical
777 Montane Forest in Rwanda Mvukiyumwami , Kanyoyo Ka Kajondo , Timothy C . Moer-
778 mond Published by : The Association for Tropical Biology and Conservation Stable URL :
779 <http://www.jstor.org/stable/2389053>. **28**: 668–681.
- 780 **Tang J, Körner C, Muraoka H, Piao S, Shen M, Thackeray SJ, Yang X. 2016.** Emerging
781 opportunities and challenges in phenology: A review. *Ecosphere* **7**: 1–17.
- 782 **Tela M, Cresswell W, Chapman H. 2021.** Pest-removal services provided by birds on subsis-
783 tence farms in south-eastern Nigeria. *PLoS ONE* **16**: 1–17.
- 784 **Thébault E, Fontaine C. 2010.** Stability of ecological communities and the architecture of
785 mutualistic and trophic networks. *Science* **329**: 853–856.
- 786 **Thia JA. 2014.** The plight of trees in disturbed forest: conservation of Montane Trees, Nigeria.
- 787 **Valdez-Hernández M, Andrade JL, Jackson PC, Rebolledo-Vieyra M. 2010.** Phenology
788 of five tree species of a tropical dry forest in Yucatan, Mexico: Effects of environmental and
789 physiological factors. *Plant and Soil* **329**: 155–171.
- 790 **Van Schaik CP, Terborgh JW, Wright SJ. 1993.** The phenology of tropical forests: Adap-
791 tive significance and consequences for primary consumers. *Annual Review of Ecology and*
792 *Systematics* **24**: 353–377.
- 793 **Vehtari A, Gelman A, Gabry J. 2017.** Practical Bayesian model evaluation using leave-one-

- 794 out cross-validation and WAIC. *Statistics and Computing* **27**: 1413–1432.
- 795 **Vico G, Dralle D, Feng X, Thompson S, Manzoni S. 2017.** How competitive is drought de-
796 ciduousness in tropical forests? A combined eco-hydrological and eco-evolutionary approach.
797 *Environmental Research Letters* **12**.
- 798 **Visser ME, Gienapp P. 2019.** Evolutionary and demographic consequences of phenological
799 mismatches. *Nature Ecology and Evolution* **3**: 879–885.
- 800 **Wheelwright NT. 1985.** Competition for Dispersers, and the Timing of Flowering and Fruiting
801 in a Guild of Tropical Trees. *Oikos* **44**: 465.
- 802 **White F. 1983.** *The Vegetation of Africa*. UNESCO.
- 803 **Williams LJ, Bunyavejchewin S, Baker PJ. 2008.** Deciduousness in a seasonal tropical for-
804 est in western Thailand: Interannual and intraspecific variation in timing, duration and environ-
805 mental cues. *Oecologia* **155**: 571–582.
- 806 **Williams RJ, Myers BA, Muller WJ, Duff GA, Eamus D. 1997.** Leaf phenology of woody
807 species in a North Australian tropical savanna. *Ecology* **78**: 2542–2558.
- 808 **Wright SJ, Cornejo FH. 1990.** Seasonal drought and leaf fall in a tropical forest. *Ecology* **71**:
809 1165–1175.
- 810 **Yang X, Wu J, Chen X, Ciais P, Maignan F, Yuan W, Piao S, Yang S, Gong F, Su Y, et al.**
811 **2021.** A comprehensive framework for seasonal controls of leaf abscission and productivity in
812 evergreen broadleaved tropical and subtropical forests. *Innovation* **2**: 100154.
- 813 **Zhao J, Zhang Y, Song F, Xu Z, Xiao L. 2013.** Phenological response of tropical plants to
814 regional climate change in Xishuangbanna, south-western China. *Journal of Tropical Ecology*
815 **29**: 161–172.
- 816 **Zhu M, Ester G de A, Wang Y, Xu Z, Ye J, Yuan Z, Lin F, Fang S, Mao Z, Wang X, et**
817 **al. 2022.** El Niño–Southern Oscillation affects the species-level temporal variation in seed and
818 leaf fall in a mixed temperate forest. *Science of the Total Environment* **850**.