

Long-term increases in tropical flowering activity across growth forms in response to rising CO₂ and climate change

Stephanie Pau¹  | Daniel K. Okamoto² | Osvaldo Calderón³ | S. Joseph Wright³

¹Department of Geography, Florida State University, Tallahassee, FL, USA

²Department of Biological Sciences, Florida State University, Tallahassee, FL, USA

³Smithsonian Tropical Research Institute, Ancón, Panama

Correspondence

Stephanie Pau, Department of Geography, Florida State University, Tallahassee, FL, USA.

Email: spau@fsu.edu

Abstract

Mounting evidence suggests that anthropogenic global change is altering plant species composition in tropical forests. Fewer studies, however, have focused on long-term trends in reproductive activity, in part because of the lack of data from tropical sites. Here, we analyze a 28-year record of tropical flower phenology in response to anthropogenic climate and atmospheric change. We show that a multidecadal increase in flower activity is most strongly associated with rising atmospheric CO₂ concentrations using yearly aggregated data. Compared to significant climatic factors, CO₂ had on average an approximately three-, four-, or fivefold stronger effect than rainfall, solar radiation, and the Multivariate ENSO Index, respectively. Peaks in flower activity were associated with greater solar radiation and lower rainfall during El Niño years. The effect of atmospheric CO₂ on flowering has diminished over the most recent decade for lianas and canopy trees, whereas flowering of midstory trees and shrub species continued to increase with rising CO₂. Increases in flowering were accompanied by a lengthening of flowering duration for canopy and midstory trees. Understory treelets did not show increases in flowering but did show increases in duration. Given that atmospheric CO₂ will likely continue to climb over the next century, a long-term increase in flowering activity may persist in some growth forms until checked by nutrient limitation or by climate change through rising temperatures, increasing drought frequency and/or increasing cloudiness and reduced insolation.

KEYWORDS

climate change, CO₂ fertilization, El Niño, lifeforms, reproduction, solar irradiance, solar radiation

1 | INTRODUCTION

Increasing evidence indicates long-term directional trends in tropical forests. Increases in forest biomass, reproduction, and recruitment, changes in tree growth and productivity, as well as shifts in species composition suggest that anthropogenic global change is altering the ecology of tropical forests (reviewed in Clark, 2007; Lewis, Lloyd, Sitch, Mitchard, & Laurance, 2009; Wright, 2010). How tropical forests respond to anthropogenic change is of global importance because tropical forests account for 33% of terrestrial productivity,

store 25% of the carbon in the terrestrial biosphere, and are home to more than 50% of the known species on Earth (Bonan, 2008; Dirzo & Raven, 2003; Lambin et al., 2001; Saatchi et al., 2011; Saugier, Roy, & Mooney, 2001).

The changing ecology of tropical forests has been attributed to a suite of environmental drivers, at both global and regional scales. Globally, atmospheric CO₂ concentrations and temperature are rising, with temperatures rising by about 0.26° per decade in most tropical regions (Malhi & Wright, 2004). Rising atmospheric CO₂ concentrations have been linked to increasing water-use

efficiency (Holtum & Winter, 2010), increasing aboveground biomass (Lewis et al., 2009), increasing reproductive activity (Clark, Clark, & Oberbauer, 2013), and shifts in species composition (e.g., importance of lianas; reviewed by Schnitzer & Bongers, 2011) in tropical forests. Rising nighttime temperatures have been associated with increasing respiration costs and slower rates of wood production (Clark et al., 2013; Dong et al., 2012; Feeley, Joseph Wright, Nur Supardi, Kassim, & Davies, 2007). Rising daytime temperatures have also been associated with greater flowering activity (Pau et al., 2013).

Forest responses to rising atmospheric CO₂ and temperature will be complicated by regional anthropogenic changes, including nutrient deposition and altered hydrological regimes. Increases in the frequency and severity of drought will have negative impacts on forest biomass (Phillips et al., 2009) and lead to shifts to more drought-tolerant species (Feeley, Davies, Perez, Hubbell, & Foster, 2011). "Normal" variation in dry season water stress can also reduce aboveground biomass production (Clark et al., 2013). Changes in cloudiness and atmospheric transmissivity to solar irradiance affect photosynthesis, vegetative growth, and reproduction (Asner & Alencar, 2010; Graham, Mulkey, Kitajima, Phillips, & Wright, 2003; Nemani et al., 2003; Wright & Calderón, 2006). Increased emissions and deposition of anthropogenic nitrogen (N) are widespread across the tropics (Hietz et al., 2011). Although many tropical forests are already N-rich, increasing N deposition has led to increased N concentrations in leaves in Panama and in wood in Brazil and Thailand (Hietz et al., 2011). Greater leaf N can increase photosynthetic capacity, but N deposition might also increase soil acidity and deplete soil nutrients with negative effects on forest productivity (Matson, McDowell, Townsend, & Vitousek, 1999). The magnitude of any effect of CO₂ fertilization will vary with nutrient availability and substrate type (Cernusak et al., 2013; Körner, 2003). Indeed, all of the drivers discussed above potentially work in concert. Many tropical forests are also recovering from past disturbances, further complicating our ability to attribute causality to the changing ecology of tropical forests.

Most studies of long-term changes in tropical forests have focused on trees, even though a high diversity of growth forms is a characteristic feature of tropical forests. Growth forms should differ in their response to anthropogenic change because their resource acquisition and allocation strategies differ (Morellato & Leitao-Filho, 1996; Santiago & Wright, 2007; Sarmiento & Monasterio, 1983). For example, canopy trees can have deep roots that access soil water at great depths and provide a buffer against droughts and dry season water deficits (Bennett, McDowell, Allen, & Anderson-Teixeira, 2015; Hutyra et al., 2007; Meinzer et al., 1999; Nepstad et al., 1994). In contrast, smaller understory growth forms tend to have shallower root systems and to be more susceptible to changes in water availability (Becker & Castillo, 1990; Opler, Frankie, & Baker, 1980; Wright, 1991). For example, a dry season forest irrigation experiment did not alter the phenology of most canopy tree species (Wright & Cornejo, 1990), but had widespread effects on the timing of leafing, flowering, and fruiting of

understory species (Tissue & Wright, 1995; Wright, 1991). As another example, woody vines or lianas are a characteristic feature of tropical forests (Gentry, 1991) and are increasing in importance in many Neotropical forests (reviewed by Schnitzer & Bongers, 2011; Wright, Sun, Pickering, Fletcher, & Chen, 2015). It has been hypothesized that the liana growth form allows liana seedlings to capitalize on CO₂ fertilization through lateral growth to understory sunflecks and gaps, while tree seedlings must wait for canopy openings overhead (Granados & Körner, 2002). These examples raise the possibility that different long-term changes expressed by different growth forms might provide insight into the mechanisms involved.

A limited number of studies have focused on long-term trends in tropical reproductive activity, in part because of the lack of data from tropical sites (Cook et al., 2012). The level of reproduction has increased broadly over decadal time scales in Panama, Costa Rica, and the Ivory Coast (Clark et al., 2013; Polansky & Boesch, 2013; Wright & Calderón, 2006) and has increased in many species and decreased in many others in Uganda (Chapman et al., 2005). In temperate regions, "spring advancement" including earlier bud burst and flowering is associated with rising temperatures and longer growing seasons (CaraDonna, Iler, & Inouye, 2014; Menzel & Fabian, 1999; Menzel, Sparks, Estrella Koch, Aasa A, & Chmielewski, 2006; Peñuelas et al., 2013; Settele et al., 2014). The lack of a season inhospitable to flowering and the diversity of flowering strategies complicate the detection of shifts in the timing of flowering in the tropics. For example, hundreds of species flower in every month of the year in humid tropical forests (Croat, 1978) and the duration of annual flowering varies among species from a few days to year-round (Newstrom, Frankie, Baker, & Newstrom, 1994). Nonetheless, most tropical species have a limited flowering window tied to climatic seasonality (Morellato et al., 2000; van Schaik, Terborgh, Wright, & van Schaik, 1993; Zimmerman, Wright, Calderón, Pagan, & Paton, 2007). Thus far, it is unclear whether longer flowering duration is limited to temperate regions, or whether an extension of flowering duration is also evident in the tropics. An extended flowering duration could indicate weakened synchrony within species.

We previously used one of the longest tropical flowering records from Barro Colorado Island (BCI), Panama, to compare different climatic drivers of flowering activity over seasonal, interannual, and decadal timescales. We showed that seasonal and interannual variation in community-wide flowering activity was driven by changes in light availability associated with cloud cover (Wright & Calderón, 2006; Zimmerman et al., 2007), whereas decadal variation appeared to match rising temperatures and/or varying rainfall (Pau et al., 2013). Here, we focus on decadal trends, and examine how hypothesized climatic drivers, including rainfall, light, temperature, and ENSO teleconnections, affect flowering activity of different growth forms. We also consider possible effects of rising atmospheric CO₂ (Clark et al., 2013). We evaluate annual flowering activity, measured through weekly censuses of flower presences in 200 passive traps, and flowering duration, measured in weeks for each species and the number of species flowering.

2 | MATERIALS AND METHODS

2.1 | Flower and climate data

Barro Colorado Island (BCI) supports tropical moist forest in the Holdridge Life Zone system (Croat, 1978). The movements of the intertropical convergence zone (ITCZ) largely determine seasonal variation in climate. Annual rainfall averages 2600 mm, with a pronounced dry season from January through April. Many species concentrate flowering during the dry season, when cloud cover is minimal and incoming solar irradiance averages 48% greater than during the wet season (Wright & Calderón, 2006; Wright & Van Schaik, 1994; Zimmerman et al., 2007).

We censused fallen flowers weekly starting in February 1987 using 200 traps within a 50-ha plot (Wright & Calderón, 2006). Each trap had an effective surface area of 0.5 m² (71 cm on each side) and consisted of a 1-mm mesh screen bag mounted 80–100 cm

above the ground on a PVC frame. All plant reproductive parts captured by the traps were identified to species each week. We treated each flower species–trap–census combination as a flower presence and summed flower presences to quantify relative annual flowering activity (Figure 1a). For individual species, this measure of flowering activity integrates the number of flower presences per census (intensity) and the number of weekly censuses with flowers (duration). To separate intensity and duration, we quantified flowering duration as the number of weeks that each species flowered each year. Finally, we quantified the number of species flowering as the number of species present averaged over censuses for each year.

We assigned species to a growth form, summed flower presences to yearly values by growth form, and averaged flower duration to yearly values by growth form. Growth forms were lianas (woody vines), canopy trees (maximum height >20 m), midstory trees (10 m < maximum height <20 m), understory treelets (5 m < maximum height <10 m), and shrubs (maximum height <5 m). Epiphytes,

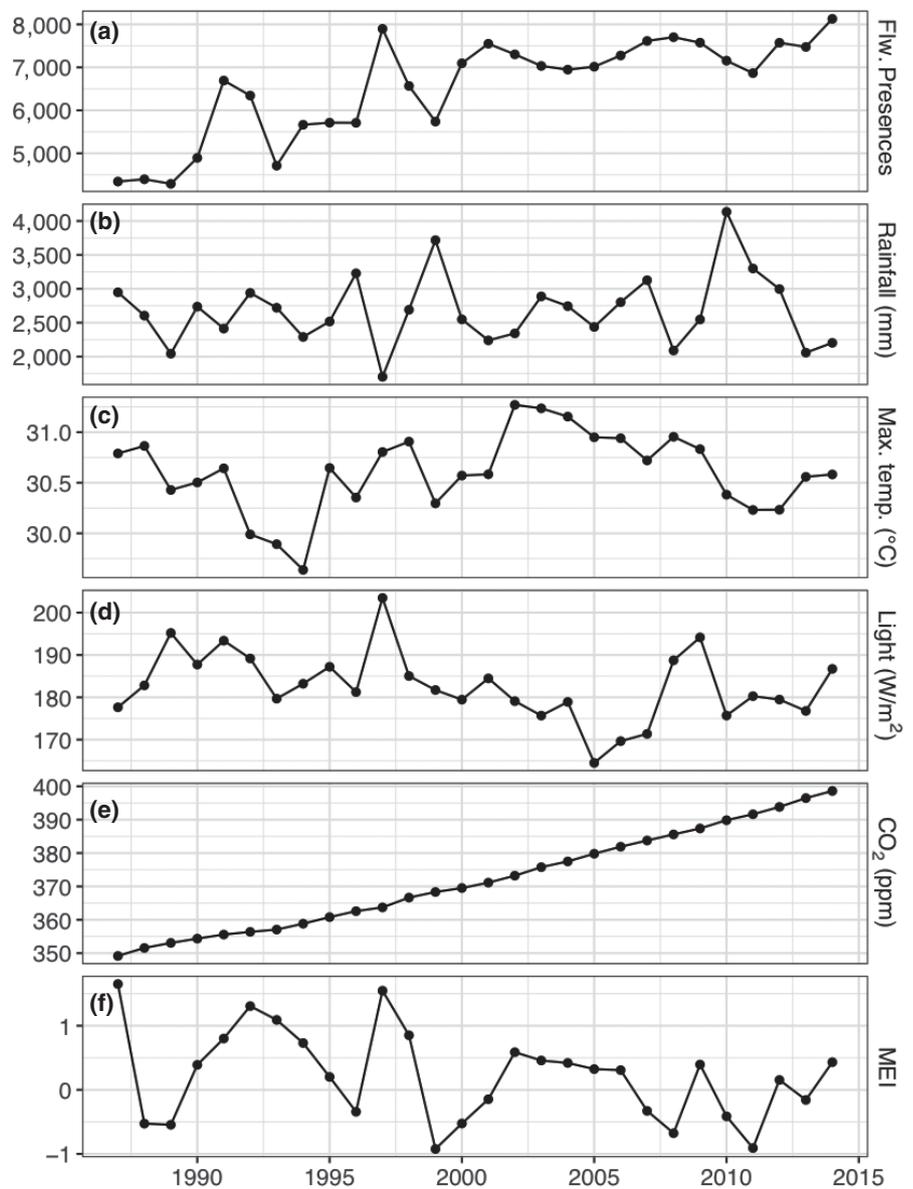


FIGURE 1 Long-term variation in flower presences and climate at Barro Colorado Island, Panama (1987–2014). Flower presences were summed over 200 traps, 52 weekly censuses, and all flowering species. “MEI” refers to the Multivariate ENSO Index where large positive values indicate El Niño conditions and large negative values indicate La Niña conditions. See Methods for details about climatic variables

hemiepiphytes, parasites, vines, and unidentified species (or unassigned to a growth form) together comprised ~17% of the flower presences and are not considered further.

Rainfall was measured using a tipping bucket (Li-Cor 1400-106 tipping bucket, Lincoln, NE, USA) and summed to yearly values (mm; 1 January through 31 December). Minimum and maximum temperatures were measured daily using manual thermometers and averaged to yearly values (°C). Solar radiation was measured using a pyranometer (Li-Cor Silicon Pyranometer, Lincoln, NE, USA) placed on top of a tower above the forest canopy at 42 m. In 2006, the tower was extended and the pyranometer was moved to the new top at 48 m. The top of the forest canopy remained at least 2 m below the sensor before 2006 so the move should not have affected the solar radiation measurements. Solar radiation was recorded every 15 min and averaged to yearly values (W/m²). Detailed information about BCI meteorological measurements, including instrumentation, calibration, and location changes can be found at <https://repository.si.edu/handle/10088/29560> (<https://doi.org/10.5479/data.stri/10088/29560>).

Global mean annual atmospheric carbon dioxide (CO₂) concentrations (ppm) were obtained from the NOAA ESRL (Earth Systems Research Laboratory) website (<https://www.esrl.noaa.gov/gmd/ccgg/trends/full.html>). The Multivariate ENSO Index (MEI) was also obtained from the NOAA ESRL website (<http://www.esrl.noaa.gov/psd/enso/mei/>). The MEI scales from large positive values during El Niño events to large negative values during La Niña events (Wolter & Timlin, 2011).

2.2 | Statistical analyses

We examined relationships between flower presences, climatic variables (light, temperature, rainfall, MEI), and atmospheric CO₂ using 28 years of annual data for each growth form (1987–2014; Figure 1). We used a linear model that accounted for serial correlation among growth forms to evaluate relationships between flower presences, independent variables, and their interactions across growth forms. Different autoregressive–moving average (ARMA) error correlation structures (within-lifeform) were compared using the Akaike information criterion corrected for small sample sizes (AICc) (Table S1). Autocorrelation plots of model residuals were examined to confirm there was no serial correlation although there was remaining autocorrelation at year 4 (Figure S1). We assumed the error correlation structure and parameters were the same among growth forms (i.e., there was no ARMA–growth form interaction). Separate variances for each growth form were used to reduce heteroscedasticity (i.e., the estimate for each growth form coefficient was associated with a separate standard error). Linear models were estimated using generalized least squares (Pinheiro & Bates, 2000; Pinheiro, Bates, DebRoy, & Sarkar, 2017). We compared the full model (light, minimum or maximum temperature, rainfall, atmospheric CO₂, MEI, and their interactions with growth form) to all possible reduced models using AICc (Burnham & Anderson, 2010; Tables S2 and S3). Minimum and maximum temperatures were compared using

the full model (i.e., including all other independent variables), and were considered equivalent based on AICc (i.e., $\Delta\text{AICc} < 2$; Burnham & Anderson, 2010). Thus, we compared both minimum and maximum temperatures in two sets of model comparisons of the full model and all possible reduced models (Tables S2 and S3).

We compared the flowering record analyzed in this study (1987–2014) to a shorter period of observation (1987–2009) from a previous analysis (Pau et al., 2013), in which we did not undertake statistical analyses of yearly flowering data, to examine the consistency of hypothesized climatic drivers over time (Table S4).

Model averaging using AICc weights was performed four ways: full and conditional averaging over all models and over equivalent best-fit models only. Equivalent best-fit models have $\Delta\text{AICc} < 2$ (Burnham & Anderson, 2010). Model averaging allows inference about regression parameters to incorporate model uncertainty and reduce bias from potential spurious correlations (Lukacs, Burnham, & Anderson, 2010). To calculate full-average models, parameter coefficients missing from the full or best model are set to zero before averaging. To calculate conditional-average models, parameter coefficients missing from the full or best model are excluded so that those missing parameter coefficients do not contribute to average values. The average coefficients of parameters in the best-fit models are robust to the four possible model averaging procedures (i.e., full vs. conditional averaging over all vs. equivalent best-fit models) because models including these parameters have the largest AIC weights (Tables S5 and S6). For climate variables with a significant interaction with growth form, post hoc linear contrasts were performed to test the null hypothesis that the slope differed significantly from zero for each growth form. Data were centered and standardized to 1 standard deviation. After this standardization of the data, estimated model coefficients correspond to the change in flower presences associated with a one standard deviation change in the independent variable.

We examined long-term trends in flower presences, flowering species richness, and flowering duration using the calendar year as a predictor in separate linear models for each growth form. We also used Pearson correlations to evaluate relationships between flower presences, flowering species richness, and flowering duration.

Finally, to examine nonlinear relationships between flower presences, climatic variables, and atmospheric CO₂, we used a generalized additive model (GAM) using monthly aggregated data (weekly flower censuses and rainfall were summed, and temperature and light were averaged). Whereas the linear model using yearly data provides an estimate of cumulative annual relationships with each predictor, GAMs estimate flexible (potentially nonlinear) and independent smoothing functions to predictors and response variables (Venables & Ripley, 1999; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). We used a Poisson likelihood and estimated relationships between the monthly log-flowering response and each predictor in the GAM using a cubic regression spline, hereafter referred to as a “smooth term”. Using the GAM, we estimated additive smooth terms, light, temperature, rainfall, atmospheric CO₂, MEI, and month (to account for seasonality in flower production) and accounted for

within-growth form serial autocorrelation in the error term using an AR(1). Because our primary focus was on interannual variability (i.e., not what drives the seasonal dynamics), we used yearly anomalies from monthly means for all predictors except for atmospheric CO₂ and the MEI. We used seasonally adjusted global atmospheric CO₂ values (instead of raw CO₂ measurements) provided by NOAA (<https://www.esrl.noaa.gov/gmd/ccgg/trends/full.html>). The use of seasonally adjusted CO₂ values, anomalies from the monthly mean from raw CO₂ measurements, or raw CO₂ measurements did not qualitatively change results.

3 | RESULTS

Lianas and canopy trees made the largest contributions to total flower presences, 19.4% and 28.4%, respectively, and comprised about 10.0% and 17.8% of total flowering species richness, respectively. Midstory and understory trees contributed 13.1% and 10.1% of total flower presences and comprised about 7% and 13.8% of all species, respectively. Shrubs contributed only 3.3% of total flower presences, but are the most species-rich group comprising about 18.4% of all species. Variation in flower presences across years was similar for all growth forms, with slightly higher variation for shrubs and understory treelets (coefficient of variation ~30%).

All growth forms showed a significant and positive long-term trend in flower presences except for understory trees (all $p < .001$;

lianas $r^2 = .36$; canopy trees $r^2 = .69$; midstory trees $r^2 = .90$; shrubs $r^2 = .30$; Figure 2). All growth forms showed a significant and positive long-term trend of increasing flowering species richness (all $p < .05$; lianas $r^2 = .31$, canopy trees $r^2 = .34$; midstory trees $r^2 = .13$; understory trees $r^2 = .17$; shrubs $r^2 = .17$). All growth forms showed a significant and positive long-term trend in flower duration (number of weeks flowers were present) except for lianas and shrubs (all $p < .001$; canopy trees $r^2 = .40$; midstory trees $r^2 = .61$; understory trees $r^2 = .40$; Figure 3). Years with greater flower presences were associated with a greater number of species flowering for all growth forms except for midstory trees ($p < .001$; lianas $r = .62$; canopy trees $r = .80$; shrubs $r = .66$; $p < .02$ understory trees $r = .44$). Years with greater flower presences were also associated with longer flowering duration for all growth forms except for understory trees (all $p < .001$; lianas $r = .81$; canopy trees $r = .67$; midstory trees $r = .79$; shrubs $r = .52$).

The best-fit models after comparing all possible models included growth form, rainfall, light, CO₂, and the MEI as predictors of annual flower presences (i.e., all independent variables except for minimum or maximum temperatures; Tables S2 and S3). There were also significant interactions between CO₂ and growth form and MEI and growth form. The two best models ($\Delta\text{AICc} < 2$) comprised 60.4% of the AICc weight and differed in whether an interaction between MEI and growth form was included. Growth form was consistent in the top-ranked models, and the sum of AICc weights for all models with growth form was over 99% (Tables S2). CO₂ was also

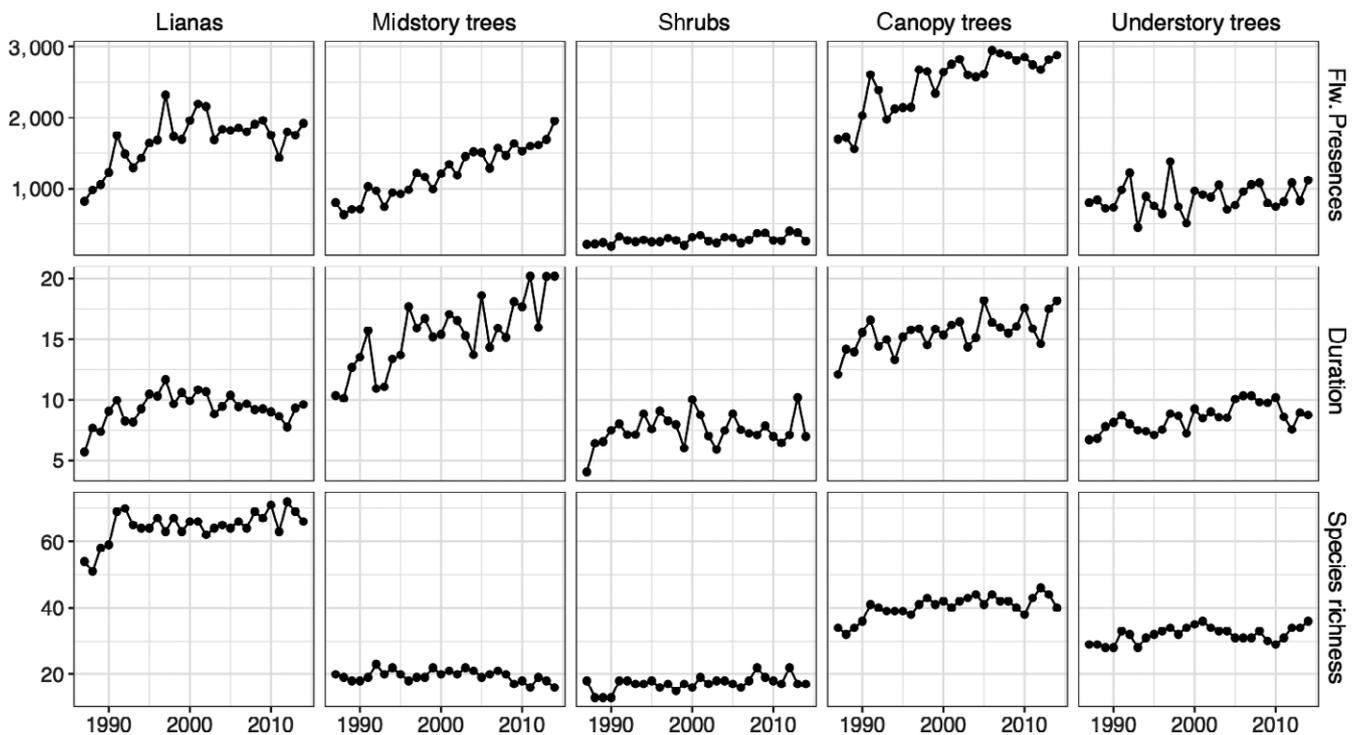


FIGURE 2 Long-term variation in flowering activity at Barro Colorado Island (BCI), Panama (1987–2014). Flower presences were summed over 200 traps, 52 weekly censuses, and all flowering species. Flower duration was calculated as the number of weeks that each species flowered each year and then assigned to a growth form. Flowering species richness was the total number of species present in each census averaged each year

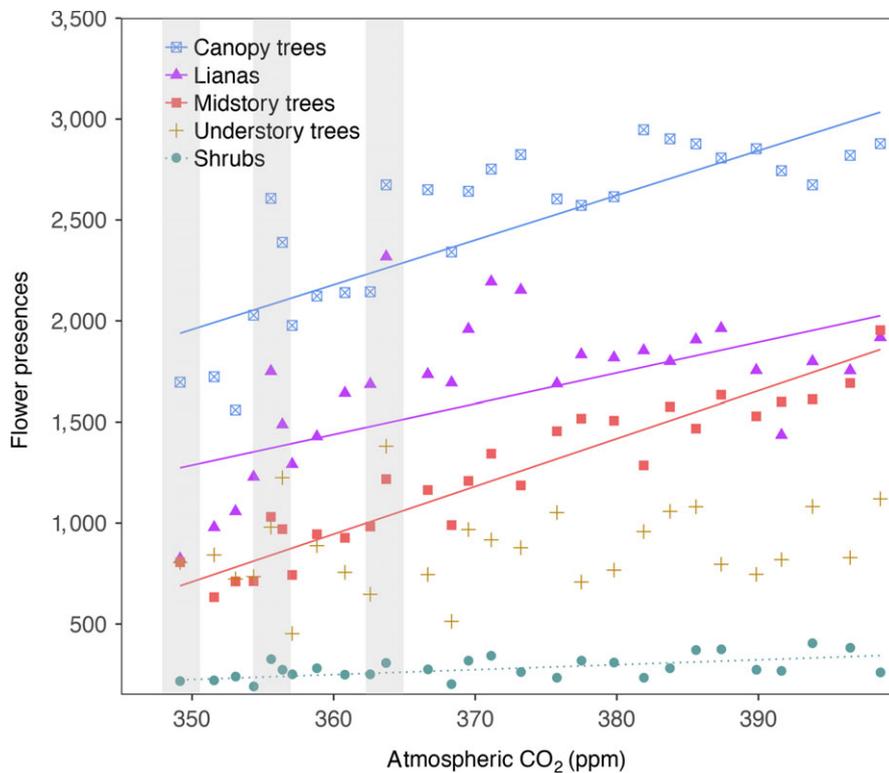


FIGURE 3 Linear relationships between flower presences and atmospheric CO₂ concentrations using yearly data. All growth forms responded significantly and positively to CO₂ except shrubs (marginally significant; $p = .07$) and understory trees (see Table 2). Solid and dashed lines represent significant and marginally significant relationships for individual growth forms. Gray bars represent the three strongest El Niño years (1987, 1992, 1997) based on the Multivariate ENSO Index (MEI)

consistent in the top-ranked models, and the sum of AICc weights for all models with CO₂ was over 99%. The sum of AICc weights for all models in which a variable appeared was then highest for light (94%), MEI (91%), and rainfall (87%). CO₂ had the largest effect on flower presences (Table 1). CO₂ had approximately five times the effect of MEI on flower presences and approximately three to four times the effect of rainfall or light.

TABLE 1 Models of yearly flower presences using averaged coefficients of the best-fit models with $\Delta\text{AICc} < 2$. Interactions between CO₂ and growth form and the Multivariate ENSO Index (MEI) and growth form were also in the best-fit models using data from 1987 to 2014 (Table 2; Figure 3). In comparison with a shorter record of observation (1987–2009), temperature and not the MEI was included in the best-fit models. The only interaction with growth form in the best-fit models was with CO₂

1987–2014 (28 years)					
	Estimate	SE	Adjusted SE	z-value	Pr(> z)
Rainfall	−21.09	8.15	8.21	2.57	0.01
Light	17.90	7.94	8.01	2.24	0.03
CO ₂	71.16	36.15	36.46	1.95	0.05
MEI	13.86	8.04	8.11	1.71	0.09
1987–2009 (23 years)					
	Estimate	SE	Adjusted SE	z-value	Pr(> z)
Rainfall	−34.08	8.88	8.97	3.81	<0.001
Light	11.59	6.52	6.59	1.76	0.08
CO ₂	70.65	30.50	30.83	2.29	0.02
Temperature	−8.75	6.77	6.84	1.28	0.20

Interactions between CO₂ and growth form showed that all growth forms produced significantly more flowers as CO₂ increased except shrubs (only marginally significant) and understory trees (Table 2; Figure 3). The interaction between MEI and growth form was in one of the two best-fit models, and only midstory trees had a significant relationship with MEI. Years with a higher positive MEI value, that is, increasing strength of El Niño, were associated with more flowers for midstory trees, after accounting for variation in rainfall, light, and CO₂, which were also in the best-fit models. However, increases in flower presences for other growth forms during strong El Niño events may be apparent as well (Figure 3).

In comparison with the shorter record of observation (1987–2009), two of the four equivalent best-fit models included temperature, two included light, all included CO₂ and rainfall, none included the MEI, and all included the interaction between CO₂ and growth form (Tables S4 and Table 1). When CO₂ and MEI were not included in the model, similar to the previous analysis of the shorter record (Pau et al., 2013), temperature was still in one of the two best-fit models, and the coefficient was positive but not significant; there was no significant interaction between growth form and temperature.

Whereas linear models showed that flowering by lianas, canopy trees, midstory trees, and shrubs on average increased with CO₂ (Table 2; Figure 3), the nonlinear model showed evidence that this effect was strong between 1987 and 2000 and then diminished after 2000. The increase by lianas and canopy trees appears driven by stronger responses before atmospheric CO₂ reached c. 370 ppm, after which, flowering flattens and responses to CO₂ saturated (Figure 4). Midstory trees continue to increase flowering past this period

TABLE 2 Interactions between CO₂ and growth form and the Multivariate ENSO Index (MEI) and growth form in the model of flower presences with all hypothesized predictors (Figure 3). Only one of the two best-fit models included an interaction between MEI and growth form. Values are slope coefficients (SE). The interaction between flowering activity and CO₂ was marginally significant for shrubs ($p = .07$). *** $p < .001$, ** $p < .01$, * $p < .05$

Interaction	Lianas	Canopy trees	Midstory trees	Understory trees	Shrubs
CO ₂ *growth form	264.66 (72.29)**	399.12 (75.30)***	363.37 (30.42)***	108.90 (57.09)	35.65 (12.08)
MEI*growth form	20.66 (39.93)	75.17 (41.59)	66.72 (16.80)**	52.64 (31.53)	6.09 (6.67)

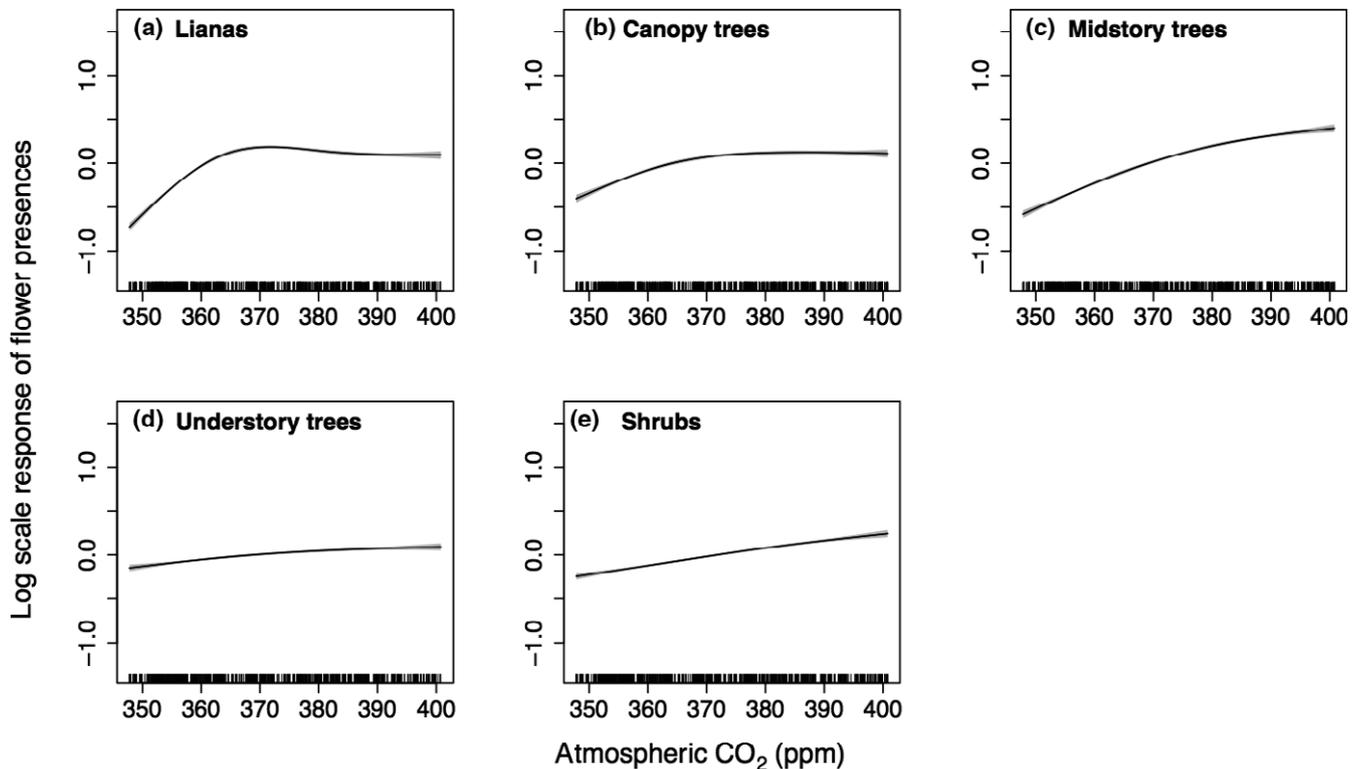


FIGURE 4 Log-scale response of monthly flower presences to atmospheric CO₂ using a cubic regression spline estimated in the GAM. Log-scale responses shown are centered at their mean and accounting for monthly seasonality in flowering and holding all other climatic factors (temperature, rainfall, light, and MEI) at their mean. Gray shading indicates two standard errors. All smooth terms were significant ($p < .001$)

(Figure 2), as does the response to CO₂ in the nonlinear model (Figure 4). Shrubs steadily increase flowering throughout the record, and the nonlinear model showed the proportional flowering response to CO₂ accelerates in recent years (Figures 3 and 4). Understory trees consistently showed no long-term increase in flowering and no effect of CO₂ in both linear and nonlinear models. There was evidence for nonlinear responses to all other climatic predictors as well. All nonlinear smooth terms were significant ($p < .01$) except for the response of shrubs to light (Figures S3–S6).

4 | DISCUSSION

Here, we use one of the longest records of tropical phenology to show that rising atmospheric CO₂ concentrations are associated with a three-decade 3% per year increase in flowering activity on

Barro Colorado Island, Panama. Other climatic variables have significant but weaker effects on flowering activity. We also show that including growth form, which should represent different resource acquisition and allocation strategies, improves fitted models. Linear models at the annual scale showed that on average, the strongest relationships between increasing CO₂ and flowering were for lianas, canopy, and midstory trees, although there was evidence that these responses slowed after global atmospheric CO₂ reached c. 370 ppm (around the year 2000). After this period, flowering flattened for lianas and canopy trees, as did their responses to CO₂, whereas flowering by midstory trees continued to increase, as did their response to CO₂. The saturation point of photosynthesis is c. 1000 ppm (reviewed in Körner, 2006; Cernusak et al., 2013; Franks et al., 2013), well above the threshold observed in here for flowering activity of canopy growth forms. Some have hypothesized that the growth of light-limited understory plants may be more

stimulated by CO₂ compared to canopy trees because the efficiency of photosynthesis per unit light absorbed is dependent on CO₂ (Ehleringer & Björkman, 1977; Körner, 2006; Lloyd & Farquhar, 2008). In this record, flowering of understory treelets did not respond as strongly to increases in CO₂ in both linear and nonlinear models, perhaps because understory trees have less extensive root systems resulting in limited water and/or nutrient availability (Opler et al., 1980; Becker & Castillo, 1990; Wright, 1991). However, shrubs showed a steady increase of flowering in response to CO₂ in both linear and nonlinear models. Increased reproductive activity by shrub species may indicate how rising CO₂ will affect future shifts in species composition if communities are recruitment limited (Hubbell et al., 1999; Muller-Landau, Wright, Calderón, Hubbell, & Foster, 2002).

We also show that when MEI is included as a predictor variable, the effect of temperature suggested in a previous analysis (Pau et al., 2013) is no longer apparent. CO₂ and MEI were not included in the previous analysis. When we compared the full suite of hypothesized climatic drivers of flowering to the shorter record of the previous study (1987–2009), we found that temperature was included in equivalent best-fit models whereas the MEI was not (Table 1). These results highlight the importance of long-term ecological records in revealing underlying relationships (Clark et al., 2013; Cohen, 1992). During El Niño years, BCI experiences especially dry, sunny, and warm conditions, and some degree of correlation between rainfall, light, and temperature is inevitable. Drier conditions are accompanied by fewer clouds and increased solar radiation reaching the forest, which increases both light and temperature. Wright and Calderón (2006) analyzed species level flower production and showed that interannual variation in cloud cover and light availability were strongly coupled to El Niño dynamics, with greater reproductive output during El Niño years. Later work examining long-term trends revealed that there are no long-term changes in cloud cover and solar irradiance (Pau et al., 2013). Interannual changes in temperature are captured in the MEI through reduced cloud cover and increased radiative warming during El Niño years. Here, accounting for the steady increase in CO₂ shows that interannual peaks in flowering activity, that is, residual variance around a monotonic increase, appear to coincide with El Niño events (Figure 3). Comparisons of models with and without each of the climatic factors associated with El Niño (rainfall, temperature, and light) suggested that light was the most important variable to include for predicting flower presences because the sum of AIC weights for all models in which a variable appeared was highest for light; however, light and rainfall had similar effect sizes.

Flower production (i.e., number of flowers) is known to increase in response to experimental manipulations of CO₂. A meta-analysis of 110 studies calculated an average 19% increase in flower production in both crop and wild species exposed to CO₂ enrichment compared to ambient conditions (Jablonski, Wang, & Curtis, 2002). In addition to changes in allocation, species could be reaching reproductive age earlier, resulting in greater reproductive output. Rising atmospheric CO₂ concentrations are known to cause reproduction at

younger ages and higher levels of reproduction (LaDeau & Clark, 2001, 2006). A free-air CO₂ enrichment (FACE) experiment in a loblolly pine plantation demonstrated that CO₂-fertilized trees reached reproductive age sooner and produced more seeds than trees in ambient CO₂ conditions (LaDeau & Clark, 2001, 2006).

As flowering activity increases at BCI for some species, woody growth rates may be slowing (Dong et al., 2012; Feeley et al., 2007). However, these studies of woody growth rates did not examine data after 2005 and only included four- to five-year census intervals (1985–2005). Another study showed that aboveground woody biomass varied little at BCI between 1985 and 2005 with no consistent trend (Chave et al., 2008). Furthermore, slow-growing heavy-wooded species appear to be increasing in dominance relative to fast-growing lighter-wooded species (Chave et al., 2008; Feeley et al., 2011), which is inconsistent with the expectations of carbon fertilization (Laurance et al., 2004). Stable isotope analysis of tropical tree rings from three continents indicated that intrinsic water-use efficiency had increased in canopy and understory trees in response to rising atmospheric CO₂ (van der Sleen et al., 2015). Yet there were no concurrent increases in growth ring width, suggesting that changes in other climatic stressors masked the positive effects of CO₂ on woody growth or that assimilates from enhanced photosynthesis were allocated to reproduction or root biomass and not to wood production (van der Sleen et al., 2015). In Costa Rica, wood production, leaf, reproductive, and twig litterfall mass (Mg/ha/year) exhibited distinct responses to interannual and long-term climate change (Clark et al., 2013). Of these four components of net primary productivity (NPP), only reproductive litterfall exhibited a long-term increasing trend over a period of 12 years, and its increase was associated with increases in CO₂ (Clark et al., 2013).

Recovery from past disturbances such as human clearing of trees, and drought and fires associated with El Niño events may have set many forests on a successional trajectory, making it difficult to isolate the effects of current climate change (Chave et al., 2008; Muller-Landau, 2009; Wright, 2005). Piperno (1990) examined plant phytoliths (silica structures with taxa-specific morphologies) recovered from the soils of our study site and found no evidence of the distinctive phytoliths of corn and other agricultural crops and the continuous presence of phytoliths of many species of forest trees from surface soils to 70 cm depth. Given this paleobotanical evidence, we can discount the possibility that past human disturbance of the study site contributed to increasing flower activity between 1987 and 2014.

The BCI forest might, however, be recovering from a severe El Niño drought in 1983 (Feeley et al., 2011; Swenson et al. 2012). Although a shift toward drought-tolerant species was previously suggested, including the increasing abundance of large-statured trees (Feeley et al., 2011), more recent work documents only a weak shift in community composition since 1982 driven by changing abundances of a handful of species (Katabuchi et al., 2017). There was no consistent trend for species with functional traits associated with drought tolerance to show increases in abundance (Katabuchi et al., 2017).

There is little information on long-term changes in the timing of tropical plant phenology (Chambers et al., 2013). Here, we show that at BCI, long-term increases in flower presences were driven in part by extended flowering durations for most growth forms. While the growing season in the humid tropics is already 365 days long and cannot lengthen as it has at higher latitudes (Cook et al., 2012; Menzel et al., 2006), the extended flowering duration observed for most growth forms suggests that the window of favorable conditions has widened for the average species. Extended flowering duration could increase temporal overlap in flowering by different species, with consequences for competition for pollinators and other biotic and abiotic resources. Understory trees have been increasing their flowering duration, but flower presences for this group have not been increasing. This indicates that flowering synchrony has declined for understory trees. In contrast, lianas and shrubs have increased flower presences but not flower duration, suggesting either a more concentrated peak in flowering or elevated flowering throughout the entire flowering period.

Tropical forests face an uncertain future. A large portion of the tropics experiences strong teleconnections with ENSO (Ropelewski & Halpert, 1987). Predictions of more frequent and extreme El Niño events in response to warming are supported by recent climate models (Cai et al., 2014; Collins et al., 2010; Power, Delage, Chung, Kocub, & Keay, 2013; Santoso et al., 2013). Cai et al. (2014) find strong multimodel consensus for a doubling of extreme El Niño events over the next two centuries with future greenhouse gas scenarios. There is, however, ambiguity in predicting the numerous amplifying and dampening feedbacks associated with ENSO and its teleconnections (Collins et al., 2010). Alternatively, the “rich get richer” (i.e., “wet get wetter”) hypothesis may lead to rainier conditions in equatorial areas subject to the intertropical convergence zone (ITCZ) (Chou, Neelin, Chen, & Tu, 2009; Durack, Wijffels, & Matear, 2012). Because the pronounced seasonality at BCI is associated with the movement of the ITCZ, this may result in a cloudier wet season and a reduction in productivity due to light limitation. Interannual variation in light and rainfall will interact with the strong positive increase of CO₂. Given sufficient nutrient availability, rising CO₂ might intensify the positive effects of sunny and dry El Niño conditions on flowering activity or offset the negative effects of cloudier and wetter conditions on flowering.

Observed changes in mean annual temperature did not have a large impact on flowering activity; however, continued warming is predicted under all greenhouse gas emission scenarios (IPCC 2014). Tropical regions may experience temperatures outside of their historical range sooner than other regions (Mora et al., 2015). Some tropical forests may already be near a high temperature threshold (Clark, Piper, Keeling, & Clark, 2003; Doughty & Goulden, 2008). There is thus far no evidence that leaf respiration and flowering activity have approached a high temperature threshold on BCI and elsewhere in central Panama (Pau et al., 2013; Slot et al., 2014). The impact of anthropogenic global change on tropical forest growth and reproduction is a critical uncertainty. Experimental work

disentangling resource availability and limitation of multiple factors, as well as allocation to reproduction, should complement observational evidence from diverse natural communities. Long-term records in tropical forests are rare, yet establishing these records across different sites and species should be a priority.

ACKNOWLEDGEMENTS

The Environmental Sciences Program of the Smithsonian Institution supported all data collection. We thank Raul Rios, Brian Harvey, and Steve Paton for maintaining the BCI climate monitoring program. We thank Deborah A. Clark and three anonymous reviewers for helpful comments on a previous draft of the manuscript.

ORCID

Stephanie Pau  <http://orcid.org/0000-0001-8135-9266>

REFERENCES

- Asner, G. P., & Alencar, A. (2010). Drought impacts on the Amazon forest: The remote sensing perspective. *New Phytologist*, *187*, 569–578. <https://doi.org/10.1111/j.1469-8137.2010.03310.x>
- Becker, P., & Castillo, A. (1990). Root Architecture of shrubs and saplings in the understory of a tropical moist forest in lowland Panama. *Biotropica*, *22*, 242–249. <https://doi.org/10.2307/2388534>
- Bennett, A. C., McDowell, N. G., Allen, C. D., & Anderson-Teixeira, K. J. (2015). Larger trees suffer most during drought in forests worldwide. *Nature Plants*, *1*, 15139. <https://doi.org/10.1038/nplants.2015.139>
- Bonan, G. B. (2008). Forests and climate change: Forcings, feedbacks, and the climate benefits of forests. *Science*, *320*, 1444–1449. <https://doi.org/10.1126/science.1155121>
- Burnham, K. P., & Anderson, D. R. (2010). *Model selection and multimodel inference: A practical information-theoretic approach*, 2nd edn. New York, NY: Springer.
- Cai, W., Borlace, S., Lengaigne, M., Van Rensch, P., Collins, M., Vecchi, G., ... England, M. H. (2014). Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change*, *4*, 111–116. <https://doi.org/10.1038/nclimate2100>
- CaraDonna, P. J., Iler, A. M., & Inouye, D. W. (2014). Shifts in flowering phenology reshape a subalpine plant community. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 4916–4921. <https://doi.org/10.1073/pnas.1323073111>
- Cernusak, L. A., Winter, K., Dalling, J. W., Holtum, J. A., Jaramillo, C., Körner, C., ... Wright, S. J. (2013). Tropical forest responses to increasing [CO₂]: Current knowledge and opportunities for future research. *Functional Plant Biology*, *40*, 531–551. <https://doi.org/10.1071/FP12309>
- Chambers, L. E., Altwegg, R., Barbraud, C., Barnard, P., Beaumont, L. J., Crawford, R. J. M., ... Wolfaardt, A. C. (2013). Phenological Changes in the Southern Hemisphere. *PLoS One*, *8*. <http://doi.org/10.1371/journal.pone.0075514>
- Chapman, C. A., Chapman, L. J., Struhsaker, T. T., Zanne, A. E., Clark, C. J., & Poulsen, J. R. (2005). A long-term evaluation of fruiting phenology: Importance of climate change. *Journal of Tropical Ecology*, *21*, 31–45. <https://doi.org/10.1017/S0266467404001993>
- Chave, J., Condit, R., Muller-Landau, H. C., Thomas, S. C., Ashton, P. S., Bunyavejchewin, S., ... Feeley, K. J. (2008). Assessing evidence for a pervasive alteration in tropical tree communities. *PLoS Biology*, *6*, e45. <https://doi.org/10.1371/journal.pbio.0060045>

- Chou, C., Neelin, J. D., Chen, C.-A., & Tu, J.-Y. (2009). Evaluating the "rich-get-richer" mechanism in tropical precipitation change under global warming. *Journal of Climate*, 22, 1982–2005. <https://doi.org/10.1175/2008JCLI2471.1>
- Clark, D. A. (2007). Detecting tropical forests' responses to global climatic and atmospheric change: Current challenges and a way forward. *Biotropica*, 39, 4–19. <https://doi.org/10.1111/j.1744-7429.2006.00227.x>
- Clark, D. A., Clark, D. B., & Oberbauer, S. F. (2013). Field-quantified responses of tropical rainforest aboveground productivity to increasing CO₂ and climatic stress, 1997–2009. *Journal of Geophysical Research: Biogeosciences*, 118, 783–794.
- Clark, D. A., Piper, S. C., Keeling, C. D., & Clark, D. B. (2003). Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 5852–5857. <https://doi.org/10.1073/pnas.0935903100>
- Cohen, J. (1992). A power primer. *Psychological Bulletin*, 112, 155–159. <https://doi.org/10.1037/0033-2909.112.1.155>
- Collins, M., An, S.-I., Cai, W., Ganachaud, A., Guilyardi, E., Jin, F. F., ... Vecchi, G. (2010). The impact of global warming on the tropical Pacific Ocean and El Niño. *Nature Geoscience*, 3, 391–397. <https://doi.org/10.1038/ngeo868>
- Cook, B. I., Wolkovich, E. M., Davies, T. J., Ault, T. R., Betancourt, J. L., Allen, J. M., ... Lancaster, L. T. (2012). Sensitivity of spring phenology to warming across temporal and spatial climate gradients in two independent databases. *Ecosystems*, 15, 1283–1294. <https://doi.org/10.1007/s10021-012-9584-5>
- Croat, T. B. (1978). *Flora of Barro Colorado Island*. Stanford, CA: Stanford University Press.
- Dirzo, R., & Raven, P. H. (2003). Global state of biodiversity and loss. *Annual Review of Environment and Resources*, 28, 137–167. <https://doi.org/10.1146/annurev.energy.28.050302.105532>
- Dong, S. X., Davies, S. J., Ashton, P. S., Bunyavejchewin, S., Supardi, M. N., Kassim, A. R., ... Moorcroft, P. R. (2012). Variability in solar radiation and temperature explains observed patterns and trends in tree growth rates across four tropical forests. *Proceedings of the Royal Society Biological Sciences*, 279, 3923–3931. <https://doi.org/10.1098/rspb.2012.1124>
- Doughty, C. E., & Goulden, M. L. (2008). Are tropical forests near a high temperature threshold? *Journal of Geophysical Research*, 113, 1–12.
- Durack, P. J., Wijffels, S. E., & Matear, R. J. (2012). Ocean salinities reveal strong global water cycle intensification during 1950 to 2000. *Science*, 336, 455–458. <https://doi.org/10.1126/science.1212222>
- Ehleringer, J., & Björkman, O. (1977). Quantum yields for CO₂ uptake in C₃ and C₄ plants dependence on temperature, CO₂, and O₂ concentration. *Plant Physiology*, 59, 86–90. <https://doi.org/10.1104/pp.59.1.86>
- Feeley, K. J., Davies, S. J., Perez, R., Hubbell, S. P., & Foster, R. B. (2011). Directional changes in the species composition of a tropical forest. *Ecology*, 92, 871–882. <https://doi.org/10.1890/10-0724.1>
- Feeley, K. J., Joseph Wright, S., Nur Supardi, M. N., Kassim, A. R., & Davies, S. J. (2007). Decelerating growth in tropical forest trees. *Ecology Letters*, 10, 461–469. <https://doi.org/10.1111/j.1461-0248.2007.01033.x>
- Franks, P. J., Adams, M., Amthor, J. S., Barbour, M., Berry, J. A., Ellsworth, D., ... von Caemmerer, S. (2013). Sensitivity of plants to changing atmospheric CO₂ concentration: From the geological past to the next century. *New Phytologist*, 197, 1077–1094. <https://doi.org/10.1111/nph.12104>
- Gentry, A. H. (1991). The distribution and evolution of climbing plants. In F. E. Putz, & H. A. Mooney (Eds.), *The biology of vines* (pp. 3–49). Cambridge, UK: Cambridge University Press.
- Graham, E. A., Mulkey, S. S., Kitajima, K., Phillips, N. G., & Wright, S. J. (2003). Cloud cover limits net CO₂ uptake and growth of a rainforest tree during tropical rainy seasons. *Proceedings of the National Academy of Sciences of the United States of America*, 100, 572–576. <https://doi.org/10.1073/pnas.0133045100>
- Granados, J., & Körner, C. (2002). In deep shade, elevated CO₂ increases the vigor of tropical climbing plants. *Global Change Biology*, 8, 1109–1117. <https://doi.org/10.1046/j.1365-2486.2002.00533.x>
- Hietz, P., Turner, B. L., Wanek, W., Richter, A., Nock, C. A., & Wright, S. J. (2011). Long-term change in the nitrogen cycle of tropical forests. *Science*, 334, 664–666. <https://doi.org/10.1126/science.1211979>
- Holtum, J. A. M., & Winter, K. (2010). Elevated [CO₂] and forest vegetation: More a water issue than a carbon issue? *Functional Plant Biology*, 37, 694–702. <https://doi.org/10.1071/FP10001>
- Hubbell, S. P., Foster, R. B., O'Brien, S. T., Harms, K. E., Condit, R., Wechsler, B., ... De Lao, S. L. (1999). Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, 283, 554–557. <https://doi.org/10.1126/science.283.5401.554>
- Hutyra, L. R., Munger, J. W., Saleska, S. R., Gottlieb, E., Daube, B. C., Dunn, A. L., ... Wofsy, S. C. (2007). Seasonal controls on the exchange of carbon and water in an Amazonian rain forest. *Journal of Geophysical Research: Biogeosciences*, 112, 1–16.
- IPCC (2014). Summary for policymakers. In C. B. Field, V. R. Barros, D. J. Dokken, K. J. Mach, M. D. Mastrandrea, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea & L. L. White (Eds.), *Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of working group II to the fifth assessment report of the intergovernmental panel on climate change* (pp. 1–32). Cambridge, UK and New York, NY, USA: Cambridge University Press.
- Jablonski, L. M., Wang, X., & Curtis, P. S. (2002). Plant reproduction under elevated CO₂ conditions: A meta-analysis of reports on 79 crop and wild species. *New Phytologist*, 156, 9–26. <https://doi.org/10.1046/j.1469-8137.2002.00494.x>
- Katabuchi, M., Wright, S. J., Swenson, N. G., Feeley, K. J., Condit, R., Hubbell, S. P., & Davies, S. J. (2017). Contrasting outcomes of species- and community-level analyses of the temporal consistency of functional composition. *Ecology*, 98, 2273–2280. <https://doi.org/10.1002/ecy.1952>
- Körner, C. (2003). Ecological impacts of atmospheric CO₂ enrichment on terrestrial ecosystems. *Philosophical Transactions of the Royal Society London A*, 361, 2023–2041. <https://doi.org/10.1098/rsta.2003.1241>
- Körner, C. (2006). Plant CO₂ responses: An issue of definition, time, and resource supply. *New Phytologist*, 172, 393–411. <https://doi.org/10.1111/j.1469-8137.2006.01886.x>
- LaDeau, S., & Clark, J. S. (2001). Rising CO₂ levels and the fecundity of forest trees. *Science*, 292, 95–98. <https://doi.org/10.1126/science.1057547>
- LaDeau, S. L., & Clark, J. S. (2006). Elevated CO₂ and tree fecundity: The role of tree size, interannual variability, and population heterogeneity. *Global Change Biology*, 12, 822–833. <https://doi.org/10.1111/j.1365-2486.2006.01137.x>
- Lambin, E. F., Turner, B. L., Geist, H. J., Agbola, S. B., Angelsen, A., Bruce, J. W., ... George, P. (2001). The causes of land-use and land-cover change: Moving beyond the myths. *Global Environmental Change*, 11, 261–269. [https://doi.org/10.1016/S0959-3780\(01\)00007-3](https://doi.org/10.1016/S0959-3780(01)00007-3)
- Laurance, W. F., Oliveira, A. A., Laurance, S. G., Condit, R., Nascimento, H. E., Sanchez-Thorin, A. C., ... Dick, C. W. (2004). Pervasive alteration of tree communities in undisturbed Amazonian forests. *Nature*, 428, 171–175. <https://doi.org/10.1038/nature02383>
- Lewis, S. L., Lloyd, J., Sitch, S., Mitchard, E. T. A., & Laurance, W. F. (2009). Changing ecology of tropical forests: Evidence and drivers. *Annual Review of Ecology, Evolution and Systematics*, 40, 529–549. <https://doi.org/10.1146/annurev.ecolsys.39.110707.173345>

- Lloyd, J., & Farquhar, G. D. (2008). Effects of rising temperatures and [CO₂] on the physiology of tropical forest trees. *Philosophical Transactions of the Royal Society B*, 363, 1811–1817. <https://doi.org/10.1098/rstb.2007.0032>
- Lukacs, P. M., Burnham, K. P., & Anderson, D. R. (2010). Model selection bias and Freedman's paradox. *Annals of the Institute of Statistical Mathematics*, 62, 117–125. <https://doi.org/10.1007/s10463-009-0234-4>
- Malhi, Y., & Wright, J. (2004). Spatial patterns and recent trends in the climate of tropical rainforest regions. *Philosophical Transactions of the Royal Society Biological Sciences*, 359, 311–329. <https://doi.org/10.1098/rstb.2003.1433>
- Matson, P. A., Mcdowell, W. H., Townsend, A. R., & Vitousek, P. M. (1999). The globalization of N deposition: Ecosystem consequences in tropical environments. *Biogeochemistry*, 46, 67–83.
- Meinzer, F. C., Luis, J., Goldstein, G., Holbrook, N. M., Cavelier, J., & Wright, S. J. (1999). Partitioning of soil water among canopy trees in a seasonally dry tropical forest. *Atomic Energy*, 121, 293–301.
- Menzel, A., & Fabian, P. (1999). Growing season extended in Europe. *Nature*, 397, 659. <https://doi.org/10.1038/17709>
- Menzel, A., Sparks, T. H., Estrella Koch, N., Aasa A, Ahas. A. R.,... Chmielewski, F. M. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology*, 12, 1969–1976. <https://doi.org/10.1111/j.1365-2486.2006.01193.x>
- Mora, C., Caldwell, I. R., Caldwell, J. M., Fisher, M. R., Genco, B. M., & Running, S. W. (2015). Suitable days for plant growth disappear under projected climate change: Potential human and biotic vulnerability. *PLOS Biology*, 13, e1002167. <https://doi.org/10.1371/journal.pbio.1002167>
- Morelato, L. P. C., & Leitao-Filho, H. F. (1996). Reproductive phenology of climbers in a southeastern Brazilian forest. *Biotropica*, 28, 180–191. <https://doi.org/10.2307/2389073>
- Morelato, L. P. C., Talora, D. C., Takahasi, A., Bencke, C. C., Romera, E. C., & Zipparro, V. B. (2000). Phenology of Atlantic rain forest trees: A comparative study. *Biotropica*, 32, 811–823. <https://doi.org/10.1111/j.1744-7429.2000.tb00620.x>
- Muller-Landau, H. C. (2009). Sink in the African jungle. *Nature*, 457, 969–970. <https://doi.org/10.1038/457969a>
- Muller-Landau, H. C., Wright, S. J., Calderón, O., Hubbell, S. P., & Foster, R. B. (2002). Assessing recruitment limitation: Concepts, methods, and case studies from a tropical forest. In D. J. Levey, W. R. Silva & M. Galetti (Eds.), *Seed dispersal and frugivory: Ecology, evolution and conservation* (pp. 35–53). Oxfordshire, UK: CAB International.
- Nemani, R. R., Keeling, C. D., Hashimoto, H., Jolly, W. M., Piper, S. C., Tucker, C. J.,... Running, S. W. (2003). Climate-driven increases in global terrestrial net primary production from 1982 to 1999. *Science*, 300, 1560–1563. <https://doi.org/10.1126/science.1082750>
- Nepstad, D. C., de Carvalho, C. R., Davidson, E. A., Jipp, P. H., Lefebvre, P. A., Negreiros, G. H.,... Vieira, S. (1994). The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature*, 372, 666–669. <https://doi.org/10.1038/372666a0>
- Newstrom, L. E., Frankie, G. W., Baker, H. G., & Newstrom, L. E. (1994). A New Classification for Plant Phenology Based on Flowering Patterns in Lowland Tropical Rain Forest Trees at La Selva, Costa Rica. *Biotropica*, 26, 141–159.
- Opler, P. A., Frankie, G. W., & Baker, H. G. (1980). Comparative phenological studies of treelet and shrub species in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology*, 68, 167–188. <https://doi.org/10.2307/2259250>
- Pau, S., Wolkovich, E. M., Cook, B. I., Nytch, C. J., Regetz, J., Zimmerman, J. K., & Wright, S. J. (2013). Clouds and temperature drive dynamic changes in tropical flower production. *Nature Climate Change*, 3, 838–842. <https://doi.org/10.1038/nclimate1934>
- Peñuelas, J., Sardans, J., Estiarte, M., Ogaya, R., Carnicer, J., Coll, M.,... Filella, I. (2013). Evidence of current impact of climate change on life: A walk from genes to the biosphere. *Global Change Biology*, 19, 2303–2338. <https://doi.org/10.1111/gcb.12143>
- Phillips, O. L., Aragão, L. E. O. C., Lewis, S. L., Fisher, J. B., Lloyd, J., López-González, G.,... Der Van Heijden, G. (2009). Drought sensitivity of the Amazon rainforest. *Science*, 323, 1344–1347. <https://doi.org/10.1126/science.1164033>
- Pinheiro, J. C., & Bates, D. M. (2000). *Linear mixed-effects models: Basic concepts and examples in mixed-effects models in S and S-Plus*. New York, NY: Springer.
- Pinheiro, J. C., Bates, D. M., DebRoy, S., Sarkar, D., & R Core Team (2017). *nlme: Linear and Nonlinear Mixed Effects Models*. R package version 3.1-131. Retrieved from <https://CRAN.R-project.org/package=nlme>
- Polansky, L., & Boesch, C. (2013). Long-term changes in fruit phenology in a West African lowland tropical rain forest are not explained by rainfall. *Biotropica*, 45, 434–440. <https://doi.org/10.1111/btp.12033>
- Piperno, D. (1990). Fitolitos, arqueología y cambios prehistóricos de la vegetación en un lote de cincuenta hectáreas de la isla de Barro Colorado. In E. G. Leigh Jr, A. S. Rand, & D. M. Windsor (Eds.), *Ecología de un Bosque Tropical* (pp. 153–156). Washington, DC: Smithsonian Institution Press.
- Power, S., Delage, F., Chung, C., Kociuba, G., & Keay, K. (2013). Robust twenty-first century projections of El Niño and related precipitation variability. *Nature*, 502, 541–545. <https://doi.org/10.1038/nature12580>
- Ropelewski, C. F., & Halpert, M. S. (1987). Global and regional scale precipitation patterns associated with the El Niño/Southern Oscillation. *Monthly Weather Review*, 115, 1606–1626. [https://doi.org/10.1175/1520-0493\(1987\)115<1606:GARSPP>2.0.CO;2](https://doi.org/10.1175/1520-0493(1987)115<1606:GARSPP>2.0.CO;2)
- Saatchi, S. S., Harris, N. L., Brown, S., Lefsky, M., Mitchard, E. T., Salas, W.,... Petrova, S. (2011). Benchmark map of forest carbon stocks in tropical regions across three continents. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 9899–9904. <https://doi.org/10.1073/pnas.1019576108>
- Santiago, L. S., & Wright, S. J. (2007). Leaf functional traits of tropical forest plants in relation to growth form. *Functional Ecology*, 21, 19–27.
- Santoso, A., McGregor, S., Jin, F.-F., Cai, W., England, M. H., An, S. I.,... Guilyardi, E. (2013). Late-twentieth-century emergence of the El Niño propagation asymmetry and future projections. *Nature*, 504, 126–130. <https://doi.org/10.1038/nature12683>
- Sarmiento, G., & Monasterio, M. (1983). Life forms and phenology. In F. Bourliere (Ed.), *Ecosystems of the world XIII. Tropical savannas* (pp. 79–108). Amsterdam, Netherlands: Elsevier.
- Saugier, B., Roy, J., & Mooney, H. A. (2001). Estimations of global terrestrial productivity: Converging on a single number? In J. Roy, B. Saugier & H. A. Mooney (Eds.), *Terrestrial global productivity* (pp. 543–557). San Diego, CA: Academic Press. <https://doi.org/10.1016/B978-012505290-0/50024-7>
- van Schaik, C. P., Terborgh, J. W., Wright, S. J., & van Schaik, C. P. (1993). The phenology of tropical forests: Adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics*, 24, 353–377. <https://doi.org/10.1146/annurev.es.24.110193.002033>
- Schnitzer, S. A., & Bongers, F. (2011). Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. *Ecology Letters*, 14, 397–406. <https://doi.org/10.1111/j.1461-0248.2011.01590.x>
- Settele, J., Scholes, R., Betts, R., Bunn, S. E., Leadley, D., Nepstad, J. T., & Taboada, M. A. (2014). *Climate change 2014: Impacts, Adaptations, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel and Climate Change*. 271–359 pp.
- van der Sleen, P., Groenendijk, P., Vlam, M., Anten, N. P. R., Boom, A., Bongers, F.,... Zuidema, P. A. (2015). No growth stimulation of tropical trees by 150 years of CO₂ fertilization but water-use efficiency increased. *Nature Geosciences*, 8, 24–28. <http://doi.org/10.1038/ngeo2313>
- Slot, M., Rey-Sánchez, C., Gerber, S., Lichstein, J. W., Winter, K., & Kitajima, K. (2014). Thermal acclimation of leaf respiration of tropical

- trees and lianas: Response to experimental canopy warming, and consequences for tropical forest carbon balance. *Global Change Biology*, 20, 2915–2926. <https://doi.org/10.1111/gcb.12563>
- Swenson, N. G., Stegen, J. C., Davies, S. J., Erickson, D. L., Forero-Montaña, J., Hurlbert, A. H., . . . Zimmerman, J. K. (2012). Temporal turnover in the composition of tropical tree communities: Functional determinism and phylogenetic stochasticity. *Ecology*, 93, 490–499. <http://doi.org/10.1890/11-1180.1>
- Tissue, D. T., & Wright, S. J. (1995). Effect of seasonal water availability on phenology and the annual shoot carbohydrate cycle of tropical forest shrubs. *Functional Ecology*, 9, 518–527. <https://doi.org/10.2307/2390018>
- Venables, W. N., & Ripley, B. D. (1999). *Modern applied statistics with S*, 4th edn. New York, NY: Springer. <https://doi.org/10.1007/978-1-4757-3121-7>
- Wolter, K., & Timlin, M. S. (2011). El Niño/Southern Oscillation behaviour since 1871 as diagnosed in an extended multivariate ENSO index (MEI.ext). *International Journal of Climatology*, 31, 1074–1087. <https://doi.org/10.1002/joc.2336>
- Wright, S. J. (1991). Seasonal drought and the phenology of understory shrubs in a tropical moist forest. *Ecology*, 72, 1643–1657. <https://doi.org/10.2307/1940964>
- Wright, S. J. (2005). Tropical forests in a changing environment. *Trends in Ecology and Evolution*, 20, 553–560. <https://doi.org/10.1016/j.tree.2005.07.009>
- Wright, S. J. (2010). The future of tropical forests. *Annals of the New York Academy of Sciences*, 1195, 1–27. <https://doi.org/10.1111/j.1749-6632.2010.05455.x>
- Wright, S. J., & Calderón, O. (2006). Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecology Letters*, 9, 35–44.
- Wright, S. J., & Cornejo, F. H. (1990). Seasonal drought and leaf fall in a tropical forest. *Ecology*, 71, 1165–1175. <https://doi.org/10.2307/1937384>
- Wright, S. J., Sun, I. F., Pickering, M., Fletcher, C. D., & Chen, Y. Y. (2015). Long-term changes in liana loads and tree dynamics in a Malaysian forest. *Ecology*, 96, 2748–2757. <https://doi.org/10.1890/14-1985.1>
- Wright, S. J., & Van Schaik, C. P. (1994). Light and the phenology of tropical trees. *The American Naturalist*, 143, 192–199. <https://doi.org/10.1086/285600>
- Zimmerman, J. K., Wright, S. J., Calderón, O., Pagan, M. A., & Paton, S. (2007). Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: The role of annual changes in irradiance. *Journal of Tropical Ecology*, 23, 231. <https://doi.org/10.1017/S0266467406003890>
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer. <https://doi.org/10.1007/978-0-387-87458-6>

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Pau S, Okamoto DK, Calderón O, Wright SJ. Long-term increases in tropical flowering activity across growth forms in response to rising CO₂ and climate change. *Glob Change Biol*. 2017;00:1–12. <https://doi.org/10.1111/gcb.14004>