



# The effects of seasonal and long-term climatic variability on Neotropical flowering phenology: An ecoinformatic analysis of aerial pollen data



Derek S. Haselhorst<sup>a</sup>, David K. Tcheng<sup>b</sup>, J. Enrique Moreno<sup>c</sup>, Surangi W. Punyasena<sup>a,d,\*</sup>

<sup>a</sup> Program in Ecology, Evolution and Conservation Biology, University of Illinois, Urbana, IL, United States

<sup>b</sup> Illinois Informatics Institute, National Center for Supercomputing Applications, University of Illinois, Urbana, IL, United States

<sup>c</sup> Center for Tropical Paleocology and Archaeology, Smithsonian Tropical Research Institute, Panama, Panama

<sup>d</sup> Department of Plant Biology, University of Illinois, Urbana, IL, United States

## ARTICLE INFO

### Keywords:

Climate  
Ecology  
Ecoinformatics  
Palynology  
Phenology  
Pollen

## ABSTRACT

The phenological behavior of tropical forests changes in response to seasonal, annual, and long-term variation in temperature, precipitation, and solar irradiance. However, detecting the respective influence of these variables is difficult due to the relatively small range of change that is observed in the tropics. Analysis is further constrained by the limited duration of many phenological datasets. To address these limitations, we developed a predictive ecoinformatic model using multivariate linear regression and slope correlation analysis that can uncover statistically significant biological responses within short, noisy ecological time series. Our approach correlates all possible combinations of climatic and taxonomic variables using a series of random determination trials on shuffled environmental data. Seasonal and annual fluctuations in temperature, precipitation, and sunlight were used to predict the reproductive response of each individual taxon. This predictive model was applied to two seasonally sampled aerial pollen records collected between 1996 and 2006 from two Panamanian forests, Barro Colorado Island and Parque Nacional San Lorenzo. Our results highlight the degree to which pollen output responds to fine-scale variability in climate. Our results lend support to the hypothesis that the pollen output of tropical species is diminished with prolonged periods of heavy rainfall and that pollen output is sensitive to small, seasonal increases in temperature. Our ecoinformatic approach can be expanded to other observational phenological datasets to better understand how communities will respond to climate change and our results demonstrate the ability of aerial pollen data to track long-term changes in flowering phenology.

## 1. Introduction

Changes in the magnitude and timing of phenological events represent some of the most sensitive and most obvious biological responses to climate change (Caradonna et al., 2014; Pau et al., 2011). In plant communities, reproductive changes in response to seasonal and annual increases in temperature are not uniform across species, leading to changes in community composition over time (Caradonna et al., 2014). Long-term observations are needed to more accurately assess the relationship between phenological patterns and climate across different systems, as the response of individual species can be used to help predict how populations may expand or decline in the future (Miller-Rushing and Primack, 2008; Parmesan and Yohe, 2003). Furthermore, temporal shifts in the timing of plant reproductive events can have cascading effects, disrupting the timing of biological interactions and life histories of organisms across multiple trophic levels (Hegland et al., 2009; Yang and Rudolf, 2010).

In temperate communities, phenological events ranging from spring flowering to avian migration and pollinator activity are well-documented as occurring earlier than they did in the past for many species (Bertin, 2008; Chambers et al., 2013; Miller-Rushing and Primack, 2008). A comparison of first flowering dates in 296 taxa using historical and modern records collected from Concord, Massachusetts from 1852 to 2006 revealed that, on average, plants are flowering 3.3 days earlier for every 1 °C increase in mean monthly temperature (Miller-Rushing and Primack, 2008). However, for tropical latitudes, characterized by small variations in intra-annual temperature, environmental controls on the reproductive behavior of taxa are not as well understood. One prediction is that tropical species will be forced to shift their ranges or adapt in response to warmer temperatures, whereas temperate species will be more likely to respond by shifting phenological events in time (Pau et al., 2011; Wright et al., 2009). The uncertainty in the sensitivity of tropical species to changes in temperatures or precipitation stems from the paucity of long-term empirical phenological data across

\* Corresponding author at: 139 Morrill Hall, 505 S. Goodwin Ave., Urbana, IL 61801, United States.  
E-mail address: [punyasena@life.illinois.edu](mailto:punyasena@life.illinois.edu) (S.W. Punyasena).

<http://dx.doi.org/10.1016/j.ecoinf.2017.06.005>

Received 15 January 2017; Received in revised form 21 June 2017; Accepted 26 June 2017

Available online 12 July 2017

1574-9541/ © 2017 Elsevier B.V. All rights reserved.

different habitats (e.g. Pau et al., 2013). This underscores the need for continued ecological monitoring of flowering events in tropical communities in a warming world (Wolkovich et al., 2012).

An overlooked source of flowering frequency data comes from aerial pollen traps. Environmental pollen networks capture airborne pollen, which correlate with anthesis, the period when floral buds are fully developed and open. A limited number of studies have used long-term pollen rain data to study flowering phenology, substituting pollen counts for visual assessments of flowering. Examples include a 33-year pollen time series from Denmark used to analyze pollen-climate relationships and an extensive 31-year pollen record from the Netherlands (Nielsen et al., 2010; Vliet et al., 2002). In Denmark, it was observed that inter-annual variability in pollen counts correlated with changes in precipitation and temperature, with increased pollen abundance in *Betula*, *Fagus*, *Quercus*, *Tilia*, and *Ulmus* following summers characterized by high temperatures (Nielsen et al., 2010). The Dutch study was able to reproduce observations of spring advancements in flowering using pollen data from 14 taxa (Vliet et al., 2002). Similarly, long-term tropical pollen samples can also be used to track how climate influences the seasonal and inter-annual flowering behavior of species-rich tropical forest communities (Haselhorst et al., 2013). These pollen records have the potential to greatly expand the limited observational phenological data available for tropical ecosystems.

We use pollen data in this study as a proxy for flowering phenology. We hypothesize that climatic variability will have a greater influence on pollen abundance, and therefore flowering behavior, in more seasonal tropical forest environments characterized by greater intra-annual variation in precipitation, solar irradiance, and temperature. Prior comparisons of flowering behavior between seasonally dry and aseasonal tropical forest environments using visual flowering observations have suggested that reproductive periodicity is an adaptation to increased variation in the seasonal availability of these variables (Frankie et al., 1974; Pau et al., 2013; Zimmerman et al., 2007). These studies have concluded that with increased seasonality, flowering activity is more likely to be restricted to a single season (dry or wet) in many species. Of these variables, we hypothesize temperature will exert a greater influence, as suggested by the results of a recent analysis which concluded that seasonal and long-term flowering outputs are greatest during warmer periods (Pau et al., 2013).

To test these hypotheses, we analyzed two 10-year pollen rain records from two lowland Panamanian forests characterized by differences in dry seasonality and species composition, Barro Colorado Island (BCI) and Parque Nacional San Lorenzo (PNSL). Samples were collected twice a year, at the start of the wet and dry seasons. Seasonal and annual variability in mean temperature, precipitation, and solar irradiance over the 10 years and between the two sites provide a natural experiment. However, the average climatic variation experienced at BCI and PNSL in these timeframes is relatively small, and the corresponding biological response is therefore difficult to detect using standard statistical approaches. Detecting a response is made even more challenging as aerial pollen influx data are non-normally distributed as some pollen types are represented in much greater abundance than others due to floral structure, mode of pollination syndrome, and natural reproductive variability in flowering behavior occurring over both seasonal and annual sampling intervals.

To measure correlations between natural variability in climate and observed pollen data, a predictive ecoinformatic pollen response model was developed that could both maximize the amount of ecological information derived from our relatively short, noisy pollen time series data without overestimating the strength of the relationship between our explanatory climate and pollen (taxonomic) response variables. We used an iterative multivariate linear regression machine-learning approach to identify statistically significant biological signals in our data. We developed a simple response prediction model that uses cross-validation to explore a landscape of models that correlate the phenological behavior of individual taxa with our measured climate variables:

seasonal and annual mean temperature, precipitation, and available sunlight. To address which of these predictor variables was driving the observed phenological response, we used a sign slope sensitivity analysis of each linear model that tallied positive and negative slope correlations of a taxon's phenological behavior to our environmental and null variables.

## 2. Methods

### 2.1. Study sites

Pollen data were collected from two lowland tropical forest sites in Panama: Barro Colorado Island (BCI) and Parque Nacional San Lorenzo (PNSL). Forest composition in the region is shaped by the differential water requirements of plant species, as species found on the wetter, Atlantic side of the isthmus tend to be more drought-sensitive than species on the substantially drier Pacific side (Comita and Engelbrecht, 2009; Engelbrecht et al., 2007). Across Panama, the magnitude of seasonal drought conditions also acts as one of the strongest controls on physiological growth, leaf flushing, flower, and fruit developmental patterns, limiting water transport and photosynthetic assimilate levels needed to maintain different developmental and reproductive phases in different species (Comita and Engelbrecht, 2009; Engelbrecht et al., 2007; Santiago and Mulkey, 2004; Wright et al., 1999).

BCI (09° 10'N, 79° 51'W) is a tropical moist forest centrally located within the Panama Canal in Lake Gatún. A 50-ha study plot was established on BCI in 1980, providing an exceptional setting to study long-term changes in species diversity and reproductive dynamics within a tropical plant community (Wright and Calderón, 2006). The island is characterized by a pronounced 4- to 5-month dry season, typically beginning in mid-December and ending in mid-April, sometimes extending into early May. During this time period, the island is characterized by decreased cover and diminished rainfall, sometimes receiving as little as 100 mm of its ~2600 mm of annual rainfall total (Croat, 1978; Leigh, 1999). Long-term analyses of flowering and fruiting phenology have been reported using comprehensive datasets from Barro Colorado Island, revealing marked differences in the composition and magnitude of phenological outputs in relation to seasonal and annual climatic conditions (Pau et al., 2013; Wright and Calderón, 2006; Wright and Muller-Landau, 2005; Zimmerman et al., 2007).

PNSL (09° 16'N, 79° 58' 14" W) neighbors the Atlantic entrance to the Panamá Canal, approximately 19 km to the northwest of BCI. A 5.96 ha Smithsonian Tropical Research Institute (STRI) study plot and canopy crane was established within the PNSL protected area in September of 1997 (Condit and Aguilar, 2004). PNSL is substantially wetter than BCI, receiving ~3000 mm of rainfall annually, and is characterized by temperatures ranging from 26.8 to 27.7 °C between September and April (Weaver & Bauer, n.d.; Pyke et al., 2001; Engelbrecht et al., 2007). Despite receiving more rainfall, PNSL also maintains a well-defined dry season from January through April, receiving between 42 and 125 mm of rainfall a month during this duration (Weaver and Bauer, 2004).

### 2.2. Pollen rain datasets

The BCI and PNSL pollen rain datasets were sampled seasonally using aerial pollen traps arranged vertically in 5 m increments from the forest floor. On BCI, traps were affixed to the 48-m Lutz weather tower and on PNSL, the traps were placed on the 55-m STRI canopy crane. Pollen traps were constructed following Haselhorst et al. (2013), and were set for collection at the beginning of the dry and wet seasons and collected at the end of the season. As a result, both pollen records provided a continuous sample of the aerial pollen rain that can be analyzed at both seasonal and annual time steps. Pollen traps were arranged at 5 m intervals on each tower from 0 to 45 m. Pollen samples from the 0, 5, 20, and 25 m sampling heights from both sites were

counted and analyzed. This allowed us to capture the range of compositional variability in the pollen influx in both the forest understory (0, 5 m) and canopy (20, 25 m) (Haselhorst et al., 2013).

The BCI dataset spans 11 years (1996–2006). Samples were collected each year with the exception of 1998. Previously analyzed and published pollen influx to these traps revealed a strong compositional variability in the sampled pollen rain on a seasonal and inter-annual basis (Haselhorst et al., 2013). To compare the relationship between pollen productivity and climate at PNSL to the same extent as BCI, the PNSL dataset provides a near complement to the BCI dataset (~10-years; 1997–2006). The STRI canopy crane was not established until the summer of 1997, and as a result, the PNSL pollen rain dataset lacks a 1996 sampling year and the 1997 sampling year was limited to the wet season only.

### 2.3. Pollen counts and identifications

At the end of each season, each the rayon fiber from each pollen trap was collected and transferred to Whirl-Pak bags and stored at a controlled temperature of 4 °C at STRI's Center for Tropical Palaeoecology and Archaeology (CTPA) in Panama City, Panama. At CTPA, each sample was processed according to the laboratory protocol outlined in Haselhorst et al. (2013).

Pollen counts were completed of prepared slides at 400 × magnification using a transmitted light microscope. Samples were counted until ≥ 300 identified pollen grains were tallied for each sample, at which point the remainder of each slide was scanned for rare pollen types that had yet to be recorded within the previous 300 identified grains (Haselhorst et al., 2013). We then pooled counts from all four sampling heights so that each time step analyzed included a pollen sum of ~1200 grains. This reduced the number of individual pollen sampling observations from PNSL and BCI to 10 and 11 annual, and 19 and 20 seasonal, time steps, respectively. The threshold of ≥ 300 pollen grains per sample has been used in previous analyses of the BCI pollen rain (Bush and Rivera, 1998, 2001) and other studies of tropical pollen have similarly aggregated counts from multiple pollen traps to achieve pollen sums of ≥ 500 (Burn et al., 2010; Gosling et al., 2009).

Pollen identifications were made using a guide of BCI pollen and spore types as well as previously published pollen photographs from the Lutz tower record (Haselhorst et al., 2013; Roubik and Moreno, 1991). Final pollen identifications were completed at CTPA using a pollen reference collection of over 25,000 tropical plant species. A total of 170 pollen types were recognized in the PNSL pollen rain, including 22 pollen types that could not be assigned a family, genus, or species level name. Due to morphological similarities within related taxa, most pollen identifications were made at the genus and family level. The complete list of pollen types is available from the University of Illinois' Illinois Digital Environment for Access to Learning and Scholarship (IDEALS) website (Table S1, [https://doi.org/10.13012/B2IDB-2059727\\_V1](https://doi.org/10.13012/B2IDB-2059727_V1)). To maintain consistency between the BCI and PNSL records, pollen counts from BCI were revised based on updated taxonomic classifications, totaling 138 pollen types identified.

Pollen influx was calculated using the number of exotic *Lycopodium* spores recorded in each pollen sample; a known quantity (~10,700) was added to each sample during laboratory processing (Stockmarr, 1971). To account for differences in the duration of the BCI and PNSL dry and wet seasons, pollen influx was then standardized by the number of days each trap was sampled (pollen grains/cm<sup>2</sup>/day). Similarly, annual pollen influx data was calculated by pooling pollen counts from the dry and wet seasons.

### 2.4. Meteorological datasets

Data for our three climate variables were obtained from STRI and the Panama Canal Authority (ACP) meteorological monitoring instruments. Climate data for BCI was obtained from the Lutz tower

(temperature and solar irradiance) and El Claro clearing (precipitation). Climate data for PNSL was obtained from monitoring instruments on the canopy crane. Values for temperature (°C/day; Novalynx 210-4411 standard thermometer), precipitation (mm/day; Novalynx rain gauge), and solar irradiance (MJ/m<sup>2</sup>/day; LiCor LI200X pyranometer) were averaged for the duration of each seasonal pollen sample. Annual averages are for the combined dry and wet seasons for each sampling year. Two gaps in solar irradiance and rainfall data from the canopy crane (9/25/2005–2/15/2006 and 4/20/2006–6/19/2006) were obtained from the nearest ACP meteorology and hydrology station located at the Gatún Locks (09° 16' 06" N, 79° 55' 14" W) 5.5 km away. A summary of the climatic data for each sampling period has been included in a Supplemental table (Table S2, [https://doi.org/10.13012/B2IDB-8658584\\_V1](https://doi.org/10.13012/B2IDB-8658584_V1)).

### 2.5. Evaluating compositional differences

Correspondence analysis (CA) (R, package *vegan*) was used to assess differences in pollen rain composition and taxon abundances sampled from the BCI and PNSL forest communities (Legendre and Legendre, 1999; Oksanen et al., 2017; R Core Team, 2016). To visualize the taxa that were driving the separation observed in the ordination, axis 1 loadings were plotted for 37 taxa exceeding 1% in either the total BCI or PNSL pollen rain captured. CA was also used to measure variation in the composition of the pollen influx that results from differences in sampling length. This was accomplished by time-averaging samples using moving windows of varying sampling lengths: one, three, five, seven, and 10 years. In order to minimize misidentifications and to increase the consistency of our identifications, multiple species were combined to form the following pollen classifications: *Alchornea* spp., *Cedrela* spp., *Cordia* spp., *Eugenia* spp., *Machaerium* spp., *Myrcia* spp., *Vismia* spp., *Vochysia* spp., and *Zanthoxylum* spp. (Table S1, [https://doi.org/10.13012/B2IDB-2059727\\_V1](https://doi.org/10.13012/B2IDB-2059727_V1)). The species represented in these genus-level groupings may be different at BCI and PNSL. A familial grouping (cf. Rubiaceae spp.) was also created, combining taxonomic components previously identified as cf. *Ixora* and cf. *Warszewiczia* (Haselhorst et al., 2013).

### 2.6. Modeling pollen response to climatic variability

Pollen response prediction models were developed to evaluate the predictive effect of our three climatic variables on pollen productivity using a machine-based iterative multivariate linear regression on multiple driver and response variables. The Java code used to complete the analysis is published in a GitHub repository (<https://github.com/surangipunyasena/TimeSeriesPredictor>).

The nature of the analysis was as follows. A model space was first created by testing all possible combinations of driver (climatic) and response (pollen influx) variables. The models tested included one time-based model and nine single environmental variable models incorporating temperature, precipitation, or solar irradiance and lags of 0, 1, or 2 time steps (season or year). The time-based model acted as our control, or baseline model, to which the respective influence of each climatic driver variables could be compared. Failure to beat the time-based model would indicate that the contemporaneous and lagged climatic variables tested had a relatively small influence on our observed pollen counts. Lagged climatic models were developed by comparing pollen data from the current sampling period (season or year) to the climatic conditions observed during the preceding sampling period(s).

For each variable, a linear model was formed to predict the productivity of individual pollen types in response to variability in our climatic variables. Our analysis first incorporated the total number of problems solved (i.e. the influx of unique pollen types with observations/counts greater than zero), then determined the number of instances in which pollen productivity was positively or negatively correlated with a specific explanatory climate variable using a sign

distribution analysis. This approach provided a tally of the number of taxa from BCI (138) and PNSL (170) that responded positively or negatively to each driver variable (climate variable) tested.

A simple tally is susceptible to information loss, as it does not identify the extent to which any individual taxon or the overall pollen rain responded to climatic variability. So, to ensure that all taxa were analyzed on the same scale, pollen influx data across all taxa were normalized prior to testing the significance of each driver variable. Applying z-score normalization to our pollen influx data allowed us to more accurately account for differences in pollen output on a per taxon basis. That is, a taxon that produces more pollen (e.g. an anemophilous species) was not given more weight in the analysis than a species that produces little pollen.

Given the large number of individual pollen types and combinations included in each analysis, normal significance testing over a series of linear models would lead to inflated measurements of significance. To address this, a baseline test for significance was calculated using 8192 determination trials on randomized data, providing an empirical distribution of z-scores and p-values. The predictive model was also run using relative pollen abundance data in lieu of pollen influx data. Both sets of results are presented in this paper.

Each synthetic random determination trial was generated using shuffled environmental data where the slope of each pollen response variable to our environmental variables was centered on zero. This approach incorporated all data in each slope correlation analysis, averaging the number of pollen prediction slopes across taxa as more data were included. This generated a null probability distribution by capturing the skewness of the data itself, analogous to a Monte-Carlo randomization. Significance was determined by looking at the distribution of the slope values across taxa, computing the mean, standard deviation, and standard error, and then testing to see if the mean was significantly higher than zero using a two-tailed test. Using our best observed z-score as a baseline, we were then able to determine if the predicted pollen response to each climatic variable was significantly higher or lower than zero ( $p < 0.05$ ).

We analyzed both seasonal and annual pollen influx data sampled from BCI (138 taxa) and PNSL (170 taxa). The analysis incorporated all taxa and was further subdivided into separate liana and tree form datasets based on the taxonomic affinities of known pollen taxa. This allowed us to address whether there were differences in the phenological responses of different plant functional types. Categorization of pollen types into functional types is included in the online supplement, available through the University of Illinois Data Bank (Table S3, [https://doi.org/10.13012/B2IDB-7821127\\_V1](https://doi.org/10.13012/B2IDB-7821127_V1)).

### 3. Results

Pollen sums for each season ranged from 974 grains (BCI dry season 2001) to 1319 grains (BCI dry season 1997). The mean pollen sum was  $1228.6 \pm 81.0$ . Correspondence analysis revealed distinct differences in the taxonomic composition of the sampled pollen rain of BCI and PNSL (Fig. 1a). The PNSL pollen samples were more variable in composition year-to-year than those from BCI. This indicates that flowering patterns are more irregular for PNSL than BCI. It is not until the sample window is extended to seven or more years that the PNSL pollen rain begins to capture the full range of natural variability in flowering behavior that can be observed over a decade.

The BCI and PNSL pollen rain were characterized by different taxonomic components. To visualize the taxa that were driving the separation observed in the ordination, axis 1 loadings were plotted for 37 taxa exceeding 1% in either the BCI or PNSL 10-year pollen rain record (Fig. 1b). The pollen taxa that most strongly characterize the pollen signature of BCI include: *Faramea occidentalis* (Rubiaceae), *Genipa* (Rubiaceae), cf. *Alchornea* sp. (Euphorbiaceae), *Alseis* (Rubiaceae), *Uncaria tomentosa* (Rubiaceae), *Anacardium* (Anacardiaceae), and *Maripa panamensis* (Convolvulaceae). Taxa that most strongly

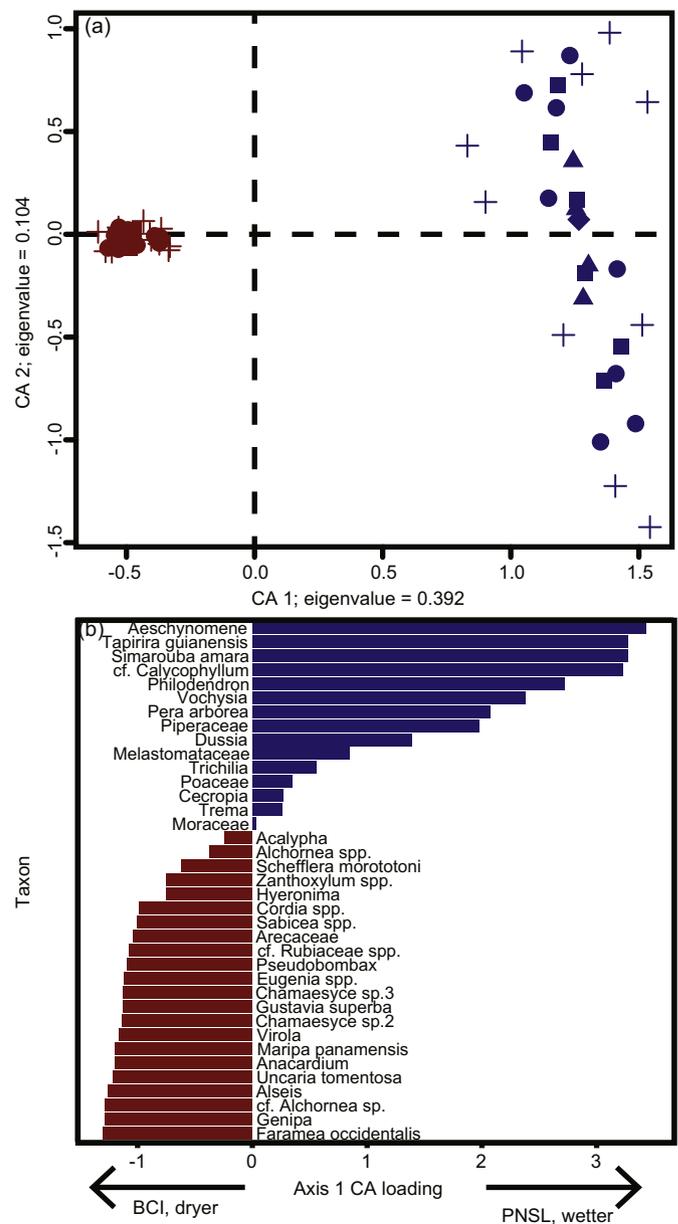


Fig. 1. (a) Results of the CA comparing compositional differences in BCI (red) and PNSL (blue) pollen assemblages for pollen samples aggregated over one, three, five, seven, and ten years, for each sampling height. Sampling length is represented as crosses (1 year), circles (3 years), squares (5 years), triangles (7 years), and diamonds (10 years). (b) Axis 1 loadings for 37 abundant taxa exceeding 1% of the pollen rain from BCI or PNSL. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

characterize PNSL include: *Aeschynomene* (Fabaceae – Faboideae), *Tapiriira guianensis* (Anacardiaceae), *Simarouba amara* (Simaroubaceae), cf. *Calycophyllum* (Rubiaceae), and *Philodendron* (Araceae).

In most models tested, pollen influx was more responsive to variability in climatic conditions at BCI than at PNSL, particularly in response to precipitation and temperature (Fig. 2). Over both seasonal and annual sampling durations, mean pollen response values were centered more closely on zero at PNSL (Fig. 2b, d), reflecting the reduced variability in intra-annual climatic conditions observed and their effect at the site. Differences between plant functional types were not observed, as, overall, pollen types characteristic of lianas and trees responded similarly across all models (Fig. 2).

Our results show, generally, that there is a negative correlation across taxa between pollen influx and the current year or season's

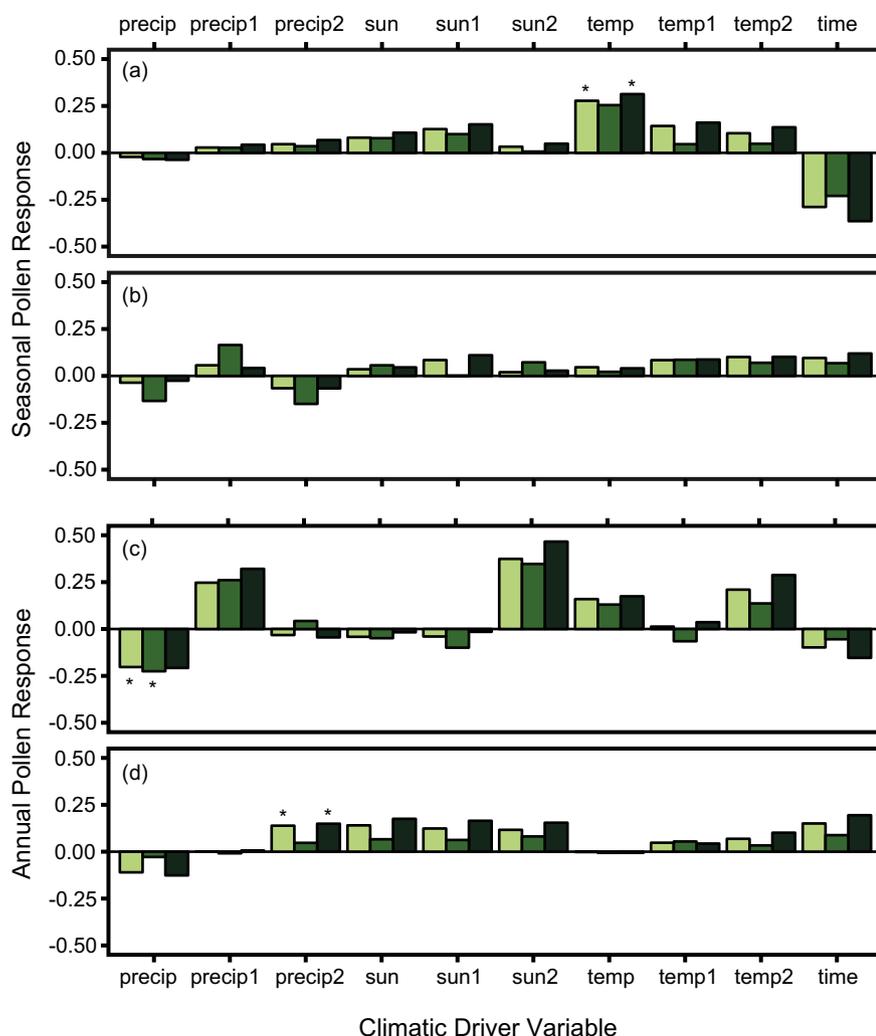


Fig. 2. Seasonal and annual model predictions of pollen influx at BCI (a, c) and PNSL (b, d) in response to climatic variability using time and three climatic variables: precipitation (precip), solar irradiance (sun), and temperature (temp). Lagged climatic effects of one or two seasons are represented with a 1 or 2 respectively. Significant effects ( $p < 0.05$ ) are denoted with an \*. Models with an overall magnitude of response centered around zero indicate that the climatic variable is exerting little influence on the observed phenological response. In addition to the full dataset (light), separate analyses were run on pollen types corresponding to different growth forms to determine whether trees (dark) and lianas (medium) responded similarly to variability in our climatic variables.

rainfall and a positive correlation between pollen influx and the previous years' rainfall. There are significant reductions in pollen influx with increased rainfall at BCI (Fig. 2c) and a parallel but not significant result at PNSL (Fig. 2d). There was a pronounced lagged effect to annual precipitation, as increases in pollen productivity followed wetter years at both sites (Fig. 2c, d). This result was significant for trees at PNSL, but not lianas (Fig. 2d). The response to seasonal precipitation was more modest at both BCI and PNSL (Fig. 2a, b). Solar irradiance, in contrast, had a generally positive but limited effect on pollen influx. No relationship at either site, however, was significant (Table S3, [https://doi.org/10.13012/B2IDB-7821127\\_V1](https://doi.org/10.13012/B2IDB-7821127_V1)).

Modeled results of the effect of temperature indicated an increase in pollen influx during warmer periods, particularly for BCI. Temperature significantly affected seasonal patterns of pollen influx at BCI when all taxa were included, and within trees, but not in lianas (Fig. 2a). A similar, but less significant, pattern was observed at annual scales (Fig. 2c). These results suggest that at the community level, the phenological activity of more seasonal tropical forests is more responsive to elevated temperature than precipitation and sunlight.

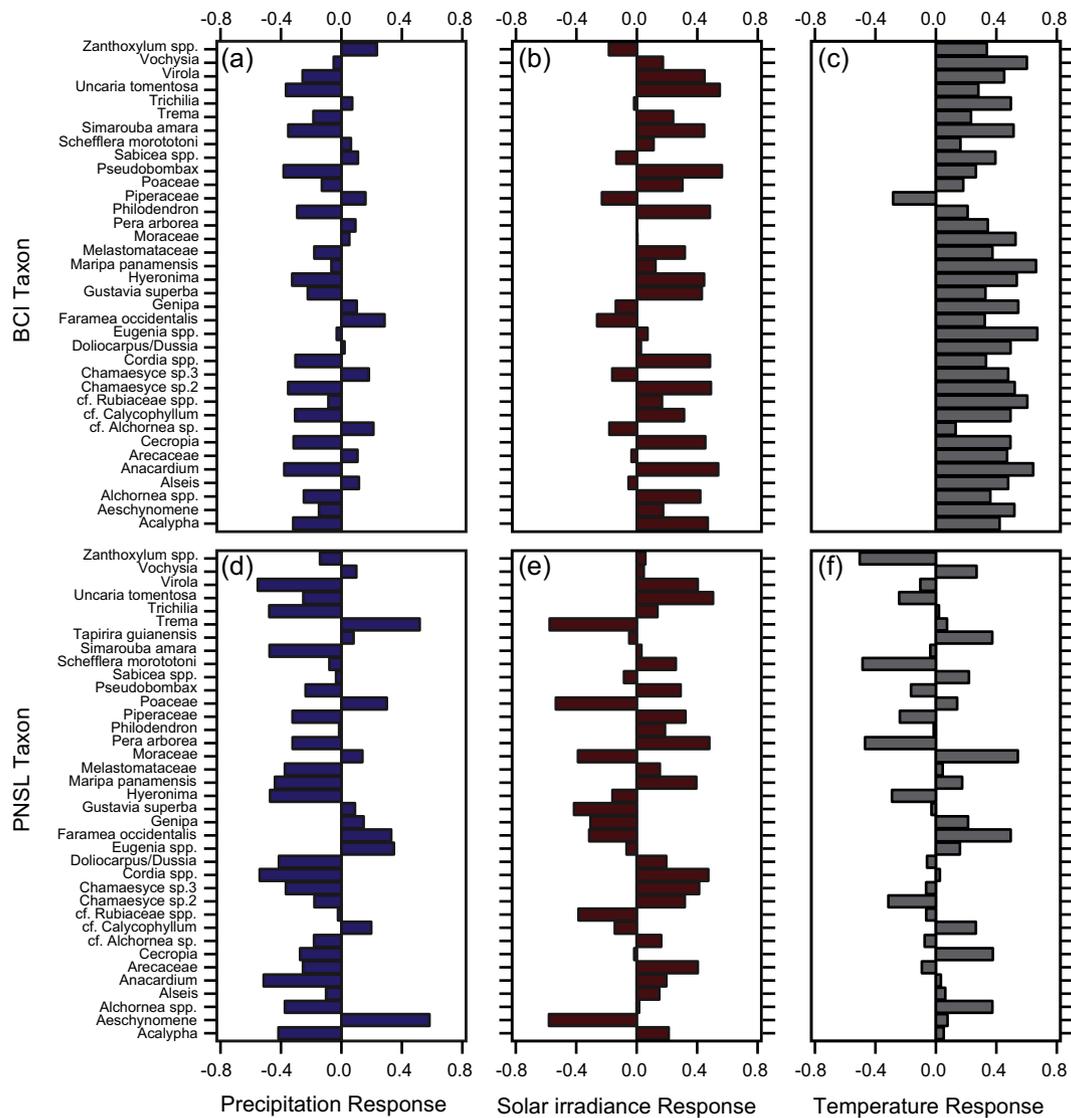
To visualize how individual taxa responded to seasonal climatic variability at BCI and PNSL, individual taxon responses from our ecoinformatic analysis were plotted for the 37 taxa included in our CA (Fig. 3). These were the most abundant taxa, exceeding 1% of the pollen rain sampled at either site.

The response to precipitation and solar irradiance was more tightly correlated at BCI than PNSL (Fig. 3a, b). At both sites, the majority of taxa either increased during periods of high sunlight and low

precipitation, or during periods of low sunlight and high precipitation. This pattern was more pronounced at BCI than at PNSL. The taxa whose pollen outputs increased during drier periods and periods of increased solar irradiance were primarily dry-season flowering species; e.g. *Uncaria tomentosa* (Rubiaceae), *Pseudobombax* (Malvaceae – Bombacoideae), *Cordia* spp. (Boraginaceae) and *Anacardium* (Anacardiaceae). This pattern was more pronounced at BCI (Fig. 3a, b) than at PNSL (Fig. 3d, e). At BCI, just two taxa, *Schefflera morototoni* (Araliaceae) and cf. *Dussia* (Fabaceae – Faboideae), broke from this observed pattern (Fig. 3a, b), whereas at PNSL, five taxa did: *Vochysia* (Vochysiaceae), *Sabicea* spp. (Rubiaceae), *Hyeronima* (Euphorbiaceae), cf. Rubiaceae spp., and *Cecropia* (Urticaceae) (Fig. 3d, e).

The taxonomic correlations from the BCI pollen dataset showed a positive response to increases in seasonal temperature in all but one taxon (Piperaceae) (Fig. 3c). The taxa most positively influenced by temperature were: *Anacardium* (Anacardiaceae), *Maripa panamensis* (Convolvulaceae), and *Eugenia* spp. (Myrtaceae) (Fig. 3c). In contrast, PNSL taxa had more variable responses to temperature. While select pollen types consistent with *Anacardium*, *Maripa panamensis*, and *Eugenia* spp. all exhibited increased pollen productivity during sampling periods characterized by higher temperatures, the magnitude of response was weaker at PNSL than BCI (Fig. 3f). Furthermore, unlike BCI, 17 of our 37 most abundant taxa at PNSL decreased their pollen output when temperature increased (Fig. 3f).

The annual reproductive response of individual taxa at BCI and PNSL (Fig. 4) was similar to the seasonal response. At BCI, all taxa showed a positive response to increases in temperature, with the



**Fig. 3.** Modeled response of 37 individual taxa to seasonal climatic variability at BCI (a–c) and PNSL (d–f) under varying levels of precipitation (left column), solar irradiance (middle column), and temperature (right column). Values of individual pollen response slopes were plotted for the same 37 taxa included in our correspondence analysis (Fig. 1b).

exception of Piperaceae (Fig. 4c). The overall negative response to higher levels of rainfall is also evident at BCI (Fig. 4a). Piperaceae was the only taxon to exhibit increased pollen production in response to increases in precipitation (Fig. 4a).

Modeled predictions using relative pollen abundance instead of pollen influx emphasize overall compositional changes, and produced a similar pattern of results, but were of lower significance (Fig. 5). The response to seasonal increases in temperature was no longer significant for BCI ( $p = 0.07$ ), though the overall response narrowly missed our threshold for significance for all taxa ( $< 0.05$ ) (Fig. 5a). Increased pollen production in response to temperature was also still observed at BCI over annual time intervals, but not when lianas were analyzed separately (Fig. 5c). An overall negative response to precipitation was still observed at both sites, but this result was no longer significant over annual sampling intervals at BCI (Fig. 5c), though notably, pollen composition appears to change as a lagged response to annual precipitation at PNSL (Fig. 5d). Similarly, a positive, but not significant, response to increased solar irradiance was observed at both BCI and PNSL seasonally (Fig. 5a, b).

#### 4. Discussion

Our modeled responses for BCI and PNSL reveal that aerial pollen trap data can be used to determine the sensitivity of flowering to fine-scale climatic variability in forest communities. At the community level (Fig. 2), our results are consistent with previous studies concluding that with less seasonal climate, the timing of phenological events is more asynchronous and less likely to be restricted to a single season in many species (Bawa et al., 2003; Borchert et al., 2004; Frankie et al., 1974). At PNSL, the less seasonal wet forest, we observed both increased year-to-year compositional variability in flowering outputs (Fig. 1), and a lesser influence of climate on pollen productivity (Figs. 2 and 5).

While our predictive modeling approach could not explicitly address how the effects of resource allocation (Sakai et al., 2006; Singh and Kushwaha, 2006; Wright et al., 1999), competition for pollinators (Lobo et al., 2003; Poulin and Wright, 1999), and variability in photoperiod (Borchert et al., 2005; Stevenson et al., 2008) may influence phenological variability in some taxa, our results indicate that differences in the magnitude of the phenological responses detected at BCI and PNSL can also be attributed to prevailing differences in the seasonality of climate observed at each site. Previous studies have demonstrated that strong temporal variation in one or more limiting

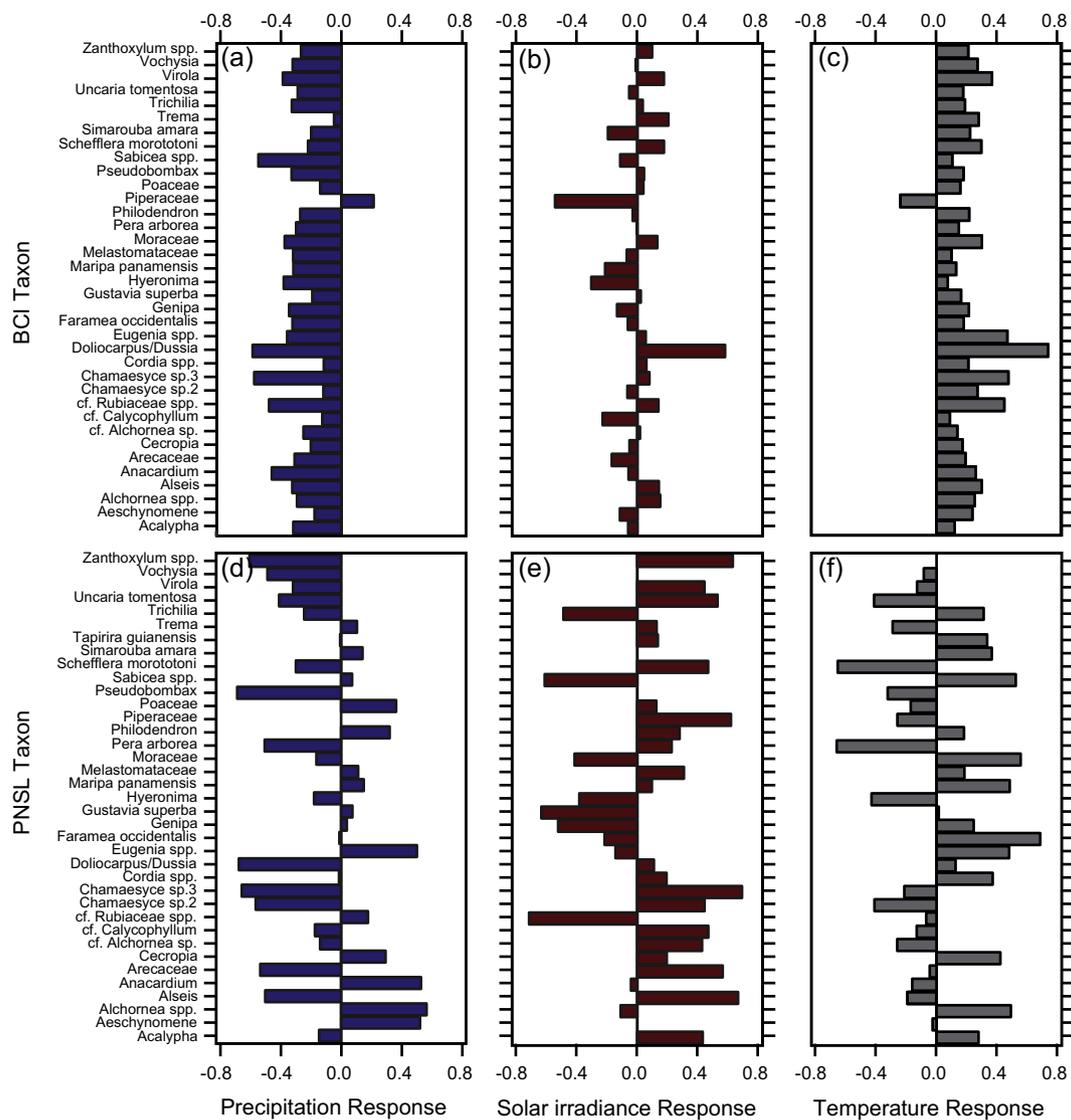


Fig. 4. Modeled response of 37 individual taxa to annual climatic variability at BCI (a–c) and PNSL (d–f) under varying levels of precipitation (left column), solar irradiance (middle column), and temperature (right column). Values of individual pollen response slopes were plotted for the same 37 taxa included in our correspondence analysis (Fig. 1b).

environmental factors is needed for phenological selection (Wright and van Schaik, 1994; Zimmerman et al., 2007). The dry season at BCI was characterized by greater seasonal variation in solar irradiance (4.61 MJ/m<sup>2</sup>/day) and temperature (0.45 °C/day). The seasonality of solar irradiance (3.28 MJ/m<sup>2</sup>/day) and temperature (0.07 °C/day) was lower at PNSL. Of the three climatic variables tested, solar irradiance had the weakest effect on pollen productivity (Fig. 2, Table S3, [https://doi.org/10.13012/B2IDB-7821127\\_V1](https://doi.org/10.13012/B2IDB-7821127_V1)), failing to support the hypothesis that community plant reproduction should occur during the dry season when levels of solar irradiance are highest (Wright and van Schaik, 1994; Wright et al., 1999).

Seasonal increases in precipitation were similar during the BCI (6.34 mm/day) and PNSL (6.66 mm/day) wet seasons. Our results revealed a reduction in reproductive productivity during periods of increased rainfall at the community level (Fig. 2), and are in general disagreement with previous studies suggesting that rainfall events may act as a reproductive cue for flowering events (Opler et al., 1976; Reich and Borchert, 1984). That hypothesis, however, may be better addressed on a species-by-species basis (Figs. 3 and 4), particularly in deciduous taxa characterized by distinct seasonal variation in growth and reproductive cycles (e.g. *Cordia alliodora*) (Bawa and Opler, 1975; Frankie et al., 1974; Opler et al., 1975, 1976; Reich and Borchert,

1984). The responses of individual taxa were consistent with observations that some drought-sensitive species (e.g. *Faramea occidentalis*) flower in the early wet season as conditions become more favorable (Reich and Borchert, 1984; Wright and van Schaik, 1994) (Fig. 4). Overall, the results of our precipitation models support previous studies indicating that plant reproductive effort is reduced during tropical wet seasons (Wright et al., 1999). The pronounced one to two-year lags in response to precipitation at BCI and PNSL (Figs. 2 and 5) are consistent with observations that species that fail to flower or fruit under periods of prolonged rainfall suppress reproductive activity until environmental conditions become more favorable (Condit, 1998). Furthermore, many of the individual taxa that demonstrated the strongest response to low rainfall are high light-demanding taxa (e.g. *Uncaria tomentosa*, *Pseudobombax*, *Cordia*, and *Anacardium*) that have been previously identified as dry-season flowering species (Croat, 1978).

Within a single genus, tropical species have been observed to exhibit contrasting phenological responses to environmental cues, even when under experimental conditions (Tissue and Wright, 1995; Wright, 1991; Wright and Cornejo, 1990). Irrigation experiments in the abundant *Psychotria* (Rubiaceae) and *Piper* (Piperaceae) species during the BCI dry season failed to produce shared phenological responses across species, indicating that the reproductive behavior of some species is

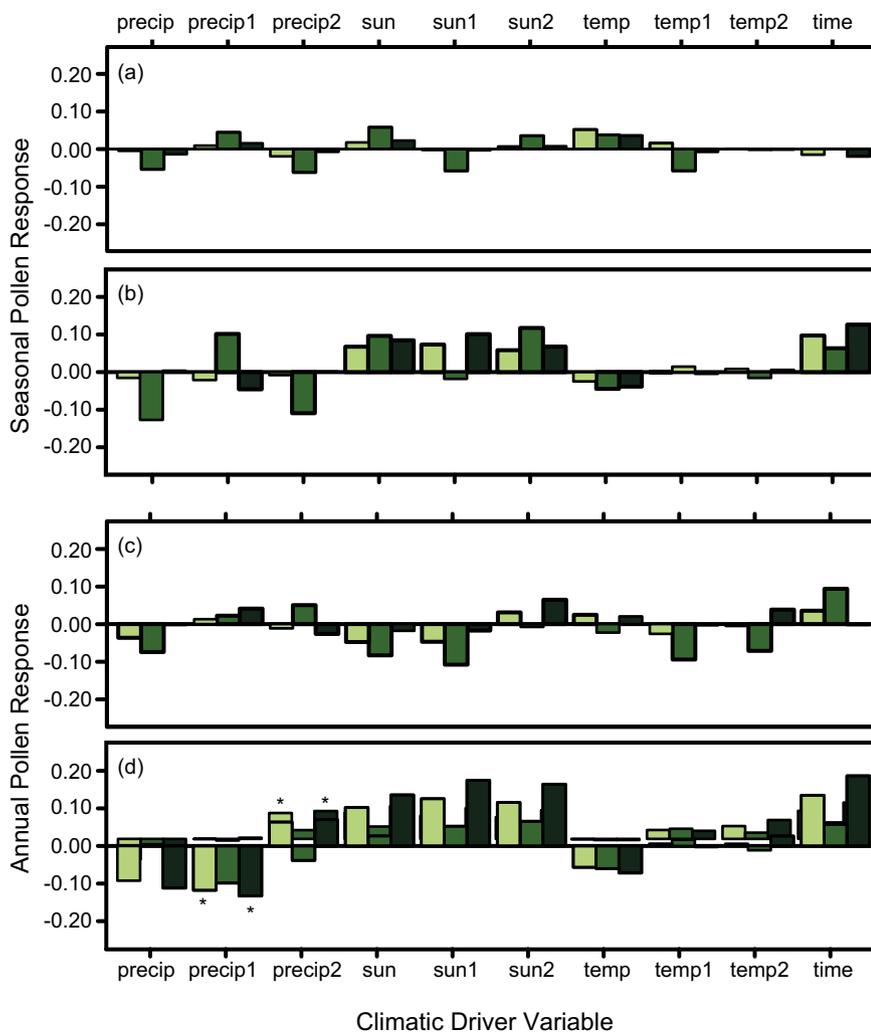


Fig. 5. Seasonal and annual model predictions of relative pollen abundance at BCI (a, c) and PNSL (b, d) in response to climatic variability using time and three climatic variables: precipitation (precip), solar irradiance (sun), and temperature (temp). Lagged climatic effects of one or two seasons are represented with a 1 or 2 respectively. Significant effects ( $p < 0.05$ ) are denoted with an \*. Models with an overall magnitude of response centered around zero indicate that the climatic variable is exerting little influence on the observed phenological response. In addition to the full dataset (light), separate analyses were run on pollen types corresponding to different growth forms to determine whether trees (dark) and lianas (medium) responded similarly to variability in our climatic variables.

likely the result of endogenous controls, and not a response to seasonal climatic cues (Wright, 1991). While our results also reveal similar phenological disagreement in the response of pollen types identified to genus- and family-level groupings at BCI and PNSL (Figs. 3 and 4), they also highlight the need for continued long-term observations in response to seasonal and interannual variability in temperature, as short-term experimental studies can misconstrue phenological responses.

Until recently, experimental studies on tropical plant phenology have largely focused on the effects of precipitation and solar irradiance, as temperature is fairly uniform throughout the course of the year irrespective of season (Tissue and Wright, 1995; Wright, 1991; Wright and Cornejo, 1990). As a consequence, these experimental studies have largely ignored how phenology may be responding to seasonal and long-term changes in temperature. The direction and magnitude of plant responses to warmer temperatures is not always consistent between observational and experimental studies (Wolkovich et al., 2012). Short-term (one-to-four year) experimental studies often capture more transient, or plastic, phenological responses that do not represent how plant community dynamics will respond under longer-term changes to temperature. Our results underscore the need for more spatially and temporally extensive observations of flowering productivity. Furthermore, our results demonstrate that even relatively small variations in wet and dry seasonal temperatures ( $0.45\text{ }^{\circ}\text{C}/\text{day}$ ) can significantly alter the phenological responses of tropical plant taxa (Fig. 2). Considering that the magnitude of predicted temperature change in tropical latitudes is expected to far exceed this value over the next century (Wright et al., 2009), we predict that the flowering patterns of these tropical

forests will be profoundly altered. Continued monitoring of phenological responses to temperature takes on added importance.

Our results most strongly corroborate a recent analysis demonstrating that flowering increases during periods characterized by elevated temperatures on BCI (Pau et al., 2013). Like species located in temperate latitudes (Caradonna et al., 2014; Miller-Rushing and Primack, 2008), the phenology of tropical species may also change in response to increases in temperature, particularly in more seasonal habitats characterized by a higher degree of intra-annual variation in temperature. This phenological response may be diminished in less seasonal forests where temperature is buffered by increased cloud cover and precipitation throughout the year.

Some of the observed differences in pollen response predictions between BCI and PNSL may also be a result of differences in the local abundances of the plant species represented in the pollen rain and the different degree of taxonomic resolution possible with various pollen types. There may be phenotypic plasticity within individual species, varying in responses between sites due to underlying differences in environmental attributes and climatic conditions (Pau et al., 2011). We restricted our analysis to the most common shared pollen types, but some taxa were not as abundant in both sites. From detailed vegetation surveys across Panama, we know that taxa such as *Dussia mundia* (Fabaceae), *Marila laxiflora* (Clusiaceae), *Pera arborea* (Euphorbiaceae), and *Tapirira guianensis* (Anacardiaceae) are primarily restricted to forest environments receiving  $> 3000\text{ mm}$  of rainfall a year (e.g. PNSL) (Santiago and Mulkey, 2004). For taxa that were abundant in one site, but poorly represented in another, more observations may be needed in

order to identify a general pattern (Condit et al., 1996).

One potential source of error is in our analysis lies in our estimates of pollen influx (pollen grains/cm<sup>2</sup>/day) for each plant taxon, which were measured using *Lycopodium* spores. These marker spores are added during sample processing to help standardize pollen counts. However, because pollen density is measured relative to the number of *Lycopodium* spores within a pollen sample, there is a high degree of internal correlation of taxa in our influx estimates, particularly in pollen samples with low *Lycopodium* counts. In these instances, the response of taxa within these samples to the environmental variables is exaggerated, introducing noise into the analysis. As we continue to sample the pollen rain at BCI and PNSL and process additional samples, future analyses will benefit from the addition of more *Lycopodium* tablets during processing, with the aim of achieving a 1:1 ratio of marker to counted grains (Maher, 1981). However, we expect that the effect of low *Lycopodium* densities in our current analysis is limited. Only 3 out of 82 PNSL and 7 out of 84 BCI samples had < 5 *Lycopodium* spores, and, because our analysis pools four sampling heights, the total number of *Lycopodium* spores ranged from 17 to 403 for seasonal samples, with a mean of  $147.3 \pm 80.0$ .

A final shortcoming to our study is that ten years was not a sufficient sampling length to gauge the influence of episodic climate phenomena, such as the El Niño Southern Oscillation (ENSO), which would be expected to have a significant influence on phenology. Increased community flowering and fruiting activity have been described previously as a general feature of El Niño (Wright and Calderón, 2006). Longer sampling windows would likely capture a parallel pattern in pollen production. Continued observation of the pollen rain may also improve our analysis across different plant functional types, as liana species are hypothesized to increase flowering activity under protracted El Niño drought events, due to their affinity for sunlight and reduced precipitation and soil moisture demands relative to other species (Croat, 1975; Srygley et al., 2010). We intend to continue our sampling of the BCI and PNSL pollen rain in the hope of capturing this larger pollen response.

## 5. Conclusions

Seasonal and interannual phenological patterns in many tropical forest taxa are still poorly resolved (Eamus, 1999). Long-term monitoring of aerial pollen trap data provides a cost efficient and convenient way to track the phenological flowering response of diverse tropical plant communities to seasonal and interannual climate variability in changing forest environments. Observed differences in community-level (Figs. 2 and 5) and individual taxonomic (Figs. 3 and 4) pollen response patterns emphasize the need to monitor long-term phenological responses across habitats and on a species-by-species basis as reproductive outputs may vary according to underlying climatic and environmental differences. The Isthmus of Panama, in particular, provides a unique setting from which to study phenological response patterns. Detailed community inventories and climatic data are available for a network of sites across the environmental gradient (Condit et al., 2013; Pyke et al., 2001).

The mean annual temperature of modern closed-canopy forests is projected to increase by 3.3 °C over the next century. There is a clear need to identify temperature-sensitive taxa as these increases in temperature pose a risk to the continued persistence of many species (Wright et al., 2009). Changes to the timing, magnitude, and frequency of seasonal reproductive outputs can be used to predict how communities may be shaped in the future, as temporal asynchrony in reproductive outputs among taxa can be used to inform models of species recruitment and coexistence (Usinowicz et al., 2012). Consequently, extended analyses comparing pollen data to climatic variation can also be used to further identify the most climatically sensitive, and thus most ecologically informative, taxonomic components for paleoecological interpretations from fossil pollen material (Bush and Colinvaux, 1990).

Aerial pollen data can be used to quickly expand the number of long-term phenological datasets needed to predict how individual species and community dynamics will respond to climate change. Pollen trap data can be correlated to climatic data over annual, seasonal, and even monthly time steps using predictive models like those presented here. Furthermore, the relationship between pollen outputs and climate variables could be improved as predictive models are trained on more observations and by improving the taxonomic resolution of pollen types currently identified at the genus or family level (Mander and Punyasena, 2014). This can be done by utilizing high-resolution microscopy techniques and automated pollen identifications made using high-throughput computational algorithms (Mander and Punyasena, 2014; Mander et al., 2013; Punyasena et al., 2012). Aerial pollen samples represent a largely untapped source of phenological data for understudied systems like tropical forests.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.ecoinf.2017.06.005>.

## Acknowledgements

We thank the Smithsonian Tropical Research Institute (STRI) for access to the BCI Lutz tower, the Sherman Crane, and the use of the Center for Tropical Paleocology and Archaeology research facilities. We additionally thank STRI for the BCI and PNSL climate data used in our analyses. Initial funding for this research was provided by the University of Illinois Campus Research Board (Grants 09236 and 11239) to SWP and a University of Illinois Center for Latin American and Caribbean Studies Tinker Travel Grant to DSH. Support for DSH, DKT, and SWP was provided by the U.S. National Science Foundation (NSF EF-1137396 to SWP and DKT).

We additionally thank the anonymous reviewer whose suggestions substantially improved this paper.

## References

- Bawa, K., Opler, P., 1975. Dioecism in tropical forest trees. *Evolution* (N. Y.) 29, 167–179.
- Bawa, K., Kang, H., Grayum, M., 2003. Relationships among time, frequency, and duration of flowering in tropical rain forest trees. *Am. J. Bot.* 90, 877–887.
- Bertin, R.I., 2008. Plant phenology and distribution in relation to recent climate change. *Plant phenology and distribution in relation to recent climate change. J. Torrey Bot. Soc.* 135, 126–146.
- Borchert, R., Meyer, S.A., Felger, R.S., Porter-Bolland, L., 2004. Environmental control of flowering periodicity in Costa Rican and Mexican tropical dry forests. *Glob. Ecol. Biogeogr.* 13, 409–425.
- Borchert, R., Renner, S.S., Calle, Z., Navarrete, D., Tye, A., Gautier, L., et al., 2005. Photoperiodic induction of synchronous flowering near the Equator. *Nature* 433, 627–629.
- Burn, M.J., Mayle, F.E., Killeen, T.J., 2010. Pollen-based differentiation of Amazonian rainforest communities and implications for lowland palaeoecology in tropical South America. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 295, 1–18.
- Bush, M., Colinvaux, P., 1990. A pollen record of a complete glacial cycle from lowland Panama. *J. Veg. Sci.* 1, 105–118.
- Bush, M.B., Rivera, R., 1998. Pollen dispersal and representation in a neotropical rain forest. *Glob. Ecol. Biogeogr.* 7, 379–392.
- Bush, M.B., Rivera, R., 2001. Reproductive ecology and pollen representation among neotropical trees. *Glob. Ecol. Biogeogr.* 10, 359–367.
- Caradonna, P.J., Iler, A.M., Inouye, D.W., 2014. Shifts in flowering phenology reshape a subalpine plant community. *PNAS* 111, 4916–4921.
- Chambers, L.E., Altwegg, R., Barbraud, C., Barnard, P., Beaumont, L.J., Crawford, R.J.M., et al., 2013. Phenological changes in the Southern Hemisphere. *PLoS One* 8.
- Comita, L.S., Engelbrecht, B.M.J., 2009. Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. *Ecology* 90, 2755–2765.
- Condit, R., 1998. Ecological implications of changes in drought patterns: shifts in forest composition in Panama. *Clim. Chang.* 39, 413–427.
- Condit, R., Aguilar, S., 2004. Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *J. Trop. Ecol.* 20, 51–72.
- Condit, R., Hubbell, S., Foster, R., 1996. Assessing the response of plant functional types to climatic change in tropical forests. *J. Veg. Sci.* 405–416.
- Condit, R., Engelbrecht, B.M.J., Pino, D., Pérez, R., Turner, B.L., 2013. Species distributions in response to individual soil nutrients and seasonal drought across a community of tropical trees. *Proc. Natl. Acad. Sci. U. S. A.* 110, 5064–5068.
- Croat, T., 1975. Phenological behavior of habit and habitat classes on Barro Colorado Island (Panama Canal Zone). *Biotropica* 7, 270–277.
- Croat, T.B., 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford, California.

- Eamus, D., 1999. Ecophysiological traits of deciduous and evergreen woody species in the seasonally dry tropics. *Trends Ecol. Evol.* 14, 11–16.
- Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L., et al., 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 447, 80–82.
- Frankie, G., Baker, H., Opler, P., 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62, 881–919.
- Gosling, W.D., Mayle, F.E., Tate, N.J., Killeen, T.J., 2009. Differentiation between Neotropical rainforest, dry forest, and savannah ecosystems by their modern pollen spectra and implications for the fossil pollen record. *Rev. Palaeobot. Palynol.* 153, 70–85.
- Haselhorst, D.S., Moreno, J.E., Punyasena, S.W., 2013. Variability within the 10-year pollen rain of a seasonal neotropical forest and its implications for paleoenvironmental and phenological research. *PLoS One* 8, e53485.
- Hegland, S.J., Nielson, A., Lazaro, A., Bjerknes, A.-L., Totland, O., 2009. How does climate warming affect plant-pollinator interactions? *Ecol. Lett.* 12, 184–195.
- Legendre, P., Legendre, L., 1999. *Numerical Ecology*, 3<sup>rd</sup> edition. Elsevier, Amsterdam.
- Leigh, E.G., 1999. *Tropical Forest Ecology: A View from Barro Colorado Island*. Oxford University Press, New York, New York.
- Lobo, J.A., Quesada, M., Stoner, K.E., Fuchs, E.J., Herreras-Diego, Y., Rojas, J., et al., 2003. Factors affecting phenological patterns of bombacaceous trees in seasonal forests in Costa Rica and Mexico. *Am. J. Bot.* 90, 1054–1063.
- Maher Jr., L.J., 1981. Statistics for microfossil concentration measurements employing samples spiked with marker grains. *Rev. Palaeobot. Palynol.* 32, 153–191.
- Mander, L., Punyasena, S.W., 2014. On the taxonomic resolution of pollen and spore records of Earth's vegetation. *Int. J. Plant Sci.* 175, 931–945.
- Mander, L., Li, M., Mio, W., Fowlkes, C.C., Punyasena, S.W., 2013. Classification of grass pollen through the quantitative analysis of surface ornamentation and texture. *Proc. R. Soc. B* 280, 20131905.
- Miller-Rushing, A., Primack, R., 2008. Global warming and flowering times in Thoreau's concord: a community perspective. *Ecology* 89, 332–341.
- Nielsen, A.B., Møller, P.F., Giesecke, T., Stavngaard, B., Fontana, S.L., Bradshaw, R.H.W., 2010. The effect of climate conditions on inter-annual flowering variability monitored by pollen traps below the canopy in Draved Forest, Denmark. *Veg. Hist. Archaeobotany* 19, 309–323.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., et al., 2017. *vegan: Community Ecology Package*. R package version 2.4-2. <https://CRAN.R-project.org/package=vegan>.
- Opler, P., Baker, H., Frankie, G., 1975. Reproductive biology of some Costa Rican *Cordia* species (Boraginaceae). *Biotropica* 7, 234–247.
- Opler, P., Frankie, G., Baker, H., 1976. Rainfall as a factor in the release, timing, and synchronization of anthesis by tropical trees and shrubs. *J. Biogeogr.* 3, 231–236.
- Parmesan, C., Yohe, G., 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421, 37–42.
- Pau, S., Wolkovich, E.M., Cook, B.I., Davies, T.J., Kraft, N.J.B., Bolmgren, K., et al., 2011. Predicting phenology by integrating ecology, evolution and climate science. *Glob. Chang. Biol.* 17, 1–11.
- Pau, S., Wolkovich, E.M., Cook, B.I., Nyctch, C.J., Regetz, J., Zimmerman, J.K., et al., 2013. Clouds and temperature drive dynamic changes in tropical flower production. *Nat. Clim. Chang.* 3, 838–842.
- Poulin, B., Wright, S., 1999. Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. *J. Trop. Ecol.* 15, 213–227.
- Punyasena, S.W., Tchong, D.K., Wesseln, C., Mueller, P.G., 2012. Classifying black and white spruce using layered machine learning. *New Phytol.* 196, 937–944.
- Pyke, C.R., Condit, R., Aguilar, S., Lao, S., Christopher, R., 2001. Floristic composition across a climatic gradient in a neotropical lowland forest floristic composition across a climatic gradient in a neotropical lowland forest. *J. Veg. Sci.* 12, 553–566.
- R Core Team, 2016. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria URL: <https://www.R-project.org/>.
- Reich, P., Borchert, R., 1984. Water stress and tree phenology in a tropical dry forest in the lowlands of Costa Rica. *J. Ecol.* 72, 61–74.
- Roubik, D.W., Moreno, J.E., 1991. *Pollen and Spores of Barro Colorado Island*. Missouri Botanical Gardens, St. Louis, Missouri.
- Sakai, S., Harrison, R., Momose, K., Kuraji, K., Nagamasu, H., Yasunari, T., et al., 2006. Irregular droughts trigger mass flowering in aseasonal tropical forests in Asia. *Am. J. Bot.* 93, 1134–1139.
- Santiago, L.S., Mulkey, S.S., 2004. Leaf productivity along a precipitation gradient in lowland Panama: patterns from leaf to ecosystem. *Trees* 19, 349–356.
- Singh, K.P., Kushwaha, C.P., 2006. Diversity of flowering and fruiting phenology of trees in a tropical deciduous forest in India. *Ann. Bot.* 97, 265–276.
- Srygley, R.B., Dudley, R., Oliveira, E.G., Aizprúa, R., Pelaez, N.Z., Riveros, A.J., 2010. El Niño and dry season rainfall influence hostplant phenology and an annual butterfly migration from Neotropical wet to dry forests. *Glob. Chang. Biol.* 16, 936–945.
- Stevenson, P.R., Castellanos, M.C., Cortés, A.I., Link, A., 2008. Flowering patterns in a seasonal tropical lowland forest in Western Amazonia. *Biotropica* 40, 559–567.
- Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. *Pollen Spores* 13, 615–621.
- Tissue, D.T., Wright, S.J., 1995. Effect of seasonal water availability on phenology and the annual shoot carbohydrate cycle. *Funct. Ecol.* 9, 518–527.
- Ustinowicz, J., Wright, S.J., Ives, A.R., 2012. Coexistence in tropical forests through asynchronous variation in annual seed production. *Ecology* 93, 2073–2084.
- Vliet, A.J.H.V.A.N., Overeem, A., Groot, R.S.D.E., Jacobs, A.F.G., Spijksma, F.T.M., 2002. The influence of temperature and climate change on the timing of pollen release in the Netherlands. *Int. J. Climatol.* 1767, 1757–1767.
- Weaver, P.L., Bauer, G.P., 2004. *The San Lorenzo Protected Area: A Summary of Cultural and Natural Resources*. Gen. Tech. Rep. IITF-25 Department of Agriculture, Forest Service, International Institute of Tropical Forestry, San Juan, PR: U.S.
- Wolkovich, E.M., Cook, B.I., Allen, J.M., Crimmins, T.M., Betancourt, J.L., Travers, S.E., et al., 2012. Warming experiments underpredict plant phenological responses to climate change. *Nature* 485, 494–497.
- Wright, S., 1991. Seasonal drought and the phenology of understory shrubs in a tropical moist forest. *Ecology* 72, 1643–1647.
- Wright, S.J., Calderón, O., 2006. Seasonal, El Niño and longer term changes in flower and seed production in a moist tropical forest. *Ecol. Lett.* 9, 35–44.
- Wright, S., Cornejo, F., 1990. Seasonal drought and leaf fall in a tropical forest. *Ecology* 71, 1165–1175.
- Wright, S., Muller-Landau, H., 2005. Annual and spatial variation in seedfall and seedling recruitment in a Neotropical forest. *Ecology* 86, 848–860.
- Wright, S.J., van Schaik, C.P., 1994. Light and the phenology of tropical trees. *Am. Nat.* 143, 192–199.
- Wright, S., Carrasco, C., Calderon, O., Paton, S., 1999. The El Niño southern oscillation, variable fruit production, and famine in a tropical forest. *Ecology* 80, 1632–1647.
- Wright, S.J., Muller-Landau, H.C., Schipper, J., 2009. The future of tropical species on a warmer planet. *Conserv. Biol.* 23, 1418–1426.
- Yang, L.H., Rudolf, V., 2010. Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecol. Lett.* 13, 1–10.
- Zimmerman, J.K., Wright, S.J., Calderón, O., Pagan, M.A., Paton, S., 2007. Flowering and fruiting phenologies of seasonal and aseasonal neotropical forests: the role of annual changes in irradiance. *J. Trop. Ecol.* 23, 231.