Proposing the solar-wind energy flux hypothesis as a driver of inter-annual variation in tropical tree reproductive effort

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PREMISE: The El Niño Southern Oscillation (ENSO) affects tropical environmental conditions, potentially altering ecosystem function as El Niño events interact with longer-term climate change. Anomalously warm equatorial Pacific Ocean temperatures affect rainfall and temperature throughout the tropics and coincide with altered leaf flush phenology and increased fruit production in wet tropical forests; however, the understanding of mechanisms underlying this pattern is limited. There is evidence that increases in tropical tree reproduction anticipate El Niño onset, motivating the continued search for a global driver of tropical angiosperm reproduction. We present the solar-wind energy flux hypothesis: that physical energy influx to the Earth's upper atmosphere and magnetosphere, generated by a positive anomaly in the solar wind preceding El Niño development, cues tropical trees to increase resource allocation to reproduction.

METHODS: We test this hypothesis using 19 years of data from Luquillo, Puerto Rico, correlating them with measures of solar-wind energy.

RESULTS: From 1994 to 2013, the solar-wind energy flux into Earth's magnetosphere (E_{in}) was more strongly correlated with the number of species fruiting and flowering than the Niño 3.4 climate index, despite Niño 3.4 being previously identified as a driver of interannual increases in reproduction.

CONCLUSIONS: Changes in the global magnetosphere and thermosphere conditions from increased solar-wind energy affect global atmospheric pressure and circulation patterns, principally by weakening the Walker circulation. We discuss the idea that these changes cue interannual increases in tropical tree reproduction and act through an unidentified mechanism that anticipates and synchronizes the reproductive output of the tropical trees with El Niño.

KEY WORDS El Niño Southern Oscillation; flowering; fruiting; Luquillo; reproductive phenology; solar wind; solar-wind energy flux; tropical trees.

INTRODUCTION

Global climate oscillations and variation in tropical forest reproduction

Interannual fluctuations in global climate, such as ENSO (Moy et al., 2002; McPhaden et al., 2006; Vecchi et al., 2006; Power et al., 2013), influence tropical forest energy flux (e.g., change in forest temperature or rates of nutrient cycling; Malhi and Wright, 2004; Levine et al., 2018) including biomass accretion (Phillips et al., 1998), carbon dynamics (Brienen et al., 2015; Liu et al., 2017), and the reproductive phenologies of tropical trees (Wright and Calderón, 2006; Zimmerman et al., 2007, 2018; Chang-Yang et al., 2016; Pau et al., 2018; Sakai and Kitajima, 2019). Because tropical forests account for approximately one-third of the global carbon cycle (Beer et al., 2010; Pan et al., 2011), understanding how such interannual climate drivers affect

their reproduction is important for long-term projections of tropical forests dynamics, including their carbon storage potential. Changes in the local environment, such as solar irradiance, temperature, and precipitation, only partly describe the variability in leaf and reproductive phenologies of tropical trees (Lasky et al., 2016; Chapman et al., 2018; Chen et al., 2018; Wright and Calderón, 2018). A positive ENSO anomaly increases soil moisture deficit, solar radiation, and vapor pressure deficit in much of the terrestrial tropics (Detto et al., 2018; He et al., 2018; Rafai et al., 2019), during which, many tropical forests exhibit increased reproduction (Wright and Calderón, 2006; Chang-Yang et al., 2016; Chapman et al., 2018; Pau et al., 2018; Zimmerman et al., 2018). For example, the masting of Asian dipterocarps in ENSO years can increase up to 8-fold from non-ENSO years (Ashton et al., 1988; Curran and Leighton, 2000; Willamson and Ickes, 2002; Chen et al., 2018).

Yet, how can it be that certain species mast at the regional and global scales (Koenig and Knops, 1998)? How can forests from across the world respond similarly, in terms of productivity and reproductive output, to global-scale interannual climate cycles like ENSO (Asner et al., 2000)? If it were merely a function of resource allocation within trees and response to local abiotic-environmental drivers, one would predict canopy-damaging disturbance, e.g., frost events (Chang-Yang et al., 2016) or hurricanes (Zimmerman et al., 2018), to disrupt the coordination of ENSO and increased reproductive activity among forests. Yet globally, despite disturbance, trees in wet tropical forests seem to coordinate resource allocation to increase reproductive effort coinciding almost perfectly with the timing of environmental conditions conducive to high rates of seed survival and germination (i.e., the high light and dry conditions that typically accompany El Niño in tropical wet forests) (Williamson and Ickes, 2002; Detto et al., 2018). We posit that trees can anticipate ENSO through a yet undetermined physiological cue. Here, we do not attempt to identify the specific cue that may trigger flowering but suggest that such a cue would be adaptive for species that could anticipate the positive changes that an ENSO event might have on tree reproduction.

On one hand, tropical trees may be adapted to trade off the timing of leaf flush and fruiting phenologies to maximize the exploitation of solar insolation by new leaves with the investment of sugars into fruits under dry conditions to avoid drought stress (Detto et al., 2018). A developing El Niño event may trigger a switch in resource investment from leaves to flowers and fruits. On the other, by synchronizing an increased volume of fruit production among individuals or species across years, the per-seed cost of negative density-dependent effects, such as exposure to fungal pathogens or seed predation, is minimized (Janzen, 1970; Aston et al., 1988; Curran and Leighton, 2000; Williamson and Ickes, 2002; Pearse et al., 2016). Thus, there is an inherent fitness implication to this adaptive behavior at the population and community scales (Crawley and Long, 1995; Kelly et al., 2000), and evolution may have selected for species with higher sensitivity to phenological cues that result in community synchrony in reproduction via increased survival and recruitment of their seeds (Williamson and Ickes, 2002). However, in regard to reproductive effort (i.e., timing and output), individual trees are likely insensitive to the benefits of density-dependent effects acting of offspring (Salisbury, 1942; Crawley and Long, 1995; Connell and Green, 2000), and the development time for most tropical fruits is several to many months (Zimmerman et al., 2007), suggesting a separate abiotic cue that allows them to forecast the onset of ENSO.

The solar wind, the Earth system, and the El Niño Southern Oscillation

The solar wind, a continuous flow of charged particles (i.e., electrons, protons, and alpha particles) ejected from the Sun's surface, induces energy into the Earth system through its interaction with Earth's magnetic field (i.e., magnetosphere) and upper atmosphere (i.e., the ionosphere 220–300 km above sea level) (Akasofu, 1981; Hasegawa et al., 2004). Wang et al. (2013) implemented a three-dimensional magnetohydrodynamic model to simulate the solar wind–magnetosphere–ionosphere system and compute a parameterization of the solar-wind energy flux into the magnetosphere, which depends on solar wind plasma parameters. Recently, He et al. (2018) applied this parameterization to in situ spacecraft data on solar-wind plasma parameters (collected by NASA's Advanced Composition Explorer) to estimate the solar-wind energy flux into the magnetosphere (E_{in}), identifying a 2–4-year interannual and 11-year quasi-decadal periodicity in E_{in}. They further identified a statistically significant relationship between the mean annual strength of the solar wind and subsequent early winter ENSO onset, concluding that increased E_{in} leads to cascading changes in the Earth's atmospheric and oceanic currents. Such cascading effects include a weakening in the Walker circulation (Rasmusson and Carpenter, 1982b; Vecchi et al., 2006; He et al., 2018) and a strengthening in the Bjerknes feedback (Rasmusson and Carpenter, 1982b; McPhaden et al., 2006; He et al., 2018), which allow a positive ENSO to develop. However, these solar-wind-induced climate feedbacks have not, as of yet, been clearly linked to plant lifecycles in any capacity. From 1964 to 2013, positive anomalies in E_{in} preceded the onset of sea level pressure and Walker circulation anomalies by several months to a year (He et al., 2018). Moreover, tropical cyclone and geomagnetic activity have been linked to E_{in} positive anomalies potentially via uneven heating of the thermosphere (80–100 km above sea level) from increased solar wind activity (Li et al., 2018). Such changes to the Earth's atmospheric and oceanic circulations potentially describe a mechanism by which tropical trees may anticipate ENSO and adds to evidence that solar wind–Earth system interactions may potentially drive interannual and quasi-decadal fluctuations in the Earth's climate, including ENSO (Hocke, 2009).

Lagged time-series correlations between the community phenological response (the number of species in fruit or flower) for two extensively-studied neotropical forests, Barro Colorado Island (BCI), Panama, and Luquillo, Puerto Rico have revealed negative lags, particularly with respect to temperature (Wright and Calderón, 2006; Zimmerman et al., 2007, 2018). Thus, it is reasonable to consider that tropical trees anticipate ENSO, irrespective of any identifiable cue. To maximize fruit production by the time an ENSO has fully developed, trees would need to anticipate the event and shift the allocation of resources to reproduction well in advance of local environmental changes. On the basis of these observations, we propose a new hypothesis that integrates space weather and provides a scenario that allows trees to initiate flowering in advance of ENSO events.

Hypothesis

Explicitly, the solar-wind energy flux hypothesis as a cue for tropical tree reproduction states:

> That due to positive energy anomalies in solar-wind energy and its interaction with the Earth system's upper atmosphere (the magnetosphere and thermosphere), tropical trees are physiologically cued to

shift resource allocation away from photosynthesis and growth and toward fruit production in preparation for the favorable environmental conditions that will develop during El Niño.

Although we are unable to identify the precise physiological mechanism by which tropical trees are cued to increase reproduction in anticipation of El Niño, it may be linked to solar-wind driven changes in tropical atmospheric circulation currents, temperature, pressure, and energy flow which feedback to affect soil moisture (i.e., land-atmospheric coupling). Such atmospheric changes have been related to a physical energy increase in the Earth's magnetosphere and upper atmosphere from the solar wind (He et al., 2018; Li et al., 2018). Atmospheric conditions and soil moisture are both affected under positive ENSO conditions (Rasmusson and Carpenter, 1982a; Sun et al., 2014; Detto et al., 2018; Levine et al., 2018) and have feedbacks on tropical forest productivity (Asner et al., 2000; Liu et al., 2017; Levine et al., 2018); therefore, it is reasonable to hypothesize they may exert some effect on tropical forest reproduction. Next, we provide a case study that illustrates a stronger correlative relationship to solar-wind energy anomalies than ENSO itself, as preliminary evidence.

MATERIALS AND METHODS

Measuring forest phenology using seed traps at Luquillo

Fortnightly surveys of all plant reproductive parts were conducted for 120 stationary traps located in the 16-ha Luquillo Forest Dynamics Plot (18°20′N, 62°49′W) in the northwestern section of the Luquillo Experimental Forest in eastern Puerto Rico beginning in March 1992. The forest community at Luquillo is a Caribbean subtropical montane forest (below 600 m a.s.l.) dominated by the palm *Prestoea acuminata* var. *montana* (Graham) A.J.Hend. & Galeano and *Dacryodes excelsa* Vahl. (Burseraceae), with a species richness of 44 tree species per hectare that are ≥1 cm diameter at 1.3 m height (Thompson et al., 2002). Flower presence–absence and seed and fruit abundances are recorded by species for each trap. Fruits were converted to seed abundances using the number of seeds per fruit determined for each species (Wright and Calderón, 2006; Zimmerman et al., 2007). We limited analyses to species that were recorded in greater than six traps, ensuring that multiple individuals were sampled (Zimmerman et al., 2007). Altogether in 23 years of monitoring, 89 species were found in flower, and 76 were found in seed or fruit, with 71 species recorded in both flower and fruit (Zimmerman et al., 2018). Seed-trap size was increased from 0.16 to 0.5 m² in 2006, and traps were run concurrently for a year. Seed abundances from the smaller traps were corrected based on the slope of the regression for pairwise flower presences (1.26) and seed abundances (1.61; additional details are described by Zimmerman et al., 2018).

Wavelet analysis

We used a continuous multivariate Morlet wavelet transformation to calculate the timescale of coherent patterns in community flower and seed abundances. Recent research on the phenology of tropical trees (Lasky et al., 2016; Detto et al., 2018) has demonstrated the utility of wavelet analyses in detecting community-level responses of species-rich communities. Wavelet analysis allows for the identification of synchronous and compensatory trends at the scale of climate oscillation recurrence (i.e., timescales greater than

1 year; the scale was specified from 0.5 to 10 years for the analysis). Accordingly, we use a continuous multivariate Morlet wavelet to visualize the multivariate matrix of species phenology at the community level and determine the timescale of community synchrony in phenology at Luquillo. The continuous multivariate wavelet transform is: $w_k(t,s) = s^{-1} \int_{-\infty}^{\infty} x_k(\tau) \varphi\left(\frac{t-\tau}{s}\right) d\tau$, where $\varphi(t)$ is the wavelet function and $x_k(\tau)$ is the presence count of flowers or abundance of seeds for the kth species at time τ, and s is the wavelet scale. The Morlet wavelet function used is $\varphi(t) = \pi^{-\frac{1}{4}} e^{\left(2\pi i \tau - \frac{1}{2}\tau^2\right)}$ (Morlet et al., 1982). Once data are in wavelet form, one can compute the wavelet modulus ratio, a measure of time series coherency at a given timescale, represented by the coefficient of the aggregate temporal variation over the marginal temporal variation of individual species. Coherency via the wavelet modulus ratio was estimated with respect to wavelet scale using $\rho(t,s) = \frac{\Lambda_{t,s}(|\sum_k w_k(t,s)|)}{\Lambda_{t,s}(\sum_k |w_k(t,s)|)}$, where $\Lambda_{ts}(\cdot) = \int_{-\infty}^{\infty} e^{-\frac{1}{2}\left(\frac{t-\tau}{s}\right)^2} (\cdot) d\tau$ and $|\cdot|$ is the complex norm (i.e., modulus of a complex number) (Keitt, 2008, 2014). Wavelet modulus ratios near 1 correspond to community synchrony, while ratios near 0 show community compensation. Statistical significance was determined using a phase-randomization, nonparametric bootstrapping method using 999 randomizations, where the observed wavelet modulus ratio was compared to a null distribution in which wavelet scale and response variables are randomized [wmr.boot() function of Keitt (2014)]. Analyses were carried out in R v.3.5.2 (R Core Team, 2017) using the mvcwt package (Keitt, 2014).

Seasonal detrending of the phenology data and correlations with solar-wind, climate indices, and the local environment

Using the same fortnightly survey data, the phenological response of the forest was defined as the number of species in either fruit or flower at the monthly-scale, because that is the scale for ENSO climate indices. We seasonally detrended monthly time series of the number of species in flower and seed using seasonal-trend decomposition by locally weighted regression (i.e., Loess; also known as STL: Cleveland et al., 1990; see appendix 2 of Zimmerman et al., 2018). From the trend, annual open, high, low, close (OHLC) moving averages were computed. We obtained annual normalized E_{in} values from 1993 to 2012 from He et al. (2018). Space weather data on sunspot number (SSN), the solar radio flux at 10.7 cm frequency (F107), and total solar irradiation (TSI) were downloaded from the NASA ONMIweb database (omniweb.gsfc.nasa.gov) and monthly Niño 3.4 data were obtained from NOAA (esrl.noaa.gov/psd/enso/dashboard.html). SSN, F107, and TSI are commonly used as proxies for solar weather activity. We compared the OHLC moving averages to annualized mean anomalies for E_{in}, SSN, F107, TSI, and ENSO 3.4 from 1992 to 2012. OHLC moving averages were used to best capture the annual average and variability of the phenological response over time, by weighting the temporal variation in the data (i.e., yearly open and close values) equal to the range of the data (i.e., annual high and low values). All indices were normalized, and the average annual anomaly was calculated. Time-series correlations between the seasonally detrended OHLC (open, high, low, close) moving average of the number of species in flower or seed and the normalized anomaly for the E_{in} and ENSO 3.4 were done using annual data from 1993 to 2012 (df = 18). Similarly, to identify the effect of E_{in} on the local climate of Luquillo, we performed annual time series correlations between E_{in} and annual rainfall, temperature (maximum and minimum annual averages), and sunlight environment (photosynthetically active

radiation and incoming solar shortwave radiation). Time-series correlations were implemented using the ccf() function in R.v3.5.2 (R Core Team, 2017), which adequately accounts for temporal autocorrelation within a time series.

RESULTS

Assessing the interannual synchrony in tropical tree reproductive output

To help visualize the community composition of fruits and flowers collected in the phenology traps and display time scales at which coherency occurs, we present a Morlet wavelet analysis of flower and fruit abundances. It illustrates supra-annual coherency in a 22-year time series of flower and fruit production at Luquillo (Fig. 1). Community synchrony in flower and seed production occurred at the interannual scales consistent with ENSO, despite a large disturbance in September 1998, Hurricane Georges, which nullified flower and fruit production of the community for roughly three months. More temporally consistent community synchrony is evident for flowers than for seeds (Fig. 1A) and extended from a timescale of ca. 2 years and beyond. The entire top portion of Fig. 1A is statistically significant as the bold lines delimiting areas of significance using $\alpha = 0.05$ do not connect along the upper boundary. For seed production, the strongest community synchrony occurs between 2 and 5 years and is strongest during the 1997–1998 ENSO (Fig. 1B). Therefore, flower production in the community is regularly synchronized, but seed production is only synchronized interannually and coincides with the timing and periodicity of ENSO.

Correlation of forest reproduction with the solar-wind energy flux
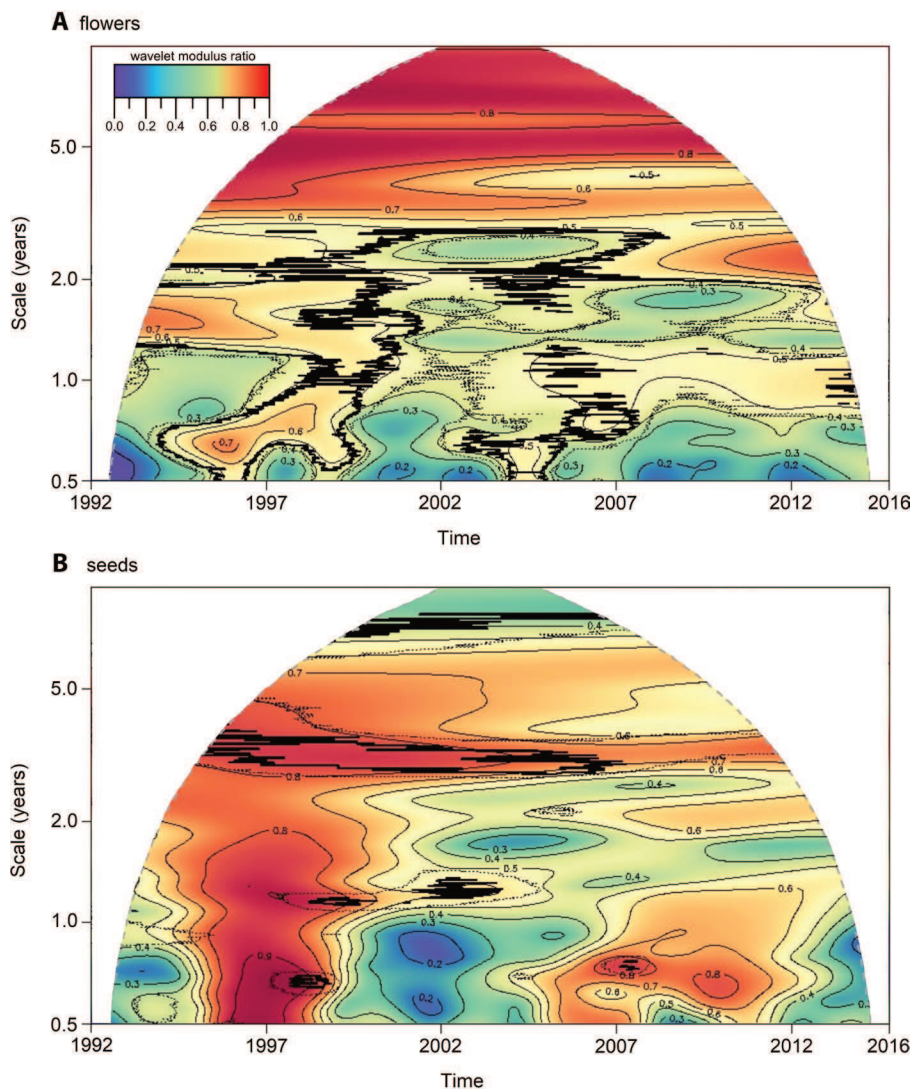

FIGURE 1. Morlet wavelet modulus ratios over time using seed trap abundances of (A) flowers and (B) seeds for the tree community of the Luquillo Forest Dynamics Plot, Puerto Rico. The vertical axis (log scale) represents the scale of the Morlet wavelet modulus, ranging from half a year to 10 years. Colors within the heatmaps denote the magnitude of the wavelet modulus ratio scaled from 0 (dark blue) corresponding to strong compensatory dynamics to 1 (dark red) denoting strong community synchrony. Note that the community synchrony (i.e., the red area) extends down to the smallest scale in part B, illustrating the effect of Hurricane Georges in 1998. Contours are wavelet modulus ratio–magnitude isotherms. Dotted and bold lines delimit areas of statistical significance at $\alpha = 0.1$ and 0.05, respectively, using 999 bootstrapped resamples (see Methods).

In this context, we were interested in preliminarily exploring how E_{in} related to forest-level flower and seed production. In previous work, ENSO 3.4 was the strongest correlated El Niño-related climate index to the phenology of the trees in Luquillo (Zimmerman et al., 2018). Pearson correlations between the normalized annual E_{in} anomalies and open, high, low, close (OHLC) annual average of the seasonally detrended number of species in flower ($r = -0.635$, $t = -3.48$, df = 18, $p < 0.01$) and seed ($r = 0.443$, $t = 2.97$, df = 18, $p < 0.05$) were both statistically significant. Those relationships were stronger than their respective correlations with normalized annual anomalies of ENSO 3.4 (flowers: $r = 0.019$, $t = 0.08$, df = 18, $p = 0.938$, seeds: $r = 0.253$, $t = 1.11$, df = 18, $p = 0.28$). Relationships

between other measures of space weather activity (SSN. F107, and TSI) and the OHLC annual average of the seasonally detrended annual number of species in flower or seed were similar those of E_{in}, but weaker (Fig. 2). Correlations were nonsignificant between the phenological responses and TSI, F107 and SSN, except between that of flowers and SSN ($r = -0.504$, $t = -2.33$, df = 18, $p < 0.05$).

DISCUSSION

The community synchrony in the abundance of flowers and fruits counts at 4–6-year timescales is consistent with recurring ENSO
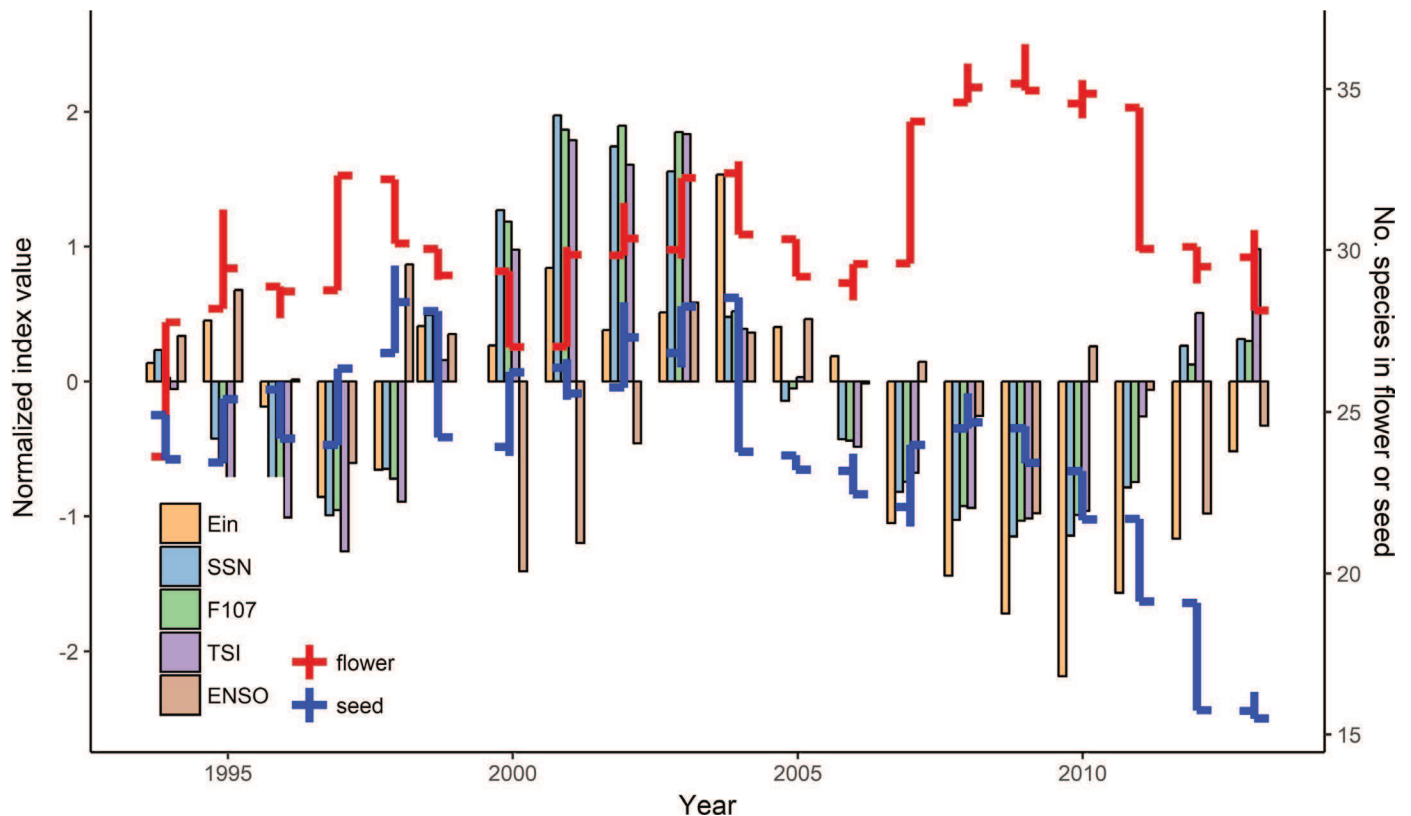
FIGURE 2. Annual normalized solar-wind energy flux into the magnetosphere (E_{in}), sunspot number (SSN), solar radio flux at 10.7 cm frequency (F107), total solar irradiation (TSI), and ENSO 3.4 indices from 1993 to 2013 with OHLC (Open: left-facing horizontal line, High: maximum of annual range, Low: minimum, Close: right-facing horizontal line) bars for the seasonally detrended number of species in flower (red) or seed (blue) at Luquillo, Puerto Rico. Years in which fewer species producing seed coincide with years with negative normalized index values related to solar-wind energy-flux into the atmosphere (E_{in}, SSN, TSI, and F107) (i.e., less energy input from the solar wind into the Earth system). See Appendix S1 for complete time-series correlations.

positive anomalies (Fig. 1). Therefore, the signal of ENSO on community synchrony in the reproductive effort of tropical trees in Luquillo exists despite a dynamic tree community situated in an aseasonal, disturbance-affected forest (Zimmerman et al., 2007; Hogan et al., 2016, 2018). A positive ENSO has no effect on rainfall at Luquillo but decreases temperature (strongest relationship at 2- to 4-month lead, i.e., before ENSO) and increases solar radiation (photosynthetic photon flux density, strongest relationship at 7-month lag) (Zimmerman et al., 2018). Luquillo is considerably wetter (no month receives <100 mm of rainfall) and less seasonal than many other tropical forests (e.g., BCI, the Amazon), where ENSO can interact with seasonal dynamics to strengthen or lengthen the dry season (Detto et al., 2018; Rafai et al., 2019). At the annual scale at Luquillo, relationships with measures of solar-wind energy more closely tracked the number of species in flower or seed over time than the ENSO 3.4 anomalies (Fig. 2). E_{in} was found to have no statistically significant relationship with annual total rainfall or average temperatures (minimum or maximum), or solar radiation (Appendix S1) yet was strongly related to flower and seed reproductive effort of trees. These results suggest that the correlation between the solar-wind energy flux and annual reproductive effort at Luquillo is not mediated through changes in commonly studied phenological cues, such as temperature, rainfall or sunlight. Further investigation is needed to determine whether neotropical forests or

tropical forests in other parts of the world (i.e., Asia and Africa) respond similarly.

In conclusion, the sub-annually lagged E_{in}–ENSO teleconnection occurs most strongly over Southeastern Asian and northern Australia, creating a strong Walker circulation divergence there, and several convergence centers over the eastern Pacific (Rasmussen and Carpenter, 1982b; He et al., 2018). These global-scale changes in sea level pressure and atmospheric circulation conditions that extend at least 1000 km above the Earth's surface (He et al., 2018) can be linked to climate, geomagnetic energy, and global cyclonic activity (Li et al., 2018). ENSO acts as an established global climatic driver of supra-annual cycles in tropical tree phenology (Wright and Calderón, 2006; Chang-Yang et al., 2016; Detto et al., 2018; Pau et al., 2018; Zimmerman et al., 2018). Increased E_{in} results in significantly greater sea level pressure over equatorial Southeastern Asia at 130°E longitude, and significantly lower sea level pressures over the American Pacific Ocean at 30° N and S latitude and 130° W longitude (He et al., 2018). Therefore, although no direct physiological cue can be identified from this work, we suspect the effects of atmospheric-mediated, solar-wind energy input to the Earth system to affect both Neotropical and Southeastern Asian tropical forest most-strongly, albeit potentially via differing effects on the local environment. Indeed, Liu et al. (2017) showed that Neotropical

and Southeastern Asian tropical forests had the greatest carbon cycle anomolies (i.e., differences in net biosphere exchange) during the 2015–2016 El Niño. Evidence for ENSO influence on the phenology of African forests is mixed (Babweteera et al., 2018; Chapman et al., 2018), and variable (Adamescu et al., 2018). Moreover, the relationship between ENSO and changes in local environmental conditions of tropical Africa is weaker (Mahli and Wright, 2004).

The mechanism behind the interannual variation and El Niño-related increase in reproductive effort of tropical trees is difficult to identify, owing to the subtlety and complexity of climatic teleconnections and the need for long-term records of forest reproduction (Pearse et al., 2016; Abernethy et al., 2018; Wright and Calderón, 2018). At Luquillo after accounting for seasonal variation, decreased E_{in} results in more species producing flowers, but a decrease in species producing seed (Fig. 2). These patterns appear to be influenced by negative trends in solar-wind energy flux and declines in seed production after 2005. Whether this relationship holds at other neotropical sites remains to be investigated. At BCI, Panama, similar coherency in community reproduction and leaf flush have been observed at 4- to 7-year timescales (Detto et al., 2018), pointing to the widespread effect of ENSO on tropical tree reproductive effort. However, in contrast to Luquillo, there have been steady increases in fruit and flower production over the 28-year record at BCI (Pau et al., 2018). Notably, we identified no effects between E_{in} and temperature or precipitation for Luquillo using annual data, although previous work has shown ENSO to affect temperature and solar radiation at the sub-annual (i.e., monthly) scale. Likely the interactions between fluctuations in solar-wind energy into the Earth system and tropical tree reproduction are complex and occur at timescales finer than the annual scale as the solar wind intensity fluctuates with solar activity. Thus, finer temporal resolution in the analysis may prove to be insightful. Furthermore, species could potentially vary in their sensitivity to solar-wind energy flux, although there exists very little understanding of how extraplanetary energy affects plant reproductive physiology. Future research should work to identify how solar-wind energy flux and other measures of solar weather relate to changes in the local environment or directly cue tropical tree phenology at broader spatial and temporal scales.

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AUTHOR CONTRIBUTIONS

J.A.H. conceived the idea, analyzed the data, and wrote the manuscript. J.K.Z. and J.E.B. collected the data. All authors, especially C.J.N., edited manuscript drafts and contributed intellectually.

COMPETING INTERESTS

The authors declare no competing interests.

FUNDING INFORMATION

DATA AVAILABILITY

Data on the phenology of trees and shrubs from the Luquillo Forest Dynamics Plot can be found on the Luquillo LTER website: data set 88: http://luq.lter.network/data/luqmetadata88.

SUPPORTING INFORMATION

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

APPENDIX S1. Complete time-series correlations between solar wind measures, the phenological response, and local meteorological conditions at Luquillo.

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