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Extreme drought disrupts plant phenology: Insights from 35 years of cloud forest data in Venezuela

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Abstract

The potential effects of climate change on plant reproductive phenology include asynchronies with pollinators and reductions in plant fitness, leading to extinction and loss of ecosystem function. In particular, plant phenology is sensitive to extreme weather events, which are occurring with increasing severity and frequency in recent decades and are linked to anthropogenic climate change and shifts in atmospheric circulation. For 15 plant species in a Venezuelan cloud forest, we documented dramatic changes in monthly flower and fruit community composition over a 35-year time series, from 1983 to 2017, and these changes were linked directly to higher temperatures, lower precipitation, and decreased soil water availability. The patterns documented here do not mirror trends in temperate zones but corroborate results from the Asian tropics. More intense droughts are predicted to occur in the region, which will cause dramatic changes in flower and fruit availability.

KEYWORDS
cloud forest, phenological asynchrony, reproductive phenology, soil moisture, tropical diversity

INTRODUCTION

Increases in global mean temperatures are causing changes in flowering phenologies around the world (Cleland et al., 2007; Gordo & Sanz, 2010), including in tropical forests (Corlett & Lafrankie, 1998). The tropical cloud forests of northern South America are characterized by high levels of diversity but are also among the least studied ecosystems in the world (Doumenge et al., 1995). These forests are likely to be threatened by changes in precipitation and temperature patterns that are characteristic of global climate change (Bonan, 2008) (Figure 1A), and these threats will be aggravated in the near future by increases in the frequency of extreme weather events (Sillmann & Roeckner, 2008). Because of

climate-dependent phenological synchronies with beneficial animals, such as pollinators and dispersers, understanding the reproductive phenology of plants within any biotic community can help identify species that are likely to be vulnerable to climate change as well as those that are most resistant to climate-driven extinction (Wilmers, 2007). Flowers and fruits are an important resource for animals, and reproductive phenologies can create pulses of resource availability in specific time periods, such that alterations of these phenological patterns are likely to cascade to entire communities (Abernethy et al., 2018; Chapman et al., 2005; Glaum et al., 2021). Fruits and flowers that are synchronous among individuals and species can be characterized as temporal assemblages, and these communities of reproductive parts are influenced
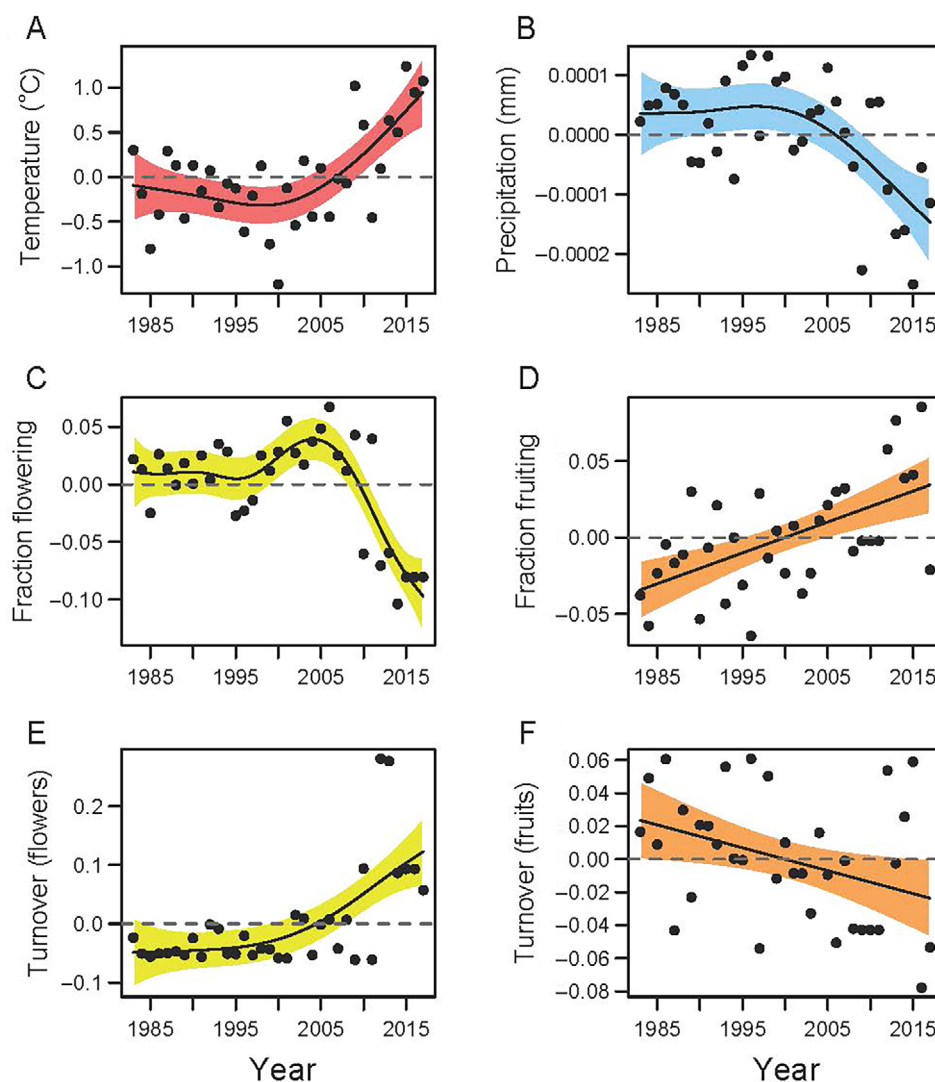
FIGURE 1   Annual variation in temperature (A) and precipitation (B), estimates of flowering (C) and fruiting (D) intensity, and average turnover (E, F) among months for 15 cloud forest species from 1983 to 2017; turnover was calculated for each month relative to the previous month within each year and then averaged across months, such that a high turnover shown here indicates a year with high levels of divergence in the flowering or fruiting communities among months. In all panels, *y*-axes are deviations from the mean, with the horizontal line indicating the average across the time series for visual reference. Curves and associated 95% CIs for the visualization of change over time were generated using general additive models (GAMs), with year as the smoothed term and Gaussian error. Panel-specific GAM results are as follows: (A) $R^2 = 0.47$, generalized cross-validation score (GCV) = 0.18; (B) $R^2 = 0.40$, GCV < 0.01; (C) $R^2 = 0.67$, GCV < 0.01; (D) $R^2 = 0.31$, GCV < 0.01; (E) $R^2 = 0.43$, GCV < 0.01; (F) $R^2 = 0.11$, GCV < 0.01.

by seasonal climatic fluctuations in precipitation and temperature (Zhao et al., 2013).

It is well established that climate change will alter both the means and variances of important weather variables that affect ecosystems, such as precipitation and soil moisture (Todman et al., 2018), and understanding these impacts depends on long-term data quantifying ecological interactions (Siteur et al., 2016). The disturbances associated with climate change are impacting life cycles of plants and their phenophases, resulting in phenological mismatches between plants and other organisms that can contribute to declines in species richness and interaction diversity (Bush et al., 2020; Dyer et al., 2014; Poisot et al., 2016; Renner & Zohner, 2018). Due to changes in diversity and interactions, many ecosystems are reaching critical transitions, changing to relatively unstable states, but the complexities of ecosystems make it difficult to predict when these transitions will occur or what the attributes of the alternative functional states will be (Bonan, 2008; Majumder et al., 2019; Todman et al., 2018). This is especially true for phenomena like plant–pollinator and fruit–disperser dynamics, and increases in extreme weather events are contributing to potentially catastrophic changes in these biotic networks (Dyer & Letourneau, 2013). These phenological asynchronies are

relatively well established in temperate ecosystems, where plant phenology is largely dependent on the prolonged cold of winter, and climate change has had clear effects on the timing of leaf, fruit, and flower production as a result of earlier onset of spring (Gordo & Sanz, 2010; Piao et al., 2019). Phenological mismatches can be with interacting animals or microbes (reviewed by Renner & Zohner, 2018; Rudgers et al., 2020), but also with other plants, changing the makeup of flower or fruit assemblages (i.e., all species that are flowering or fruiting together) at any given time (Ims, 1990; Pesendorfer et al., 2021). In the tropics, we do not know whether sustained and prolonged warming and increases in extreme weather cause synchronous changes in flowering and fruiting or idiosyncratic changes in flower and fruit assemblages at any given seasonal period. Because most species on Earth live in tropical regions, this issue of potentially variable response to climate change across latitudes is fundamental to our understanding of the Anthropocene.

To advance our knowledge of climate change impacts on tropical latitudes, we used a long-term phenological data set of 15 cloud forest plant species in northern Venezuela to address the following questions: (1) How have long-term temperature increases and changes in precipitation patterns affected assemblages of flowers and fruits within a cloud forest community across different seasons? (2) Have the impacts across plant species been divergent, or have changes in temperature and precipitation caused changes in synchronous flowering and assemblages of flowers and fruits? If climate impacts are heterogeneous across cloud forest tree species, it is likely that assemblages in different seasons will change, since individual phenologies change at different rates, and flowering and fruiting synchronies are altered by temperature and water availability (Abernethy et al., 2018; Ims, 1990). In addition to documenting how annual intensity of flowering and fruiting changes over time, a number of community parameters are relevant to these two questions about how shifts in phenology change assemblages of flowers and fruits available in any given month in a Neotropical cloud forest. We investigated changes in four of the most commonly used measures of how assemblages change: (1) ordination of species composition, (2) dominance, (3) turnover, and (4) overlap of species of fruits and flowers (using two measures of synchrony) (Gouhier & Guichard, 2014; Hallett et al., 2016; Hu et al., 2019).

METHODS

Study site

The study site, about 1 km² total area, is located along the northern ocean-facing slopes of the "Cordillera de la Costa"

in northern Venezuela. The specific location is known as Altos de Pipe (10.397, −66.985), at 1747 m above sea level (asl), 11 km from Caracas along the Pan-American Highway. The annual mean precipitation is 1200 mm, with a dry season from January to March and a rainy season from June to November. A wet-to-dry transition occurs in November–December and the dry-to-wet transition is April–May. Mean annual temperature is 19°C. The soils of the study site are clay loam and acidic, with a low cation exchange capacity and a high aluminum content. The dominant vegetation at the study site can be characterized as cloud forest, composed of three strata. The emergent stratum is 25–30 m in height and is dominated by *Aspidosperma fendleri* Woodson (Apocynaceae) and *Podocarpus salicifolius* Klotzsch & H.Karst. ex Endl (Podocarpaceae). The canopy (second stratum) is approximately 15 m in height and includes a rich mix of species, including *Richeria grandis* Vahl (Phyllanthaceae) and *Protium tovarense* Pittier (Burseraceae). The understory stratum has high densities of shrubs in the Melastomataceae and Rubiaceae families, including the melastome shrub, *Miconia dodecandra* Cogn, and the rubiaceous shrub, *Palicourea fendleri* Standl (Flores et al., 2005).

Phenology and climate

For 35 continuous years, every month, the reproductive status of five individuals in 15 focal tree species in 12 families (Appendix S1: Tables S1 and S4, Figures S1–S4) was recorded (Flores, 2022); distances between individuals within a species were 5–20 m. Trees were tagged and numbered for monthly observations and subsequent identification, and voucher specimens were deposited at the herbarium of the Instituto Venezolano de Investigaciones Científicas (IVIC). These 15 species were selected as important exemplars of cloud forest trees, all of which are restricted to cloud forests; they are characterized by a mix of reproductive life histories and dispersal and pollination syndromes and are a large part of the forest biomass (Appendix S1: Table S1). For each species, each month five branches were randomly selected, and notes were recorded for each species, with a focus on the presence of flowers and fruits (Appendix S1: Table S1). An individual was considered to be in bloom when at least one flower bud or flower in anthesis was noted, so a single inflorescence on one of the five branches was recorded as in flower. Similarly, an individual was recorded as being in fruit when a fully formed fruit was noted or an infructescence on one of the five branches was recorded on an individual. The total number of individuals with flowers or fruits (zero to five individuals per species) were counted and

recorded monthly for each species. Only the number of trees with reproductive parts was noted (not the identity of the individual), so this approach did not allow for statistics focused on variation within a species. Fraction of individuals in flower or fruit was used for summary statistics in figures. Climate data were collected from a station (INAME IVIC 82-90) within 1 km of the study site, managed by the Centro de Ciencias Atmosfericas y Biogeoquímica (reconstructed by Kalnay et al., 1996); these data were available as monthly values for temperature (mean average degree Celsius temperature per month), precipitation (mm/mo), and soil moisture (volumetric percentage). Time series allowed for summaries of phenological and climatic variables from 1983 to 2017. The availability of only monthly values for both plants and climate variables prevented us from asking questions about finer-scale turnover of flower or fruit assemblages or effects of within-month variances in climate variables.

Synchrony and community measures

All R (version 4.1.0) script for estimates of community parameters and all statistical analyses are provided in Flores (2022) at https://doi.org/10.5281/zenodo.7662623. We calculated the degree of overlap (synchrony) between the monthly flowering and fruiting of pairs of species using a modified Primack index (X_i), and for community-wide synchrony (Y) we utilized the Loreau and de Mazancourt (2008) index. Both measures were included to allow for an examination of how community synchrony of individual species changed over time (X_i) and to examine how the entire community synchrony (Y) was affected by climate variables. The Primack index measures the synchrony of an individual species (flower or fruit, i) with other individuals within that assemblage, and it is defined as

$$X_i = \left(\frac{1}{n-1}\right)\left(\frac{1}{f_i}\right)\sum_{j=1}^{n} e_{i \neq j},$$

where e_i is the number of months both individuals i and j are flowering/fruiting synchronously, f_i is the number of months that individual i is flowering/fruiting, and n is the number of individuals in the population. This index ranges between 0 (no overlap) and 1 (complete overlap). When $X = 1$, perfect synchrony occurs; all flowering months of individual i overlap with all flowering months of all other individuals, ($i \neq j$), in the population; when $X = 0$, individual i is asynchronous with all others in the population (Augspurger, 1983). This yielded one estimate per species per year.

Community-wide synchrony (Y) is the temporal variance for full communities divided by the temporal SD for the time series of all species (Loreau & de Mazancourt, 2008), as summarized in the following equation:

$$Y = \frac{\sigma^2_{xT}}{\left(\sum \sigma_{x_i}\right)^2}.$$

The term in the numerator of this equation is simply the variance (with month as the temporal unit) of the fraction fruiting/flowering time series for all species, and the denominator is simply the squared sum of the SDs of time series for individual species. This measure of synchrony, which yielded one estimate per year, is standardized between 1, which represents perfect synchrony among all flowers or fruits, and 0, which is perfect asynchrony. This measure makes no assumptions about abundances and variances of the species of flowers or fruits (Loreau & de Mazancourt, 2008).

Total turnover (T) was calculated to examine monthly community changes from one year to the next and was simply the proportion of species bearing flowers or fruits that differed between months (Hallett et al., 2016); this yielded one estimate per year:

$$T = \frac{G + L}{S},$$

where G is a species with flowers or fruits acquired from the previous month, L is a species with flowers or fruits lost from the previous month, and S is the total species richness (for species bearing flowers or fruits) for the two months.

Dominance was measured in terms of ranks, which were summarized by rank abundance clocks, which start at a vertical axis (12:00) and move over time around the clock (the units are months within years), with abundances increasing toward the outer rings and different colors used for different species. These heuristic figures illustrate changes in the top ranked species (Hallett et al., 2016), depicting different community change scenarios over time, from complete reshuffling of ranks (i.e., continual community changes, with colors crossing as one moves from 12:00 to 11:00) to stability in the dominance of a single species.

Annual intensity of flowering and fruiting was also calculated as the sum of flowering and fruiting per species per month. Communities of flowering and fruiting plants (among those censused) were summarized using a traditional principal component analysis (PCA) of species assemblages (Herbold, 1984). The covariance matrix for flower and fruit PCAs was derived from all of

the monthly assemblages of reproductive parts across the 35 years. Each monthly census constituted a unique assemblage, so for each species the fraction of total individuals bearing reproductive parts contributed to the quantitative assemblage, for a total of 420 measured assemblages of species bearing flowers or fruits. For this approach, flower or fruit species that occur together frequently, for example in the wet season, will have larger loadings on the same principal components. The PCA utilized the full correlation matrix (i.e., fraction flowering and fruiting were centered and scaled) for the monthly values of fraction flowering or fruiting across all years of the study. We also used a PCoA with Bray Curtis dissimilarity matrix, but results from these two approaches (PCA and principal coordinates analysis [PCoA]) were similar, so the first two PCs from the PCA were used in susbsequent models to examine associations between temperature and precipitation variables and the eigenvectors representing reproductive assemblages (for each month of the study), as well as to examine changes in assemblages over time.

Structural equation models

Structural equation models (SEM) were used to examine associations between mean monthly temperature, precipitation, soil moisture, fraction bearing reproductive parts, turnover, synchrony, and the eigenvectors from the PCA that summarized the assemblages of reproductive parts (PC1 and PC2). Only temperature was treated as an exogenous variable, which was based on the assumption that increases in temperature over the decades have caused changes in precipitation and soil moisture (even though feedback from changes in the latter two variables could also affect temperature). All variables, except PC1 and PC2, were z-transformed prior to analysis. We used the global estimation method in the lavaan package version 0.6–3 in R version 3.5.3 to generate five different models for both fruit and flower assemblages. The models differed only by the presence of one of the focal endogenous variables: fraction flowering or fruiting, turnover, synchrony, PC1, and PC2. Model fit for each of these was assessed by comparing them to more saturated reference models, which included year as the only exogenous variable, plus all of the variables and associations that were in the five unique models; comparisons were made using the difference in Akaike information criterion (dAIC). This approach allows for changes in reproductive phenology over the course of the study, as the path coefficients account for change in endogenous variables over time. We report standardized path coefficients

and illustrate the structural equation modeling results using standard path diagrams.

Bayesian temporal models

Eigenvectors from the PCA were used in hierarchical Bayesian models to examine changes in flowering and fruiting assemblages over time (months nested within years), as measured by the first two eigenvectors from the PCA of correlation matrices for flowers and fruits separately. We report results from four models: one model per reproductive assemblage (monthly values of PC1 and PC2) for flowers and for fruits. The models followed methods from other global change studies (Salcido et al., 2020; Wagner et al., 2021) and treat parameter estimates of change over decades as random variables, yielding distributions of parameter estimates related to shifts in assemblages toward those that had been found more frequently in the dry season. Specifically, we used multilevel Bayesian models to estimate coefficients for the relationship between year, month nested within year, and monthly PC1 values (eigenvector for species assemblages). Models were fit in JAGS utilizing the rjags package in R using (for each analysis) two Markov chains and one million steps each. Performance was assessed through an examination of chain histories (burn-in was not required), effective sample sizes, and the Gelman and Rubin convergence diagnostic. Response variables were modeled as normal distributions with means dependent on an intercept plus predictor variables, and we used uninformative priors. The priors on beta coefficients (for year and climatic variables) were normal distributions with a mean of zero and precision of 0.001 (variance = 1000). Priors on precisions were modeled as gamma distributions with rate = 0.1 and shape = 0.1. Scaling and centering were applied to all variables (except scores from PCA) prior to analysis.

RESULTS

Temperatures throughout the Cordillera de la Costa have been increasing over the past 30 years (0.05°C/year; Figure 1A), and precipitation has been declining, with an increase in drought conditions reflected in the number of dry years (Figure 1B). For our cloud forest site, the period from 2011 to 2015 included records of historically high temperatures, while the lowest recorded levels of precipitation were between 2006 and 2017.

Concomitant with these climate trends, there were substantial changes in phenology of reproductive parts on our focal tree species, with overall decreases in the

fraction of trees flowering and increases in the fraction fruiting (Figure 1). Since these data are based on point visits, they are as likely to reflect changes in flowering or fruiting windows as they are a measure total fraction with reproductive parts during a given month. Because fruits are longer lived than flowers, it was more likely to encounter fruits, and the patterns over time that we documented for fraction flowering or fruiting are consistent with the hypothesis that flowering windows decreased while fruiting windows increased. Changes in fraction flowering for a species at any given time measured in this way will still lead to changes in synchrony for an individual species as well as community-wide synchrony, and we detected declines in paired (X_i) and community-wide (Y) synchrony (Figure 2, Appendix S1: Figure S2) for many of the individual species and for the full communities of flowers (Appendix S1: Figure S2). These changes contributed to increases in turnover of flowering communities across years (i.e., the changes in flower communities encountered from one month to the next continuously increased over the years) and decreases in turnover in fruiting communities across years (Figure 1). The most pronounced changes in flowering and fruiting times started in 2009, matching declines in precipitation (Figure 1).

Community ordination values for both flowers and fruits (analyzed separately) each produced axes that represented communities of flowers or fruits (PC1 in both cases) that dominate in the rainy (negative loadings) or dry (positive loadings) season versus communities that dominate in the two transition periods (PC2 for both flowers and fruits), with wet-to-dry transition flower or fruit communities producing negative values for PC2 and the dry-to-wet transition communities yielding positive values for PC2. For both the fruit and flower PCAs, the first five eigenvalues accounted for over 75% of the total variance, but only the first two axes were used in
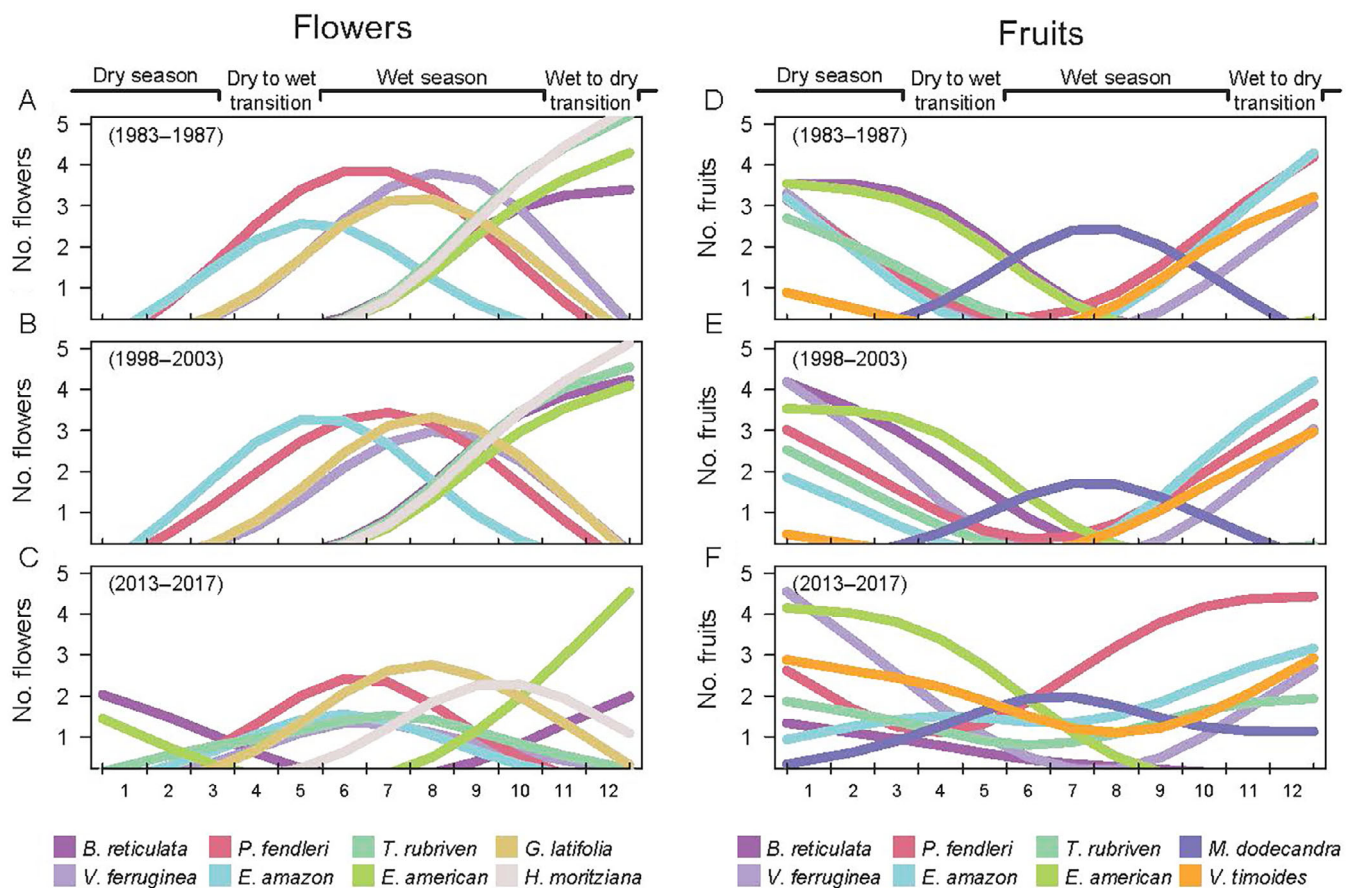

FIGURE 2 Seasonal dynamics of selected species, illustrating shifts in flowering (A–C) and fruiting (D–F) phenology for three intervals of years; x-axes are months of the year (note description of seasons along the top), and y-axes are average numbers of flowers (A–C) or fruits (D–F) per species within months and within the 5-year windows shown here. For example, flowering in early years (panels A and B) was characterized by a set of midyear species and another set of species with later phenology; in the most recent years (panel C) that pattern has mostly broken down, with more dispersed flowering times across species and season. Smoothed curves are splines fit for each species with 4 df.

subsequent analyses since they were good representations of the seasonal (dry, rainy, and transitions) assemblages. PC1 accounted for 33% and 29% of the variance for fraction of individuals flowering and fruiting, respectively, while PC2 accounted respectively for 20% and 19% of the variance in fraction flowering and fruiting (Appendix S1: Table S2). Community changes over time were unique for different months, with PC1 changing more for the ends of the dry or wet seasons and PC2 changing more for the transition months, and these changes intensified over the years of the study as precipitation declined (Figures 3, Appendix S1: Figures S1 and S2). For example, November and December (wet-to-dry transition) experienced strong shifts toward communities that were dominated by wet-season flowers but dry-season fruits.

SEMs supported the hypothesis that changes in the communities of flowering and fruiting plants were due to direct effects of changes in temperature, precipitation, and soil moisture rather than regular changes over time. We selected models that consistently had lower AIC values, were consistent with prior knowledge about causal relationships, and were good fits based on these criteria for all of the community endogenous variables (fraction flowering or fruiting, turnover across years, PC1, PC2). Models with years and precipitation as exogenous variables were poorer fits to the data (Appendix S1: Table S3). When the years were included in these models, the effect of time was close to zero, and the path coefficients for the other relationships were not altered. Increases in temperature caused lower fraction of individuals bearing fruits and flowers (partly through declines in soil moisture), higher turnover, and strong shifts in the overall community (Figure 3, Appendix S1: Figure S2). Increases in precipitation and associated higher soil moisture caused greater proportions of reproductive parts, along with greater turnover and flowering/fruiting community changes (Figure 3).

Based on 95% credibility intervals for monthly changes in PC1 and PC2 over the full time series, there were strong shifts from June to October toward assemblages dominated by dry-season flowers (positive shifts in PC1); these are months that normally see flowering by wet-season and wet-to-dry transition flowers (Figure 3). There were also strong September to December (wet and transition to dry season) shifts in fruiting assemblages toward wet-season fruits (Figure 3). Dry-season months (January–March) experienced shifts toward wet-season assemblages of flowers and dry-to-wet transition assemblages of fruits (Figure 3). Compositional changes are shown for a subset of species in Figure 2 (and additional subsets in Appendix S1: Figure S3), where a breakdown of historically coflowering and cofuiting assemblages is evident in the comparison of early suites of years (1983–1987 and 1998–2003) with later years (2013–2017).

DISCUSSION

Trends in the reproductive phenology of plants over time are potentially complex and could reflect plasticity, senescence, or other aspects of plant biology, so it is challenging to document the effects of climate change on phenology. In the Venezuelan cloud forest site where our study took place, increases in mean annual temperature and declining precipitation led to lower soil moisture, which in turn yielded declines in the observed fraction of plants flowering and increases in the fraction fruiting when controlling for other abiotic factors shifting over time. The observed fraction of plants flowering or fruiting likely reflected changes in the available windows of time for reproduction in the focal plant species, with contrasting effects leading to decreases for flowers and increases for fruits. Changes in fraction bearing fruits and flowers at any given time will lead to changes in turnover and synchrony, whether due to changes in windows of availability or changes in fraction bearing reproductive parts in a month. Monthly turnover among flower and fruit assemblages increased over the time series, and there was a strong shift toward assemblages dominated by dry-season flowers and fruits appearing during the rainy season. Trends in synchrony over time for flowering and fruiting were variable for individual species, but community synchrony decreased for flowers and increased slightly for fruits over the 35-year time series. While many of these changes in reproductive phenology were directly associated with the increases in temperature and declining rainfall, all the responses were mediated by declining soil moisture. These direct and indirect effects of changes in temperature and precipitation over time were strong and accounted for most of the explained variance in phenology metrics over the time series.

The changes in the flower and fruit assemblages documented here (Figure 1) reflected a variety of shifts in reproductive phenologies for all the species examined (Figure 2, Appendix S1: Figures S1–S3). For example, for *P. fendleri* and *Tetrorchidium rubrivenium* a shift toward earlier flowering time was observed in later years, while for many species fruiting phenology has apparently become less concentrated in particular seasons (Figure 2, Appendix S1: Figure S3); for other species, fruits and flowers appear to be disappearing. For *M. dodecandra* and *Clusia multiflora*, reproductive parts have not been observed on the individuals at our study site for the past 5 years. Such losses of fruit resources for long time periods have been documented for other tropical plants and are potentially a response to climate change (Chapman et al., 2005). Climate change can affect plant flowering and fruiting phenology by many direct and
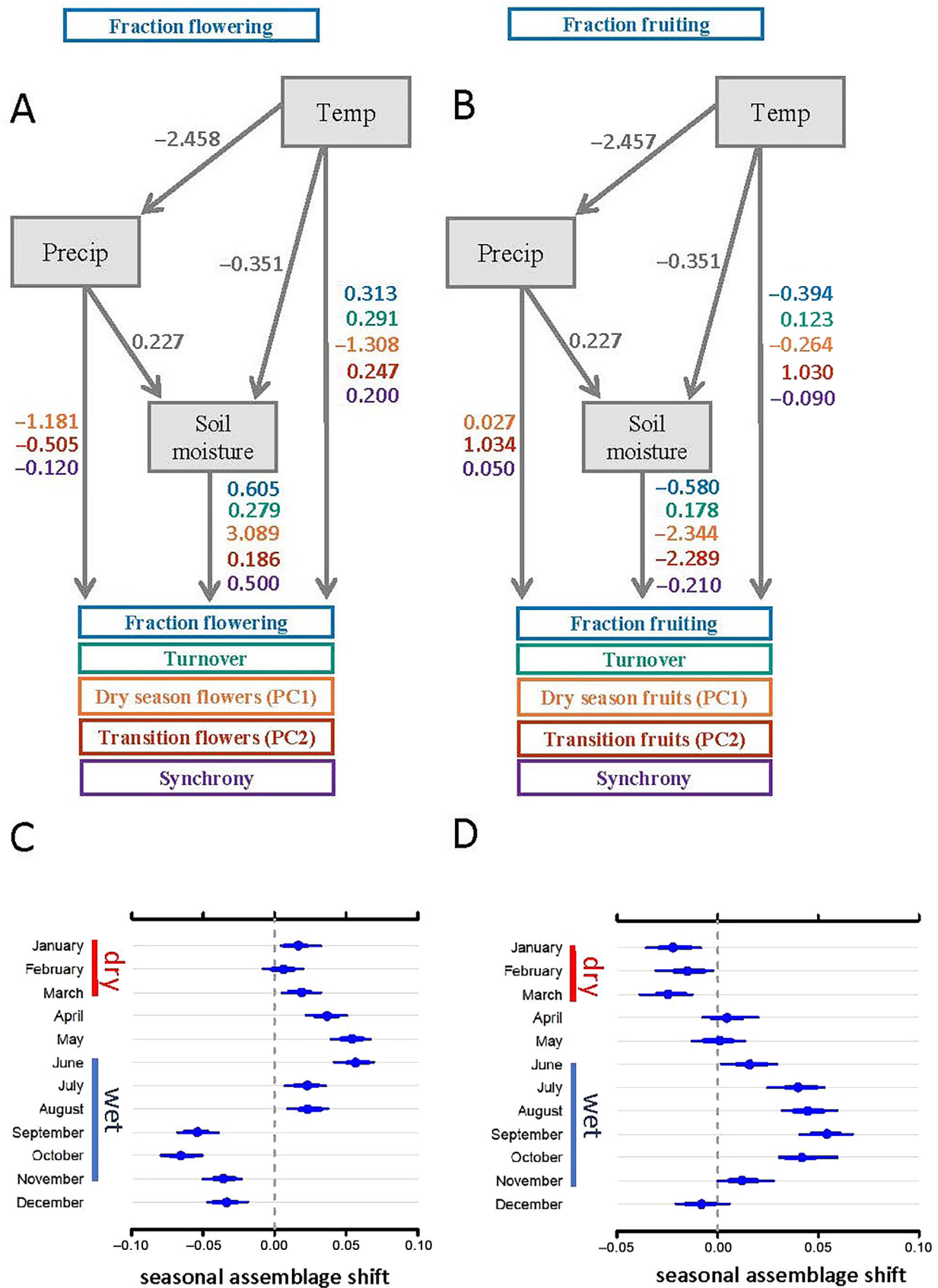
FIGURE 3 Legend on next page.

indirect mechanisms, including the direct effects of temperature increases and decreases in precipitation, as well as indirect effects via soil moisture (Figure 3). Increases in temperature can cause drastic decreases in soil moisture that affect plant physiology; cloud forest soils are composed of a root mat in the upper few centimeters, which can quickly lose water, which leads to the death of many plant seedlings or established plants. Other mechanisms by which climate change affects flowering and fruiting phenology include decreased efficacy of nitrogen utilization, drought stress, modified growth, changes in root architecture, stomata closing patterns, and specific tissue responses that alter cellular signals (Parmesan & Hanley, 2015). These and associated changes to plant biology cause early flowering or slowed growth mediated by phytohormones that regulate responses to high temperatures, drought, or insufficient water. Similar to corals, trees have a fairly inflexible damage threshold, and there is little plasticity related to responses to water stress, which is an especially difficult problem for plants in cloud forests, where in recent decades there have been decreases in soil water and nutrient availability (Hu & Riveros-Iregui, 2016).

Some plant attributes may render species more adaptable to warmer and drier climates. For the tree species examined here, there was variation in phenological responses to climate change, with some species, such as *A. fendleri*, much less affected than others. Plant phenologies in a cloud forest are diverse and complex, and there are both overlapping and disparate phenologies, such that when the leaves of one species are falling, multiple other species are leafing out. In terms of availability of fruits and flowers to consumers at any given point in time, tropical cloud forests historically have been characterized by great interspecific variation in flowering times and are mosaics of species that exhibit both synchronous and asynchronous intraspecific reproductive phenologies. For example, in the current study *A. fendleri*, *P. tovarense*, *R. grandis*, *Graffenrieda latifolia*, *Vismia ferruginea*, and *P. fendleri* are all asynchronous for flowering, while the other species in this study are at least partially synchronous. As a consequence, flowers and fruits for these and other species at our study site are available year round, which could potentially act as a buffer to unpredictable resource availabilities caused by changing phenologies, synchronies, and predictability. Regardless of the flowering or fruiting synchrony for individuals within a tree species, the shifts in reproductive phenologies recorded here are likely to alter the diversity and consistency of resource availability for animals. In particular, these phenological changes can lead to asynchronies with associated pollinators and fruit dispersers, especially for specialists (Maglianesi et al., 2020; Memmott et al., 2007; Warren et al., 2011).

For temperate forests, some synthesis has allowed for analyses of how phenological shifts in plant reproduction have affected mutualisms with animals. The best data for understanding the effects of these shifts on mutualists are for pollinators (Rafferty et al., 2015). In Europe, phenological shifts in flowering have affected thousands of species of pollinators such that there could be declines in the functional redundancy and complementarity of pollinator assemblages (Duchenne et al., 2020). More generally, Rafferty et al. (2015) argued that most mutualisms were likely to be disrupted by phenological shifts, especially those that are facultative, generalized, temporally ephemeral, and nonsymbiotic. However, it is difficult to say what these shifts in flower and fruit assemblages mean for intimate, specialized relationships that are common in tropical ecosystems (Forister et al., 2015), particularly endemic interactions in tropical cloud forests. The natural history of insects associated with our focal plant species is replete with examples of very specialized symbiotic relationships that likely depend on very specific phenologies. For example, seeds of *P. tovarense* are infested by specialized braconid

FIGURE 3 Causal hypotheses for relationships between temperature, precipitation, soil moisture, and reproductive phenology variables were tested with structural equation models, with the best-fit models summarized here. Standardized path coefficients for the best-fit models are next to arrows and are color coded based on the community metrics; missing path coefficients indicate that those relationships were not included in the best-fit models. The effects of variation in temperature, precipitation, and soil moisture were consistent for different community metrics for flowers (A and C) and fruits (B and D), including fraction of individuals with flowers or fruits, turnover, and principal components (PC1, PC2) for the assemblages. PC1 represents assemblages of flowers or fruits that dominate in the rainy (negative values) or dry (positive values) season, while PC2 represents assemblages that dominate in the two transitions between seasons. Changes in the assemblages over the full time series were estimated with a hierarchical Bayesian model, yielding an estimated change (with thin lines for 80% and thick lines for 50% credible intervals) for each month across the full time series for PC1 flowers (C) and PC1 fruits (D). Dry-season months are January–March, wet-season months are June–November, and other months are considered transitions. Negative estimates indicate shifts toward species that traditionally flower or fruit in the wet season (to the left of zero on the x-axis), while positive estimates indicate shifts toward dry-season (toward the right) assemblages. For example, there were strong shifts from June to October toward assemblages dominated by dry-season flowers (positive shifts in PC1) and strong September to December (wet and transition to dry season) shifts in fruiting assemblages toward wet-season fruits. Temp, temperature; Precip, precipitation.

wasp larvae, *Bracon phytophagus* Quicke (Flores et al., 2005), which is a very unique life history characteristic for the subfamily Braconinae. Many other obligate, specialized interactions of animals with tropical plants are likely to be abundant locally but not across the tropical landscape, which suggests that small local changes in climate and in resource availability (in this case, flowers and fruits) could drive these animals locally extinct (Sudta et al., 2022).

It is clear that we are living in a changing climate, with recent decades being characterized by dramatic increases in minimum temperatures, maximum temperatures, sea surface temperatures, intensification of the El Niño Southern Oscillation, and increases in the frequency and intensity of other extreme weather events (Ummenhofer & Meehl, 2017). Our work demonstrates that over the last 35 years, climate change has begun to affect the reproductive dynamics of important cloud forest plant species. Changes in precipitation, temperature, and soil moisture have profound implications for the conservation of diverse tropical forests. For our focal cloud forest, there were multiple periods of historically low rainfall during dry seasons over the three decades of the study and relatively low rainfall during the rainy season of drier years, and these changes were associated with shifts in the availability of fruits and flowers to pollinators, seed dispersers, and flower or fruit parasites. Strong shifts in tropical flower and fruit assemblages will dramatically change the ecology and evolution of tropical plants and will likely lead to altered community dynamics in tropical forests.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT
Data and R scripts for statistical analyses (Flores, 2022) are available in Zenodo at https://doi.org/10.5281/zenodo.7662623.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.