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

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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 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

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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 samples 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