





# Revisiting the phenology of El Triunfo cloud forest, Mexico, 30 years later

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## Research Article

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### Abstract

Climatic conditions have changed within the cloud forests of southern Mexico, but the effects of these changes on tree phenology are not well understood. Our study aimed to determine relationships between seasonal patterns of flowering and fruiting and the annual and long-term changes in temperature and rainfall in El Triunfo Biosphere Reserve, Mexico. Flowering and ripe fruiting intensity and fruit number were recorded for 158 trees of 21 zoochorous species during 17 months in 2019–2021. Circular statistics, synchronization calculations, and generalized linear mixed models were used to determine phenological patterns and relationships between phenophases and temperature, rainfall, and solar radiation. Flowering was most closely associated (negatively) with rainfall, whereas ripe fruiting was positively associated with solar radiation. We compared recent fruiting seasonality with phenological data collected in 1991–1993. The mean date of community fruiting in 2019–2020 was earlier (April 4) than in 1992 (May 1) and 1993 (May 13). Community fruit number in 2020–2021 decreased in comparison to 2019–2020. Our results suggest that decadal trends of increasing minimum daily temperature and an earlier and wetter wet season influenced the timing of community fruiting phenology, and fruit numbers varied greatly between years, possibly impacting resource availability for frugivores in El Triunfo.

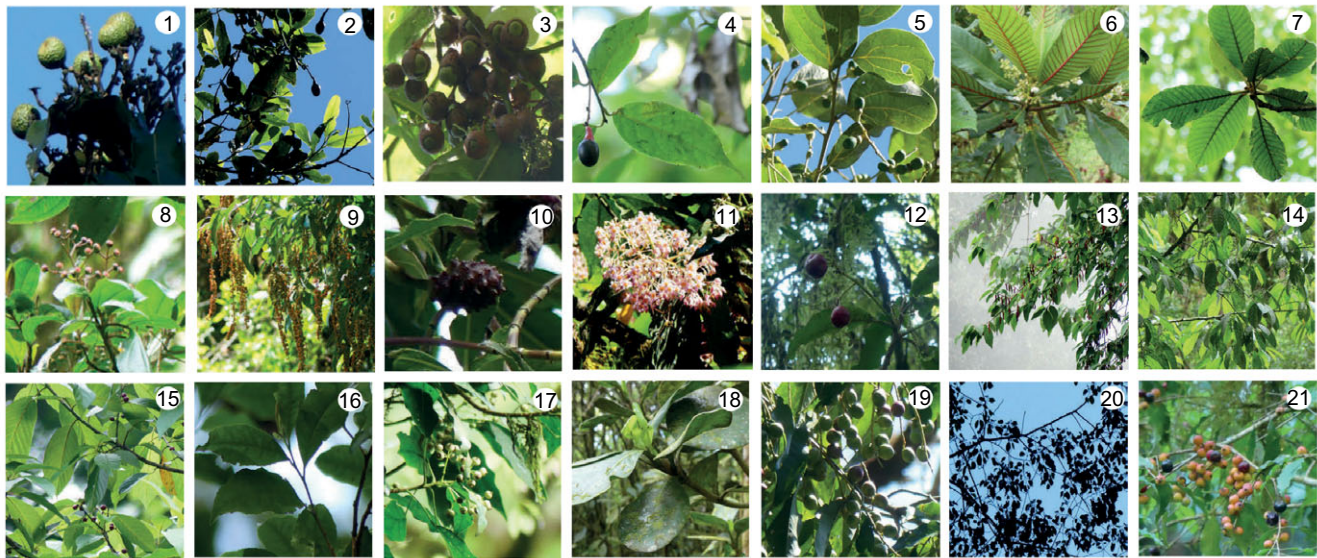
### Introduction

Yearly and long-term changes in temperature and rainfall affect flowering and fruiting patterns in tropical forests (Barnes 2015, Chapman *et al.* 2005, Du *et al.* 2020). However, long-term or comparative phenological studies are rare in higher elevation tropical cloud forests, especially in the Neotropics (Mendoza *et al.* 2017). Cloud forests provide important refuge and reproductive habitats for flora and fauna (Rojas-Soto *et al.* 2012) and contain a high diversity of endemic species (González-Espinosa *et al.* 2011). The timing of fruit presence could affect the reproduction and migration of animal species in these forests (Bustamante *et al.* 2010).

In the ecologically and climatically complex systems of wet tropical forests, factors that influence the phenology of tree communities, species or individuals of a species can be both biotic and abiotic. Biotic factors include the timing of interactions between flower production and the seasonal fluctuations in abundance of pollinators (Xu & Servedio 2021), niche partitioning between fruit production characteristics and frugivore dispersers (Todeschini *et al.* 2020), changes in the allocation of resources between growth and reproduction (Wheelwright 1986), and the time between flower pollination and fruit production (Bendix *et al.* 2006). Biotic factors often influence the numbers of fruits produced and length of fruiting period (Brito *et al.* 2017, Oshima *et al.* 2015), whereas abiotic factors influence the timing of phenological patterns (Mendoza *et al.* 2017, Van Schaik *et al.* 1993).

Abiotic factors include both environmental conditions where intra-annual changes are consistent between years (e.g., solar radiation and daylength; Numata *et al.* 2003) or vary over longer time periods (e.g., temperature, rainfall, and relative humidity; Bendix *et al.* 2006, Dunham *et al.* 2018). Pau *et al.* (2011) discussed the possibility that species with similar phenological patterns from year to year are influenced by factors that change little between years. Species with changes in the timing of phenological patterns between years may be more influenced by factors with yearly variation such as temperature and rainfall (Pau *et al.* 2020).

The causes of changing phenological patterns within a tropical tree community may be difficult to determine, as species with different life histories can have varying phenological responses to the same climatic factors (Boyle & Bronstein 2012). The diversity of species and phenological patterns in the cloud forests of southern Mexico (Solórzano *et al.* 2010) indicate that climatic factors may have different influences on individual species within a forest community in areas like the El Triunfo Biosphere Reserve.



**Figure 1.** Photos of the 21 tree species included in this study in the cloud forest of polygon 1 of El Triunfo, Mexico. Species shown are as follows: (1) *Ocotea chiapensis*, (2) *Nectandra rudis*, (3) *Licaria excelsa*, (4) *Ocotea acuminatissima*, (5) *Cinnamomum zapatae*, (6) *Saurauia madrensis*, (7) *Saurauia yasicae*, (8) *Conostegia volcanalis*, (9) *Citharexylum mocinnii*, (10) *Hedyosmum mexicanum*, (11) *Ardisia compressa*, (12) *Ardisia verapazensis*, (13) *Morus insignis*, (14) *Trophis cuspidata*, (15) *Frangula capreifolia*, (16) *Symplocarpun purpusii*, (17) *Dendropanax arboreus*, (18) *Clusia salvinii*, (19) *Prunus brachybotrya*, (20) *Prunus tetradenia*, and (21) *Eugenia capuli*.

El Triunfo is located in the Sierra Madre de Chiapas, in southern Mexico. It was established in 1990 with the goal to conserve endemic species and biodiversity of the region, especially within the higher elevation cloud forests. These forests are important reproductive habitats for bird and mammal species, which share fruit species as their feeding resources in this area (Ávila *et al.* 1996, González-García *et al.* 2017, Lira-Torres *et al.* 2004).

In the years after the establishment of the Reserve, Solórzano *et al.* (2000) recorded the number of fruits present in a community of trees producing the feeding resources of quetzals (*Pharomachrus tucicinnus*) in 1991–1993. The patterns of some tree species observed within this study indicate phenological influences from variable climatic conditions. For example, two species within the avocado family Lauraceae, *Nectandra rudis* and *Ocotea chiapensis*, showed different monthly patterns of fruit occurrence in 1992 and 1993.

In our study, we revisited the same area of El Triunfo nearly 30 years later to determine if phenological patterns had changed. Like Solórzano *et al.* (2000), we focused on the fruits consumed by quetzals (Figure 1), which were the majority of the common tree species producing fleshy animal dispersed fruits (subsequently referred to as zoochorous community; Figure 1, Table S1). As climate trends occur, changes in the timing of flower and fruit production of some tree species may cause shifts in the overall phenological patterns of this community.

Climate seasonality can be less distinct in tropical mountain environments, where high humidity continues throughout the year from fog and orographic rainfall (Bruijnzeel *et al.* 2011, Loope & Giambelluca 1998). However, in the higher elevations of the Sierra Madre, seasonal climatic differences are evident, most notably in rainfall and minimum daily temperatures (CONAGUA (Comisión Nacional del Agua) 2021). Since 1990, there have been significant trends in temperature and rainfall in the Sierra Madre (Wootton *et al.* 2023). Within El Triunfo, the wet season has trended earlier in the year and has become wetter. The dry season has also trended earlier in the year, and rainfall has decreased from October to December during the transition to the dry season. In the higher elevation areas of El Triunfo, minimum daily temperatures have

increased, particularly in the colder months of January and February, and maximum daily temperatures have decreased (Wootton *et al.* 2023).

In addition to yearly climatic influences, extreme weather conditions (e.g., strong wind and hail) could affect short-term phenology through the destruction of flowers and fruits (Bustamante *et al.* 2010, Butt *et al.* 2015). Hurricane winds are rare in the Sierra Madre (Tejeda-Cruz & Sutherland 2005). However, during the study period from 2019 to 2021, Hurricane Eta hit the west coast of Southern Mexico, bringing maximum wind speeds of 124–170 km/hr to the study area between October 31 and November 6, 2020.

The objectives of this study were to determine (a) the seasonality and synchronization of flower and fruit presence in the zoochorous tree species community; (b) the relations between these phenophases and climatic variables (temperature, rainfall, and solar radiation); (c) changes in the timing of seasonal fruiting between periods separated by ~30 years, 1992–1993 and 2019–2020; and (d) changes in the timing of seasonal fruiting and number of fruits produced between 2019–2020 and 2020–2021.

## Methods

### Study area

The study area is in the central zone of Polygon 1 in the El Triunfo Biosphere Reserve, Chiapas, Mexico (15° 39' 23.8"N, 92° 48' 29.3" W; Figure S1), within a valley at the higher elevations of the Sierra Madre de Chiapas. Phenological observation points were established along 3 km sections of four trails within the valley, mountain crests, and the higher elevation Pacific coastal slope of this area (Figure S1). These trails range in elevation between 1970 and 2100 m a.s.l., where forest composition and diversity vary greatly among riparian, sheltered, and higher wind-exposed areas (Breedlove 1981, Long & Heath 1991, Solórzano 1995).

Four climate variables, linked to phenological patterns in other wet tropical forests (Pau *et al.* 2020, Zimmerman *et al.* 2007), were included in this study. These were monthly rainfall, average

monthly minimum (T<sub>min</sub>) and maximum (T<sub>max</sub>) daily temperature, and monthly averages of daily solar radiation. Temperature and rainfall data were obtained from the automated El Triunfo weather station at 1972 m a.s.l. located at the central camp in Polygon 1 (CONAGUA (Comisión Nacional del Agua) 2021). Solar radiation was estimated using the Hargreaves-Samani temperature-based model (Hargreaves & Samani 1985), which has been determined to provide an accurate estimate of solar radiation where direct measurements are not available (Almorox *et al.* 2013). This method uses inputs of day of the year and latitude to estimate daily total extraterrestrial radiation and daily temperature range to account for cloud cover and atmospheric transmittance of radiation in the model (Quej *et al.* 2016).

In the study area, during the period from 2019 to 2021, T<sub>min</sub> was the lowest during December to February (6 °C) and the highest during June (12 °C). T<sub>max</sub> is less variable throughout the year and ranges from 23 °C in January to 25 °C in May. Rainfall is the greatest during June (600 mm) with another peak in September (550 mm) and the lowest (100 mm or less) during December to April (Figure S2), and solar radiation is the greatest during March–April (21–22 MJm<sup>-2</sup> day<sup>-1</sup>) and the lowest during October–January (15–16 MJm<sup>-2</sup> day<sup>-1</sup>), depending on cloud cover conditions.

### Phenological surveys

Phenological observations were done around the third week of each month from March 2019 to March 2020 (excluding July and November 2019) and were meant to continue throughout 2020. However, due to pandemic travel restrictions, observations were postponed until December 2020 (the month after hurricane Eta) and continued monthly until May 2021. A total of 158 individual trees were selected under the criteria of being: 1) mature trees (similar tree sizes to those of the same species observed producing fruits) of 21 fleshy-fruit producing species, and 2) trees that could be observed from the trails (near to the trail and also further away) based on the visibility of the crown of the tree to observe flower and fruit presence (Figure 1, Tables S1 and S2).

The number of trees per species was selected based on the estimated proportion of each species within the community, following the methods used by Solórzano *et al.* (2000). However, the number of tagged trees per species and the species included differed from Solórzano *et al.* (2000) due to differences in estimated species compositions between the early 1990s and 2020s and differences in the species of fruits observed to be consumed by quetzals in more recent years (detailed composition results in Wootton 2022). For some rarer species in the study area, we tagged less than the five trees per species recommended by Frankie *et al.* (1974) (Table S1). However, these species were included in the community analysis because a high diversity of fruit species may be important for frugivores in El Triunfo (González-García *et al.* 2017, Solórzano *et al.* 2000) and provided a better understanding of community patterns.

Phenological observations focused on reproductive phenophases. These were intensity of flowering (flowers in anthesis), fruiting (unripe and ripe), and the number of ripe fruits per tree. Intensity observations were done by estimating the percentage of the crown of each tree surveyed with flowers, unripe fruits, and ripe fruits. These percentages represented intensity scores of 0 (0%), 1 (1–20%), 2 (21–40%), 3 (41–60%), 4 (61–80%), and 5 (81–100%) (Fournier 1974).

The number of ripe fruits on each tree surveyed was estimated by counting the number of fruits in the entire tree with the use of

binoculars. Where the entire crown was not visible or there were large amounts of fruits in the tree, the number of fruits in a portion of the tree, usually one branch, was counted, and this number was multiplied by the estimated remainder of the tree. Some species, such as *Citharexylum mocinnii*, produced large amounts of fruits in bunches. In this case, the average number of fruits was estimated for each bunch, and this was multiplied by the estimation of the number of bunches in each tree.

Calculations of overall zoochorous community values of flowering, unripe fruiting, and ripe fruiting intensity were done by adding monthly intensity scores of all trees in the study for each phenophase. Community fruit number values were the sum of logarithmically transformed fruit counts/estimations of all trees. Fruit number values were logarithmically transformed to avoid large fruit number biases from some species within the community values. To determine differences in fruit number between years, monthly sums of fruit number without the transformation were used.

To compare fruiting patterns between 1992, 1993, and 2019–2020, the monthly number of ripe fruits at the community level was calculated by logarithmically transforming the average number of fruits of each species each month and then adding these values to obtain a community value. This was done to standardize the number of fruits per tree per species between the 1992–1993 and 2019–2021 studies, which had different numbers of trees observed per species. For these comparisons, we only included those tree species that were observed both in 1992–1993 and 2019–2021. For the months when observations could not be obtained (July and November 2019), phenophase values of the tagged trees were estimated from the mean values of the logarithmically transformed fruit number data for each tree from the adjacent months. Fruit number data from months without observations in 1992 (January, May, July, and October) and 1993 (May, August, and September) were estimated from the mean values of adjacent months of the logarithmically transformed fruit number data for each tree species.

### Statistical analysis

Circular statistics were used to determine the seasonality of each of the observed phenophases during April 2019–March 2020. Months with phenological data were converted to angles around a circle, with January converted to 15° and each month after at 30° intervals. The following calculations and tests of seasonality were done in R version 4.2 (R Core Team 2022) using scripts adapted from Mendoza (2020): (a) the average angle (date) of the distribution of data; and *r* vector, which is a proxy of the degree of seasonality of flowering and fruiting with a range of 0 to 1, where 0 is without seasonality with the presence of flowers and fruits distributed uniformly during the year and 1 is very seasonal with all the presence in one month (Cox 2004, Morellato *et al.* 2010).

Phenophase synchronization in populations of 12 species with greater than five trees observed and in the overall zoochorous community was calculated using the following index developed by Freitas & Bolmgren (2008).

$$d_i = \frac{1}{T_i} \frac{1}{N-1} \sum_{j=1}^N \sum_{t=1}^T \sqrt{f_{i,t} f_{j,t}}, \quad j \neq i$$

Where:

$d_i$  = Individual tree synchronization in relation to other trees of the same species included in the observations (*j*)

$f$  = Phenophase intensity converted to a scale from 0 to 1

$T_i$  = Number of times during the 17 months of observations where  $f_i > 0$  (months when there were flowers or fruits on the tree)  
 $N$  = Number of trees observed per species  
 $j$  = Individual tree in a species population  
 $t$  = Month observation number (1–17)  
 $T$  = Number of months when there were flowers/fruits on any tree per species (when  $f_j > 0$ )

$$S = \sum \frac{d_i}{N}$$

$S$  = Species synchronization

The above calculation was also used to determine community synchronization by including all 158 trees observed. This index ranges from 0 (no synchronization) to 1 (full population or community synchronization) using phenophase intensity values of individual trees observed. The calculation of the index was done using Java programming language (Arnold *et al.* 2005).

Relations between climatic variables (rainfall,  $T_{min}$ ,  $T_{max}$ , and solar radiation) and phenophases (flowering, unripe and ripe fruiting intensity, and log-transformed fruit number) recorded between March 2019 and May 2021 were analyzed using generalized linear mixed models (GLMMs) to determine the best fit models. GLMMs were performed with the *glmer* function of *lme4* (version 1.1-30) library in R (Bates *et al.* 2015). Models with an Akaike information criterion (AIC) less than or equal to 2 from the top-ranked model were considered significantly best fit. Climatic variables and phenophases were defined as fixed factors and individual tree as a random factor. The family distribution was defined as negative binomial due to the overdispersion of count data (Finch *et al.* 2021). Climate variables that were significantly correlated (Spearman correlation,  $p < 0.05$ ) were not included as covariates in models (similarly to Chapman *et al.* 2018, Finch *et al.* 2021). These included rainfall with  $T_{min}$ ,  $T_{min}$  with  $T_{max}$ , and  $T_{max}$  with solar radiation.

The Watson-Wheeler test (Batschelet 1981, Mendoza 2020) was used to determine significant differences in the mean date (angle) of seasonal ripe fruit production between adjacent years and periods separated by ~30 years. Fruiting seasonality of two years in the 1990s, February–December 1992 and January–December 1993 (Solórzano *et al.* 2000), were compared with our observations from April 2019–March 2020 in the program Oriana 4.02 (Kovach Computing Services 2013).

To compare fruiting characteristics between adjacent years, we used observations from the same months in 2019–2020 and 2020–2021: April, May, and December 2019, January, February, and March 2020 (2019–2020), and December 2020 to May 2021 (2020–2021). Seasonal differences in the timing of ripe fruit production between these half-year periods were also determined using the Watson-Wheeler test. A paired sample t-test was used to determine if there were differences in fruit numbers between the years.

## Results

### Seasonality and synchronization of flowering and fruiting

During the year-long observation period (April 2019–March 2020), trees within the zoochorous community displayed a mean date of flowering on February 6 ( $r = 0.46$ ), unripe fruiting on November 10 ( $r = 0.11$ ), and ripe fruiting on March 9 ( $r = 0.25$ ) (Figure 2). The mean date of community fruiting (using the

circular mean of the logarithmically transformed fruit number) was also March 9 ( $r = 0.22$ ) (Table S3, Figure 3). All flowering and fruiting patterns were significantly seasonal ( $p < 0.05$ ). Community ripe fruiting peaks (the circular mode) were greatest at the end of the drier period in El Triunfo during March (Figure 3).

Community synchronization of ripe (0.47) and unripe (0.47) fruiting was greater than flowering (0.30). Community synchronization was generally greater than that at the species population level. The species with the greatest synchronization of flowering was *Ardisia compressa* (0.41) and of unripe fruiting was *Conostegia volcanalis* (0.40). These species produced flowers and unripe fruits during a longer period throughout the year. In contrast, species with the highest synchronization of ripe fruiting, *Citharexylum mocinnii* (0.34) and *Morus insignis* (0.36), had short fruit production periods of higher intensity, whereas *Nectandra rudis* (0.31) had a longer period of fruit production (Table 1). Overall, there was low synchronization at the population level of flowering and fruiting (Table 1).

### Relations between climatic variables and phenological patterns

Based on the AIC, the best fitting models ( $\Delta AIC > 2$ ) for the relation between a climate variable and community flowering included both rainfall (negative) and rainfall (negative) with solar radiation (positive). For unripe fruiting, this included only  $T_{max}$  (negative), and for ripe fruiting intensity, this included solar radiation (positive) with rainfall (negative). The best fitting model with fruit number included solar radiation (positive) with  $T_{min}$  (negative) (Table 2).

### Seasonality differences between years and 30-year periods

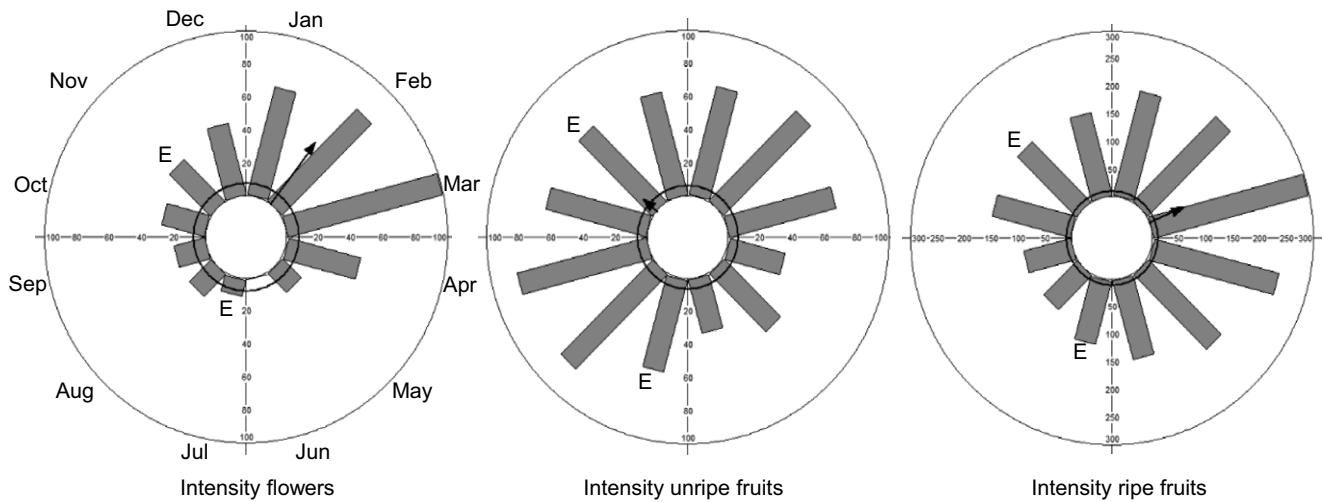
When only the 16 species observed in both Solórzano *et al.* (2000) and our study were included, the mean date of ripe fruit presence was May 1 in 1992 ( $r = 0.13$ ), May 13 in 1993 ( $r = 0.19$ ), and April 4 in 2019–2020 ( $r = 0.24$ ) (Figure 3). Mean dates of seasonal fruiting phase were marginally different between both 2019–2020 and 1992 (Watson-Wheeler  $W = 5.04$ ,  $p = 0.08$ ) and 2019–2020 and 1993 (Watson-Wheeler  $W = 4.96$ ,  $p = 0.084$ ). Mean dates of fruiting were not significantly different between 1992 and 1993 (Watson-Wheeler  $W = 0.11$ ,  $p = 0.95$ ). Of the species that produced fruits in all the observation years, seven had earlier mean dates of seasonal fruiting phase in 2019–2020 than in 1992 or 1993, whereas six species had later or similar mean dates (Table S4).

The mean date of community fruiting (number of ripe fruits) estimated during the December–May half-year period in 2019–2020 was March 8 ( $r = 0.69$ ) and in 2020–2021 was March 20 ( $r = 0.70$ ) (Figure 3). Mean dates of community fruiting between 2019–2020 and 2020–2021 were significantly different (Watson-Wheeler  $W = 14.4$ ,  $p < 0.01$ ). There was a significant difference in community fruit number between the periods in 2019–2020 (monthly mean =  $71674 \pm 39016$ ) and 2020–2021 (monthly mean =  $20683 \pm 15512$ ) ( $t(5) = -3.28$ ,  $p = 0.02$ ).

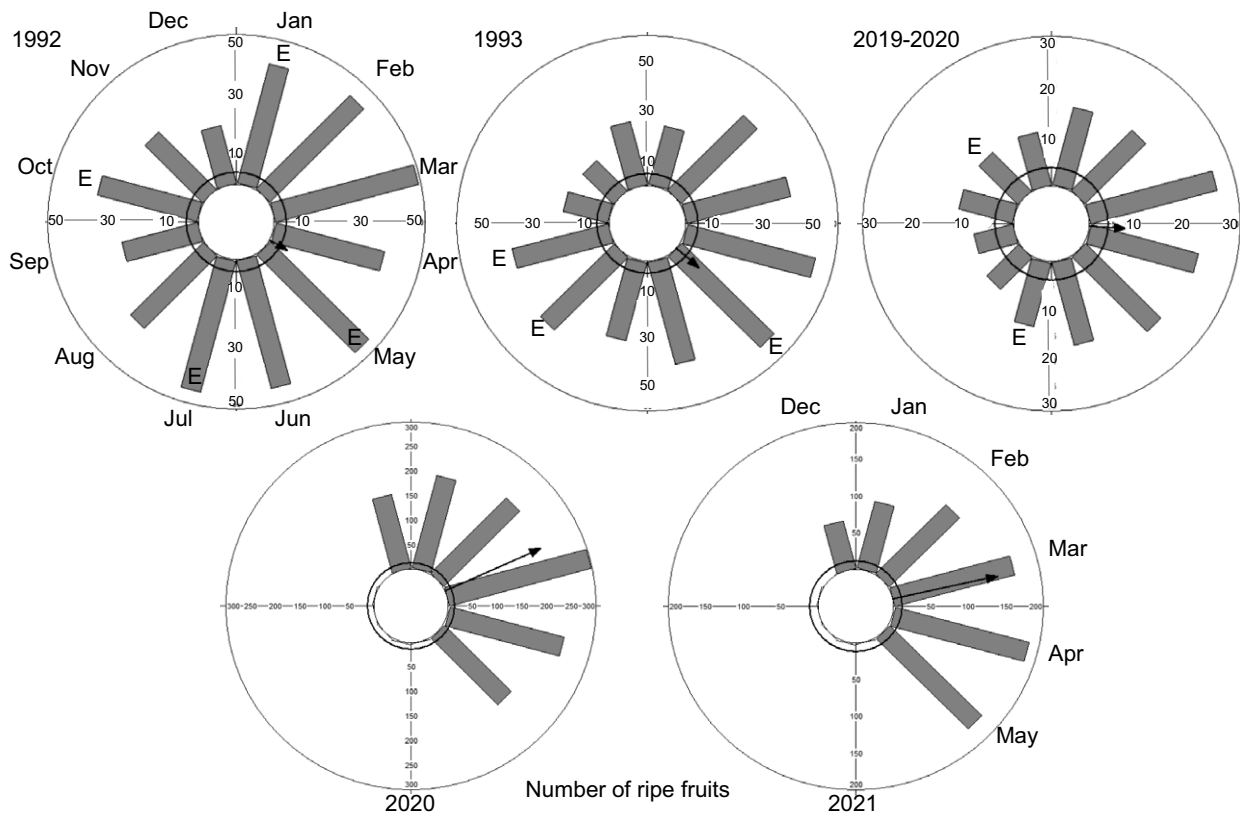
## Discussion

### Phenological patterns

An overall community peak in ripe fruiting occurred during the end of the dry/beginning of the wet season in the cloud forest of El Triunfo between 2019 and 2021. This pattern contrasted with most



**Figure 2.** Circular histograms of flowering, unripe fruiting, and ripe fruiting intensity in the zoochorous community in El Triunfo, Mexico, during April 2019–March 2020. Months without observations but including estimated flowering and fruiting values are shown with an E. Arrows indicate the degree of seasonality ( $r$  value). Numbers in histograms are the sums of intensity scores for all trees observed in the study.



**Figure 3.** Circular histograms of number of ripe fruits in the zoochorous tree community in El Triunfo, Mexico, during: (1992) January–December 1992, (1993) January–December 1993 (Solórzano *et al.* 2000), and April 2019–March 2020 (2019–2020) in the upper row; and April, May, and December 2019 and January–March 2020 (2020), and December–May 2021 (2021) in the lower row. Months without observations but including estimated flowering and fruiting values are shown with an E. Arrow length indicate the degree of seasonality (significant  $r$  value; Table S3). Numbers in histograms are sums of the logarithmically transformed number of ripe fruits estimated monthly in all trees observed.

community fruit peaks in the lower elevation tropical rainforests of the Neotropics, which often occur during the wet season (Mendoza *et al.* 2017). These temporal phenological differences may be related to the different climatic conditions according to elevation (Hu & Riveros-Iregui 2016, Mendoza *et al.* 2017) and to the different composition of tree species of temperate and tropical origin

in the higher elevation cloud forests (Borchert *et al.* 2005, González-Espinosa *et al.* 2011). In Mesoamerican cloud forests, community fruiting peaks at the end of the dry season were also recorded in El Triunfo, Chiapas, 30 years earlier (Solórzano *et al.* 2000), in Jalisco, Mexico (Zárate-Cuevas *et al.* 2022), and in the Cordillera de Talamanca, Costa Rica (Camacho & Orozco 1998). In contrast,

**Table 1.** Synchronization of flowering, unripe fruiting, and ripe fruiting in 12 species and the overall zoochorous community in El Triunfo, Mexico. Values range from 0 representing no synchronization of phenophases and 1 full synchronization

Species	Flowering	Unripe fruiting	Ripe fruiting
<i>Ardisia compressa</i>	0.405	0.238	0.154
<i>Citharexylum mocinnii</i>	0.216	0.323	0.337
<i>Conostegia volcandis</i>	0.121	0.402	0.228
<i>Eugenia capuli</i>	0.070	0.001	0.028
<i>Hedyosmum mexicanum</i>	0	0.062	0.176
<i>Licaria excelsa</i>	0.033	0.054	0.016
<i>Morus insignis</i>	0.212	0.333	0.358
<i>Nectandra rudis</i>	0.137	0.196	0.313
<i>Ocotea chiapensis</i>	0.128	0.128	0.145
<i>Prunus brachybotrya</i>	0.008	0.112	0.256
<i>Saurauia madrensis</i>	0.081	0.173	0.093
<i>Trophis cuspidata</i>	0.058	0.014	0.006
Community	0.303	0.471	0.466

two distinct peaks (during both dry and wet periods) were recorded in Veracruz, Mexico (Williams-Linera 1997) and in Monteverde, Costa Rica (Dinerstein 1986).

Cloud forests have some unique characteristics and conditions that may influence community fruiting patterns. These include a high diversity of endemic tree species, animal dispersers of fruit that migrate altitudinally throughout the year (Boyle 2010), and a longer duration of humidity and water availability from cloud cover, which could also influence solar radiation (Jarvis & Mulligan 2011). Cloud forests also receive some of the largest quantities of rainfall in Mexico, which in the Sierra Madre has been increasing at a greater rate than the adjacent lower elevation regions (Wootton *et al.* 2023). Fruit ripening peaked just before the wettest period began, when solar radiation was the highest, and after a period of flower production during the time of the year when T<sub>min</sub> was the lowest. Fruiting was also the highest during the reproductive and resident period of many bird species in El Triunfo when altitudinal migrants are in the cloud forest (Gómez de Silva *et al.* 1999).

In addition to climatic influences, various tree species within the zoochorous community showed phenological characteristics influenced by biotic interactions. Some species, such as *Ardisia compressa*, had low synchronization among individuals and low overall seasonality, which may be a strategy to disperse seeds throughout the year by a specialized animal disperser (Van Schaik *et al.* 1993). The distinct seasonal peaks in ripe fruiting of eight species in our study may be linked to the arrival times of migratory bird (Gómez de Silva *et al.* 1999) or mammal (González-Zamora *et al.* 2009) species. For example, *Trophis cuspidata* had an average fruiting phase date in September, four months later than the overall community dates. Some bird species (e.g., White-throated Thrush *Turdus assimilis*, Highland Guan *Penelopina nigra*) migrate to higher elevations during autumn in El Triunfo and have been observed consuming this fruit species (Gómez de Silva *et al.* 1999), possibly due to its fruit production patterns (Boyle 2010). Climate-influenced changes in tree species' fruiting patterns could affect seasonal migration and composition of animal species in the reserve (Ramos-Robles *et al.* 2016).

*Ocotea chiapensis* produced various peaks in ripe fruiting throughout the year. This may be important for food availability for animals that stay year-round in the cloud forest, during the summer wet season when fruit is scarcer in this forest, and can facilitate seed dispersal when there is less competition for frugivore dispersers (Wheelwright 1985). Most of the species produced many fruits one year and few or no fruits the next year. These included the species in the Lauraceae family, which Wheelwright (1986) suggested was a strategy to allocate resources between reproduction and vegetative growth between years.

There were some limitations to recording phenological patterns due to the natural conditions of the study area. The timing of greatest fruiting in El Triunfo coincided with the breeding season of several frugivore species (Ávila *et al.* 1996, González-García *et al.* 2017), when fruit consumption needs are the greatest (Ávila *et al.* 1996). The consumption of these ripe fruits before they could be observed could affect the apparent fruiting seasonality of some tree species.

### Climatic-influenced flowering and fruiting patterns

Community flowering was greatest during the driest part of the year (January–April), which may coincide with a higher abundance of pollinators and lower potential for storm damage (Van Schaik *et al.* 1993, Xu & Servedio 2021). Flowering mainly occurred during the months of the year with the lowest temperatures (January–March), although in 2021, there was also high flower presence in April, which is a warmer month. Ramírez & Davenport (2016) discussed that some species within tropical regions that are related to species in temperate regions, such as *Prunus* sp., may require a dormant period during cooler temperatures to initiate flower production. We also observed this in *Prunus brachybotrya* trees in the studied community.

Unripe fruiting was most associated (negatively) with T<sub>max</sub>. The development of unripe fruits is dependent on the timing of flowering patterns, so the timing of fruit development may be due more to flowering times (Bendix *et al.* 2006) than T<sub>max</sub> patterns, which do not change drastically throughout the year. Rainfall was the climate variable least associated with unripe fruiting intensity. This may be related to the lower seasonality of unripe fruit presence, which lasts throughout both the dry and wet periods.

Community ripe fruiting was most associated (positively) with solar radiation. Solar radiation is an important factor influencing plant transpiration (Turc 1961), which increases water and nutrient flow through the tree (Montanaro *et al.* 2010) and can influence fruit development (de Azevedo *et al.* 2007). It also has been shown to be directly an important factor in fruit ripening in other tropical forests (Chapman *et al.* 2018, Zimmerman *et al.* 2007).

Some tree species showed high variation within populations in synchronization and the timing of fruit presence, and some species had fruiting peaks during the wettest period of the year. Community patterns may be due to individual tree patterns rather than species composition (although some species, such as *Morus insignis*, had high seasonality and synchronization between individuals). Therefore, climatic factors may be affecting the tree community patterns independently from individual species phenological behaviors.

### Effects of climate on long term and yearly phenological patterns

Between 1990 and 2020, there was a 30-year trend of increasing T<sub>min</sub> and decreasing T<sub>max</sub> in El Triunfo (Wootton *et al.* 2023).

**Table 2.** Results of the best-fitting models for the relations between phenophases (flowering, unripe fruiting, ripe fruiting, and number of fruits) and climate variables in El Triunfo, Mexico, using generalized linear mixed model analysis. Climate variables are monthly rainfall (rain), minimum daily temperature (Tmin), maximum daily temperature (Tmax), and monthly averages of daily solar radiation (solar). \* Models with a  $\Delta AIC > 2.0$  were considered significant for the best fit

Phenophase	AIC	$\Delta AIC$	Weight	Log-likelihood	Model climate variable z-values				
					Intercept	Rain	Tmin	Tmax	Solar
Flowering									
<i>Rain</i> *	3211.9	0	0.53	-1601.9	-10.82	-10.25	-	-	-
<i>Rain + Solar</i> *	3213.2	1.3	0.28	-1601.6	-5.33	-9.86	-	-	0.80
Unripe fruiting									
<i>Tmax</i> *	3992.4	0	0.99	-1992.2	4.360	-	-	-6.87	-
Ripe fruiting									
<i>Solar + Rain</i> *	4894.3	0	0.77	-2442.1	-4180.79	-2.25	-	-	132.07
No. of fruits									
<i>Solar + Tmin</i> *	7081.6	0	0.74	-3535.8	-2582.14	-	-31.29	-	105.09

Rainfall patterns shifted earlier in the year: the start and end of the wet season trended earlier in the year, and rainfall peaks shifted from late in the wet season (September) to early (June). These changes in temperature and rainfall seem to have influenced the earlier shift in the overall seasonal patterns of zoochorous community fruiting between 1992–1993 and 2019–2020, although this was variable amongst species.

Warmer and wetter trends have also been recorded in parts of Africa where there have been longer term phenological observations. In Uganda, Chapman *et al.* (2005) determined that as these climate trends occurred, a higher proportion of trees produced fruits, but some species rarely produced fruits in the later years. We observed few fruits during 2019–2021 in comparison to records from the 1990s in some species such as *Symplocarpun purpusii*, although this species seems to have interannual variability in fruit production and production may be higher in years outside of our observations. Fruit production also increased greatly between 1992–1993 and 2019–2020 in two of the most common Lauraceae species in El Triunfo, *Ocotea chiapensis* and *Nectandra rudis*.

Increasing rainfall trends have also been linked to the number of species with fruits and timing of fruiting within tropical tree communities. Dunham *et al.* (2018) recorded a higher richness of species producing fruits and a greater intensity of fruiting in Madagascar during a period of increasing rainfall. In this area, after dry seasons receiving less rainfall than normal, there was a later shift in fruiting patterns in the next year (Dunham *et al.* 2018). 1990 and 1991 were exceptionally dry years in Chiapas and around the world (Murray-Tortarolo *et al.* 2017). This drought may have influenced the later fruiting patterns observed in 1992–1993 in El Triunfo than in 2019–2021.

Changes in air temperature may have also affected fog conditions. Solórzano *et al.* (2000) described months during their phenological observations when it was not possible to count fruits due to heavy fog. But there were no months during our observations when fog was so thick that fruits could not be observed. Less fog cover could increase the amounts of solar radiation reaching the forest and decrease available water during the dryer period of the year (Giambelluca *et al.* 2011). This may have influenced the higher seasonality of ripe fruit in comparison to 1992–1993, with peaks in March and April before increased cloud cover during the wet season would have resulted in decreased solar radiation reaching the forest canopy.

Solar radiation was estimated at the site of the El Triunfo weather station. However, the actual solar radiation affecting each tree observed could vary from this estimation due to local factors such as cloud and fog cover, slope aspect, and forest canopy conditions. These conditions change greatly throughout the valleys and slopes of the study area and between tree species heights.

The reduction in fruit number between December–May in 2019–2020 and 2020–2021 shows the variation in seasonal patterns during the period when the greatest fruit production occurs. Strong wind and rain from Hurricane Eta may have caused flowers and unripe fruits to fall, disrupting the patterns of ripe fruit production and lowering the number of fruits present in the zoochorous community during 2020–2021. This reduction in community fruiting is like what occurred after Hurricane Hugo in Puerto Rico (Wunderle 1995) and Hurricane Karl in Veracruz, Mexico (Williams-Linera *et al.* 2021). The production of flowers once again after Hurricane Eta may have resulted in a later ripe fruit development in comparison to earlier years. Changes between years in fruit number may also be due to natural cycles between reproductive and vegetative growth of some species (Wheelwright 1986).

### Ecological implications for the El Triunfo Biosphere Reserve

Shifts in phenological patterns related to climate trends show changing ecological conditions within cloud forests. Some of the factors influencing climate trends in the Sierra Madre de Chiapas since 1990 are cyclical over longer time periods (Fuentes-Franco *et al.* 2015), so their effects on fruiting patterns during the next 30 years may be different than the past 30 years. However, severe weather events like tropical storms and droughts are expected to occur more frequently in the next decades in Mexico (Murray-Tortarolo 2021). Our results suggest that climate trends have influenced shifts in the timing and seasonality of fruit production, and fruit number fluctuated greatly between years possibly due to extreme weather, both conditions having long- and short-term consequences for the availability of fruit for wildlife in the reserve.

**Supplementary material.** To view supplementary material for this article, please visit <https://doi.org/10.1017/S0266467424000191>

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