

1 **Title:** Proposing the solar wind-energy-flux hypothesis as a driver of interannual
2 variation in tropical tree reproductive effort
3 tropical tree reproduction

4
5 **Authors:** J. Aaron Hogan^{1*}, Christopher J. Nytch², John E. Bithorn^{2,3} & Jess K.
6 Zimmerman^{2,3}

7 **Institutional Affiliations:**

8 1 International Center for Tropical Botany, Department of Biological Sciences, Florida
9 International University, Miami, FL 33175, USA

10 2 Department of Environmental Sciences, University of Puerto Rico-Río Piedras, San
11 Juan, PR, 00925, USA

12 3 El Verde Field Station, km 19.5 PR-186, Rio Grande, PR 00745, USA

13 *corresponding author, email: jhogan@fiu.edu

14 **Author contributions:** J.A.H conceived the idea, analyzed the data, and wrote the
15 manuscript. J.K.Z. and J.E.B collected the data. All authors contributed intellectually
16 and provided insight and comments on manuscript drafts.

17 **Competing interests:** The authors declare no competing interests.

18 **Materials & Correspondence:** Materials and correspondence should be addressed to
19 J.A.H.

20

21 **Content type:** Letter

22

23 **Keywords:** solar wind-energy-flux, reproductive phenology, tropical trees, Ein, ENSO,
24 Luquillo.

25 **Abstract**

26 A growing body of research documents how the El Niño Southern Oscillation (ENSO)
27 results in short-term changes in terrestrial environmental conditions, with the potential to
28 drive ecosystem processes as the duration and severity of ENSO events increases with
29 anthropogenic climate change. An ENSO positive phase results in anomalous patterns
30 of rainfall and temperature throughout the tropics that coincide with leaf flush and
31 increased fruit production in tropical forests worldwide. However, our understanding of
32 possible mechanisms underlying this natural phenomenon is limited. Furthermore,
33 flowering in tropical trees anticipates ENSO development, motivating the continued
34 search for a global phenological cue for tropical angiosperm reproduction. We propose
35 the solar energy flux hypothesis: that a physical energy influx in the Earth's upper
36 atmosphere and magnetosphere generated by a positive anomaly in the solar wind
37 preceding ENSO development, cues tropical trees to increase allocation of resources to
38 reproduction. We show that from 1994-2013, the solar wind energy flux into the Earth's
39 magnetosphere (E_{in}) is more strongly correlated with the number of trees in fruit or
40 flower in a Puerto Rican wet forest than the Niño 3.4 climate index, despite Niño 3.4
41 being a previously identified driver of interannual increases in reproduction. We discuss
42 the idea that changes in the global magnetosphere and thermosphere conditions via
43 solar wind-effects on global atmospheric circulation, principally a weaker Walker
44 circulation, cue interannual increases tropical tree reproduction. This may be a
45 mechanism that synchronizes the reproductive output of the tropical trees to changes in

- 46 environmental conditions that coincide with ENSO. Thus, space weather patterns may
- 47 help explain terrestrial biological phenomena that occur at quasi-decadal scales.

48 **Global climate oscillations and variation tropical forest reproduction:**

49 Interannual fluctuations in global climate, such as ENSO (McPhaden et al. 2006;
50 Moy et al. 2002; Power et al. 2013; Vecchi et al. 2006), influence tropical forest energy
51 flux (e.g. change in forest temperature or rates of nutrient cycling, Malhi and Wright
52 2004, Levin et al. 2018) including biomass accretion (Phillips et al. 1998), carbon
53 dynamics (Brienen et al. 2015), and reproductive phenologies of tropical trees (Chang -
54 Yang et al. 2016; Lasky et al. 2016; Pau et al. 2018; Wright and Calderón 2006;
55 Zimmerman et al. 2007; Zimmerman et al. 2018). As tropical forests account for
56 approximately one-third of the global carbon cycle (Beer et al. 2010, Pan et al 2011),
57 understanding how such interannual climate drivers affect their reproduction is
58 important for long-term projections of tropical forests dynamics, including their carbon
59 storage potential. Changes in the local environment, such as solar irradiance,
60 temperature, and precipitation, only partly describe the variability in leaf and
61 reproductive phenologies of tropical trees (Chapman et al. 2018; Chen et al. 2018;
62 Lasky et al. 2016; Wright and Calderón 2018). A positive ENSO anomaly increases soil
63 moisture deficit, solar radiation, and vapor pressure deficit (Detto et al. 2018; He et al.
64 2018), during which, tropical trees exhibit increased reproduction (Chang - Yang et al.
65 2016; Pau et al. 2018; Wright and Calderón 2006; Zimmerman et al. 2018). For
66 example, the masting of Asian Dipterocarps in ENSO years can increase up to 8-fold
67 from non-ENSO years (Curran and Leighton 2000; Chen et al. 2018).

68 Yet, how can it be that species mast at the regional and global scales (Koenig
69 and Knops 1998)? How can forests from across the world respond similarly to global-
70 scale interannual climate cycles like ENSO (Asner et al. 2000)? If it were merely a

71 function of resource allocation within trees and response to local abiotic-environmental
72 drivers, one would predict canopy-damaging disturbance, e.g. frost events (Chang -
73 Yang et al. 2016), or hurricanes (Zimmerman et al. 2018), to disrupt the coordination of
74 ENSO and increased reproductive activity among forests. Yet globally, despite
75 disturbance, trees coordinate resource allocation to maximize reproductive effort that
76 coincides almost perfectly with the timing of environmental conditions conducive to high
77 rates of seed survival and germination (i.e. the high light and dry conditions of a positive
78 ENSO). We posit that trees can anticipate ENSO using a yet undetermined
79 physiological cue, which is related to a physical energy increase in the Earth's
80 magnetosphere and upper atmosphere.

81 On one hand, tropical trees may be adapted to trade-off the timing of leaf flush
82 and fruiting phenologies to maximize the exploitation of solar insolation by new leaves
83 with the investment of sugars into fruits under dry conditions to avoid drought stress
84 (Detto et al. 2018). A developing ENSO event may trigger a switch in resource
85 investment from leaves to flower and fruits. On the other, by synchronizing an
86 increased volume of fruit production among individuals or species across years, the per-
87 seed cost of negative density-dependent effects, such as exposure to fungal pathogens
88 or seed predation, is minimized (Curran and Leighton 2000; Janzen 1970; Pearse et al.
89 2016). There is an inherent fitness implication to this adaptive behavior at the
90 population and community scales (Crawley and Long 1995; Kelly et al. 2000), and
91 evolution may have selected for species with higher sensitivity to phenological cues that
92 result in community synchrony in reproduction via increased survival of their seeds.
93 However, in regard to reproductive effort (i.e. timing and output), individual trees are

94 likely insensitive to the benefits of post-fruit production density-dependent effects
95 (Connell and Green 2000; Crawley and Long 1995; Salisbury 1942), and the gestation
96 time for most tropical fruits is several months, suggesting a separate abiotic cue that
97 allows them to forecast the onset of ENSO. We contend that this cue may be
98 electromagnetic or energetic in nature and is likely mediated through subtle changes in
99 the Earth's upper atmosphere and magnetosphere (i.e. temperature, vapor pressure,
100 atmospheric conductivity) that results from increased energy input from the solar wind.

101 **The solar wind and the El Niño Southern Oscillation**

102 Recently, using a new modeling approach for solar wind dynamics, He et al.
103 (2018) discovered both a 2-4-year interannual and 11-year quasi-decadal periodicity in
104 E_{in} . They further identified a statistically significant relationship between the mean
105 annual strength of the solar wind and subsequent early winter ENSO onset, concluding
106 that increased E_{in} leads to cascading changes to the Earth's atmospheric and oceanic
107 currents. Such cascading effects include a weakening in the Walker circulation
108 (Rasmusson and Carpenter 1982b, He et al. 2018; Vecchi et al. 2006) and a
109 strengthening in the Bjerknes feedback (Rasmusson and Carpenter 1982b, He et al.
110 2018; McPhaden et al. 2006), which allow a positive ENSO to develop, however, these
111 climate feedbacks have not, as of yet, been undoubtedly linked to positive anomalies in
112 the solar wind energy flux into the Earth system (Hocke 2009) or to plant lifecycles in
113 any capacity. From 1964 to 2013, positive anomalies in E_{in} preceded the onset of sea
114 level pressure and Walker circulation anomalies by several months to a year (He et al.
115 2018). Moreover, tropical cyclone and geomagnetic activity have been linked to E_{in}
116 positive anomalies potentially via uneven heating of the thermosphere (80-100 km

117 above sea level) from increased solar wind activity (Li et al 2018). This describes a
118 potential mechanism by which tropical trees may anticipate ENSO and adds to evidence
119 that solar wind-Earth system interactions may potentially drive interannual and quasi-
120 decadal fluctuations in the Earth's climate, including ENSO (Hocke 2009).

121 Simple time series correlations between the community phenological response
122 (the number of species in fruit or flower) for two extensively-studied Neotropical forests,
123 Barro Colorado Island (BCI), Panama and Luquillo, Puerto Rico have revealed negative
124 lags, particularly with respect to temperature (Wright and Calder 2006; Zimmerman
125 et al. 2007; Zimmerman et al. 2018). Thus, it is reasonable to consider that tropical
126 trees anticipate ENSO irrespective of any cue in the immediate environment (although
127 the cue may be environmentally regulated to some degree through potential positive or
128 negative feedbacks); i.e. to maximize fruit production by the time an ENSO has fully
129 developed, trees must anticipate the event and shift the allocation of resources to
130 reproduction well in advance of local environmental changes. Based on these
131 observations, we propose a new hypothesis that integrates space weather.

132 **Hypothesis**

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

135 *due to positive energy anomalies in solar wind energy and its interaction with the*
136 *Earth system's upper atmosphere (the magnetosphere and thermosphere),*
137 *tropical trees are physiologically cued to shift resource allocation away from*
138 *photosynthesis and growth and toward maximum fruit production in preparation*
139 *for the favorable environmental conditions that will develop during ENSO.*

140 We posit that the physiological mechanism by which tropical trees are cued is linked to
141 changes in tropical atmospheric circulation currents, temperature, vapor pressure which
142 feedback to affect soil moisture (i.e. land-atmospheric coupling) that are possibly driven
143 by solar wind anomalies. Atmospheric conditions and soil moisture are both affected
144 under positive ENSO conditions (Rasmusson & Carpenter 1982a, Sun et al. 2014; Detto
145 et al. 2018, Levin et al. 2018), and have feedbacks on tropical forest productivity (Asner
146 et al. 2000, Levin et al. 2018), therefore it is reasonable to hypothesize they may exert
147 some effect on tropical forest reproduction. Next, we provide a case study that
148 illustrates a stronger correlative relationship to solar-wind energy anomalies than ENSO
149 itself, as preliminary evidence.

150 **Methods:**

151 *Measuring forest phenology using seed traps at Luquillo*

152 Fortnightly surveys of all plant reproductive parts were conducted for 120
153 stationary traps located in the 16-ha Luquillo Forest Dynamics Plot (18°20' N, 62°49' W)
154 in the northwest section of the Luquillo Experimental Forest in eastern Puerto Rico from
155 March 1992 through 2015. The forest community at Luquillo is a Caribbean subtropical
156 montane forest (below 600 m.a.s.l.) dominated by the palm *Prestoea acuminata* var.
157 *montana* (Graham) A.J.Hend. & Galeano and *Dacryodes excelsa* Vahl. (Burseraceae),
158 with a species richness of 44 tree species per ha ≥ 1 cm diameter at 1.3 m height
159 (Thompson et al. 2002). Flower presence-absence and seed and fruit abundances are
160 recorded by species for each trap. Fruits were converted to seed abundances using the
161 number of seed per fruit determined for each species (Wright and Calderón 2006;
162 Zimmerman et al. 2007). We limit analyses to species that were recorded in greater

163 than six traps, ensuring that multiple individuals were sampled (Zimmerman et al 2007).
164 Altogether in 23 years of monitoring, 89 species were found in flower and 76 were found
165 in seed or fruit, with 71 species recorded in both flower and fruit (Zimmerman et al.
166 2018). Seed-trap size was increased from 0.16 to 0.5 m² in 2006, and traps were run
167 concurrently for a year. Seed abundances from the smaller traps were corrected based
168 on the slope of the regression for pairwise flower presences (1.26) and seed
169 abundances (1.61, for additional details see methods in Zimmerman et al. 2018).

170 *Wavelet analysis*

171 We used a continuous multivariate Morlet wavelet transformation to calculate the time-
172 scale of coherent patterns in community flower and seed abundances. Wavelet
173 analysis allows for the identification of synchronous and compensatory trends at the
174 scale of climate oscillation recurrence (i.e. time scales greater than one year; the scale
175 was specified from 0.5 to 10 years for the analysis). The continuous multivariate
176 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
177 function and $x_k(\tau)$ is the presence count of flowers or abundance of seeds for the k^{th}
178 species at time τ , and s is wavelet scale. The Morlet wavelet function used is (Morlet et
179 al. 1982): $\varphi(t) = \pi^{-\frac{1}{4}} e^{(2\pi i t - \frac{1}{2} t^2)}$. Once data are in wavelet form, one can compute
180 wavelet modulus ratio, a measure of time series coherency at a given time scale,
181 represented by the coefficient of the aggregate temporal variation over the marginal
182 temporal variation of individual species. Coherency via the wavelet modulus ratio was
183 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 $\Lambda_{t,s}(\cdot) =$

184 $\int_{-\infty}^{\infty} e^{-\frac{1}{2} \left(\frac{t-\tau}{s}\right)^2} (\cdot) d\tau$ and $|\cdot|$ is the complex norm (i.e. modulus of a complex number) (Keitt

185 2008; 2014). Wavelet modulus ratios near 1 correspond to community synchrony, while
186 ratios near 0 show community compensation. Statistical significance was determined
187 using a phase-randomization, non-parametric bootstrapping method using 999
188 randomizations, where the observed wavelet modulus ratio was compared to a null
189 distribution in which wavelet scale and response variables are randomized (wmr.boot
190 function in Keitt 2014). Analyses were carried out in R v.3.2.5 (R Core Team 2016)
191 using the 'mvcwt' package (Keitt 2014).

192 *Seasonal detrending of the phenology data and correlations with solar wind and climate*
193 *indices*

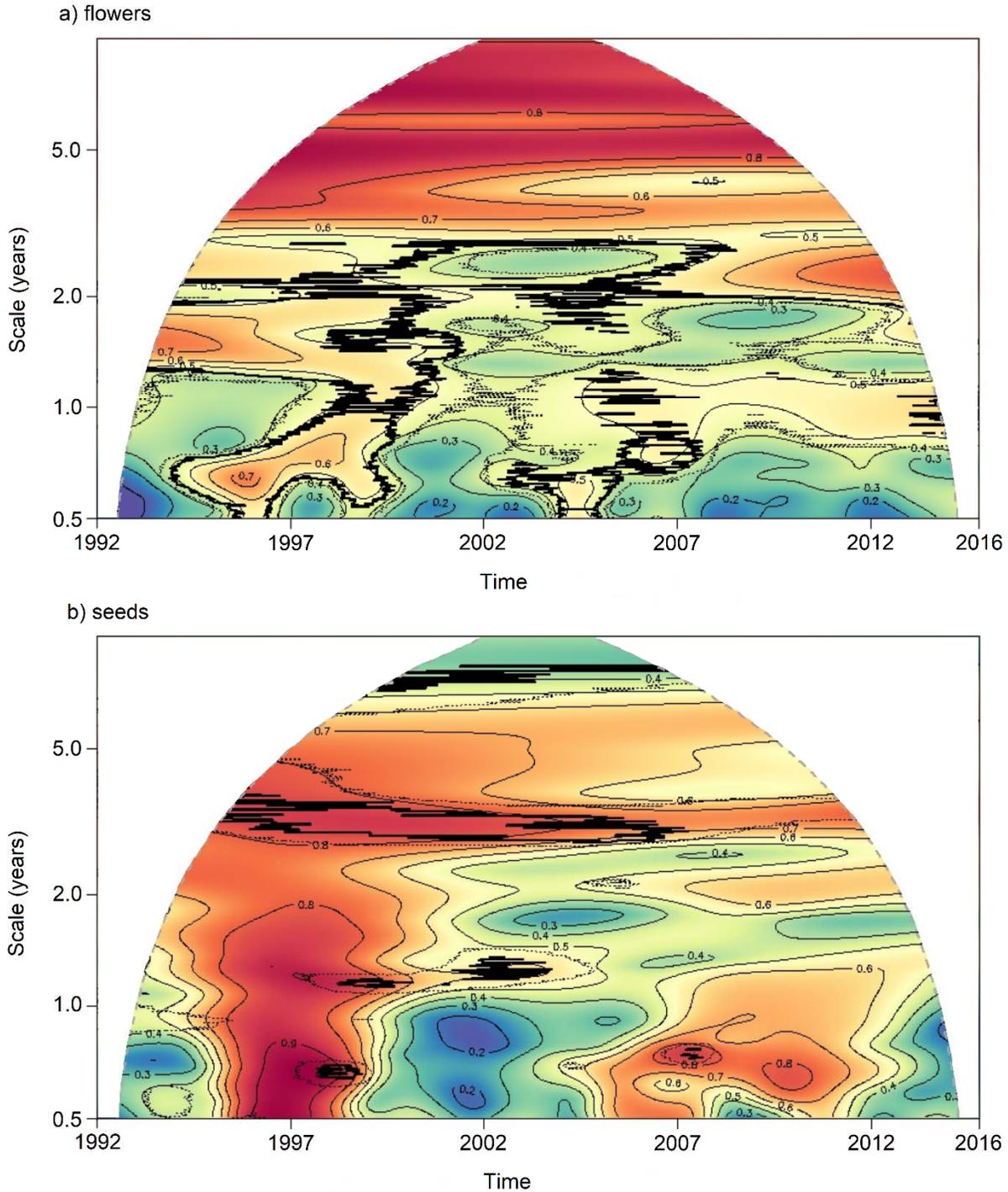
194 Using the same fortnightly survey data, the phenological response of the forest
195 was defined as the number of species in either fruit or flower at the monthly-scale,
196 because that is the scale for ENSO climate indices. We seasonally detrended monthly
197 time series of the number of species in flower and seed using seasonal-trend
198 decomposition by loess (Cleveland et al. 1990; see Appendix 2 of Zimmerman et al.
199 2018). From the trend, annual open, high, low, close (OHLC) moving averages were
200 computed. We obtained annual normalized E_{in} values from 1993-2012 from He et al.
201 (2018). Space weather data on sunspot number (SSN), the solar radio frequency at
202 10.7 cm (F107), and total solar irradiation (TSI) were downloaded from the NASA
203 ONMIweb database (omniweb.gsfc.nasa.gov) and monthly Niño 3.4 data were obtained
204 from NOAA (esrl.noaa.gov/psd/enso/dashboard.html). SSN, F107, and TSI are
205 commonly used as proxies for solar weather activity, which is primarily a function of the
206 surface mixing of Sun and solar flaring activity. We compared the OHLC moving
207 averages to annualized mean anomalies for E_{in} , SSN, F107, TSI, and ENSO 3.4 from

208 1992-2012. All indices were normalized, and the average annual anomaly was
209 calculated. Pearson correlations between the seasonally-detrended OHLC (open, high,
210 low, close) average of the number of species in flower or seed and the normalized
211 anomaly for the E_{in} and ENSO 3.4 were done using annual data from 1993-2012 (df =
212 18).

213 **Results:**

214 *Assessing the interannual synchrony in tropical tree reproductive output*

215 To help visualize the community composition of fruits and flowers, and display
216 time-scales at which coherency occurs, we present a Morlet wavelet analysis of flower
217 and fruit abundances. It illustrates supra-annual coherency in a 22-year time series of
218 flower and fruit production at Luquillo (Fig. 1). Community synchrony in flower and seed
219 production occurred at the interannual scales consistent with ENSO. This occurred
220 despite a large disturbance in September 1998, Hurricane Georges which nullified
221 flower and fruit production of the community for roughly three months. More temporally-
222 consistent community synchrony is evident for flowers than for seeds (Fig. 1a) and
223 extended from a timescale of ca. 2 years and beyond. The entire top portion of Fig. 1a
224 is statistically significant as the bold lines delimiting areas of significance using $\alpha=0.05$
225 do not connect along the upper boundary. For seed production, the strongest
226 community synchrony occurs between 2 and 5 years and is strongest during the 1997-
227 1998 ENSO (Fig. 1b). Therefore, flower production in the community is regularly
228 synchronized, but seed production is only synchronized interannually and coincides with
229 the timing and periodicity of ENSO.



230

231 **Figure 1:** Morlet wavelet modulus ratios over time using seed trap abundances of (a)

232 flowers and (b) seeds for the tree community of the Luquillo Forest Dynamics Plot,

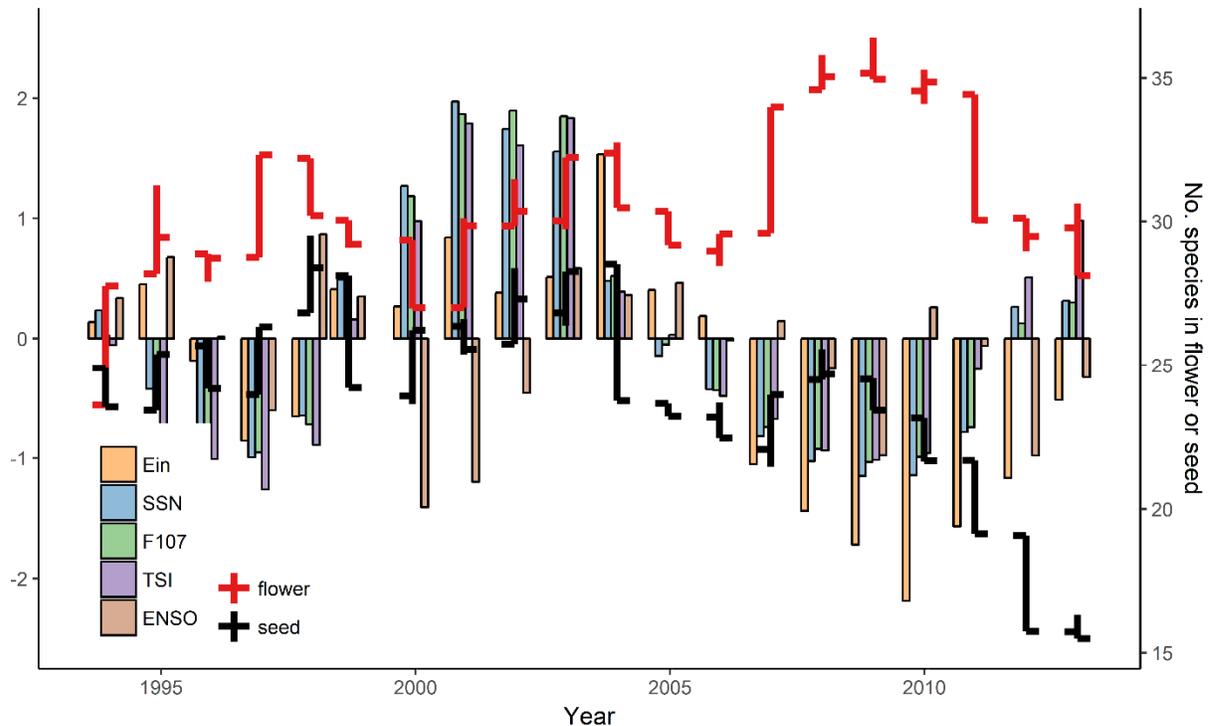
233 Puerto Rico. The vertical axis (log scale) represents the scale of the Morlet wavelet

234 modulus, ranging from a half to 10 years. Colors within the heatmaps denote the
235 magnitude of the wavelet modulus ratio scaled from 0 (dark blue) corresponding to
236 strong compensatory dynamics to 1 (dark red) denoting strong community synchrony.
237 Note that the community synchrony (i.e. the red area) extends down to the smallest
238 scale in Fig. 1b, illustrating the effect of Hurricane Georges in 1998. Contours are
239 wavelet modulus ratio-magnitude isotherms. Dotted and bold lines delimit areas of
240 statistical significance at $\alpha = 0.1$ and 0.05 , respectively using 999 bootstrapped
241 resamples (see Methods).

242

243 *Correlation of forest reproduction with the solar wind energy flux*

244 In this context, we were interested in preliminarily exploring how E_{in} related to
245 forest-level flower and seed production. In previous work, ENSO 3.4 was the strongest
246 correlated El Niño-related climate index to the phenology of the trees in Luquillo
247 (Zimmerman et al. 2018). Pearson correlations between the normalized annual E_{in}
248 anomalies and open, high, low, close (OHLC) annual average of the seasonally-
249 detrended number of species in flower ($r = -0.635$, $t = -3.48$, $df = 18$, $p = 0.0026$) and
250 seed ($r = 0.443$, $t = 2.97$, $df = 18$, $p = 0.0504$) were both statistically significant. Those
251 relationships were stronger than their respective correlations with normalized annual
252 anomalies of ENSO 3.4 (flowers: $r = 0.019$, $t = 0.08$, $df = 18$, $p = 0.938$, seeds: $r = 0.253$,
253 $t = 1.11$, $df = 18$, $p = 0.28$). Correlations of other measures of space weather activity
254 (SSN, F107, and TSI) with the OHLC annual average of the seasonally-detrended
255 annual number of species in flower or seed were like those of E_{in} , but slightly weaker
256 (Fig. 2).



257

258 **Figure 2:** Annual normalized E_{in} , SSN, F107, TSI and ENSO 3.4 indices from 1993-
259 2013 with OHLC (Open: left facing horizontal line, High: maximum of annual range, Low:
260 minimum, Close: right facing horizontal line) bars for the seasonally-detrended number
261 of species in flower (red) or seed (blue) at Luquillo, Puerto Rico. Years in which fewer
262 species producing seed coincide with years with negative normalized index values
263 related to solar energy flux into the atmosphere (E_{in} , SSN, TSI, and F107) (i.e. less
264 energy input from the solar wind into the Earth system). See supplement for complete
265 lagged time-series correlations.

266

267 **Concluding remarks**

268 The community synchrony in the abundance of flowers and fruits counts at 4-6-
269 year timescales is consistent with recurring ENSO positive anomalies (Fig.1). Therefore,
270 the signal of ENSO on community synchrony in the reproductive effort of tropical trees

271 in Luquillo exists despite a dynamic tree community situated in an aseasonal,
272 disturbance-affected forest (Hogan et al. 2016; Hogan et al. 2018; Zimmerman et al.
273 2007). A positive ENSO has no effect on rainfall at Luquillo but decreases temperature
274 (strongest relationship at 2 to 4-month lead, i.e. before ENSO) and increases solar
275 radiation (photosynthetic photon flux density, strongest relationship at 7-month lag)
276 (Zimmerman et al. 2018). Luquillo is considerably wetter (no month receives <100mm
277 of rainfall) and less seasonal than many tropical forests (e.g., BCI), where ENSO can
278 interact with seasonal dynamics to strengthen or lengthen the dry season (Detto et al.
279 2018). At the annual scale at Luquillo, relationships with measures of solar wind energy
280 more closely tracked the number of species in flower or seed over time than the ENSO
281 3.4 anomalies (Fig. 2). E_{in} was found to have no statistically significant relationship with
282 either annual total rainfall or average temperatures (minimum or maximum) yet was
283 strongly related to flower and seed reproductive effort of trees, potentially supporting the
284 idea that changes in global atmospheric circulations relate to interannual variation in
285 reproductive effort of tropical forests.

286 In conclusion, the roughly 1-year lagged E_{in} -ENSO teleconnection occurs most
287 strongly over the eastern Indo-Pacific, creating strongly anomalous Walker circulation
288 diverge there and several convergence centers over the Northeastern Pacific
289 (Rasmussen and Carpenter 1982b, He et al. 2018). These global-scale changes in
290 atmospheric conditions that extend at least 1000 km above the Earth's surface (He et al.
291 2018), can be linked to climate, geomagnetic energy and global cyclonic activity (Li et al.
292 2018). ENSO acts as an established global climatic driver of supra-annual cycles in
293 tropical tree phenology (Chang - Yang et al. 2016; Pau et al. 2018; Wright and

294 Calderón 2006; Zimmerman et al. 2018, Detto et al. 2018). The mechanism behind the
295 interannual increase in reproductive effort of tropical trees is difficult to identify, owing to
296 the subtlety and complexity of climatic teleconnections, and the need for long-term
297 records of forest reproduction (Abernethy et al. 2018; Pearse et al. 2016; Wright and
298 Calderón 2018). At Luquillo after accounting for seasonal variation, a positive E_{in}
299 anomaly results in fewer species producing flowers, but an increase in species
300 producing seed (Fig. 2). At Luquillo, these patterns appear to be influenced by negative
301 trends in solar energy flux and declines in seeds production after 2005.

302 Whether this relationship holds at other Neotropical sites remains to be investigated. At
303 BCI, Panama, similar coherency in community reproduction and leaf flush have been
304 observed at 4-7-year timescales (Detto et al. 2018), pointing to the widespread effect of
305 ENSO on tropical tree reproductive effort. However, in contrast to Luquillo, there have
306 been steady increases in fruit and flower production over the 28-year record at BCI (Pau
307 et al. 2018). Notably, we identified no effects between E_{in} and temperature or
308 precipitation for Luquillo using annual data, although previous work has shown ENSO to
309 affect temperature and solar radiation at the sub-annual (i.e. monthly) scale. Likely the
310 interactions between fluctuations in energy into the Earth system from the solar wind
311 and tropical tree reproduction are complex and occur at timescales finer than the annual
312 scale as the solar wind intensity fluctuates with solar activity. Thus, finer temporal
313 resolution in the analysis may prove to be insightful. Furthermore, individual species
314 probably vary in their sensitivity to solar wind energy flux. Future research should work
315 to identify how solar wind energy flux and other measures of solar weather influence
316 tropical tree phenology at broader spatial and temporal scales.

317

318 **Acknowledgments:**

319 We thank Drs. Shengping He, and Hui Li from the Key Lab for Space Weather at the
320 Chinese Academy of Sciences for sharing the E_{in} data and providing insights.

321 **Funding information:**

322 The Luquillo Forest Dynamics Plot is funded by the University of Puerto Rico, US NSF
323 through the LTER Program (grants BSR-8811902, DEB-9411973, DEB-9705814, DEB-
324 0080538, DEB-0218039, DEB-0620910, and DEB-1516066), the USDA International
325 Institute for Tropical Forestry, the Mellon Foundation and The Center for Tropical Forest
326 Science (Forest-GEO) at the Smithsonian.

327 **Data availability:**

328 Data on the phenology of trees and shrubs from the Luquillo Forest Dynamics Plot can
329 be found on the Luquillo LTER website: dataset 88:

330 <http://luq.lter.network/data/luqmetadata88>

331 **References:**

332 Abernethy KE, Bush R, Forget PM, Mendoza I, Morellato LPC. 2018. Current issues in tropical
333 phenology: a synthesis, *Biotropica* 50: 477-482.

334 Asner GP, Townsend AR, Braswell BH. 2000. Satellite observation of El Nino effects on
335 Amazon forest phenology and productivity, *Geophysical Research Letters* 27:981-984.

336 Beer C, Reichstein M, Tomelleri E, Ciais P, Jung M, Carvalhais N, Rödenbeck C, Arain MA,
337 Baldocchi D, Bonan GB, Bondeau A. 2010. Terrestrial gross carbon dioxide uptake:
338 global distribution and covariation with climate, *Science* 329:834-838.

- 339 Chang-Yang CH, Sun IF, Tsai CH, Lu CL, Hsieh CF. 2016. ENSO and frost codetermine
340 decade-long temporal variation in flower and seed production in a subtropical rain forest,
341 *Journal of Ecology* 104:44-54.
- 342 Chapman CA, Valenta K, Bonnell TR, Brown KA, Chapman LJ. 2018. Solar radiation and ENSO
343 predict fruiting phenology patterns in a 15-year record from Kibale National Park,
344 Uganda, *Biotropica* 50:384-395.
- 345 Chen YY, Satake A, Sun IF, Kosugi Y, Tani M, Numata S, Hubbell SP, Fletcher C, Nur Supardi
346 MN, Wright SJ. 2018. Species-specific flowering cues among general flowering Shorea
347 species at the Pasoh Research Forest, Malaysia, *Journal of Ecology* 106:586-598.
- 348 Cleveland RB, Cleveland WS, McRae JE, Terpenning I. 1990. STL: A Seasonal-Trend
349 Decomposition, *Journal of Official Statistics* 6:3-73.
- 350 Connell JH, Green PT. 2000. Seedling dynamics over thirty-two years in a tropical rain forest
351 tree, *Ecology* 81:568-584.
- 352 Crawley M, Long C. 1995. Alternate bearing, predator satiation and seedling recruitment in
353 *Quercus robur* L, *Journal of Ecology* 83:683-696.
- 354 Curran LM, Leighton M. 2000. Vertebrate responses to spatiotemporal variation in seed
355 production of mast-fruiting Dipterocarpaceae, *Ecological Monographs* 70:101-128.
- 356 Detto M, Wright SJ, Calderón O, Muller-Landau HC. 2018. Resource acquisition and
357 reproductive strategies of tropical forest in response to the El Niño–Southern Oscillation,
358 *Nature Communications* 9:913.
- 359 He SP, Wang HJ, Gao, YQ, Li F, Li H, Wang C. 2018. Influence of solar wind energy flux on the
360 interannual variability of ENSO in the subsequent year, *Atmospheric and Oceanic*
361 *Science Letters* 11:165-172.
- 362 Hocke, K. 2009. QBO in solar wind speed and its relation to ENSO, *Journal of Atmospheric and*
363 *Solar-Terrestrial Physics* 71:216-220.

- 364 Hogan JA, Zimmerman J, Thompson J, Uriarte M, Swenson N, Condit R, Hubbell S, Johnson D,
365 Sun IF, Chang-Yang CH. 2018. The frequency of cyclonic wind storms shapes tropical
366 forest dynamism and functional trait dispersion, *Forests* 9:404.
- 367 Hogan JA, Zimmerman JK, Thompson J, Nytech CJ, Uriarte M. 2016. The interaction of land-use
368 legacies and hurricane disturbance in subtropical wet forest: twenty-one years of change,
369 *Ecosphere* 7:e01405.
- 370 Janzen DH. 1970. Herbivores and the number of tree species in tropical forests, *The American*
371 *Naturalist* 104:501-528.
- 372 Keitt, TH. 2008. Coherent ecological dynamics induce by large-scale disturbance, *Nature*
373 454:331-334.
- 374 Keitt TH. 2014. mvcwt: wavelet analysis of multiple time series, <https://github.com/thk686/mvcwt>.
- 375 Kelly D, Harrison AL, Lee WG, Payton IJ, Wilson PR, Schauber EM. 2000. Predator satiation
376 and extreme mast seeding in 11 species of *Chionochloa* (Poaceae), *Oikos* 90:477-488.
- 377 Koenig WD, Knops JM. 1998. Scale of mast-seeding and tree-ring growth, *Nature* 396:225.
- 378 Lasky JR, Uriarte M, Muscarella R. 2016. Synchrony, compensatory dynamics, and the
379 functional trait basis of phenological diversity in a tropical dry forest tree community:
380 effects of rainfall seasonality, *Environmental Research Letters* 11:115003.
- 381 Levin P, Randerson J, Chen Y, Pritchard M, Xu M, Hoffman F. 2018. Soil moisture variability
382 intensifies and prolongs Eastern Amazon temperature and carbon cycle responses to El
383 Niño-Southern Oscillation, *Journal of Climate* doi: 10.1175/JCLI-D-18-0150.1
- 384 Li H, Wang C, He S, Wang H, Tu C, Xu J, Li F, Guo X. 2018. Plausible modulation of solar wind
385 energy flux input on global tropical cyclone activity, *Journal of Atmospheric and Solar-*
386 *Terrestrial Physics*.
- 387 Malhi Y, Wright SJ. 2004. Spatial patterns and recent trends in the climate of tropical rainforest
388 regions, *Philosophical Transactions of the Royal Society of London B: Biological*
389 *Sciences* 359:311-329.

- 390 McPhaden MJ, Zebiak SE, Glantz MH. 2006. ENSO as an integrating concept in earth science,
391 *Science* 314:1740-1745.
- 392 Morlet J, Arens G, Farge E, Ghil M, Gnaud P. 1992. Wave propagation and sampling theory—Part I:
393 Complex signal and scattering in multilayered media, *Geophysics* 47:203-221.
- 394 Moy CM, Seltzer GO, Rodbell DT, Anderson DM .2002. Variability of El Niño/Southern
395 Oscillation activity at millennial timescales during the Holocene epoch, *Nature* 420:162.
- 396 Pan Y, Birdsey RA, Fang J, Houghton R, Kauppi PE, Kurz WA, Phillips OL, Shvidenko A, Lewis
397 SL, Canadell JG, Ciais P, Jackson RB, Pacala SW, McGuire AD, Piao S, Rautainen A,
398 Sitch S, Hays D. 2011. A Large and Persistent Carbon Sink in the World's Forests,
399 *Science* 333,988-993.
- 400 Pau S, Okamoto DK, Calderón O, Wright SJ. 2018. Long-term increases in tropical flowering
401 activity across growth forms in response to rising CO₂ and climate change, *Global*
402 *Change Biology* 24:2105-2116.
- 403 Pearse IS, Koenig WD, Kelly D. 2016. Mechanisms of mast seeding: resources, weather, cues,
404 and selection, *New Phytologist* 212:546-562.
- 405 Phillips OL, Malhi Y, Higuchi N, Laurance WF, Núñez PV, Vásquez RM, Laurance SG, Ferreira
406 LV, Stern M, Brown S. 1998. Changes in the carbon balance of tropical forests: evidence
407 from long-term plots, *Science* 282:439-442.
- 408 Power S, Delage F, Chung C, Kociuba G, Keay K. 2013. Robust twenty-first-century projections
409 of El Niño and related precipitation variability, *Nature* 502:541.
- 410 Rasmusson EM, Carpenter TH. 1982a. The Relationship Between Eastern Equatorial Pacific
411 Sea Surface Temperature and Rainfall over India and Sri Lanka, *Monthly Weather*
412 *Review*, 111: 517-528.
- 413 Rasmusson EM, Carpenter TH. 1982b. Variations in Tropical Sea Surface Temperature and
414 Surface Wind Fields Associated with the Southern Oscillation/ El Niño, *Monthly Weather*
415 *Review*, 110: 354-384.

- 416 R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for
417 Statistical Computing, Vienna, Austria. <http://www.r-project.org>
- 418 Salisbury EJ. 1942. *The reproductive capacity of plants. Studies in quantitative biology.* G Bell &
419 Sons, London.
- 420 Sun Y-Y, Liu J-Y, Tsai H-F, Lin C-H, Kuo Y-H. 2014. The Equatorial El-Niño Oscillation
421 Signatures Observed by FORMOSAT-3/COSMIC from July 2006 to January 2012,
422 *Terrestrial, Atmospheric, and Oceanic Sciences Journal* 25:545-558.
- 423 Thompson J, Brokaw N, Zimmerman JK, Waide RB, Everham III EW, Lodge DJ, Taylor C,
424 Garcia-Montiel D, Marcheterre F. 2002. Land Use History, Environment, and Tree
425 Composition in a Tropical Forest, *Ecological Applications* 12:1344-1363.
- 426 Vecchi GA, Soden BJ, Wittenberg AT, Held IM, Leetmaa A, Harrison MJ. 2006. Weakening of
427 tropical Pacific atmospheric circulation due to anthropogenic forcing, *Nature* 441:73.
- 428 Wright SJ, Calderón O. 2006. Seasonal, El Niño and longer term changes in flower and seed
429 production in a moist tropical forest, *Ecology Letters* 9:35-44.
- 430 Wright SJ, O. Calderón 2018. Solar irradiance as the proximate cue for flowering in a tropical
431 moist forest, *Biotropica* 50:374-383.
- 432 Zimmerman JK, Hogan JA, Nycth CJ, Bithorn JE. 2018. Effects of hurricanes and climate
433 oscillations on annual variation in reproduction in wet forest, Puerto Rico. *Ecology*
434 99:1402:1410.
- 435 Zimmerman JK, Wright SJ, Calderón O, Pagan MA Paton S. 2007. Flowering and fruiting
436 phenologies of seasonal and aseasonal neotropical forests: the role of annual changes
437 in irradiance, *Journal of Tropical Ecology* 23: 231-251.