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ORIGINAL PAPER

# Spatio-temporal patterns of orchids flowering in Cameroonian rainforests

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## Abstract

We characterized the flowering patterns of 45 epiphytic orchid species occurring in Cameroonian rainforests to explore the environmental and evolutionary forces driving their phenology. We used a dataset of 3470 flowering events recorded over a period of 11 years in the Yaoundé living collection (82% of the flowering events) and from *in situ* observations (18% of the flowering events) to (i) describe flowering frequency and timing and synchronization among taxa; (ii) test flowering patterns for phylogenetic relatedness at the generic level; and (iii) investigate the spatial patterns of phenology. An annual flowering pattern prevailed among the species selected for this study. The species-rich African genera *Angraecum* and *Polystachya* are characterized by subannual and annual frequency patterns, respectively. However, in terms of flowering time, no phylogenetic signal was detected for the four most diverse genera (*Ancistrorhynchus*, *Angraecum*, *Bulbophyllum*, and *Polystachya*). Results suggest also an important role of photoperiod and precipitation as climatic triggers of flowering patterns. Moreover, 16% of the taxa cultivated *ex situ*, mostly Polystachya, showed significant differences in flowering time between individuals originating from distinct climatic regions, pointing toward the existence of phenological ecotypes. Phenological plasticity, suggested by the lack of synchronized flowering in spatially disjunct populations of *Polystachya*, could explain the widespread radiation of this genus throughout tropical Africa. Our study highlights the need to take the spatial pattern of flowering time into account when interpreting phylogeographic patterns in central African rainforests.

**Keywords** Climatic regions · Epiphyte · Orchidaceae · Phenology · Phylogeny · Shadehouse

## Introduction

Phenology is the study of recurring biological events generally associated with the changing seasons (Sakai 2001). The study of phenology provides a better understanding of environmental filtering, community composition, ecological functions, and evolutionary processes (Fenner 1998). Because phenology is at the core of many inter-specific interactions

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(Butt et al. 2015), its study is becoming increasingly important for the conservation and management of biodiversity (Wallace and Painter 2002; Zhang et al. 2014) in the current context of climate change and biodiversity loss (Chapman et al. 2005; Bertin 2008; Zalamea et al. 2011).

Despite the fact that orchids are one of the most species-rich angiosperm families and are widely known for their remarkably specialized plant-pollinator interactions, very little is known about their flowering patterns, especially in the tropics, where they are most diverse. The majority of phenological studies on orchids in the tropics focuses on one or a few taxa, with an emphasis on plant-pollinator interactions (Zimmerman et al. 1989; Parra-Tabla and Vargas 2004, 2007; Srimuang et al. 2010; Sletvold et al. 2010) or the effects of climate change (Robbirt et al. 2011; Molnár et al. 2012).

In Africa, possibly due to the difficulties involved in collecting phenological data, only nine studies have focused on species-level reproductive plant phenology over time periods of 10 years or more (Bush et al. 2016; Adamescu et al. 2018; Babweteera et al. 2018; Chapman et al. 2018; Dunham et al. 2018; Ouédraogo et al. 2018). Most studies on flowering patterns of African orchids at a regional scale were conducted in West Africa more than 40 years ago (Sanford 1971; Johansson 1974). Since most tropical orchids are epiphytic plants, their flowers are often overlooked in situ. In this case, ex situ cultivation can complement limited field observations (e.g., Sanford 1971).

A variety of evolutionary forces have been hypothesized to drive flowering patterns. These can be grouped in three main types (Ims 1990; Boulter et al. 2006):

(i) an environmental factor, which links seasonal increases in phenological activity to predictable seasonal variations, such as photoperiod, irradiance, precipitation, or temperature (Frankie et al. 1974; van Schaik et al. 1993; Wright and van Schaik 1994; Morellato et al. 2000; Hamann 2004; Zimmerman et al. 2007). Although this hypothesis is one of the most frequently studied, studies on environmental control on flowering of tropical plants, especially orchids, remain rare (Vaz et al. 2004);
(ii) a biotic/social factor such as the presence of pollinators, or pests (Zimmerman et al. 1989; Ollerton and Lack 1992; Sakai et al. 1999; Elzinga et al. 2007), which has rarely been studied in the tropics mainly due to the lack of data on biotic interactions;
(iii) a phylogenetic or internal constraint due to the organisms' endogenous rhythms. Under this hypothesis, flowering patterns are influenced or constrained by phylogeny and, as a result, the flowering times of taxonomically related species tend to be similar (Wright and Calderón 1995; Smith-Ramírez et al. 1998; Boulter et al. 2006; but see Munguía-Rosas et al. 2011).

Some studies (Sanford 1971; Schwartz-Tzachor et al. 2008) also discussed the importance of geographical patterns in interpreting flowering phenology because of the existence of phenological ecotypes (i.e., populations of the same species displaying differences in phenological activities depending on their environment). Phenological ecotypes could result from environmental, biotic, and/or phylogenetic factors (Schwartz-Tzachor et al. 2008).

Cameroon is of particular interest for studies of the orchid family in Africa. Droissart et al. (2018) have reported 445 orchid taxa from 57 genera. This is 5.6% of the 7850 indigenous and naturalized vascular plant species present in the country (Onana 2011). This high diversity is partly explained by the species' radiation into a variety of habitats (i.e., 267 habitats referenced by Letouzey (1985), of which 132 occur in evergreen and semi-deciduous forests) and climates in this region where the rainfall regime varies from unimodal (northern and western Cameroon) to bimodal (South, East, and Center regions) (Fig. 1).

The objective of the present study is to fill the gap in the current knowledge of tropical orchids by addressing the following questions: (i) what are the flowering patterns of epiphytic orchids of Cameroon?; (ii) are these patterns lineage-dependent at the genus level?; and (iii) are flowering patterns related to the geographical provenance of taxa?

In order to answer these questions, we leveraged a unique phenological dataset collected on both cultivated and field-collected specimens from Cameroon. A shadehouse was built in 2004 at Yaoundé to cultivate orchid specimens collected across the country with the aim of producing flowering material for identification purposes. More than 6000 specimens belonging to 250 species, collected from over 800 unique locations, have since been cultivated there.

## Material and methods

### Data

#### Ex situ phenological data from the Yaoundé orchid shadehouse

In the shadehouse, living epiphytic orchids are cultivated on various types of wooden supports, including wood-slat baskets, wooden rafts, and plaques, and are protected from direct sunlight by a shading net (Electronic supplementary material 1). During the dry season, plants are watered daily or once or twice a week, depending on precipitation frequency.

The annual precipitation regime in Yaoundé is bimodal with a first peak around April–May (> 200 mm) and a second peak around September–October (> 250 mm). December and January correspond to the peak of the hot and dry season with about 50 mm of rain whereas July is the peak of the shorter,

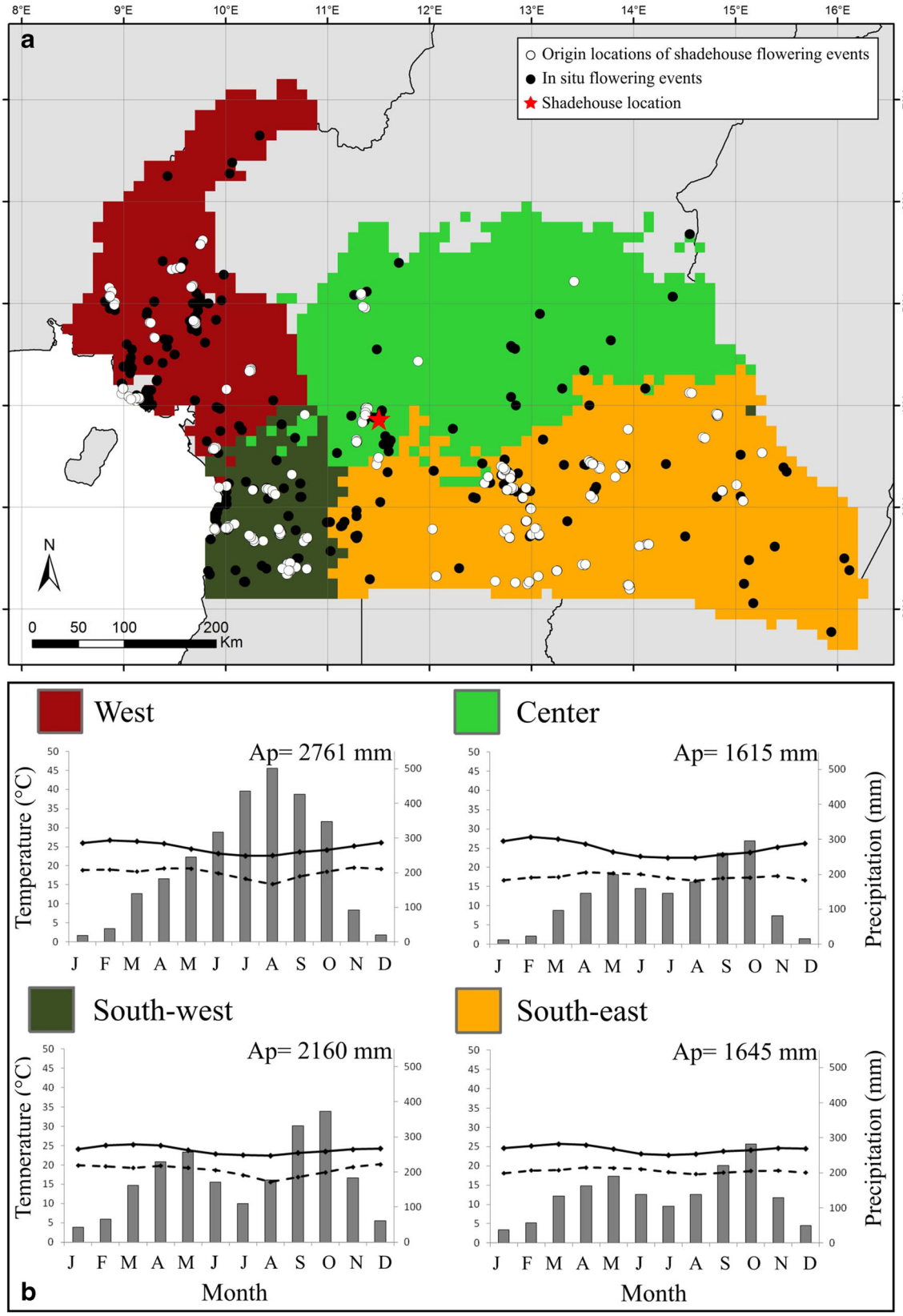



**Fig. 1** Distribution of sampling along the four climatic regions analyzed in Cameroon. Climatic regions of Cameroon were delineated using remote sense climate data. **a** Map of the four climatic regions analyzed in the present work with the origin location of specimens. **b** Annual ombrothermic diagrams of the four climatic regions of Cameroon. For each climatic region, the mean monthly precipitation (bars) and the maximum (continuous line) and minimum (dashed line) temperatures are displayed. Ap annual precipitation

cold and dry season with rainfall of 100 mm (Fig. 2). The monthly mean maximum and minimum temperature is fairly stable throughout the year (Fig. 2). However, the mean daily range exceeds the mean seasonal range (i.e., mean maximum of warmest month minus mean minimum of coldest month). Monthly photoperiod ranges from 688 min of sunlight (11h28) in December to 767 min (12h47) in June (Fig. 2).

Since 2004, the plants have been surveyed at least once a week to collect flowers for accurate identification. Flowering specimens are subsequently preserved in an alcohol solution and duplicated for the Yaoundé and the "Université Libre de Bruxelles" herbaria (respectively YA and BRLU according to Thiers (2018)). For each flowering specimen, we recorded the collection date, the taxon identity, and its geographic provenance. Following each collection (i.e., inflorescence and one leaf), no subsequent flower is collected from that particular plant during a month. After this time, any opened flower or inflorescence can then be collected, and this is considered as a new flowering event. For this study, we therefore define a flowering event as a unique and independent destructive observation of anthesis of one plant.

A complete inventory of the shadehouse was conducted in 2015 to assess mortality of individuals. Only accurately identified taxa for which we have recorded at least 20 flowering events were considered for analysis. The database consists of 2840 flowering events recorded between January 2004 and December 2014. This dataset was collected from 979 living plants belonging to 45 epiphytic taxa (species, subspecies, or varieties) and 12 genera (Table 1 and Electronic supplementary material 2) collected from the field between 2004 and 2014.

### In situ phenological data from Cameroon

In situ flowering events (Electronic supplementary material 2) for the 45 selected taxa were compiled from (i) the literature (Szlachetko and Olszewski 1998, 2001a, b; Simo 2014), (ii) herbarium records housed at BRLU, P, WAG, and YA (acronyms according to Thiers (2018)), (iii) georeferenced occurrences available from the Global Biodiversity Information Facility (www.gbif.org, accessed in December 2014), and (iv) an in situ collection of living specimens in the Dja Biosphere Reserve, Cameroon, surveyed between 2000 and 2004 (Stévart unpublished data). In an in situ flowering event, plants may be sampled in the field at any time during their flowering, whereas in an ex situ flowering event, plants are sampled as soon as the first flower opens. When the specific day of flowering was unknown (20% of records), we denoted the 15th day of the month as the flowering date. In total, 630 flowering events with dates and locations were extracted from these databases (hereafter called the "*in situ* dataset").

### Climatic data

Gridded estimates of monthly mean precipitation were acquired from the Climate Hazards Group InfraRed Precipitation with Stations version 2.0 (CHIRPS), US Geological Survey (USGS) and University of California, Santa Barbara (UCSB) (Funk et al. 2015). For the temperature data, we used the MYD11C3 version 5.0 of the Moderate Resolution Imaging Spectroradiometer (MODIS) (Wan 2014). This product provides monthly minimum and maximum temperature at 0.05 by 0.05° resolution. These data have been recently proposed as a better alternative to weather station interpolation in areas with sparse ground observations such as in Central Africa (Deblauwe et al. 2016). From the monthly time series of CHIRPS (January 1981 to December 2014) and MYD11C3 (January 2003 to December 2014), we derived monthly averages of precipitation, minimum temperature, and maximum temperature on a 0.05 by 0.05° grid of Cameroon.

### Climatic regions

To investigate the association between spatial patterns of climate and orchid flowering phenology, we performed an unsupervised classification of the climatic data described above.

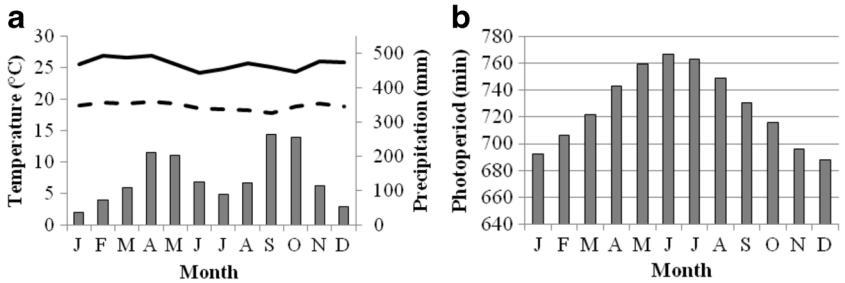



**Fig. 2** Climatic conditions of Yaoundé averaged from 2004 to 2014. **a** Mean monthly precipitation (bars) from the Climate Hazards Group InfraRed Precipitation with Stations (CHIRPS) data and the mean monthly maximum (solid line) and minimum (dashed line) land surface temperatures from the Moderate Resolution Imaging Spectroradiometer (MODIS) data. **b** Monthly photoperiod data from the Astronomical Applications Department of the US Naval Observatory http://aa.usno.navy.mil

**Table 1** Frequency, number, timing, and synchronization of flowering events at population level in the shadehouse. Frequency corresponds to the number of flowering cycles per year per taxon over the 11-year period span (see different classes in the "Material and methods" section). Timing is represented by the number of flowering events per month pooled over the 11-year period. Darkest cells have number of flowering events per month above the median. Taxa are sorted by frequency classes then by the month with highest flowering events. The *r* values (last column) represent the synchronization coefficient (or mean vector length). *Taxa determined not synchronous by the Rayleigh test

| Population frequency | Taxa | J | F | M | A | M | J | J | A | S | O | N | D | r |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sub-annual | *Bulbophyllum sandersonii* | 1 | 4 | 4 | 3 | 3 | 3 | 1 | 2 | 1 | 4 | 3 | 3 | 0.14* |
| | *Angraecum podochiloides* | 1 | 4 | 4 | 3 | 9 | 5 | 7 | 4 | 3 | 4 | 2 | 6 | 0.20* |
| | *Angraecum bancoense* | 4 | 6 | 4 | 5 | 7 | 24 | 16 | 19 | 4 | 11 | 5 | 3 | 0.38 |
| | *Angraecum distichum* | 8 | 10 | 16 | 5 | 21 | 13 | 11 | 34 | 26 | 24 | 6 | 12 | 0.24 |
| | *Polystachya rhodoptera* | 2 | 4 | 1 | 1 | | 2 | 2 | 3 | 6 | 4 | 1 | 1 | 0.26* |
| Bimodal | *Aerangis calantha* | 2 | 7 | | | 4 | 4 | 1 | 5 | 7 | 3 | | 1 | 0.18* |
| | *Bulbophyllum falcatum* var. *velutinum* | 5 | 11 | 35 | 11 | 4 | 2 | 2 | 1 | 1 | 3 | 14 | 6 | 0.51 |
| | *Bulbophyllum calyptratum* | 4 | 3 | 7 | 9 | 7 | 2 | 2 | 1 | | 1 | 5 | 4 | 0.40 |
| | *Angraecum subulatum* | | 1 | 4 | 1 | 8 | 12 | 7 | 9 | 4 | 14 | 3 | | 0.42 |
| | *Polystachya paniculata* | | | | | 8 | 30 | 25 | 6 | 12 | 18 | 6 | 1 | 0.62 |
| Annual with spread flowering events | *Bulbophyllum oreonastes* | | | 9 | 5 | 19 | 4 | 2 | | | 5 | | 1 | 0.62 |
| | *Polystachya adansoniae* | 2 | 7 | 24 | 19 | 39 | 16 | 4 | 3 | 5 | 4 | | | 0.66 |
| | *Angraecum pungens* | | | | 2 | 2 | 6 | 5 | 5 | 4 | 2 | 1 | | 0.65 |
| | *Angraecum gabonense* | | | 1 | 1 | 3 | 14 | 16 | 8 | 8 | 2 | 2 | 1 | 0.69 |
| | *Calyptrochilum christyanum* | 4 | 3 | | | 1 | 8 | 22 | 41 | 20 | 6 | 2 | 2 | 0.71 |
| | *Polystachya elegans* | | | | 3 | 7 | 14 | 8 | 16 | 6 | 4 | 2 | | 0.68 |
| | *Ancistrorhynchus capitatus* | 1 | 1 | 2 | 7 | 5 | 12 | 19 | 15 | 30 | 20 | 3 | | 0.59 |
| | *Polystachya calluniflora* | 1 | | 2 | 1 | 2 | 2 | 7 | 8 | 9 | 8 | | | 0.58 |
| | *Polystachya ramulosa* | | | 1 | 1 | 2 | 2 | 3 | 5 | 6 | 1 | 1 | 1 | 0.56 |
| | *Bulbophyllum imbricatum* | 2 | 2 | 1 | 1 | 1 | | 1 | | | 18 | 18 | 1 | 0.73 |
| | *Bulbophyllum calyptratum* var. *graminifolium* | | 1 | 1 | 4 | 1 | | | | | 1 | 18 | 2 | 0.61 |
| | *Bulbophyllum falcatum* | | 1 | 4 | 4 | | | | | | 3 | 8 | 7 | 0.54 |
| Annual synchronous | *Polystachya dolichophylla* | 17 | 9 | 1 | 1 | 1 | | | | | | | | 0.90 |
| | *Polystachya victoriae* | 2 | 27 | 2 | | | | | | | | | | 0.99 |
| | *Bulbophyllum sandersonii* subsp. *stenopetalum* | 1 | 13 | 40 | 7 | 5 | | 1 | | | | | 1 | 0.90 |
| | *Calyptrochilum emarginatum* | | | 11 | 10 | | | | 1 | | | | | 0.91 |
| | *Polystachya obanensis* | | | 5 | 5 | 20 | 2 | | | | | | | 0.91 |
| | *Ancistrorhynchus schumannii* | | | | | 2 | 14 | 9 | 5 | | | | 1 | 0.83 |
| | *Ancistrorhynchus metteniae* | | | | | | 36 | 39 | 21 | 2 | | | | 0.93 |
| | *Cyrtorchis letouzeyi* | | | | | 5 | 8 | 9 | 1 | | | | | 0.90 |
| | *Chamaeangis vesicata* | | | | | | | 5 | 60 | 54 | 7 | | | 0.96 |
| | *Polystachya stuhlmannii* | | | | | 4 | 9 | 4 | 25 | 18 | 14 | | | 0.77 |
| | *Bolusiella batesii* | | | | | | | 1 | 7 | 34 | 9 | 1 | | 0.96 |
| | *Polystachya modesta* | | | | | 1 | | 1 | 13 | 14 | 3 | 2 | | 0.87 |
| | *Polystachya coriscensis* | | | | | | 4 | 15 | 36 | 51 | 24 | 2 | | 0.87 |
| | *Podangis muscicola* | | | | | 2 | | 3 | 18 | 21 | 2 | | 1 | 0.87 |
| | *Aerangis arachnopus* | | | | | | | | 4 | 13 | 37 | | | 0.97 |
| | *Listrostachys pertusa* | | 2 | | | 1 | | 4 | 12 | 44 | 70 | 5 | | 0.89 |
| | *Polystachya pyramidalis* | | | | | | | | 1 | 16 | 64 | 23 | 8 | 0.98 |
| | *Tridactyle anthomaniaca* | | 1 | | | | | | 2 | 1 | 17 | 1 | 1 | 0.85 |
| | *Bulbophyllum maximum* | | | | | | | | | | 3 | 11 | 8 | 0.95 |
| | *Bulbophyllum falcatum var. bufo* | 1 | | 1 | | | | | | 1 | 7 | 19 | 11 | 0.91 |
| | *Polystachya polychaete* | 2 | | | | | | | | 3 | 10 | 69 | 11 | 0.95 |
| | *Polystachya affinis* | 18 | 5 | | | | | | | | | 10 | 21 | 0.91 |
| | *Podangis rhipsalisocia* | 28 | | | | | | | | | | 3 | 31 | 0.96 |

We first derived 19 climatic variables as described in the ANUCLIM scheme (Xu and Hutchinson 2011) from values of CHIRPS and MODIS to create a set of biologically meaningful descriptors of the climate. This set of variables represents annual trends (e.g., mean annual temperature, annual precipitation), seasonality (e.g., annual range in temperature and precipitation), and extreme or limiting environmental factors (e.g., temperature of the coldest and warmest month, and precipitation of the wet and dry quarters). To remove the collinearity present among these variables, we retained the first five axes of a principal component analysis (PCA), on the 19 variables, which then respectively constituted our synthetic variables. Finally, we classified the grid cells falling within the borders of Cameroon into eight groups using K-means clustering on the five synthetic variables (Fig. 1). The number of groups was optimal in that they represent the major climatic zones of the region and are congruent with the ecoregions defined by Olson et al. (2001) and global environmental zones of Metzger et al. (2013). The specimens we used came from four of these eight climatic regions (Fig. 1). The remaining regions are therefore not discussed in the present work. The South-west, South-east, and Center regions are characterized by a bimodal precipitation regime distinguished by different precipitation intensities and correspond approximately to the administrative regions of the South, the East, and the Center respectively. The West region is characterized by a unimodal regime of precipitation corresponding to the African monsoon (Fig. 1) and corresponds approximately to the Littoral, North-west, and South-west administrative regions. Mean monthly temperatures of these four climatic regions are relatively constant over the year, at around 23 °C.

## Analyses

### Flowering patterns: frequency, flowering time, and synchronization

In order to describe the complex array of tropical phenological patterns and to make objective inter-site comparisons, Newstrom et al. (1994) proposed a conceptual framework of phenology classification based on six criteria. In the present work, we used three of these criteria based on the characteristics of our data: (i) flowering frequency (the number of "on"/"off" cycles per year, one cycle consists of a flowering episode followed by a non-flowering interval); (ii) flowering time (the average flowering date of flowering events); and (iii) synchronization (the concentration of the flowering events around the average flowering date, Newstrom et al. 1994).

Part of the complexity of tropical phenology lies in the variation of patterns from one level of analysis to another (e.g., individual vs. population or community). Contrary to temperate phenology where winter synchronizes most species into annual cycles at all levels of analysis, tropical phenological patterns may differ greatly at different levels of analysis (e.g., Newstrom et al. 1994). We chose to analyze our dataset at two levels to describe the flowering patterns of orchids occurring in Cameroon: (i) the individual level (the dominant flowering pattern of distinct individuals within a taxon) and (ii) the population level (the flowering pattern produced by all the flowering events pooled for all individuals of a given taxon).

At the individual level, only the individuals cultivated for at least four years in the shadehouse were included in the analyses (405 individuals from the 45 taxa). To achieve this in the absence of an annual inventory of dead plants, we kept individuals with one flowering event recorded before January 1st, 2012 and still living in 2015, or those that have flowered at least twice within a four-year interval. At the population level, all flowering events were included (2840 events) in the analyses.

**Flowering frequency classes** The flowering frequency was described at the individual and population levels for the ex situ dataset over the 11-year time span. The patterns were further classified into (i) continual, flowering events throughout the year with sporadic breaks; (ii) sub-annual, with more than one flowering cycle per year at no specific period of the year, which includes bimodal with two flowering cycles a year at two well-defined periods; (iii) annual, with one flowering cycle per year; and (iv) supra-annual, with less than one flowering cycle per year. We defined the frequency pattern by graphical analyses of the whole time series as suggested by Newstrom et al. (1994) (Electronic supplementary material 3).

Since flowering may happen for two consecutive years in supra-annual individuals (Newstrom et al. 1994), we considered the pattern to be annual only when an individual flowered during at least three consecutive years or three times over four consecutive years. To characterize the phenology at the individual level, we used the modal frequency class of all individuals of any given taxon.

At the population level, a further subdivision was made for the annual frequency class: "annual synchronous" corresponds to taxa that are highly synchronized (see below) with one major flowering period; whereas "annual with extended flowering events" corresponds to moderately synchronous taxa (see below) with one major flowering period.

**Flowering time** Because flowering events are often not concentrated in a short period of time and may occur year-round, especially in the tropics, one has to take into account the circularity of the data (i.e., the fact that only one day separates January 1st and December 31st; Batschelet 1981; Fisher 1993; Zar 2010) to calculate the average flowering time and the synchronization of flowering events. Thus, each single flowering event was converted into an angular value representing its date linearly scaled on the circle from the 1st of January to the 31st of December.

For each taxon at the population level of analysis, the flowering time of a given taxon was calculated as the angle of the mean vector, $\Phi$, from all of these flowering events, and corresponds to the average flowering time of the taxon (Electronic supplementary material 4 and 5):

$$\Phi = \arctan(y/x) \quad \text{if } x > 0$$
or
$$\Phi = 180^{\circ} + \arctan(y/x) \quad \text{if } x < 0$$

where

$$x = \sum n_i \cos\Phi_i, y = \sum n_i \sin\Phi_i$$

$n_i$ is the number of flowering events in day $i$ and $\Phi_i$ is the angle value of day $i$. The 1st of January was chosen as 0°.

**Synchronization/regularity** We calculated a synchronization criterion ($r$) representing both the duration and the regularity of flowering events (Hamann 2004). The length of the mean vector ($\Phi$) (also called "mean resultant length"), $r$, can be viewed as a synchronization statistic ranging from 0, for asynchronous, to 1, for perfectly synchronous (all flowering events occurred the same month of the year), at the population level. At the individual level, this criterion can be viewed as a regularity statistic of flowering. It is calculated as follows:

$$r = \left(x^2 + y^2\right)^{1/2} / \sum n_i$$

We used the Rayleigh test (Batschelet 1981) to determine if the mean resultant length differs from 0, i.e., if the taxon presents a particular flowering season. We classified the flowering patterns into four classes of synchronization (or regularity for the individual level): highly synchronous ($r \geq 0.75$), moderately synchronous ($0.5 \leq r < 0.75$), slightly synchronous ($r < 0.5$), and not synchronous (null hypothesis of Rayleigh test accepted). At the individual level, regularity of a taxon was calculated as the average statistic of all its individuals.

We used the R package CIRCULAR (Lund and Agostinelli 2011; R Core Team 2015) to calculate flowering time and level of synchronization.

### Phylogenetic relatedness

The potential influence of phylogeny on the flowering frequency, synchrony, and time was tested at the genus level for the ex situ dataset by grouping the flowering events of genera comprising at least three taxa: *Ancistrorhynchus* (3), *Angraecum* (6), *Bulbophyllum* (10), and *Polystachya* (15).

The association between the taxonomic unit (i.e., the genus) and the frequency or synchronization classes at the individual and population levels of analysis was assessed using a Fisher exact test on two-way contingency tables against the null hypothesis of no association (Fisher 1950). When the Fisher exact test was significant at the 5% threshold, we compared the Freeman-Tukey deviates of each contingency table cell with the critical value proposed by Bishop et al. (1975) and modified by Sokal and Rohlf (1995) to identify the over-represented associations.

To investigate the phylogenetic constraint on flowering time, we used repeated measures ANOVA with monthly relative frequencies of flowering events per taxon treated as repeated measures, taxa as subjects, and the taxonomic unit (i.e., genus) as the grouping variable (Boulter et al. 2006). The null hypothesis is a similar monthly pattern of flowering across the genus. We calculated the monthly relative frequencies of flowering events per taxon by summing the number of flowering events that occurred every month pooled over one year and divided by the total number of flowering events of the taxon.

### Geographical patterns

At the individual level of analysis for the ex situ dataset, a Fisher exact test on two-way contingency tables (Fisher 1950; see above) was used to assess the association between the geographical origin (i.e., the four climatic regions) of the living plants and the frequency (four classes) or synchronization (four classes) of flowering.

At the population level, we investigated the intra-specific geographical patterns in flowering time for the ex situ dataset by calculating the time lag between mean flowering time of individual plants collected in the four different climatic regions. We tested pair-wise differences against the null hypothesis of no difference with the parametric bootstrap test proposed by Fisher and Hall (1990). This test does not require homogeneity of dispersion among random samples. It was performed using 10,000 replicates. To match the assumption of the test regarding sample size, we discarded for each taxon climatic regions with less than five individuals (25 taxa, 1903 events). To control for the type I error rate inflation in this multiple testing framework, the false discovery rate (FDR) was maintained below 5% by applying the procedure of Benjamini and Hochberg (1995).

Finally, we compared in situ and ex situ datasets in terms of flowering time and synchronization. To minimize the effect of in situ sampling bias, we took into account only taxa from the living collection that have an annual frequency and at least ten in situ flowering event records (ten taxa). We used the parametric bootstrap procedure described above to assess the differences in flowering time between the in situ and ex situ datasets. Differences in synchronization of flowering events per taxa were assessed with Wallraff test (Zar 2010) of angular dispersion around the mean against the null hypothesis that dispersion is equal across groups.

None of the taxa of the in situ dataset matched our criteria of at least ten flowering events in at least two climatic regions, so we could not compare patterns between geographical provenances in this dataset.

## Results

### Flowering patterns

Frequency, flowering time, and synchronization/regularity criteria of the ex situ dataset were used to describe the flowering patterns of orchids in Cameroon.

At the individual level, most taxa (21 taxa, 47%) displayed annual flowering, six taxa (13%) were sub-annual, and 18 taxa (40%) were supra-annual. No bimodal or continual pattern was observed (Electronic supplementary material 6).

When pooled together at the population level, half of the taxa displayed annual, highly synchronous patterns, and 12 taxa (27%) presented annual patterns that were moderately synchronous, with extended flowering over the year for the whole population. Taxa in these two groups mostly comprised individuals that had annual flowering patterns. However, the latter group included taxa with individuals having supra-annual flowering patterns. One or a few individuals flowered every year at the same period, even if all of them did not flower annually, resulting in a synchronous annual pattern at the population level. Five taxa with individuals that had sub-annual patterns also presented sub-annual patterns at the population level that were slightly or not synchronous. An additional five taxa also displayed a sub-annual pattern that was bimodal at the population level, but their individuals presented a mix of flowering frequency patterns and regularity (Fig. 3, Table 1 and Electronic supplementary materials 4 and 5). No supra-annual or continual pattern was observed at the population level.

Overall, flowering of orchids in Cameroon occurs throughout the year; and each month of the year corresponds to the flowering peak of at least three taxa in the ex situ dataset (Table 1).

### Phylogenetic relatedness

Fisher tests for phylogenetic constraints on flowering patterns at the individual level of analysis revealed that *Angraecum* is significantly sub-annual and moderately regular, *Polystachya* is significantly annual and highly regular, and *Bulbophyllum* is significantly supra-annual (Tables 2 and 3).

At the population level, no phylogenetic signal was observed for synchronization ($p$ value = 0.06), frequency ($p$ value = 0.20), or flowering time ($p$ value = 0.105, Table 4) at the genus level.

### Geographical origin

No significant differences ($p$ values > 0.05) were detected for frequency and synchrony patterns between climatic regions at the individual level for the ex situ dataset.

Considering the flowering time in the ex situ dataset, four taxa (out of the 25 tested), of which three belong to *Polystachya* (out of eight tested in this genus), showed significant differences between groups of distinct geographical provenance (Fig. 4 and Electronic supplementary material 7). *Bulbophyllum falcatum*, annual with extended flowering events, displays significant differences in flowering timing between the South-east and Center climatic regions, with a 117-day interval between flowering peaks of the two regions. *Polystachya adansoniae* is annual with extended flowering events; the flowering peak of its sub-population from the South-east climatic region occurred more than 45 days earlier than everywhere else. Flowering events of *P. coriscensis* individuals correspond to the main rainy season of their site of provenance (Figs. 1 and 4). The difference in flowering peaks between the South-west and West climatic regions was 46 days. Finally, *P. paniculata* (Table 1) has a bimodal flowering frequency since the flowering peak in specimens from the South-east climatic region occurs at least 90 days later than those from other regions (Fig. 4 and Electronic supplementary material 7).

Two taxa displayed differences in flowering synchronization between in situ and ex situ datasets: flowering events of *Calyptrochilum emarginatum* were significantly more dispersed in the in situ dataset ($p$ value = 0.016) whereas flowering events of *Cyrtorchis letouzeyi* were more aggregated ($p$ value = 0.014). No difference in flowering time (i.e., average flowering date) was noticed between the two datasets.

## Discussion

### A diversity of flowering patterns

Our analysis revealed significant differences in terms of frequency, synchronization, and timing of flowering in orchids in Cameroon. However, most taxa have annual patterns at the individual (21 taxa, 47%) or population (35 taxa, 78%) level of analysis, including most *Polystachya* spp. (12 out of 15 taxa).

At the population level, over half (53%) of the taxa displayed a strictly annual flowering patterns, 25% were annual with extended flowering and 22% flowered at several periods each year (sub-annual). These proportions are congruent with those reported by Sanford (1971) for 143 orchid taxa in West Africa. Likewise, Dunsterville and Dunsterville (1967) and Stévart (1998) found a similar ratio of annual flowering species for 280 Venezuelan orchids and 85 taxa in São Tomé-et-Príncipe, respectively, but a higher proportion of species displaying sub-annual flowering patterns. The results

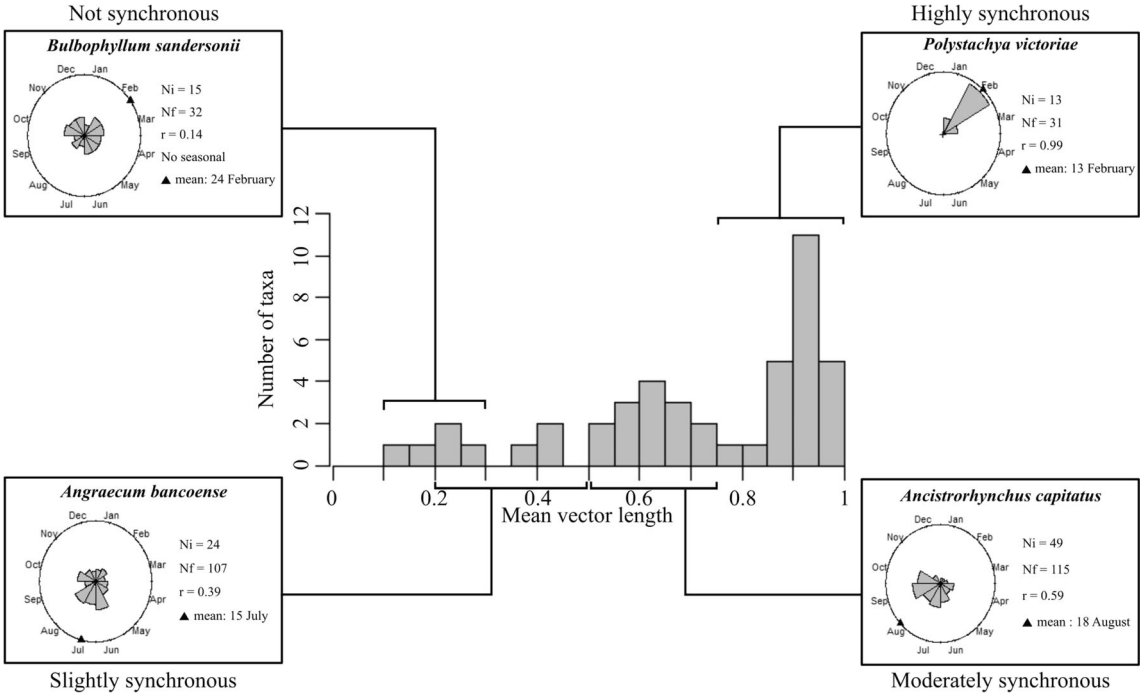



**Fig. 3** Synchronization of ex situ flowering events at the population level. Central graphic represents the distribution of the mean vector length, *r*, in the community. External graphics show examples for each group of synchronization of flowering events; graphics for the 45 studied taxa are given in Electronic supplementary materials 4 and 5. Circular graphics show the distribution of all flowering events of the taxon reported for one year. The area of monthly bins represents the relative frequency of flowering events. $N_i$ is the number of individuals, $N_f$ is the total number of flowering events for the taxon, *r* is the value of the mean vector length, and *mean* is the average flowering date

of the two latter studies should however be considered with caution because of the low number of flowering events used and the methodology employed to determine the sub-annual pattern. Nonetheless, annual flowering appears to be the prevailing pattern within tropical orchids.

Although supra-annual flowering might reduce seed predation (Curran and Webb 2000), this pattern would reduce pollinator fidelity and specialization (Bawa et al. 2003), which seems to go against the main known drivers of the orchids' extraordinary diversification (Givnish et al. 2015). In our dataset, 40% of the taxa (mostly *Bulbophyllum* spp.) displayed supra-annual patterns at the individual level. This pattern could be the result of inter-annual variations in climate (Vogt-Schilb et al. 2013). However, our results might

**Table 2** Phylogenetic constraints on flowering frequency patterns at the genus level. The table gives the value of the Freeman-Tukey deviation from a significant Fisher exact test ($p$ value < 0.001) on a two-way contingency table for the genera with at least three taxa. The frequency of flowering of their taxa is tested at the individual level of analysis. If the Freeman-Tukey value is superior to the critical value ($F$ critical = 0.2660), then the frequency class is considered significantly over-represented for this genus (values in bold)

| Frequency | | | | | |
|---|---|---|---|---|---|
| Genus | Continual | Sub-annual | Bimodal | Annual | Supra-annual |
| *Ancistrorhynchus* | 0 | − 2.0000 | 0 | − 0.1862 | − 0.8416 |
| *Angraecum* | 0 | **1.0800** | 0 | − 1.8817 | − 3.1231 |
| *Bulbophyllum* | 0 | − 3.0000 | 0 | − 2.6470 | **1.3854** |
| *Polystachya* | 0 | − 1.8452 | 0 | **1.4157** | − 2.1136 |

**Table 3** Phylogenetic constraints on flowering regularity patterns at the genus level. The table gives the value of the Freeman-Tukey deviation from a significant Fisher exact test ($p$ value = 0.002) on a two-way contingency table for the genera with at least three taxa. The regularity of flowering of their taxa is tested at the individual level of analysis. If the Freeman-Tukey value is superior to the critical value ($F$ critical = 0.5209), then the regularity class is considered significantly over-represented for this genus (values in bold)

| Regularity | | | | |
|---|---|---|---|---|
| Genus | Highly regular | Moderately regular | Lightly regular | Not regular |
| *Ancistrorhynchus* | 0.3239 | − 2.0000 | − 1.8031 | 0 |
| *Angraecum* | − 3.4760 | **0.6305** | − 0.1095 | 0 |
| *Bulbophyllum* | 0.2901 | − 1.5101 | − 1.0610 | 0 |
| *Polystachya* | **1.2385** | − 1.8452 | − 1.2779 | 0 |

**Table 4** Results of repeated measures ANOVA on monthly flowering events within the four more diverse genera of the present study (*Ancistrorhynchus*, *Angraecum*, *Bulbophyllum*, *Polystachya*). The null hypothesis (genus x month) is a similar monthly pattern of flowering between the genera tested

| Source | Df | Sum-of-squares | Mean square | *F* value | *p* value |
|---|---|---|---|---|---|
| Genus | 1 | 0.006 | 0.0064 | 0.125 | 0.724 |
| Month | 11 | 5.403 | 0.4812 | 9.58 | < 0.001 |
| Genus x month | 11 | 0.886 | 0.0805 | 1.571 | 0.105 |
| Residuals | 383 | 19.637 | 0.0513 | | |

be an overestimation given uncertainties related to potentially sub-optimal growing conditions in the shadehouse, or mortality. Sub-optimal conditions are suggested by the relatively high proportion (41%) of individuals that have flowered only once (Electronic supplementary material 6). Moreover, plant adaptation and stress associated with transplantation from the field to the shadehouse cannot be excluded. Finally, for eight of the 18 taxa considered to be supra-annual, more than half of the individuals were found to be dead when mortality of the cultivated specimens was assessed in 2015 (Electronic supplementary material 6).

## Phylogenetic relatedness

Phylogenetic effect was revealed for flowering regularity and frequency at the genus level. The genus *Angraecum* was dominated by sub-annual frequency and medium regularity ($0.5 \leq r < 0.75$) and *Polystachya* by annual frequency and high regularity ($r \geq 0.75$). These phylogenetic constraints may be related to the different growth forms of both genera: *Angraecum* has monopodial growth with axillary inflorescences which allow several flowering events on the same axis, whereas *Polystachya* presents sympodial growth with terminal inflorescences, and thus, the development of a new shoot is required before each flowering. Supra-annual frequency was predominant in *Bulbophyllum* spp., this being possibly related to their sympodial growth form and the time needed to produce new flowering shoots.

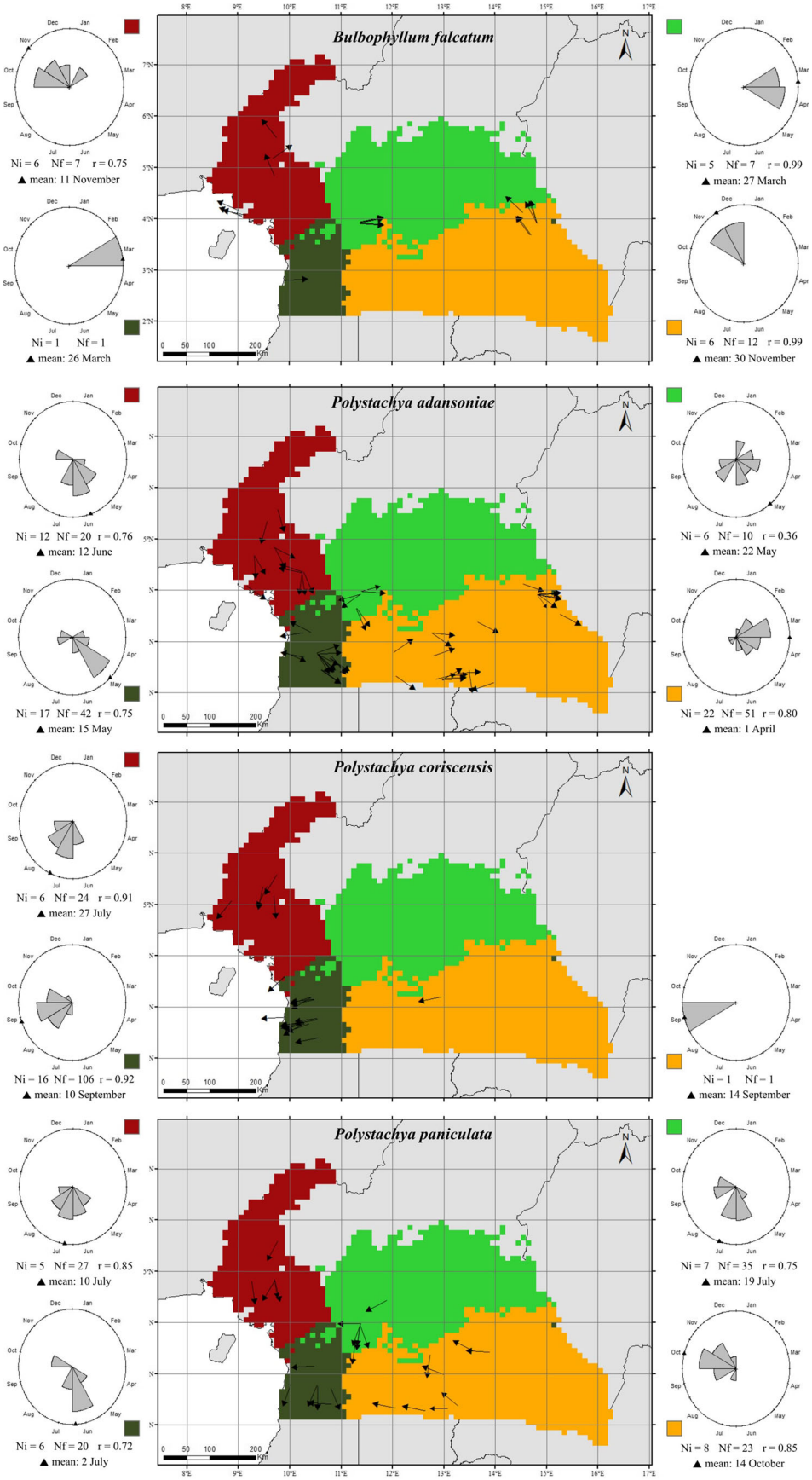
Flowering events occurred throughout the year, including for taxa with an annual frequency (Table 1). The fact that we observed no constraints in flowering time exerted by phylogenetic relationship at the genus level, unlike what has been observed in several temperate floras (Fenner 1998; Davies et al. 2013), suggests that African epiphytic orchids have been primarily subjected to a selection for a shift in flowering time by environmental or biotic factors. Nonetheless, an analysis that includes a larger number of taxa and at lower taxonomic ranks (e.g., sections or clades for *Angraecum*, *Bulbophyllum*, and *Polystachya*) should be undertaken to deepen our knowledge on phylogenetic constraints.

**Fig. 4** Geographic distribution of individuals belonging to four species with asynchronous flowering times. Arrows represent the flowering of each individual cultivated in the shadehouse in relation with its climatic region of original collection. The origin of arrows represents the exact location where the individual was initially collected. The direction of arrows represents the mean time flowering of individual with North direction representing the 1st January; time is represented clockwise. The size of arrows represents the synchronization of flowering events, maximal size corresponding to $r = 1$ and minimal size corresponding to $r = 0$. On the sides of the figure are represented the rose diagram with general data of populations for each climatic region. $N_i$ is the number of individuals, $N_f$ is the total number of flowering events for the taxa, $r$ is the value of the mean vector length, and *mean* indicates the average flowering date

## Geographical origin

The timing of flowering of individuals of four taxa (*Bulbophyllum falcatum*, *Polystachya adansoniae*, *P. coriscensis*, and *P. paniculata*) in the Yaoundé shadehouse is dependent on their geographic provenance. This suggests the existence of phenological ecotypes with desynchronized flowering times, leading to possible intra-specific breeding barriers. Because these patterns are observed within the shadehouse (i.e., after transplantation), this suggests that the flowering time for these taxa is determined by endogenous rhythms rather than being immediately dependent on environmental factors. Interestingly, Sanford's observations of Nigerian orchids (1971), specifically regarding flowering time and frequency among *Polystachya* species, disagreed with ours for seven out of ten *Polystachya* species examined in both studies, pointing to the plasticity in flowering phenology of species of this genus.

We observed timing differences between flowering of individuals of *Polystachya adansoniae* and *P. paniculata* collected in the same climatic region (Fig. 4), suggesting that this phenomenon could also occur at small geographic scales, as already observed by Sanford (1971). An important intra-specific genetic diversity (e.g., allelic endemism among different populations) that could be generated by prezygotic barriers (Hardy et al. 2013) has recently been shown for central African trees (Heuertz et al. 2014) and tropical orchids (Pinheiro et al. 2013). Evidence of prezygotic genetic isolation resulting from flowering time differences between populations of the same taxon, and generally associated with local ecological adaptations, has been found (Antonovics 2006; Hall and Willis 2006) and can lead to sympatric speciation (Savolainen et al. 2006). From our observations, we hypothesize that *Polystachya*, the third major African orchid genus (see Govaerts et al. 2018), should present an important intra-specific genetic variability associated with adaptive traits which allow significant shifts in flowering time. From our preliminary results, we suggest that the plasticity in flowering time of this genus, combined with its tendency for synchronized annual flowering pattern, might be the main reason for its wide radiation throughout the African continent.


Bulbophyllum falcatum
Ni = 6 Nf = 7 r = 0.75
▲ mean: 11 November
Ni = 1 Nf = 1
▲ mean: 26 March
Ni = 5 Nf = 7 r = 0.99
▲ mean: 27 March
Ni = 6 Nf = 12 r = 0.99
▲ mean: 30 November
Polystachya adansoniae
Ni = 12 Nf = 20 r = 0.76
▲ mean: 12 June
Ni = 17 Nf = 42 r = 0.75
▲ mean: 15 May
Ni = 6 Nf = 10 r = 0.36
▲ mean: 22 May
Ni = 22 Nf = 51 r = 0.80
▲ mean: 1 April
Polystachya coriscensis
Ni = 6 Nf = 24 r = 0.91
▲ mean: 27 July
Ni = 16 Nf = 106 r = 0.92
▲ mean: 10 September
Ni = 1 Nf = 1
▲ mean: 14 September
Polystachya paniculata
Ni = 5 Nf = 27 r = 0.85
▲ mean: 10 July
Ni = 6 Nf = 20 r = 0.72
▲ mean: 2 July
Ni = 7 Nf = 35 r = 0.75
▲ mean: 19 July
Ni = 8 Nf = 23 r = 0.85
▲ mean: 14 October
Climatic regions: South-west (G1) ; South-east (G2) ; Center (G3) ; West (G4)

### Environmental triggers for flowering

The photoperiod is particularly stable around the equator, and its effect on flowering induction might be marginal. However, Borchert et al. (2005) showed that variation of photoperiod near the equator could strongly affect flowering of tree species with synchronized or bimodal flowering patterns. According to our observations and studies in other tropical regions, the flowering of epiphytic orchids could occur during minimum (São Tomé-et-Príncipe; Stévart 1998), medium (Cameroon, Mexico; Sahagun-Godinez 1996), or maximum (Rwanda; Stévart et al. 2010) day length conditions. Contrary to some experimental studies that highlight the role of extreme day lengths (e.g., long days in Vaz et al. (2004), short days in Lopez and Runkle (2005)) as factors for flowering in orchids, we suggest that the variation of photoperiod is more complex. Triggering of flowering events of annual and highly synchronized taxa all through the year could suggest that day length required to induce flowering is taxon-dependent. Identical timing was observed for in situ and ex situ flowering events at the population level despite differences in climatic conditions, nutrient availability, or biotic factors. This suggests that photoperiod, which is the least variable environmental factor throughout the region, could be a crucial parameter to allow simultaneous flowering of all individuals from a given taxon, independently of the climate seasonality of their area of provenance.

In tropical regions, phenological variations are generally related to water availability (Fenner 1998). Moisture availability is however not recognized by Sanford (1971) as a potential inductor of flowering in West African orchids. Nevertheless, in the present study (Fig. 1, Table 1, and Electronic supplementary materials 4 and 5) and as reported for São Tomé-et-Príncipe (Stévart 1998), Kinshasa (Mbale et al. 2014), Rwanda (Stévart et al. 2010) and for some orchids of West Africa (Johansson 1974), it is clear that most taxa produce flowers at the beginning of and during the main rainy season, which could support the hypothesis of a minimal moisture level required for flowering. Therefore, and contrary to Sanford (1971), we suggest that precipitation and more specifically moisture availability, in combination with other climatic factors (e.g., photoperiod, irradiance, temperature), also plays a key role in flowering induction of African epiphytic orchids.

## Conclusion

Although no phylogenetic constraint on flowering time was observed at the genus level, this does not mean that it does not have an influence on other taxonomic ranks, as suggested by the phenological ecotypes observed in the shadehouse. Observed intra-specific variation in flowering time among individuals from different geographic regions may have a genetic basis as a result of local adaptation or genetic drifts. If flowering time is determined by endogenous rhythm rather than an environmental factor, timing of flowering would diverge and be much less synchronous during a long time of cultivation.

The role played by climatic factors on flowering patterns was difficult to evaluate due to scarce and imprecise data. However, the recent meteorological station established in the shadehouse will provide more accurate daily data to further explore these parameters.

For future perspectives, we propose to implement in situ surveys of orchids flowering along climatic gradients, especially for taxa with potential phenological ecotypes. A detailed analysis of ecology, flowering time, and phylogeographic analysis of these latter taxa would bring crucial information on prezygotic barriers acting as diversification process within Orchidaceae.

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**Author contributions** N.T. conceived the study under direction of V.Dr. and V.De. N.T. designed and performed the analysis with assistance from V.De. for circular statistics and climate classification. T.S., B.S., M.S.-D., L.A., M.-N.D., G.K., N.K., S.M., and L.Z. collected data. R.B. contributed to the interpretation of the results. N.T. wrote the manuscript with the assistance of V.De., R.B., and V.Dr. and all other co-authors.

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