

Continental-scale patterns of *Cecropia* reproductive phenology: evidence from herbarium specimens

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Plant phenology is concerned with the timing of recurring biological events. Though phenology has traditionally been studied using intensive surveys of a local flora, results from such surveys are difficult to generalize to broader spatial scales. In this study, contrastingly, we assembled a continental-scale dataset of herbarium specimens for the emblematic genus of Neotropical pioneer trees, *Cecropia*, and applied Fourier spectral and cospectral analyses to investigate the reproductive phenology of 35 species. We detected significant annual, sub-annual and continuous patterns, and discuss the variation in patterns within and among climatic regions. Although previous studies have suggested that pioneer species generally produce flowers continually throughout the year, we found that at least one third of *Cecropia* species are characterized by clear annual flowering behaviour. We further investigated the relationships between phenology and climate seasonality, showing strong associations between phenology and seasonal variations in precipitation and temperature. We also verified our results against field survey data gathered from the literature. Our findings indicate that herbarium material is a reliable resource for use in the investigation of large-scale patterns in plant phenology, offering a promising complement to local intensive field studies.

Keywords: climate seasonality; reproductive patterns; Fourier spectral and cospectral analyses; herbarium collections; Neotropics; pioneer plants

1. INTRODUCTION

Plant phenology can be defined as the study of the timing of recurring biological events, its causes with regard to biotic and abiotic forces, and the relation among phases of the same or different species [1]. The most common method to assess plant phenology is to survey local populations repeatedly over many years [2–5]. Correlative approaches have frequently shown phenological parameters to change in concert with environmental variables. Variation in precipitation, soil water availability, temperature, irradiance and day length seem to control the periodicity of flowering and leaf abscission in many tropical species [3–7]. Understanding the links between phenological patterns and environmental variables is crucial to advance the study of community and species dynamics under various climate change scenarios. By studying phenology at the continental scale, over which climate varies, we may improve our understanding of

species dynamics and their interactions with climate. In this contribution, we use herbarium collections as a data source, because they can provide valuable information on species distribution and description of reproductive patterns at large geographical scales [8,9].

The periodicity of phenological events can be classified as continuous, sub-annual, annual or supra-annual [10]. However, there is no consensus on the appropriate statistical method to characterize these patterns. Circular statistics are frequently used to analyse phenology, though these methods fail to describe sub-annual and supra-annual patterns [5]. In contrast, Fourier spectral analysis allows for a more general investigation of periodic patterns in spatial and temporal contexts [11–13]. Although Fourier spectral analysis has been used to study periodic patterns in many datasets (e.g. [14]), it has not yet been used to explore phenological patterns.

The Neotropical genus *Cecropia* Loebl. (Urticaceae) includes 61 species distributed across a wide range of climates from southern Mexico to northern Argentina [15]. With some very widespread species, *Cecropia* is an emblematic genus of pioneer trees in the Neotropics [15]. Published observations on *Cecropia* phenology are scarce. Zalamea *et al.* [16] found flowering to be strongly annual in *C. sciadophylla* in Colombia and French

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Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2010.2259> or via <http://rsob.royalsocietypublishing.org>.

Guiana, though, in their systematic monograph of the genus, Berg & Franco [15] indicate that most *Cecropia*, including *C. sciadophylla*, produce flowers and fruits throughout the year. These apparently contradictory results may arise from variation in phenology among regions, illustrating the importance of studying phenology at large geographical scales.

In this study, we examined the temporal patterns in *Cecropia* reproductive phenology throughout the Neotropics using Fourier spectral analyses. Following the hypothesis that climate seasonality is a primary driver of *Cecropia* phenology, we defined geographical regions comprising similar bioclimatic conditions, and we assessed the strength of climatic determinants on *Cecropia* phenology. Furthermore, we tested whether the periodic structures are related to rainfall and temperature seasonality using cospectral analysis and non-parametric tests. Finally, we surveyed the available literature on *Cecropia* phenology to determine the consistency of patterns inferred from herbarium specimens and field surveys.

2. MATERIAL AND METHODS

(a) *Assignment of bioclimatic regions*

We investigated whether climate seasonality could drive *Cecropia* phenology and generate within-species, as well as among-species, variation. We gathered interpolated monthly averages of precipitation, and minimum and maximum temperatures from 1950 to 2000 (WorldClim dataset, <http://worldclim.org> [17]). We then divided the study area (i.e. terrestrial portion of the area between 24° N, 104° W and 31° S, 34° W) into 20 by 20 km pixels (i.e. 44 385 pixels in total) and averaged the bioclimatic values within each pixel. We performed a principal component analysis (PCA) of these pixel data and performed a *k*-means classification of the resulting scores to get bioclimatic regions (figure 1). We classified the pixels into nine regions because this is the finest scale at which we could analyse the available data, and these regions were largely congruent with more classical, descriptive classifications (see [18]). The nine bioclimatic regions were characterized by (i) low precipitation and low temperature (Andes and Central America mountains), (ii) a dry season in the first half of the year and low annual precipitation (dry Central America and Caribbean), (iii) a dry season in the first half of the year and high annual precipitation (Orinoquia and humid Central America), (iv) no seasons and very high annual precipitation (West Amazonia and Choco), (v) a dry season in the middle of the year and high annual precipitation (South Amazonia), (vi) a dry season in the second half of the year (Guiana Shield), (vii) a dry season in the middle of the year and low variation in temperature (Caatinga and Cerrado), (viii) a dry season in the middle of the year, high variation in temperature and predominance of dry months (West Austral zone), and (ix) a dry season in the middle of the year, high variation in temperature and predominance of humid months (East Austral zone).

(b) *Herbarium dataset*

We examined *Cecropia* collections at New York Botanical Garden Herbarium (NY, $n = 880$), Colombian National Herbarium (COL, $n = 697$), Paris Natural History Museum Herbarium (P, $n = 142$), Colombian Amazon Herbarium (COAH, $n = 117$), French Guiana Herbarium (CAY, $n = 82$), University of Panama Herbarium (PMA,

$n = 58$) and Suriname National Herbarium (BBS, $n = 19$). We gathered information on collection date, species, locality and sex for a total of 1995 fertile specimens representing all 61 species described for the genus [15]. We further obtained similar information from the herbarium data presented in Flora Neotropica [15], expanding our dataset to a total of 3668 fertile specimens for the 61 *Cecropia* species. We were careful to not include the same voucher information more than once. We then attributed species and bioclimatic region labels to the herbarium specimens, and established 70 species–region combinations that included at least 15 herbarium specimens. Thirty-five different *Cecropia* species and a total of 3382 fertile specimens were represented in this subset of 70 species–regions. Given that several species of *Cecropia* have a low number of collections, we used the 15-herbarium specimens threshold as criterion to ensure that we had enough sampled species–regions for subsequent statistical analyses (for more detail in the number of specimens needed to detect periodicity in phenology, see appendix S1 in electronic supplementary material).

In herbarium samples of *Cecropia*, fruits are not easily distinguishable from female flowers, whereas the flowering stage is unambiguous for male individuals. As a preliminary analysis, we used a linear mixed effects model to check for any differences between the number of male and female collections among months. We coded collections as response variable, sex and month as fixed effects, and species as random effect, with the number of collections per month modelled as a Poisson distribution. We found no significant difference between the number of male and female collections among months ($n = 1352$ and 2030, respectively; d.f. = 1, $t = 6.021$, $p = 0.105$). Thus, we grouped male and female specimens and refer to them all as ‘flowering’ samples.

(c) *Fourier spectral and cospectral analyses*

We applied Fourier analysis to detect periodicity in the herbarium phenology data. Fourier spectral analysis decomposes a time series into a sum of sinusoidal components representing periodic trends of varying periods [19]. The analysis could detect six periodic components (i.e. 12, 6, 4, 3, 2.4 and 2 months); longer and shorter components were not detectable from the twelve-month sampling (see [20] and appendix S2 in electronic supplementary material). The normalized amplitudes of the components correspond to the percentage of variation they each explain and, altogether, comprise the Fourier spectrum. Thus, a periodic component of amplitude 0.5 explains 50 per cent of the overall variation of the time series. Phenological patterns were declared significant if the amplitude of at least one of their periodic components surpassed the 95 per cent limits of a null model with no periodic structure, which we obtained by randomly permuting the monthly data 10 000 times.

We applied this methodological framework for the species–region data, and we restricted subsequent analyses to the spectra displaying at least one significant component. We performed a PCA of the significant spectra, and a 2-means classification (*k*-means function) of their scores to test a potential dichotomy in periodic patterns for the *Cecropia* species. Thus, we sought to distinguish annual patterns from all sub-annual patterns, which include periodicities of more than one cycle per year.

We assessed whether periodic variation in phenology was related to a periodic pattern in climate variation using Fourier cospectral analyses. In these analyses, the relative

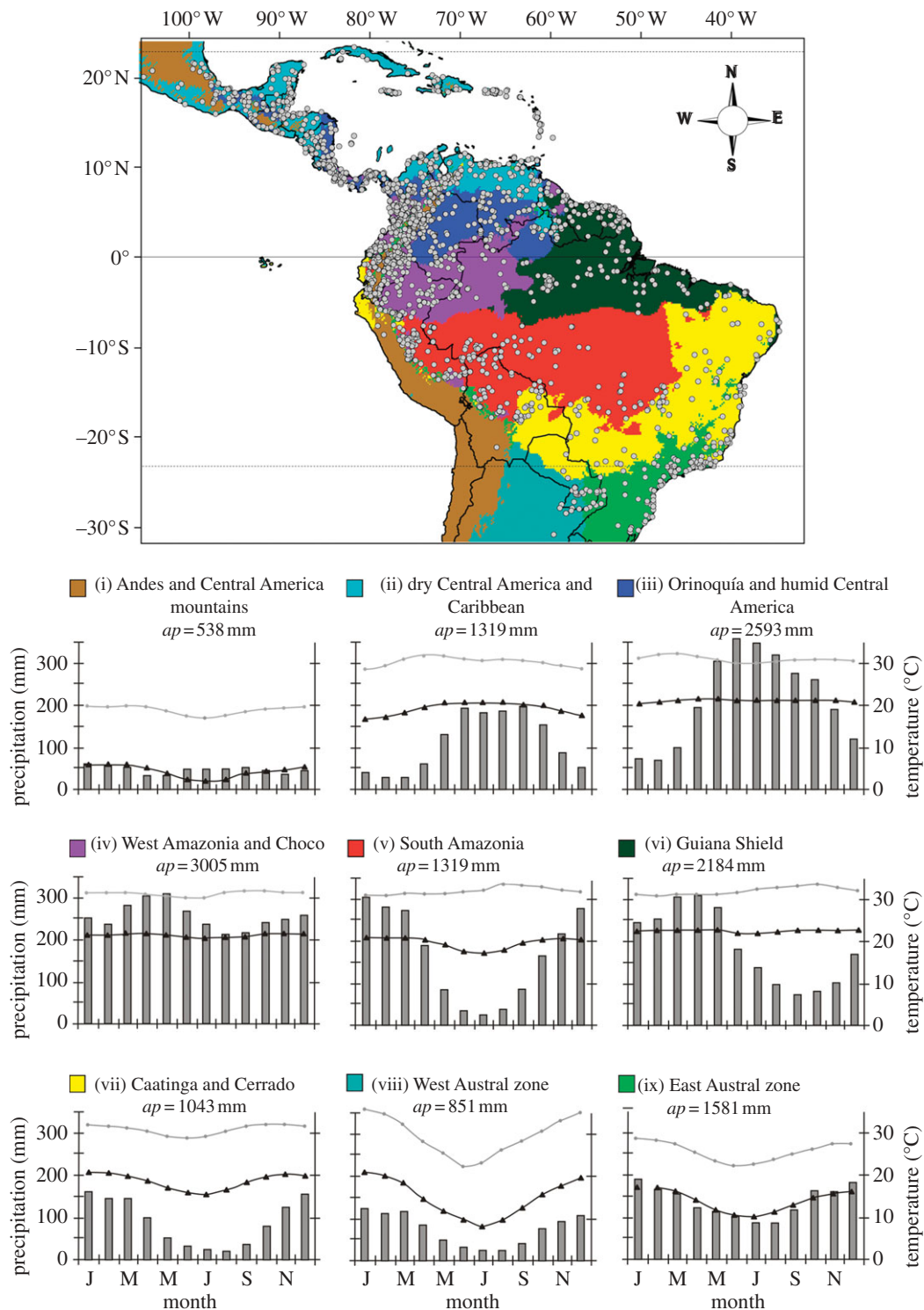


Figure 1. Nine climatic regions map delimited by a 9-means cluster analysis. The circles in the map symbolize the positions of the studied *Cecropia* herbarium specimens. In addition, for each region mean annual precipitation (bars), maximum (grey line) and minimum (black line) temperatures are showed. For all panels *ap* is the average annual precipitation in millimetres.

amplitudes of the periodic components helped to check the covariation of periodic trends [19]. We performed, analogously with the spectral analysis, 10 000 randomizations of the monthly data to determine significant periodic trends of covariation in phenological and climatic data (i.e. interpolated monthly averages of precipitation and median temperatures [17]). Any component that surpassed the 95 per cent null distribution indicated a significant association between the periodic phenological pattern and climatic variable. For any significant annual structure, we further

measured the time lag between the climatic parameter peak and the species flowering response using the corresponding phase within the Fourier cospectral analysis. Thus, when the reproductive phenology and climate variables follow an annual behaviour, an observed six-month lag refers to a reproductive peak coinciding with the minima of the climatic variable.

All analyses were performed using the R software and multivariate analyses were performed using the *ade4* package [21,22].

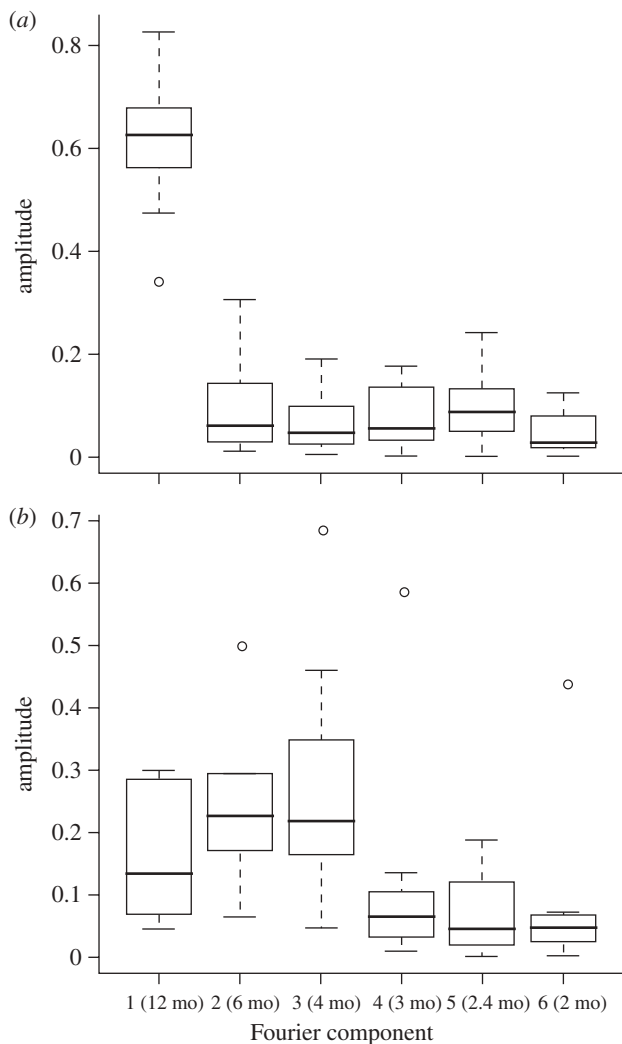


Figure 2. Box-plots representing the relative importance of periodic components in Fourier spectra for species–regions (a) with significant annual patterns in flowering (first box-plot on the left) and (b) with significant sub-annual patterns. The number of months between brackets represents the corresponding period, and the bold bar represents the median.

(d) Consistency with field-survey information

We surveyed the literature on *Cecropia* phenology to determine the extent to which flowering peaks and frequencies inferred from herbarium specimens are consistent with the published literature based on field surveys. Data gathering included our prior knowledge of the literature, and searches in Web of Science (<http://www.isiwebofknowledge.com>) and Google Scholar (<http://scholar.google.com>) using the key words ‘*Cecropia*’ and ‘phenology’.

3. RESULTS

(a) Flowering frequencies in climatic regions

The flowering phenology of 25 of the 70 species–region combinations displayed significant periodicity (randomization test, $p < 0.05$). The 2-means classification of the significant spectra distinguished 18 species–regions with a prominent first component (i.e. annual flowering pattern; figure 2a and the electronic supplementary material, table S1) and seven species–regions with stronger secondary components (i.e. sub-annual flowering patterns; figure 2b). The remaining 45 species–region

combinations did not display any significant periodicity ($p \geq 0.05$). This group included species with continuous flowering, species that flower irregularly and species with undetected patterns of periodic variation (see electronic supplementary material, appendix S1).

(b) Association of climate and phenology in annual species

Fourier cospectra of precipitation and phenology were significant for all the 18 species–region combinations displaying annual patterns, as well as for all cospectra of median temperature and phenology (randomization test, $p < 0.05$). This indicated that the annual patterns of phenology were strongly associated with annual patterns in climate. On the other hand, the phase of the cospectra, which represents the lag between the climatic and the flowering peaks, broadly varied between temperature- and precipitation-based cospectra (see electronic supplementary material, table S1).

We illustrate these results using observations from two species–regions: *C. sciadophylla* in the Guiana Shield region, and *C. mutisiana* in the Andes region (figure 3). For *C. sciadophylla*, the amplitude of the annual component of the precipitation and temperature cospectra exceeded that expected by chance, indicating a significant link between phenology and climate (figure 3e,g). For *C. mutisiana*, the precipitation cospectrum showed a significant six-month component, generated by the combination of annual variation in phenology and a bi-annual variation in precipitation (figure 3f). The temperature cospectrum, on the other hand, contained a significant annual component, as there is a single annual peak in temperature, suggesting that the annual flowering of this species could be more closely linked with temperature than with precipitation.

The number of annual flowering species in each bi-climatic region was not evenly distributed across the Neotropics; we found regions with zero, one or more annual flowering species. Table S1 in the electronic supplementary material shows that the timing of peak flowering varied within regions, among species and among regions. The flowering peaks of species were temporally synchronous in some regions, such as the Guiana Shield. *Cecropia obtusa*, *C. palmata* and *C. sciadophylla* flower during September–October, which corresponds to a six month lag with the precipitation peak, and at the time when temperatures are greatest (see electronic supplementary material, table S1). On the contrary, other species within regions are desynchronized. For example, in the dry Central America and Caribbean region, *C. peltata* flowered in July, close to the precipitation and temperature peaks, whereas *C. obtusifolia* and *C. schreberiana* flowered in March.

(c) Consistency with field-survey information

Although available observations on *Cecropia* phenology are scarce, some authors include *Cecropia* species among extensive lists of phenological information ([5]; for a detailed references list see appendix S3 in the electronic supplementary material). Table 1 provides a summary of *Cecropia* phenology data from the present study and from the field survey data gathered from the literature. We found that herbarium flowering peaks for annual species are within one month of the flowering peaks documented in the literature (table 1). However, flowering

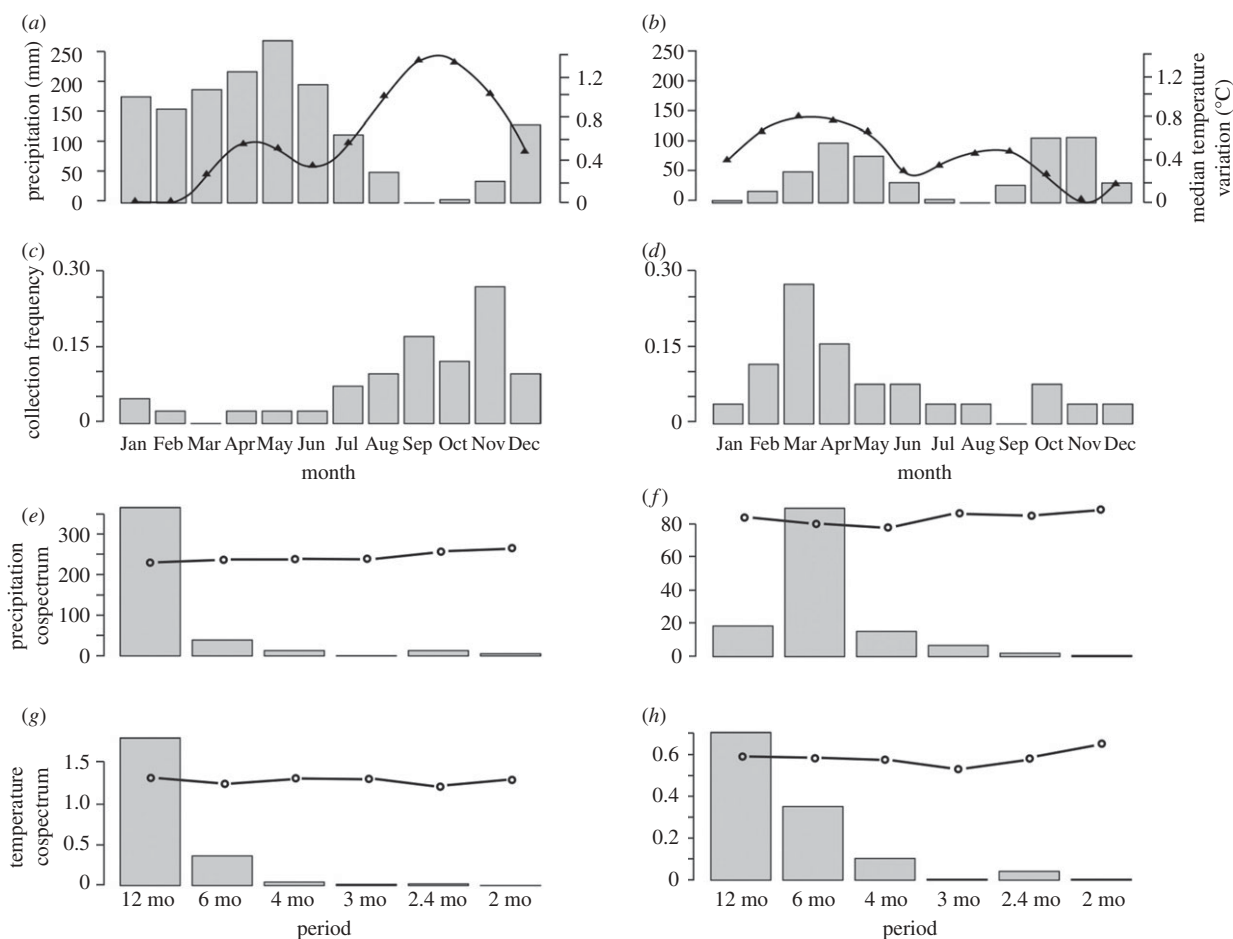


Figure 3. Monthly averages of precipitation (bars) and median temperature variation (lines) for (a) *C. sciadophylla* and (b) *C. mutisiana* collections. Median temperature variation is calculated as $(t_{\text{month}} - t_{\text{min}})/2$, where t_{month} is the temperature of each month and t_{min} is the minimum temperature. Frequency of fertile herbarium collections by month of (c) *C. sciadophylla* from the Guiana Shield region ($n = 40$; climatic region vi) and (d) *C. mutisiana* from the Andes region ($n = 25$; climatic region i). Fourier cospectra of phenology and precipitation (bars), and the 97.5% confidence limit of the null model for the Fourier cospectra (lines) for (e) *C. sciadophylla* and (f) *C. mutisiana*, as well as Fourier cospectra of phenology and median temperature (bars), and the 97.5% confidence limit of the null model for the Fourier cospectra (lines) for (g) *C. sciadophylla* and (h) *C. mutisiana*.

periods inferred from herbaria are on average two months longer than those inferred from field surveys. Furthermore, the literature suggests that *C. membranacea*, *C. hololeuca*, *C. glasiovii*, *C. angustifolia* and *C. reticulata* flower continuously throughout the year. Our results are consistent with these findings, as those species showed no significant periodic structure in our analysis (table 1). In general, our data from herbarium specimens agree with field survey data, with one exception: our analysis detected no periodic pattern for *C. latiloba*, which is reported to have annual periodicity (table 1 [23]).

4. DISCUSSION

(a) *Cecropia* flowering frequencies

We found that 18 *Cecropia* species (representing 29.5 per cent of species in the genus) and 41 per cent of the studied species flower annually. This result contrasts with the traditional view that pioneer plants in tropical forests flower copiously and continuously once they attain maturity [24]. In contrast, 13 dominant pioneer species near Manaus, Brazil have been shown to flower annually [25]. Our results reinforce and generalize the

finding of annual reproductive phenology for an emblematic genus of pioneer trees across the Neotropics.

In our survey, the group of species lacking periodic structure included some *Cecropia* species that were previously reported as continuously flowering (table 1), which is consistent with our results. However, some of the species for which we did not detect periodic structure may actually have significant flowering patterns. These patterns may be undetectable because their flowering periods or the time until fruit maturity are so lengthy that fertile specimens can be collected year-round. Another factor that may obscure periodic structure is the number of specimens used in the analysis. We evaluated the relationship between sample size and the power to detect phenological patterns with a simulation, which indicated that the type II (false negative) error rate decreases with sample size. Given simulated data with an annual pattern, there is a 70 per cent probability of failing to detect the pattern with a sample size of 15 herbarium specimens, but this probability drops to 5 per cent with a sample size of 60 specimens (see the electronic supplementary material, appendix S1). On the other hand, the type I (false positive) error rate is approximately

Table 1. Summary of *Cecropia* phenology data based on herbarium specimens and literature sources. Species are presented following the region classification used to analyse the data.

region	species	flowering (herbarium)			flowering (literature)			site	reference ^a
		period	peak	frequency	period	peak	frequency		
Andes and Central America mountains (climatic region i)									
	<i>C. mutisiana</i> ^b	Dec–Jul	Mar	annual					
	<i>C. obtusifolia</i> ^b	Dec–Jun	Mar	annual					
	<i>C. strigosa</i> ^b	Oct–Apr	Dec	annual					
	<i>C. reticulata</i> ^d	Jan–Dec		non-annual			continuous	Alto Yunda, Colombia	[1]
	<i>C. angustifolia</i> ^d	Jan–Dec		non-annual	Jan–Dec		continuous	Cotapata, Bolivia	[2]
dry Central America and Caribbean (climatic region ii)									
	<i>C. obtusifolia</i> ^b	Dec–Aug	Apr	annual	Feb–Sep	Apr	annual	BCI, Panama	[3]
	<i>C. peltata</i> ^b	Apr–Nov	Jul	annual	Feb–Oct	Jun	annual	Santa Rosa Guanacaste, Costa Rica	[4,5]
	<i>C. schreberiana</i> ^b	Jan–Sep	Apr	annual	Nov–Jun	Apr	annual	Luquillo Monuntains, Puerto Rico	[6,7]
	<i>C. longipes</i> ^c				May–Nov	Aug	annual	Panama City, Panama	[8]
	<i>C. insignis</i> ^c				Jan–Jul	Feb	annual	BCI, Panama	[3,6]
	<i>C. heterochroma</i> ^b	Jan–Apr/Jul–Sep	Mar/Aug	bi-annual					
humid Central America and Orinoquia (climatic region iii)									
	<i>C. obtusifolia</i> ^d	Jan–Dec		non-annual	Jan–Dec		continuous	La Selva, Costa Rica	[9]
	<i>C. insignis</i> ^b	Sep–Mar	Mar	annual	Feb–Jul	Apr	annual	La Selva, Costa Rica	[9,10]
	<i>C. peltata</i> ^b	Mar–Oct	Jun	annual					
	<i>C. sciadophylla</i> ^d	Sep–Mar		non-annual	Oct–Mar	Jan	annual	Tinigua NP, Colombia	[11]
	<i>C. membranacea</i> ^d	Jun–Apr		non-annual	Jan–Sep		continuous	Tinigua NP, Colombia	[12,13]
West Amazonia (climatic region iv)									
	<i>C. distachya</i> ^b	Jun–Jan	Oct	annual					
South Amazonia (climatic region v)									
	<i>C. engleriana</i> ^b	Feb–Aug	May	annual					
	<i>C. utcubambana</i> ^b	Jun–Dec	Aug	annual					
	<i>C. concolor</i> ^b	Aug–Feb	Nov	annual	Nov–Apr	Dec	annual	Santa Cruz, Bolivia	[14]
	<i>C. polystachya</i> ^b	Aug–Feb	Nov	annual					
	<i>C. purpurascens</i> ^c				Jun–Dec	Sep	annual	BDFFP, Manaus, Brazil	[15]
	<i>C. sciadophylla</i> ^d	Apr–Nov		non-annual	Aug–Feb	Oct	annual	BDFFP, Manaus, Brazil	[15]
	<i>C. latiloba</i> ^d	Jan–Dec		non-annual	Apr–Aug	May	annual	Marchantaria, Manaus, Brazil	[16–18]
Guiana Shield (climatic region vi)									
	<i>C. obtusa</i> ^b	Jun–Nov	Sep	annual	Aug–Nov	Sep	annual	Paracou, French Guiana	[19]
	<i>C. palmata</i> ^b	Aug–Jan	Oct	annual	Oct–Jan	Nov	annual	French Guiana	[20]
	<i>C. sciadophylla</i> ^b	Jul–Jan	Oct	annual	Sep–Dec	Nov	annual	ARBOCEL, French Guiana	[11,20,21]
Caatinga and Cerrado (climatic region vii)									
	<i>C. pachystachya</i> ^b	Aug–Feb	Dec	annual	Oct–May	Jan	annual	mid-west Paraná, Brazil	[22]
	<i>C. saxatilis</i> ^b	Dec–Jun	Feb	annual					
	<i>C. hololeuca</i> ^d	Jan–Dec		non-annual	Jan–Dec		continuous	São Paulo, Brazil	[23,24]
	<i>C. glaziovii</i> ^d	Jan–Dec		non-annual	Jan–Dec		continuous	São Paulo, Brazil	[24,25]

^aFor a references list, see appendix S3 in the electronic supplementary material.^bSignificant species based on a randomization test of Fourier spectra (significance level set to 5%).^cAnnual flowering species reported in the literature but not analysed in this study due to the low number of entries per region.^dNon-significant species based on the randomization test of Fourier spectra.

5 per cent, regardless of sample size. Thus, our analysis may have failed to detect some annual patterns, especially in species–region combinations with small sample sizes, but is unlikely to mistakenly report annual patterns. More than 75 per cent of the 70 species–regions used in the analysis were represented by at least 20 specimens.

(b) *Shifting patterns and association with climate seasonality*

For all annually flowering species, phenology was significantly associated with annual patterns of precipitation and mean temperature. This result supports the many studies that have shown strong associations between flowering, precipitation and temperature patterns [6,7,9]. Although our results indicate that climate seasonality is associated with *Cecropia* phenology, determining the individual roles of temperature and precipitation was not possible in this observational study. Further investigations will be necessary to clarify the specific conditions that trigger flower set. Specifically, large-scale potential habitat modelling [26] could assess the causal relationships between phenology and climate by independently investigating the spatial association of species presence/absence and bioclimatic information.

In this study, we found great variation among regions in the number of annually flowering species, which we attribute to the differences in seasonality among regions. West Amazonia is characterized by an aseasonal climate and very high annual precipitation, whereas regions such as the Guiana Shield and South Amazonia are characterized by distinct climate seasonality (figure 1). Correspondingly, the frequency of annually flowering species is greater in the Guiana Shield and South Amazonia than in West Amazonia, lending additional support to the conclusion that *Cecropia* annual reproductive phenology is linked to climate seasonality. Furthermore, when we analysed the phenology of species over their entire distribution ranges without splitting them into bioclimatic regions (results not shown), we found a reduction in the total number of species characterized by an annual flowering pattern (i.e. 11 instead of 18 species), although the detection of periodic patterns is improved when the number of samples increased (see electronic supplementary material, appendix S1). This might be due to the fact that the timing of flowering peaks may vary among climatic regions, causing the phenological structure to appear uniform at a continental scale.

An interesting case is *C. sciadophylla*, a species distributed throughout the Amazon basin, the Guiana Shield and the Orinoquía region of Colombia and Venezuela [15]. This species appeared to lack periodic structure when considered across its range, while it was clearly annual in species–region analyses (table 1). This conclusion is consistent with other studies that found annual periodicity in flower production in local populations, but with different flowering peaks throughout the year in different regions ([16,25,27,28]; J. Dalling & M. Rios 2009, personal communication.).

Non-climatic factors may also affect *Cecropia* phenology. *Cecropia latiloba* is a highly flood-tolerant species widely distributed throughout the Amazon basin, for which Schöngart *et al.* [23] found a high annual flowering periodicity in a population near Manaus. Data gathered

from herbarium specimens for South Amazonia, however, suggest a non-annual pattern for this species (table 1). The observation that flowering in *C. latiloba* is responsive to the timing of flooding may provide an explanation [23]. Variation in flooding duration and extent among rivers and years may affect *C. latiloba* phenology. Similarly, J. Dalling & M. Rios (personal communication, 2009) found that the ‘pungara’ type of *C. membranacea*, which is associated with *terra firme* forests, has a continuous flowering pattern, whereas the ‘herrerensis’ type, associated with floodplain forests, has an annual pattern at Los Amigos Biological Station, Peru [15]. Together, these observations suggest that moisture parameters other than precipitation may affect the phenology of some *Cecropia* species.

(c) *Sampling context*

Herbarium-derived datasets allow broad-based phenological analysis, but may reflect collecting biases. One of the most important issues regarding herbarium data is that collection dates of voucher specimens could be non-randomly distributed throughout the year, due to collector preferences. Boulter *et al.* [9] still showed that the total number of specimens collected in a month was randomly distributed across the course of the year for the Queensland Herbarium (BRI). Additionally, for the French Guiana Herbarium (CAY) we found that the total number of collections per month was randomly distributed throughout the year (runs test; $n = 109\,295$, $p = 0.5$). Thus, we do not believe our results to be biased by temporal patterns in botanical collecting.

Phenological field studies are, normally, detailed observations in a limited area, whereas herbarium collections cover a large spatial extent and allow a broad view of the variation in phenology throughout the range of a species [8,9]. However, inferences from herbarium-based studies could be biased by the geographical distribution of botanical collecting. In the Neotropics, botanical collections are often concentrated near cities and research stations [29]. For this study, we had relatively few specimens from the Amazonia and Orinoquía regions, limiting our scope for inference in these areas.

There is a declining trend in the collection of herbarium specimens, despite the utility of these collections in systematic, biogeographic, plant invasion and applied ecology studies [30]. The limited number of herbarium specimens available for some *Cecropia* species precluded analyses of their phenology. Our results show that herbarium reproductive phenologies are consistent with field studies and do not require as much time as field monitoring, but sample size of herbarium specimens is an important limit to their use.

(d) *Fourier analysis in phenological studies*

Most current methodologies to study phenological patterns fail to describe some phenological behaviours. For instance, recent studies in phenology have used circular statistics [2,5,31,32], but such techniques give unsatisfactory results for sub-annual and supra-annual patterns [5]. Unlike other methods used to describe phenology, Fourier analysis allows the detection of any periodic structure, as well as time lags between patterns. Although Fourier analysis has been widely used to identify periodic patterns

in many fields [11–14], to our knowledge this study represents the first time that it has been applied to phenology. We have shown that Fourier analysis can be easily applied to understand plant phenological patterns and succeeds where other methods often fail. A future challenge will be to examine supra-annual patterns, in which the reproductive pattern is characterized by mast fruiting on multi-year cycles. It is not possible to detect supra-annual pattern in data aggregated over a single series of calendar months; however, if data were aggregated over an appropriate supra-annual duration, such analyses may be feasible.

(e) Conclusions

In this study, we found that herbarium collections offer a powerful tool to determine reproductive phenology at large geographical scales, and that Fourier spectral analysis is an effective method to characterize phenological patterns. Application of these tools indicated that *Cecropia* phenology is often periodic, in accordance with climate seasonality, but that time-lags are quite variable and call for further investigation of triggering mechanisms. Phenomena such as the El Niño Southern Oscillation can induce simultaneous anomalies in temperature, precipitation and irradiance, which in turn can shift phenological patterns [3]. Thus, large-scale phenological studies are of central importance to understand how shifts in climate affect tropical forest dynamics [31]. Our study is the first to show how herbarium data can convey rich enough information on phenology to allow detailed and fruitful ecological analyses at large scales. This suggests that herbaria can be considered as retrospective observatories to investigate past, present and future plant ecology.

The authors thank the staff of New York Botanical Garden, Colombian National Herbarium, Paris Natural History Museum Herbarium, French Guiana Herbarium, Sinchi Herbarium, University of Panama Herbarium and Suriname National Herbarium for help and advice in using collections. We are grateful to S. Mori, S. Sylva, N. Pérez-Molière, C. Loup, L.-C. Jimenez, D. Cárdenas, S. Gonzalez, C. Delnatte, M. Correa and M. Werkhoven for facilitating our work with *Cecropia* collections. We also thank J. Dalling, M. Rios, C. Born, A. Jolivot and O. Taugourdeau for enlightening discussions during data analyses. The manuscript was improved thanks to valuable comments from S. Renner, D. McKey, J. Dalling, A. Roddy, N. Brokaw, H. Beeckman and three anonymous reviewers. This research was partially supported by an Ecos-Nord Colciencias and Paris 13 University grant (C08A01), an IRD (Institut de Recherche pour le Développement, France) doctoral grant and a *Proyecto Semilla* grant of Los Andes University to P.-C.Z.

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