

# Effects of hurricanes and climate oscillations on annual variation in reproduction in wet forest, Puerto Rico

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**Abstract.** Interannual changes in global climate and weather disturbances may influence reproduction in tropical forests. Phenomena such as the El Niño Southern Oscillation (ENSO) are known to produce interannual variation in reproduction, as do severe storms such as hurricanes. Using stationary trap-based phenology data collected fortnightly from 1993 to 2014 from a hurricane-affected (1989 Hugo, 1998 Georges) subtropical wet forest in northeastern Puerto Rico, we conducted a time series analysis of flowering and seed production. We addressed (1) the degree to which interannual variation in flower and seed production was influenced by global climate drivers and time since hurricane disturbance, and (2) how long-term trends in reproduction varied with plant lifeform. The seasonally de-trended number of species in flower fluctuated over time while the number of species producing seed exhibited a declining trend, one that was particularly evident during the second half of the study period. Lagged El Niño indices and time series hurricane disturbance jointly influenced the trends in numbers of flowering and fruiting species, suggesting complex global influences on tropical forest reproduction with variable periodicities. Lag times affecting flowering tended to be longer than those affecting fruiting. Long-term patterns of reproduction in individual lifeforms paralleled the community-wide patterns, with most groups of lifeform exhibiting a long-term decline in seed but not flower production. Exceptions were found for hemiepiphytes, small trees, and lianas whose seed reproduction increased and then declined over time. There was no long-term increase in flower production as reported in other Neotropical sites.

**Key words:** *El Niño Southern Oscillation; Luquillo Experimental Forest; North Atlantic Oscillation; phenology; Puerto Rico; time series analysis.*

## INTRODUCTION

The degree to which tropical forests are susceptible to changing temperature, precipitation, or other factors is an unresolved issue in ecology (Clark 2004, Wright 2005a, Feeley et al. 2007). Lacking an evolutionary history of temperature seasonality, tropical organisms might be strongly affected by rising temperatures (Janzen 1967, Wood et al. 2012, Mora et al. 2013, Perez et al. 2016). The production of flowers and fruits is highly susceptible to changes in both weather and climate (Van Schaik et al. 1993, Wright et al. 1999, Stenseth et al. 2002, Augspurger 2013, Coomes et al. 2014, Chang-Yang et al. 2015). Reproduction is resource intensive and pollen and seed dispersal could be negatively influenced by unusual weather-related disturbance events (e.g., Augspurger 2013, Chang-Yang et al. 2015). This is especially true of cyclonic storms, which severely damage forests and alter successional dynamics to leave legacies on forest structure and composition (Lugo 2008, Brokaw et al. 2012a). For example, Scatena et al. (2012) showed that reproduction in Puerto Rican wet forest ceased for six months after Hurricane Hugo and continued below normal for an additional 2.5 yr. Flower production is usually distinctly seasonal in tropical forests, even where the climate might be regarded as aseasonal (Zimmerman et al. 2007, Chang-Yang et al. 2013). In general, patterns of seasonal

irradiation (i.e., light availability) are proposed to drive reproduction in those forests where moisture availability is relatively high through much of the year (Van Schaik et al. 1993). Seasonal rains (i.e., soil moisture availability) have more control over annual patterns of reproduction in tropical dry forests (Van Schaik et al. 1993). Other factors, such as fluctuation in the climate cycles of the Pacific Ocean (e.g., El Niño Southern Oscillation; ENSO) and the Atlantic (e.g., North Atlantic Oscillation; NAO), are also known to influence reproduction patterns in tropical plant species (Stenseth et al. 2002, Wright 2005b). This has been well studied in central Panama where ENSO events provide periods of high irradiation (low cloud cover) during which many understory trees flower and fruit (Wright and van Schaik 1994, Wright 2005b). This is sometimes followed by a La Niña event that suppresses forest reproduction, leading to famine among many consumers (Wright et al. 1999). Similar cascading effects of mast events in dipterocarp forests of Southeast Asia have been linked to ENSO (Curran and Leighton 2000, Corlett and Primack 2011) and small changes in local climate (Chen et al. 2017).

Cyclonic storms are a key component of the disturbance regime in Caribbean forests (Lugo et al. 2000, Brokaw et al. 2012a). In recent decades, eastern Puerto Rico has experienced the damaging effects of two intense hurricanes, Hurricane Hugo in 1989 and Georges in 1998. Hurricanes Irma and Maria, strong Category 4 and 5 storms, followed in 2017. Hurricanes cause major changes in species composition (Uriarte et al. 2004, Heartsill Scalley et al. 2010, Uriarte et al. 2012, Hogan et al. 2016) as the abundance of

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shrubs and pioneers increase greatly following the damage to canopy trees, and then decline as the canopy closes and the understory becomes shaded (Hogan et al. 2016). Thus, lifeform would be expected to play a significant role in explaining the diverse reproductive responses of woody plants to hurricane disturbance.

The island of Puerto Rico is the eastern most of the Greater Antilles, where interannual temperature variation is strongly influenced by ENSO while rainfall variability is highly correlated with the NAO (Malmgren et al. 1998). It is located at the boundary of a transition in the seasonality of Caribbean climate; to the west and into the Caribbean basin there is a significant mid-summer dry season, while a summer drought is lacking to the east and south along the Lesser Antilles (Gamble et al. 2008). Climate change predictions into the next century suggest that with increasing global warming the temperatures in Puerto Rico will increase 4.6–9°C with potential decline in precipitation of 49.7% (averaged over regionally consistent models; Henereh et al. 2016). The number of days with 5 mm of rain is expected to decrease, causing an increase in seasonality in Caribbean montane wet forests (Waide et al. 2013). A recent parameterization of the Ecosystem Demography model (Feng et al. 2018) for Puerto Rican wet forest indicated that net ecosystem productivity of wet forest could reach 0 within 20 yr if decreased precipitation and increased temperatures occur as projected. Additionally, the frequency of intense hurricanes (categories 4 and 5 on the Saffir-Simpson scale) may increase with global warming (Knutson et al. 2010).

We analyzed monthly time series records from 1993 to 2014 of flower production for 73 species and seed rain for 76 species representing 7 different lifeforms in the Luquillo Forest Dynamics Plot (Thompson et al. 2002), located on the flanks of the Luquillo Mountains. We addressed two questions: (1) how are long-term (seasonally detrended) patterns of reproduction influenced by ENSO, NAO and hurricane disturbance? and (2) how do long-term trends in reproduction vary among lifeforms? The results provide insight into how current interannual variation in climate and storm occurrence influences long-term patterns of forest reproduction, and can inform how future anthropogenic-related changes to the biosphere may influence the status of tropical forests.

## METHODS

### *Study site*

This study was conducted near the El Verde Field Station (EVFS; 18°20' N, 65°49' W) in the northwest section of the Luquillo Experimental Forest in eastern Puerto Rico. The area supports tabonuco (*Dacryodes excelsa* Vahl.) forest in places that have not been disturbed by human activities (Thompson et al. 2002). The forest is classified as subtropical wet in the Holdridge life zone system (Ewel and Whitmore 1973). Annual rainfall averages just over 3,500 mm. Although precipitation varies seasonally, no month averages less than 200 mm, such that the climate is technically ‘aseasonal’ or ever-wet (Zimmerman et al. 2007). Major hurricanes pass directly over Puerto Rico, on average, every 60 to 80 yr (Scatena et al. 2012), although periods of shorter

return intervals can occur (Goldenberg et al. 2001) with important implications for forest structure and composition (Uriarte et al. 2009). Hurricane Hugo (September 1989) was the first major hurricane (Category 3 or higher on the Saffir-Simpson scale) in 58 yr to strike Puerto Rico and Hurricane Georges followed 9 yr later (Brokaw et al. 2012a). The storms had a strong effect on plant dynamics in the LFDP (e.g., Uriarte et al. 2004, 2012, Hogan et al. 2016), due to forest canopy damage (Brokaw and Grear 1991), and to a lesser degree stem damage to individual trees (Zimmerman et al. 1994). Following Hurricane Hugo, fruitfall in the Bissell Experimental Watersheds, 12 km to the east of El Verde, was reduced for three years compared to values prevalent before the storm (see Figure 5.6 in Brokaw et al. 2012b).

### *Data collection*

The Luquillo Forest Dynamics Plot (LFDP; 333 to 428 m a.s.l.), located ~1 km N of EVFS, is a 16-ha permanent forest dynamics plot established immediately following Hurricane Hugo in September 1989 (Thompson et al. 2002, Zimmerman et al. 2010). All self-supporting plant stems ≥1 cm diameter at 1.3 m height (dbh) are identified, mapped and measured at least once every 5 yr. Flowers, seeds, and fruits are collected from 120 stationary traps that traverse the LFDP. These traps, constructed from 1 mm mesh screening, were installed in the LFDP on March 1992, and all reproductive plant parts have been collected every two weeks since, except for a three-month period following Hurricane Georges when little reproduction was evident (Zimmerman et al. 2007). Flower presence/absence, and seed and fruit abundances are recorded by species in each trap per sampling date; fruits are converted to seed numbers using the number of seeds per fruit determined for each species.

Initially the traps were 0.16 square meters in area, but were replaced in 2006 with traps 0.5 square meters, as is the convention established by researchers at Barro Colorado Island, Panama (Wright and Calderón 2006). New traps were placed next to the old traps and both sets were followed for one year, from August 2006 to July 2007, resulting in 24 concurrent collection dates. Thereafter the smaller traps were removed and collection continued using only the larger traps. Seed abundances in large traps during the year of overlap were regressed against the small traps using all species in the community. The regression coefficient of 1.61 ( $\pm 0.15$  SE;  $R^2 = 0.59$ ;  $N = 76$  species) was applied retroactively as a correction factor for seed rain counts in the small traps. A similar analysis of traps with flowers yielded a correction factor of 1.26 ( $\pm 0.02$ ;  $R^2 = 0.97$ ;  $N = 73$  species). These values are more similar to the ratio of the linear dimensions of the two traps (1.77) than the ratio of the areas (3.125), suggesting a linear capture function – i.e., reproductive parts travel linearly in the horizontal dimension while falling and are intercepted by traps along these trajectories.

### *Data analyses*

Community-based analyses were limited to include only species that were present in six or more of either the small or large traps, ensuring that more than single individuals were

sampled (Zimmerman et al. 2007). The sample sizes for individual species are shown in Appendix S1: Table S1.

To quantify the forest-wide phenological response, we calculated the number of species found with flowers, fruits, or seeds present monthly, to match the time step of climate indices. We grouped bi-monthly observations into monthly intervals irrespective of sampling dates (i.e., by Gregorian month divisions) using the `to.monthly()` function on the phenological time series from the ‘`xts`’ package (Ryan and Ulrich 2011) in R v3.2.5 (R Core Team 2016). The influence of four monthly climate indices and four local meteorological variables on the trend in seed and flower production was evaluated using time series cross-correlations with a maximum lag of 18 months (Wright and Calderón 2006). Temperature and precipitation data were obtained from El Verde Field Station (<http://luq.lter.network/>, datasets 16, 17, and 33) and monthly averages were computed. Data on photosynthetic photon flux density (PPFD) were obtained from the Bisley Experimental Watershed (data set 90) 8 km to the east of the LFDP. Seasonality in the meteorological data was removed by subtracting from each monthly value the monthly average over the whole time series.

Prior to calculation of time series correlations, seasonality was removed from both flower and seed reproduction datasets using seasonal-trend decomposition of time series by loess (STL; Cleveland et al. 1990; Appendix S2). This procedure separates time series into a seasonal pattern and the interannual “trend” via the application of a doubly iterative “loess” (locally-weighted smoothing) regression. Once a seasonal pattern and interannual trend are identified, the procedure sets aside the “remainder” variation, or noise. We present analyses of the interannual trend without the remainder variation, although additional runs indicated that including the remainder with the interannual trend did not qualitatively change the results.

Cross-correlation analyses of the reproductive time series, monthly meteorological data, and monthly climate oscillations were conducted using the `ccf()` function in R v3.2.5 (R Core Team 2016). The `ccf` function analyzes the covariance structure of the two variables and makes an overall test of significance. We minimized the number of climate oscillations tested to avoid Type I error by limiting the number of ENSO indices to two that broadly cover the Pacific. No attempt was made to adjust *P*-values post hoc (Chang-Yang et al. 2015). From the lagged cross correlation results, we selected the largest (absolute) significant correlation coefficients and their associated lag values among the reproductive time series, meteorological time series, and ENSO12, ENSO34, NAO, and AMO (Atlantic Multidecadal Oscillation). Based on the results of cross-correlation analyses, we conducted a step-wise time series regression using the appropriately lagged variables for ENSO34, NAO, or AMO and two additional variables (and their interaction): the months since Hurricane Hugo and months since Hurricane Georges (this variable had a value of zero until the hurricane occurred in September 1998). Regression terms were added or subtracted until the model with the lowest value of the Akaike information criterion (Akaike 1974) was realized. This analysis was conducted using the `MASS` package (Venables and Ripley 2002) in R v3.2.5 (R Core Team 2016).

To determine which lifeforms were contributing to community-wide patterns, total annual cumulative fortnightly records of flower production and total annual seed production for each species were transformed to their standard normal deviates (SND) by subtracting the annual value from the mean value and dividing by one standard deviation. We compared patterns for the entire defined community and by lifeform (liana, vine, hemiepiphyte, epiphyte, large tree, medium tree, small tree, and shrub; tree sizes and shrubs as defined by Thompson et al. (2002; Appendix S1: Table S1). Patterns among lifeforms were compared using profile analysis, a direct extension of MANOVA, using the ‘`profileR`’ package (Bulut and Desjardins 2016) in R v3.2.5 (R Core Team 2016).

## RESULTS

Flower and fruit parts were found in at least five percent of traps for a total of 89 and 76 species, respectively, with 71 species represented by both phenophases (Appendix S1: Table S1). At any given time between 1992 and 2014 in the Luquillo forest, 20 to 43 species were in flower (Fig. 1) and 15 to 40 species were fruiting. There was no apparent long-term trend for species flowering, although a distinct rise in flowering appeared near the end of the series. The number of fruiting species remained relatively constant through 2003 with a decline thereafter.

Significant cross-correlations of the number of species flowering or fruiting were not found for any of the local meteorological variables (not shown). The climate index ENSO34 exhibited a significant correlation with the numbers of flowering and fruiting species (Table 1), while ENSO12 was not significant. The lag time for flowering and ENSO34 was seven months while that for fruiting was two months. Significant cross-correlations were found for both Atlantic indices and number of species flowering, with a negative correlation for NAO at a lag of 10 months and a positive correlation with AMO at 12 months.

Cross-correlations between lagged meteorological variables and climate indices were negative for ENSO and temperature (Table 2), ranging from –0.348 to –0.866, with lags ranging from negative four to one month. The negative lags between ENSO and local temperature signify that a decline in temperature anticipated a positive-phase ENSO. The ENSO indices also exhibited significant positive cross-correlations with PPFD at lags of seven to nine months, thus PPFD was greater seven to 9 months following a positive-phase ENSO. NAO was positively correlated with precipitation at a lag of zero months, was negatively correlated with minimum temperature at a lag of one month, and negatively correlated with PPFD with a lag of negative nine months. AMO was significantly positively associated with maximum and minimum temperatures at lags of negative 10 and 0 months, respectively, and was negatively related to PPFD at a lag of 13 months (Table 2).

Time series regression analysis was conducted using the appropriately lagged ENSO34, NAO and AMO climate indices (where significant), along with the times since the two hurricanes and their interaction. The best time series step-wise regressions for flowering (Table 3) included ENSO34 and time since Hurricane Hugo, both having a

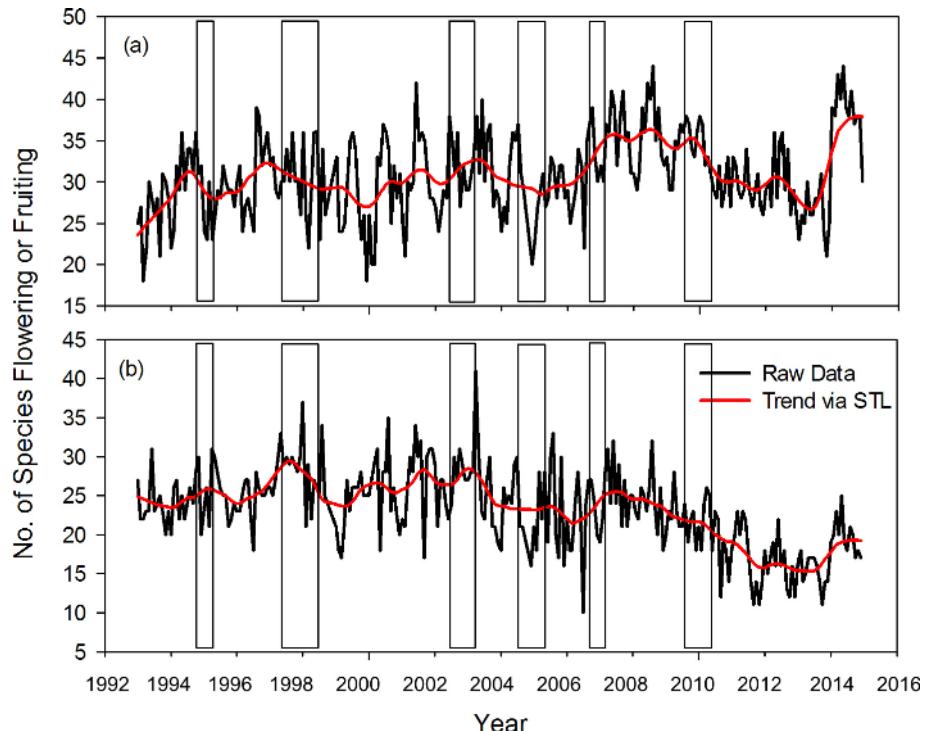


FIG. 1. (a) Changes in number of species flowering over time, showing raw data and trend established using seasonal-trend decomposition of time series by loess (STL) procedure. (b) Changes in number of species fruiting over time, showing raw data and trend established using STL procedure. Boxes show time periods when ENSO is in positive phase.

TABLE 1. The largest (absolute) cross-correlation coefficients of climatic variables vs. reproductive time series (number of species flowering or fruiting) and the corresponding time lags. Two indices of El Niño Southern Oscillation (ENSO12 and 34) are included as well as North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO). Correlations ( $P < 0.05$ ) are reported when cross-correlation analysis exhibited an overall significant result; “n.s.” noted otherwise. Lag correlations were tested up to a maximum of 18 months.

	Number of species flowering		Number of species fruiting	
	r	lag (months)	r	lag (months)
ENSO12	n.s.		n.s.	
ENSO34	0.125	7	0.218	2
NAO	-0.176	10	n.s.	
AMO	0.254	12	n.s.	

Note: Photosynthetic photon flux density (PPFD) recorded at Bisley Experimental Watersheds, 8 km distant from El Verde Field Station.

positive influence on the number of flowering species. The amount of variation explained by the model was low (~9% of variance) owing to the relatively small changes in numbers of flowering species over time (Fig. 1a). The regression model for number of fruiting species explained more of the variance in the data (~40%) and the effect of ENSO, time since Hurricane Hugo, and the interaction between time since the two hurricanes were significant. ENSO and Time since Hurricane Hugo had a positive influence on the number of flowering species while the interaction term between time since the two hurricanes was negative.

Patterns of annual flower production (presence in trap samples, accumulated for one year; Fig. 2) in the whole community showed a significant drop after 1995, remaining low until after 2007 and an uptick in 2014. Individual life-forms, particularly shrubs, appeared to differ from this overall trend, but the profile analysis found no significant interaction between time and lifeform (Wilks'  $\lambda = 0.080$ , Approximate  $F = 1.106$ ,  $df = 168$ ,  $P = 0.206$ ). The average standard normal deviate (SND) of seed production (Fig. 3) declined significantly over the time series and the profile analysis revealed significant differences among lifeform over time (Wilks'  $\lambda = 0.010$ , Approximate  $F = 1.715$ ,  $df = 176$ ,  $P < 0.0001$ ). The overall decline in the SND of seed production among all species in the community and most lifeforms matched the general decline in the number of fruiting species shown above (Fig. 1b). Hemiepiphytes, small trees, and lianas, however, differed from this overall pattern by showing a humped pattern over time or a series of peaks in seed production.

## DISCUSSION

Interannual patterns of flower and seed production in the LFDP were strongly influenced by both the history of hurricane disturbance and local climatic changes driven by global oscillations originating thousands of kilometers away. Thus, local patterns of forest reproduction integrate regional disturbance history and global variation in climate forcing, as predicted. Aside from hurricane disturbance, the Pacific El Niño (ENSO) index had the strongest influence on reproductive patterns in the LFDP. ENSO is apparently an

TABLE 2. The largest (absolute) cross-correlations coefficients and associated time-lags among local climate variables recorded at El Verde Field Station (unless otherwise noted) and indices of the El Niño Southern Oscillation and the North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO). Correlations ( $P < 0.05$ ) are reported when cross-correlation analysis exhibited an overall significant result; “n.s.” noted otherwise. Lag correlations were tested up to 18 months.

	Rainfall		Maximum temperature		Minimum temperature		PPFD	
	r	lag (months)	r	lag (months)	r	lag (months)	r	lag (months)
ENSO12	n.s.		-0.842	1	-0.866	-1	0.178	9
ENSO34	n.s.		-0.348	-2	-0.466	-4	0.231	7
NAO	0.137	0	n.s.		-0.186	1	0.176	-9
AMO	n.s.		0.320	-10	0.317	0	-0.089	13

Note: Photosynthetic photon flux density (PPFD) recorded at Bisley Experimental Watersheds, 12 km distant from El Verde Field Station.

TABLE 3. Results of step-wise linear model analyses for effects of global climate indices and time since two hurricanes on (A) the number of species flowering and (B) the number of species fruiting per month.

	Estimated coefficient	t	R <sup>2</sup>
(A) Number of species flowering			
Intercept	7.464	0.826	0.086
ENSO34 (lagged 7 months)	0.7462	2.256*	
Time since H. Hugo	0.019	4.78***	
(B) Number of species fruiting			
Intercept	0.177	0.022	0.395
ENSO34 (lagged 2 months)	0.793	2.812**	
Time since H. Hugo	0.052	2.723**	
Time since H. Georges	-0.048	-0.171	
T-Hugo:T-Georges	-0.0002	-2.296*	

\* $P \leq 0.05$ ; \*\* $P \leq 0.001$ ; \*\*\* $P \leq 0.0001$ .

integrator of changes in temperature, rainfall, irradiation, and perhaps other factors that single climate variables do not capture well (Stenseth et al. 2002, Stenseth and Mysterud 2005). While the effects of the Atlantic indices (NAO and AMO) were detected they were not included in the regression models that best explained reproductive variation. Therefore, predicting any future changes in plant reproduction at this site in the eastern Caribbean will most strongly be influenced by changes in hurricane frequency and the strength of the ENSO signal, rather than Atlantic climate indices or other changes in local meteorological conditions.

The use of cross-correlation analysis successfully recovered the demonstrated effects of ENSO and NAO on climate variability in Puerto Rico (Malmgren et al. 1998). ENSO has a positive effect on local temperatures through the influence of the eastern Pacific Ocean on local sea surface temperatures (SSTs; Malmgren et al. 1998) analyzed on an annual time step. Our analysis, conducted at a monthly time step, showed the largest correlations were negative with the ENSO indices, with a mix of positive and negative lags near zero. A negative lag in this context means that low temperatures appear in anticipation of a positive ENSO phase. The covariance structure, however, also indicates a positive relationship at some time in the future (in this case three to four months hence). Therefore, an analysis at an annual time step reveals a positive relationship, but analyses at a shorter time step appear to capture the start of a strong ENSO signal

when local SSTs are at their minimum. They then increase as the warming trend in SSTs builds from the coastal western Pacific toward the central Pacific (i.e., ENSO34 region) and eventually to the east (ENSO12 region; Trenbath and Stepaniak 2001).

We found no direct significant effects of rainfall, temperature, and irradiance on the numbers of flowering and fruiting species. Similar studies from Panama (Wright and Calderón 2006) and Taiwan (Chang-Yang et al. 2013, 2015) both showed direct effects of temperature, rainfall, and irradiance. Pau et al. (2013) found a strong positive effect of temperature on flowering using the same data from the LFDP (although a shorter time series), a pattern they attributed to seasonal (Zimmerman et al. 2007) and not interannual variation.

In contrast to the effects of local climate variables, ENSO had a consistent influence on the numbers of reproducing species, particularly fruiting, mirroring the results of both Wright and Calderón (2006) in Panama and Chang-Yang et al. (2015) in Taiwan. The magnitude of the correlations we recorded were not as high as those found in Panama (0.149 to 0.405) or, especially, Taiwan (0.337 to 0.481), perhaps owing to weaker teleconnections between Pacific-based oceanic climate drivers and conditions in Puerto Rico. Nevertheless, when the appropriately-lagged ENSO34 index was included in a regression model for the numbers of flowering or fruiting, ENSO was the only climate index retained in the final model after step-wise variable selection, emphasizing its critical influence on forest reproduction at our site. This result contributes to a well-established and growing body of knowledge that ENSO has worldwide influence on local climate and the biota of terrestrial ecosystems (Holmgren et al. 2001, Stenseth et al. 2002), particularly in tropical forests (Wright et al. 1999, Wright 2005b). We expected a priori that the Atlantic climate indices might have a strong influence on local reproductive patterns than ones originating in the Pacific. However, ENSO appears to capture a suite of climatic variables influencing plant reproduction, explaining its greater predictive power than single climate variables alone (Stenseth and Mysterud 2005).

As in Taiwan (Chang-Yang et al. 2015), we found longer lag times for ENSO effects on the numbers of flowering vs. fruiting species. We interpret this as ENSO influencing fruit development time, which varies on average between three and six months at our site (Zimmerman et al. 2007). It seems more likely that positive ENSO effects would

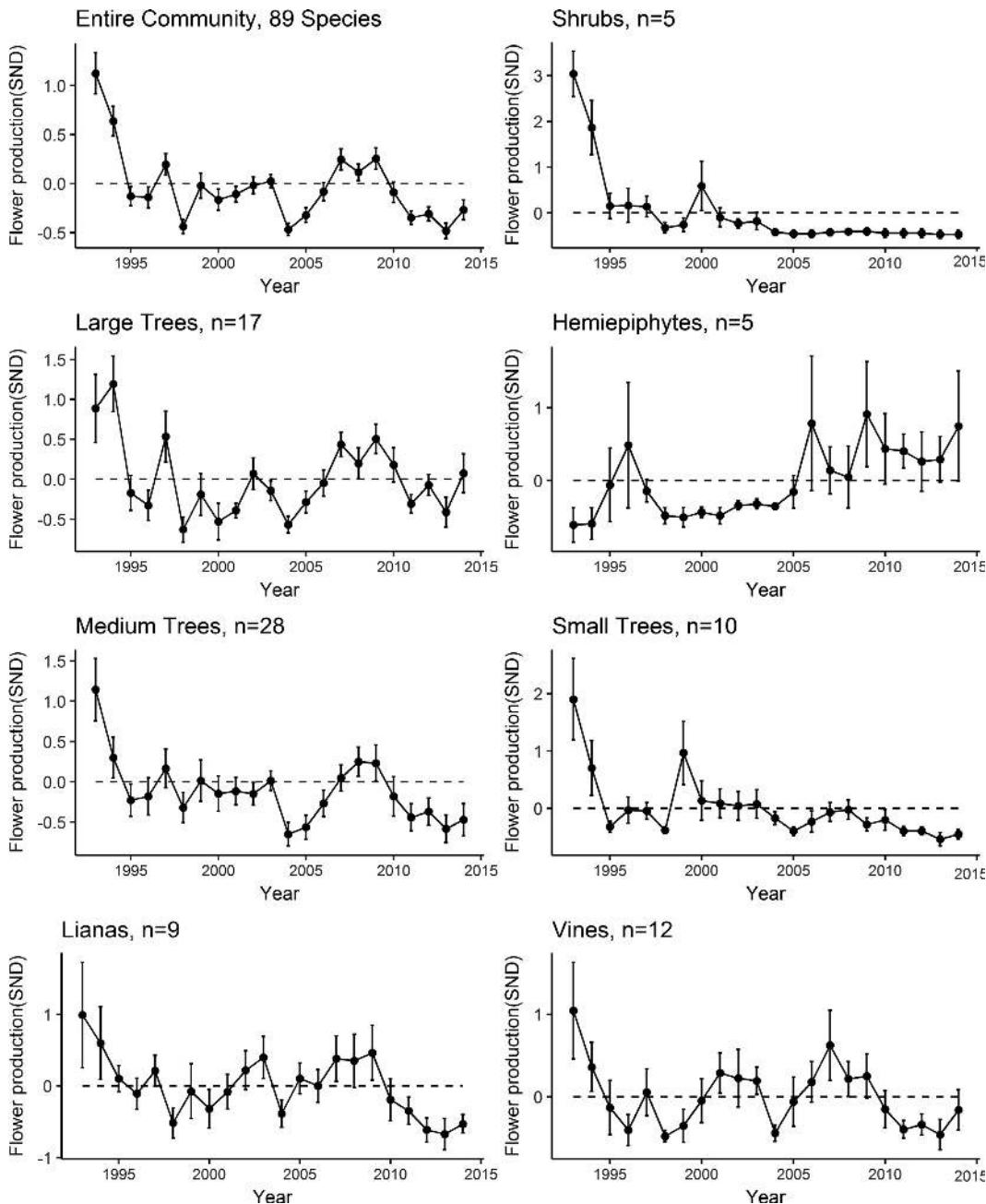


FIG. 2. Long-term patterns of annual flower production (see Methods for details) of different lifeforms. Data for individual species was converted to standard normal deviates (SND) before combining and averaging patterns within lifeforms. N denotes number of species in each lifeform. Errors bars are standard errors.

influence developing fruits prior to affecting patterns of flowering, explaining the differences in lag times. Wright and Calderón (2006) reported similar long lag times affecting flowering (seven to eight months) but reported negative lag times for numbers of fruiting species, suggesting this phenophase anticipated changes in the ENSO signal in some undetermined manner.

The influence of climate drivers on plant reproduction in the LFDP takes place in the context of hurricane disturbance (Brokaw et al. 2012a). At the beginning of this study, the numbers of reproducing species and overall levels of reproduction within species (measured through changes in

SND for individual species) were high, three years after Hurricane Hugo struck, reflecting the vigorous understory growth and reproduction of the recovering canopy at the time. The impacts of Hurricane Georges on patterns of reproduction were less apparent than those of Hurricane Hugo. The second storm had a small and significant negative effect on the numbers of fruiting species, but not the number of flowering species. The effect of Georges on reproductive output per species was small, and patterns among lifeforms were statistically parallel in the profile analysis for flower production. Increases in production of hemiepiphytes and small trees did appear following Georges, but there was

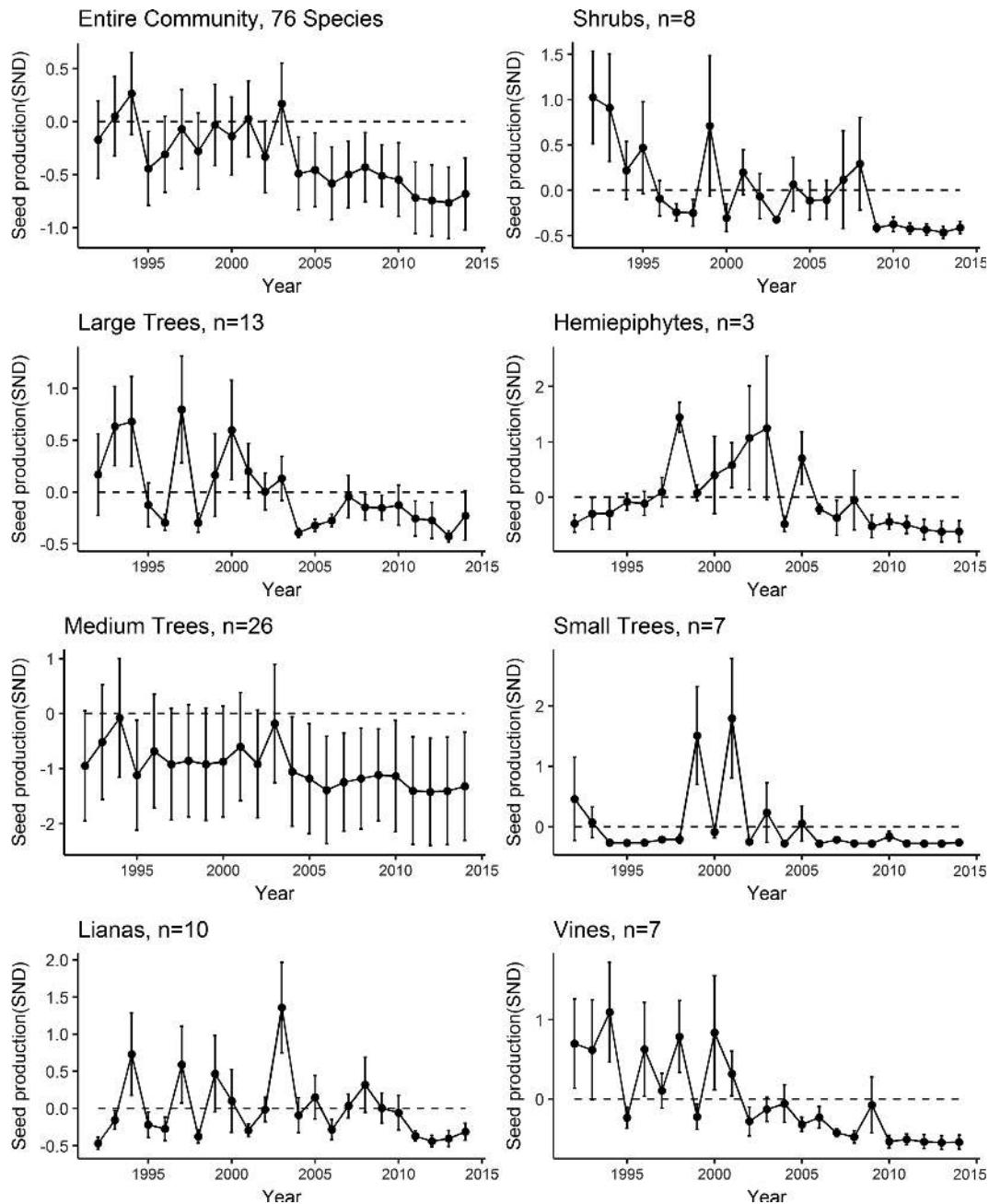


FIG. 3. Long-term patterns of annual seed production (see Methods for details) of different lifeforms. Data for individual species was converted to standard normal deviates (SND) before combining and averaging patterns within lifeforms. N denotes number of species in each lifeform. Error bars are standard errors.

no widespread positive effect of the hurricane on patterns of reproduction like those attributed to Hugo. This is explained by the relative lack of maturity of the forest canopy struck by Georges (Canham et al. 2010) and the fact that Georges was a weaker hurricane at landfall (Scatena et al. 2012). Thus, the two storms appeared to have dramatically different effects on forest reproduction, with the lessened response to Hurricane Georges conditioned on the previous, more-impactful Hurricane Hugo.

Finally, we found no long-term increases in flower production like that reported by Wright and Calderón (2006)

and Pau et al. (2017). They linked this pattern to increasing carbon fertilization from increasing atmospheric CO<sub>2</sub>. We found no comparable pattern in the entire community nor in any one lifeform in either patterns of flower production or seed production.

In summary, we found strong effects of ENSO and the history of hurricane disturbance on community-wide patterns of reproduction in the wet forest represented by the LFDP. Strong ENSO effects paralleled studies in other tropical forests, even though one might expect Caribbean forests to be more strongly impacted by geographically-closer

Atlantic indices. The first of the two hurricanes had a positive effect on reproduction at the start of the study through vigorous plant growth. A subsequent hurricane had a small negative effect on fruiting and no apparent effect on community levels of flowering.

With future climate change, how might patterns of forest reproduction in the LFDP be expected to change? Two recent articles indicate that global warming will cause an increase in frequency and intensity of ENSO events (Power et al. 2013, Cai et al. 2014). Perhaps increased flowering and fruiting can be expected in the LFDP forest community, caused by more frequent ENSO events through the 21st century. This prediction must be tempered by the possibility that climatically driven shifts in Puerto Rico's life zones (Henereh et al. 2016) may cause biotic attrition (Colwell et al. 2008) of the forest community that may disrupt forest productivity and reproduction in ways more profound than changes in ENSO (see Feng et al. 2018). Meanwhile, the frequency of hurricanes is expected to decrease over time as global climate warms through the remainder of the century, but with increased numbers of Category 4 and 5 storms as SSTs become warmer (Knutson et al. 2010). If so, frequent impacts by intense hurricanes may result in a shift in species composition toward early successional species, but without significant change in the overall frequency of flowering and fruiting by individual species. The recent impacts of Hurricanes Irma and Maria to our site provides us an opportunity to fully evaluate this hypothesis.

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#### LITERATURE CITED

- Akaike, H. 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control* 19:716–723.
- Augspurger, C. K. 2013. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. *Ecology* 94:41–50.
- Brokaw, N. V. L., and J. S. Grear. 1991. Forest structure before and after Hurricane Hugo at three elevations in the Luquillo Mountains, Puerto Rico. *Biotropica* 23:386–392.
- Brokaw, N., T. A. Crowl, A. E. Lugo, W. H. McDowell, F. N. Scatena, R. B. Waide, and M. R. Willig. 2012. A Caribbean forest tapestry: the multidimensional nature of disturbance and response. Oxford University Press, Oxford, UK.
- Brokaw, N., et al. 2012b. Response to disturbance. Pages 201–271 in N. Brokaw, T. A. Crowl, A. E. Lugo, W. H. McDowell, F. N. Scatena, R. B. Waide, and M. R. Willig, editors. A Caribbean forest tapestry: the multidimensional nature of disturbance and response. Oxford University Press, Oxford, UK.
- Bulut, O., and C. D. Desjardins. 2016. profileR: Profile Analysis of Multivariate Data in R. <https://doi.org/10.13140/rg.2.2.16269.54247>
- Cai, W., et al. 2014. Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change* 4: 111–116.
- Canham, C. D., J. Thompson, J. K. Zimmerman, and M. Uriarte. 2010. Variation in susceptibility to hurricane damage as a function of storm intensity in Puerto Rican tree species. *Biotropica* 42:87–94.
- Chang-Yang, C. H., C. L. Lu, I. Sun, and C. F. Hsieh. 2013. Flowering and fruiting patterns in a subtropical rain forest, Taiwan. *Biotropica* 45:165–174.
- Chang-Yang, C. H., I. Sun, C. H. Tsai, C. L. Lu, and C. F. Hsieh. 2015. ENSO and frost codetermine decade-long temporal variation in flower and seed production in a subtropical rain forest. *Journal of Ecology* 104:44–54.
- Chen, Y. Y., A. Satake, I. Sun, Y. Kosugi, M. Tani, S. Numata, S. P. Hubbell, C. Fletcher, M. N. N. Supardi, and S. J. Wright. 2017. Species-specific flowering cues among general flowering *Shorea* species at the Pasoh Research Forest, Malaysia. *Journal of Ecology*. <https://doi.org/10.1111/1365-2745.12836>
- Clark, D. A. 2004. Tropical forests and global warming: Slowing it down or speeding it up? *Frontiers in Ecology and the Environment* 2:73–80.
- Cleveland, R. B., W. S. Cleveland, J. E. McRae, and I. Terpenning. 1990. STL: A seasonal-trend decomposition procedure based on loess. *Journal of Official Statistics* 6:3–73.
- Colwell, R. K., G. Brehm, C. L. Cardelús, A. C. Gilman, and J. T. Longino. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258–261.
- Coomes, D. A., D. F. Burslem, and W. D. Simonson. 2014. Forests and global change. Cambridge University Press, Cambridge, UK.
- Corlett, R. T., and R. B. Primack. 2011. Tropical rain forests: an ecological and biogeographical comparison. Second edition. Blackwell, Oxford, UK.
- Curran, L., and M. Leighton. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Diptero-carpaceae. *Ecological Monographs* 70:101–128.
- Ewel, J. J., and J. L. Whitmore. 1973. The ecological life zones of puerto rico and the U.S. Virgin Islands. USDA Forest Service, Institute of Tropical Forestry, Research Paper ITF-018.
- Feeley, K. J., S. J. Wright, N. Supardi, A. R. Kassim, and S. J. Davies. 2007. Decelerating growth in tropical forest trees. *Ecology Letters* 10:461–469.
- Feng, X., M. Uriarte, G. González, S. Reed, J. Thompson, J. K. Zimmerman, and L. Murphy. 2018. Improving predictions of tropical forest response to climate change through integration of field studies and ecosystem modeling. *Global Change Biology*. <https://doi.org/10.1111/gcb.13863>
- Gamble, D. W., D. B. Parnell, and S. Curtis. 2008. Spatial variability of the Caribbean mid-summer drought and relation to the north Atlantic high circulation. *International Journal of Climatology* 28:343–350.
- Goldenberg, S. B., C. W. Landsea, A. M. Mestas-Nuñez, and W. M. Gray. 2001. The recent increase in Atlantic hurricane activity: causes and implications. *Science* 293:474–479.
- Heartsill Scalley, T., F. N. Scatena, A. E. Lugo, S. Moya, and C. R. Estrada Ruiz. 2010. Changes in structure, composition, and nutrients during 15 years of hurricane-induced succession in a subtropical wet forest in Puerto Rico. *Biotropica* 42:455–463.
- Henereh, K. A., W. A. Gould, E. Harmsen, A. Terando, M. Quiñones, and J. A. Collazo. 2016. Climate change implications for tropical islands: Interpolating and interpreting statistically down-scaled GCM projections for management and planning. *Journal of Applied Meteorology and Climatology* 55:265–282.
- Hogan, J. A., J. K. Zimmerman, J. Thompson, C. J. Nyctch, and M. Uriarte. 2016. The interaction of land-use legacies and hurricane disturbance in subtropical wet forest: twenty-one years of change. *Ecosphere* 7:e01405. <https://doi.org/10.1002/ecs2.1405>

- Holmgren, M., M. Scheffer, E. Ezcurra, J. R. Gutiérrez, and G. M. Mohren. 2001. El Niño effects on the dynamics of terrestrial ecosystems. *Trends in Ecology & Evolution* 16:89–94.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. *American Naturalist* 101:233–249.
- Knutson, T. R., J. L. McBride, J. Chan, K. Emanuel, G. Holland, C. Landsea, I. Held, J. P. Kossin, A. K. Srivastava, and M. Sugi. 2010. Tropical cyclones and climate change. *Nature Geoscience* 3:157–163.
- Lugo, A. E. 2008. Visible and invisible effects of hurricanes on forest ecosystems: an international review. *Austral Ecology* 33: 368–398.
- Lugo, A. E., J. C. Figueroa Colón, and F. N. Scatena. 2000. The Caribbean. Pages 593–622 in M. G. Barbour and W. D. Billings, editors. *North American terrestrial vegetation*. Cambridge University Press, Cambridge, UK.
- Malmgren, B. A., A. Winter, and D. Chen. 1998. El Niño-Southern Oscillation and North Atlantic Oscillation control of climate in Puerto Rico. *Journal of Climate* 11:2713–2717.
- Mora, C., A. G. Frazier, R. J. Longman, R. S. Dacks, M. M. Walton, E. J. Tong, J. J. Sanchez, L. R. Kaiser, Y. O. Stender, and J. M. Anderson. 2013. The projected timing of climate departure from recent variability. *Nature* 502:183–187.
- Pau, S., E. M. Wolkovich, B. I. Cook, C. J. Nyttch, J. Regetz, J. K. Zimmerman, and S. J. Wright. 2013. Clouds and temperature drive dynamic changes in tropical flower production. *Nature Climate Change* 3:838–842.
- Pau, S., D. K. Okamoto, O. Calderón, S. J. Wright, and S. Joseph. 2017. Long-term increases in tropical flowering activity across growth forms in response to rising CO<sub>2</sub> and climate change. *Global Change Biology*. <https://doi.org/10.1111/gcb.14004>
- Perez, T. M., J. T. Stroud, and K. J. Feeley. 2016. Thermal trouble in the tropics. *Science* 351:1392–1393.
- Power, S., C. Delage, G. Kociuba, Chung, and K. Keay. 2013. Robust twenty-first-century projections of El Niño and related precipitation variability. *Nature* 502:541–545.
- R Core Team. 2016. R: A language and environment for statistical computing. <http://www.R-project.org>
- Ryan, J. A., and J. M. Ulrich. 2011. xts: Extensible time series. R package version 0.8-2. <https://CRAN.R-project.org/package=xts>
- Scatena, F. N., J. Felipe Blanco, K. H. Beard, R. B. Waide, A. E. Lugo, N. Brokaw, W. L. Silver, B. L. Haines, and J. K. Zimmerman. 2012. Disturbance regime. Pages 164–200 in N. Brokaw, T. A. Crowl, A. E. Lugo, W. H. McDowell, F. N. Scatena, R. B. Waide, and M. R. Willig, editors. *A Caribbean forest tapestry: the multidimensional nature of disturbance and response*. Oxford University Press, Oxford, UK.
- Stenseth, N. C., and A. Mysterud. 2005. Weather packages: finding the right scale and composition of climate in ecology. *Journal of Animal Ecology* 74:1195–1198.
- Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. *Science* 297:1292–1296.
- Thompson, J., N. Brokaw, J. K. Zimmerman, R. B. Waide, E. M. Everham III, D. J. Lodge, C. M. Taylor, D. García-Montiel, and M. Fluet. 2002. Land use history, environment, and tree composition in a tropical forest. *Ecological Applications* 12:1344–1363.
- Trenbath, K. E., and D. P. Stepaniak. 2001. Indices of El Niño evolution. *Journal of Climatology* 14:1697–1701.
- Uriarte, M., R. Condit, C. D. Canham, and S. P. Hubbell. 2004. A spatially explicit model of sapling growth in a tropical forest: Does the identity of neighbours matter? *Journal of Ecology* 92:348–360.
- Uriarte, M., C. D. Canham, J. Thompson, J. K. Zimmerman, L. Murphy, A. M. Sabat, N. Fetcher, and B. L. Haines. 2009. Understanding natural disturbance and human land use as determinants of tree community dynamics in a subtropical wet forest: results from a forest simulator. *Ecological Monographs* 79:423–443.
- Uriarte, M., J. S. Clark, J. K. Zimmerman, L. S. Comita, J. Forero-Montaña, and J. Thompson. 2012. Multidimensional trade-offs in species responses to disturbance: implications for diversity in a subtropical forest. *Ecology* 93:191–205.
- Van Schaik, C. P., J. W. Terborgh, and S. J. Wright. 1993. The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annual Review of Ecology and Systematics* 24:353–377.
- Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Fourth edition. Springer, New York, New York, USA.
- Waide, R. B., D. E. Comarazamy, J. E. González, C. A. Hall, A. E. Lugo, J. C. Luvall, D. J. Murphy, J. R. Ortiz-Zayas, N. D. Ramírez-Beltran, and F. N. Scatena. 2013. Climate variability at multiple spatial and temporal scales in the Luquillo Mountains, Puerto Rico. *Ecological Bulletins* 54:21–41.
- Wood, T. E., M. A. Cavalieri, and S. C. Reed. 2012. Tropical forest carbon balance in a warmer world: a critical review spanning microbial- to ecosystem-scale processes. *Biological Reviews* 87:912–927.
- Wright, S. 2005a. The El Niño Southern Oscillation influences tree performance in tropical rainforests. Pages 295–310 in E. Birmingham, C. Dick, and C. Moritz, editors. *Tropical rainforests: past, present and future*. The University of Chicago Press, Chicago, Illinois, USA.
- Wright, S. J. 2005b. Tropical forests in a changing environment. *Trends in Ecology and Evolution* 20:553–560.
- Wright, S., and O. Calderón. 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., and C. P. van Schaik. 1994. Light and the phenology of tropical trees. *American Naturalist* 143:192–199.
- Wright, S. J., C. Carrasco, O. Calderon, and S. Paton. 1999. The El Niño Southern Oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80:1632–1647.
- Zimmerman, J. K., E. M. Everham Jr., R. B. Waide, D. J. Lodge, C. M. Taylor, and N. V. L. Brokaw. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *Journal of Ecology* 82:911–922.
- Zimmerman, J. K., S. J. Wright, O. Calderón, M. A. Pagan, and S. Paton. 2007. Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: the role of annual changes in irradiance. *Journal of Tropical Ecology* 23:231–251.
- Zimmerman, J. K., L. S. Comita, M. Uriarte, N. Brokaw, and J. Thompson. 2010. Patch dynamics and community metastability of a tropical forest: Compound effects of natural disturbance and human land use. *Landscape Ecology* 25:1099–1111.

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