

## Article

# When Are Cacti Found with Flowers and Fruits? Estimation of the Reproductive Phenology of the Genus *Xiquexique* Based on Herbarium Data

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**Abstract:** Plant phenology reflects the reproductive responses of plants to seasonal cycles and climate change. Herbarium collections can be valuable tools for filling in gaps in phenological studies. We investigated the seasonality of the reproductive phenology of *Xiquexique* species using circular statistics, estimated their flowering and fruiting periods by interpolation via inverse distance weighting based on herbarium specimens (n = 290), and analyzed the relationships among phenophases, temperature, and precipitation using generalized linear models. *Xiquexique* species flowered and fruited throughout the year, with *X. gounellei* exhibiting peak flowering in February and peak fruiting in March, while *X. tuberculatus* exhibited those peaks in August–October and August, respectively, with decreased intensity during the austral winter. The maps produced through interpolation showed higher probabilities of flowering and fruiting between February and August at sites with mean annual rainfall rates between 500 and 800 mm. Temperature and precipitation were positively correlated with flowering. *Xiquexique tuberculatus* is important for providing continuous resources to pollinators and seed dispersers in the Caatinga. Herbarium collections and interpolation methods for filling in gaps concerning the reproductive ecology of Cactaceae can aid in better understanding altered phenological patterns resulting from environmental changes.

**Keywords:** flowering; fruiting; cactaceae; herbarium records; geoprocessing; seasonality; Caatinga; dry forests



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## 1. Introduction

Phenology studies address the seasonal cycles of biological events, with species-, population-, and community-level analyses [1]. The discipline focuses on events occurring during the life cycle of plants, such as the appearance of flowers and fruits, which are often triggered by environmental stimuli [2]. The use of phenological data has become increasingly important for predicting the responses of plant species to global climate change, particularly in the Northern Hemisphere. The seasons there define distinct reproductive periods that are typically associated with higher temperatures and longer days, followed

by an interval of dormancy with cooler temperatures and shorter days [2–4]. This suggests that factors such as temperature and photoperiod play fundamental roles in regulating phenological events in these environments, highlighting the importance of such studies for understanding plant adaptations and biodiversity conservation [5,6].

Herbarium collections can play a fundamental role in phenological studies in a changing world [2,3], as they contain valuable data concerning reproductive phenology studies that can enable analyses of temporal variations of flowering, fruiting, and seed dispersal cycles [2,3,7]. Such information can play a vital role in understanding the impacts of climate change on plant biology and provide important information for conservation planning and plant resource management strategies in different environments and vegetation formations [2–5,7].

Another approach that has been used for phenological studies involves the processing of metrics available on geographic information system (GIS) platforms [8]. Geospatial data tools, such as spatial interpolation, can be used to estimate the properties of unsampled sites based on observed data values at known sites [9]. Among the various methods available, inverse distance weighting (IDW) can be an efficient tool for estimating reproductive phenology and for complementing field data with herbarium information [7].

Eastern Brazil comprises different vegetation formations [10], with the Caatinga (the most diverse and largest seasonal tropical dry forest in South America) covering most of the northeastern region of that country [11]. The semiarid Caatinga climate has well-defined seasons and contains plants adapted to drought and extreme heat, making it suitable for long-term phenological studies [11]. Among the typical plant groups found there, the cacti (Cactaceae) stand out for their unique adaptations to this semiarid environment [11]. Water and food resources are often limited in this environment, and cacti play prominent roles by providing flowers and fruits for the local fauna [12–15]. The family is represented by several genera in the Caatinga, such as *Cereus* Mill, *Melocactus* Link & Otto, *Pilosocereus* Byles & Rowley, *Tacinga* Britton & Rose, and *Xiquexique* Lavour, Calvente & Versieux, and all of them have essential ecological functions [10].

Ethnobotanical studies have highlighted the versatility and usefulness of cacti for rural communities in the semiarid region of Brazil [16]. Although these plants, particularly the *Xiquexique* species, play crucial roles in the subsistence of local human populations, few studies have focused on their regional availability [17]. Local communities rely on these plants not only as food sources, but also as forage and, notably, as living fences, which underscores their multifunctional value [16,17].

The phenology of cacti in the Caatinga is inextricably linked to the climatic characteristics of that region, with their phenologies adapted to irregular rainfall and water availability [18]. These plants are also sensitive to other factors, such as annual climatic variability, the occurrence of extreme weather events, biotic interactions, and natural or anthropogenic disturbances [18,19]. Changes in rainfall patterns, for example, can influence the timing and intensity of their flowering and fruiting [18,19]. Similarly, the activities of pollinators and dispersers play essential roles in regulating the phenologies of Cactaceae species, with these multiple interactions playing crucial roles in their life cycles [13,14].

Despite the ecological importance of cactus species, there are still considerable gaps in our knowledge of their reproductive phenologies. Projections of losses of cactus habitats due to environmental change are worrying [18], and in spite of their high levels of endemism in the Caatinga they remain largely unprotected [19]. Additionally, anthropogenic disturbances, such as extractivism, fire, invasive grasses, mining, and livestock herding (e.g., goats and cattle), can affect the survival and reproductive success of cactus species [20]. Studies of the specific timing of events such as flowering, fruiting, and seed dispersal will therefore be crucial for fully understanding the reproductive strategies of cacti under the arid and semiarid Caatinga conditions [12,14].

In this sense, cacti are an excellent plant group for long-term phenological studies based on herbarium data, as they are easily recognizable plants that are widely distributed and usually well-represented in herbarium collections.

The genus *Xiquexique* was therefore selected as a model for a pioneer phenological study based on herbarium data. It is widely distributed in the Caatinga, it plays a fundamental role in providing resources to the local fauna, including both pollinators and seed dispersers [13,21], and it has a manageable number of species.

We analyzed the reproductive phenologies of *Xiquexique* species through the examination of exsiccates available in herbarium collections to better understand their roles in providing resources to pollinators and dispersers throughout the year. We investigated the seasonality of the reproductive phenology of those *Xiquexique* species and estimated flowering and fruiting times in areas without collected samples by interpolation via inverse distance weighting. We expect that our results will allow the extension of the phenological information obtained from herbarium data to larger scales, as well as provide useful insights for planning future field research efforts.

## 2. Materials and Methods

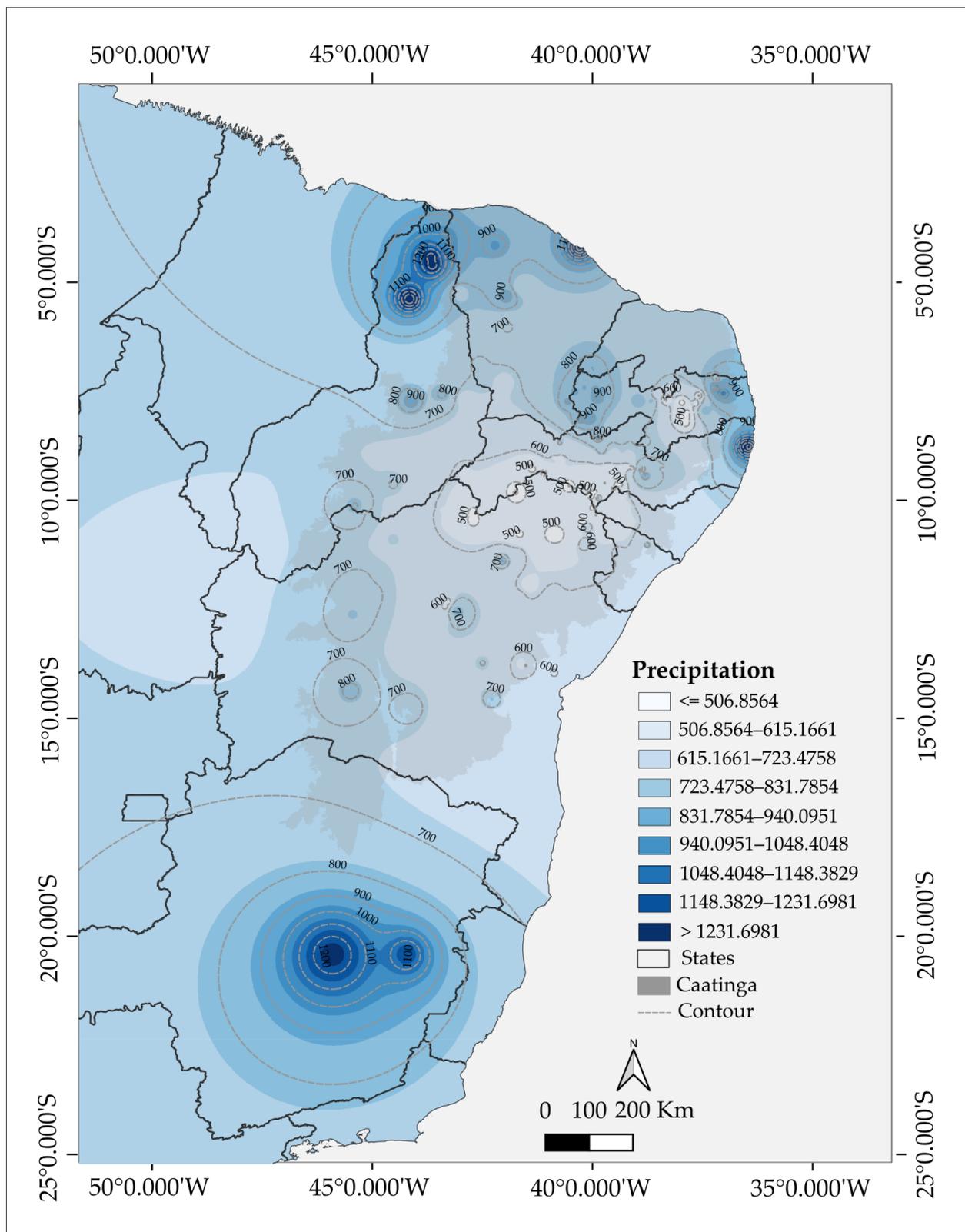
### 2.1. Species Selection and Phenological Data Collection

The recently described genus *Xiquexique* was previously classified as a subgenus within *Pilosocereus*, under the name *Pilosocereus* subg. *gounellea* Zappi [22]. *Xiquexique* comprises three species: *X. frewenii* (Zappi and N.P.Taylor) Zappi and N.P.Taylor, *X. gounellei* (F.A.C.Weber) Lavor & Calvente, *X. tuberculatus* (Werderm.) Lavor & Calvente, and the heterotypic subspecies *X. gounellei* subsp. *zehntneri* (Britton and Rose) Lavor & Calvente. They occur in eastern Brazil, particularly in the Caatinga, and are some of the most important vegetational elements in that region [10] (Figure 1).

*Xiquexique gounellei* is considered one of the most emblematic Caatinga species and has a wide distribution that includes all of the northeastern Brazilian states through to the central-northern state of Minas Gerais [10,23]. It grows on stony soils as well as on rock outcrops, and often dominates in regions with low and sparse vegetation [10] (Figure 2). *Xiquexique tuberculatus* is restricted to sandy habitats, especially old sand dunes near the São Francisco River (Figure 3). Both species produce white, tubular flowers having nocturnal anthesis, and both provide nectar as the main resource. They are frequently visited by bats and moths [12,13,21,23,24], and they produce fleshy, dehiscent fruits with many small, black seeds embedded in a pink pulp that are consumed by bats, birds, and lizards [13,21,23]. *Xiquexique frewenii* occurs on limestone outcrops in central Minas Gerais [24] and has a more restricted distribution range. It is possibly a relict species from Pleistocene drought events [10].

We conducted a comprehensive survey of herbaria specimens between October and December 2023 using the online SpeciesLink platform (<http://splink.cria.org.br/>) (accessed on 18 December 2023), a system providing free access to the collection data of various groups of organisms [2,9]. We searched for the names of the taxa and their synonyms (*Xiquexique gounellei* = *Pilosocereus gounellei*, *X. frewenii* = *P. frewenii*, and *X. tuberculatus* = *P. tuberculatus*) and identified and examined as many exsiccates as possible that contained information on their reproductive phenophases (flowering and fruiting).

The selection of the herbarium specimens was based on their careful examination and criteria such as: (1) identifications by cactus specialists; (2) the presence of flowers and fruits, or the presence of information concerning the flowers and fruits on the herbarium labels; (3) the examination of additional notes on the exsiccates; (4) the collection location; (5) the herbarium in which they were deposited; (6) the collection date; and (7) the exclusion of all duplicates or exsiccates containing only vegetative material or without any information concerning reproductive aspects (Figure 4).



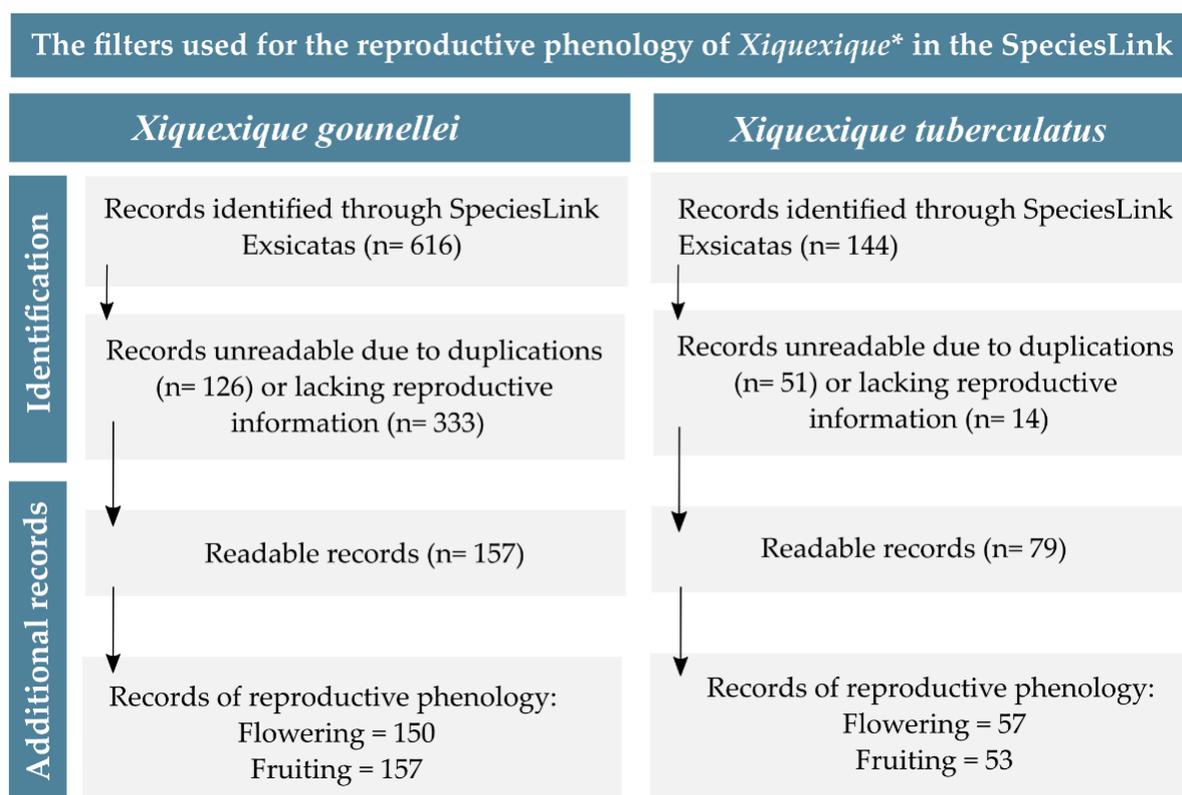
**Figure 1.** Location of the Caatinga (shaded) region in northeastern Brazil, indicating the precipitation isohyets in the region.



**Figure 2.** (A) *Xiquexique gounellei* in flower (photo: S. Albuquerque-Lima); (B) individual of *X. gounellei* in fruiting (photo: Hirandir); (C) exsiccate of *X. gounellei* (including flower), Jardim Botânico do Rio de Janeiro Herbarium; (D) exsiccate of *X. gounellei* (including fruit), Universidade Estadual de Feira de Santana Herbarium.



**Figure 3.** (A) *Xiquexique tuberculatus* in flower (photo: Sinzinando Albuquerque-Lima); (B) flower bud and fruit of *X. tuberculatus* (photo: Isadora Schulze de Albuquerque); (C) exsiccate of *X. tuberculatus* (including flower), Universidade Estadual de Feira de Santana Herbarium; (D) exsiccate of *X. tuberculatus* (including fruit), Universidade Federal Rural de Pernambuco Herbarium.



**Figure 4.** Flowchart of the filtering steps in the selection of phenological data concerning *X. gounellei* and *X. tuberculatus* on the SpeciesLink platform. \* All species belonging to the genus were filtered, but only *X. gounellei* and *X. tuberculatus* were selected for comprehensive filtering in this study.

The SpeciesLink search filtered out 780 exsicatas of *Xiquexique*, distributed among 33 herbaria. Useful collections were available from 33 herbaria (ALCB, ASE, BHZB, CEN, CSTR, EAC, EAN, FUEL, HRCB, HRSN, HST, HTSA, HUEFS, HUESB, HURB, HVASF, IPA, K, MAC, MAR, MBM, MBML, MCCA, PEUFR, RN, SPF, TEPB, UB, UEC, UESC, UFP, and VIC—acronyms according to the Index Herbariorum) (Supplementary Materials). Of the total number of selected exsicatas, only five were recorded for *X. frewenii*, 616 for *X. gounellei*, 16 for *X. gounellei* subsp. *zhentneri*, and 144 for *X. tuberculatus* (Figure 4).

In terms of *X. gounellei*, we identified 157 exsicatas that contained readable reproductive data (150 with flowers, 157 with fruits), while 333 exsicatas did not contain information concerning their respective reproductive phenophases. In addition, 126 duplicates were identified, all of which were excluded during filtering. In terms of *X. tuberculatus*, we identified 79 specimens with legible information on their reproductive phenophases (57 with flowers, 53 with fruits) available as pictures or labels with the specimens themselves. Of the 144 specimens of *X. tuberculatus*, 51 duplicates and 14 specimens were excluded due to missing information concerning their reproductive phenophases (Figure 4).

## 2.2. Data Analysis

Circular statistics were used to analyze the seasonality of the phenological data. The frequencies of the flowering and fruiting phases were calculated based on the total number of individuals/vouchers exhibiting these phases per month. Months were converted to angles and divided into 30° intervals. We calculated the mean angles and vector lengths ( $r$ ) and assessed the significance of the mean angles using the Rayleigh test ( $z$ ) for circular distributions [25]. Phenophases with vector lengths ( $r$ ) greater than 0.5, which the Rayleigh test indicated as significant ( $p < 0.05$ ), were considered seasonal [26]. Statistical analyses were performed via R software using the ‘circular’ package, version 3.2.3 [27].

Climate data in terms of mean annual temperature (bio1) and mean annual precipitation (bio12) were recorded for each collection point of *Xiquexique* species and for the genus as a whole, using WorldClim. These records cover the historical period between 1970 and 2000, and they were subsequently interpolated to reflect current conditions. Generalized linear models (GLMs), with binomial error and using the logit link function in R software version 4.0.3 [27], were used to investigate the relationship between the flowering and fruiting phases and environmental factors such as temperature and precipitation. To mitigate the influence of multicollinearity between variables, the environmental variables for each phenological stage were carefully selected based on the lowest correlation between them. Only statistically significant results ( $p < 0.05$ ) were considered in these analyses.

We used geospatial interpolation inverse distance weighting (IDW) [28] to estimate reproductive phenologies from herbarium collections, according to [7]. The IDW system is a rapid method with low operating costs, characterized as a smoothing and accurate global-type interpolator that is reasonably faithful to the sample data and has high processing speed (QGIS.org 2021). We imported and converted the group data into a vector file (shapefile) via QGIS 3.32 Lima software, and we performed interpolation using the `qgis:idw` interpolation algorithm based on the months of phenophase occurrence, resulting in a raster file. The P coefficient, an attribute that determines the power by which the distance between points is increased, was kept by default with a value of 2 (square of the distance) and, after processing, a simple false-color band was applied. Finally, resampling was performed using the bilinear method to remove the knurling effect from the image and produce a map with smooth gradients between values [7].

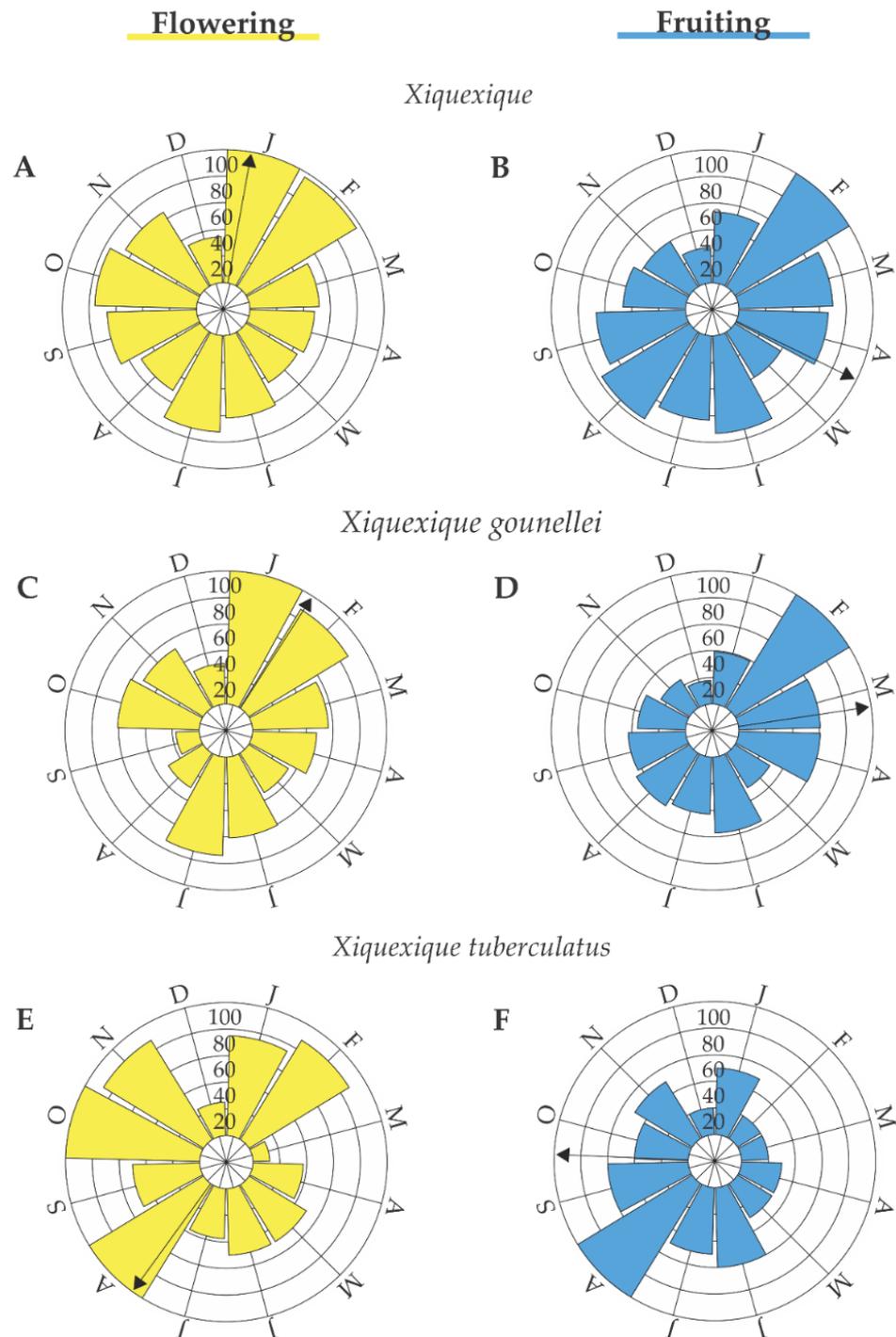
### 3. Results

Analysis of the data derived from exsiccates revealed a low seasonality of the flowering and fruiting stages of the genus *Xiquexique*, as well as for its most common species, *X. gounellei* and *X. tuberculatus*, with flower and fruit production occurring practically all year round in the arid regions of northeastern Brazil.

*Xiquexique gounellei*, however, demonstrated a notable flowering peak in February and its greatest fruiting in March (Table 1). Circular statistical analysis showed that the second day of February represented the peak of flower production ( $p < 0.05$ ), while a high proportion of individuals formed fruits on March 23 ( $p < 0.01$ ) (Table 1, Figure 5). In contrast, *X. tuberculatus* evidenced a flowering peak in August–October and a fruiting peak in August (Figure 5), with the highest proportion of individuals producing flowers on the second day of October ( $p < 0.19$ ), and the highest proportion of individuals producing fruits on August 5 ( $p < 0.02$ ) (Table 1).

**Table 1.** Results of circular statistical analysis of the occurrence of seasonality in the reproductive phenology of herbarium specimens of *Xiquexique*. Rayleigh tests were performed to evaluate the significance of the mean angle ( $\mu$ ).

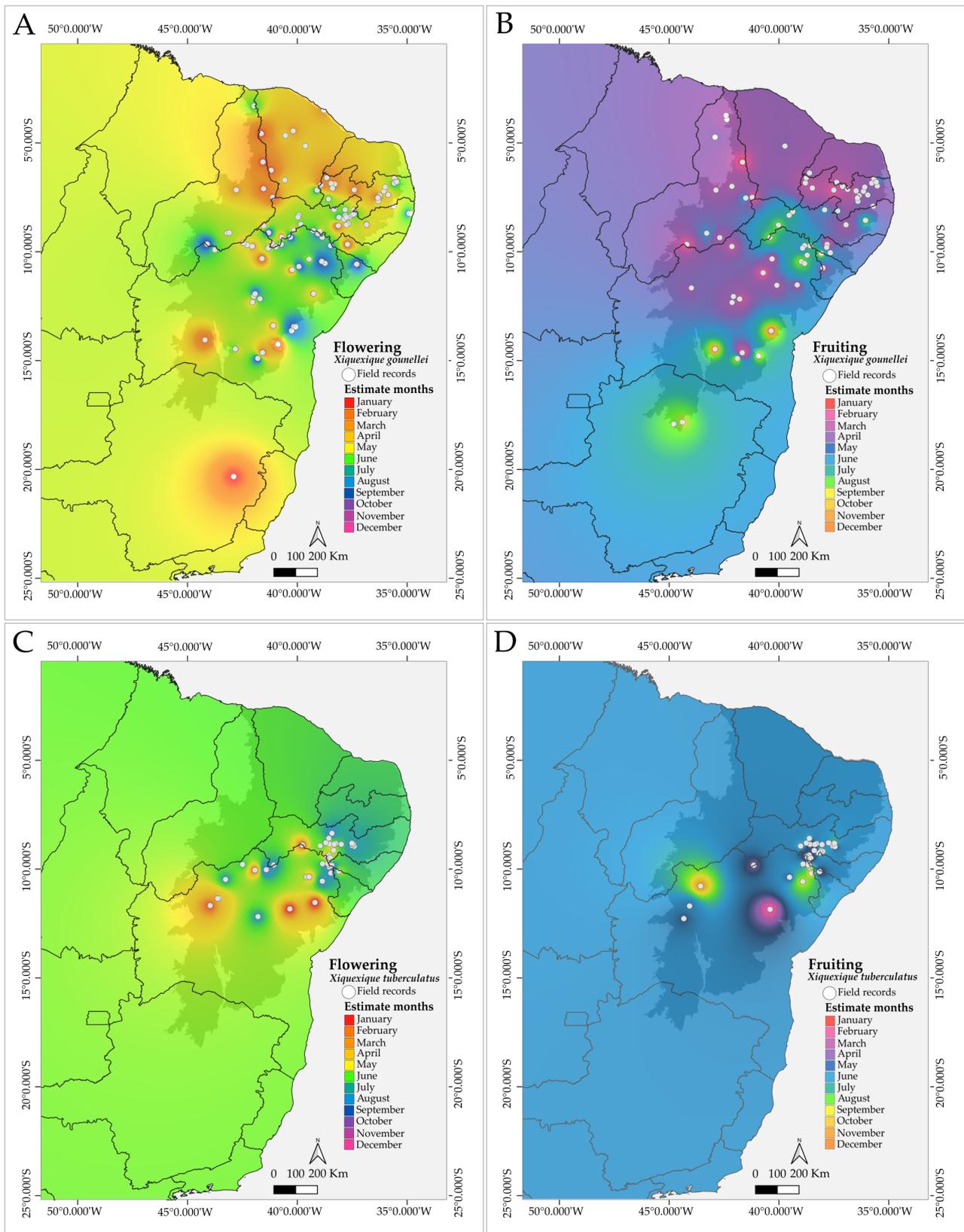
Taxon	Phenophase (n)	Mean Date	Mean Angle	Angular Standard Deviation	Mean Vector (r)	Rayleigh Test (p)
<i>Xiquexique</i>	Flowering	11/January	10.13°	120.66°	0.17	0.17
	Fruiting	27/April	116.24°	120.96°	0.08	0.17
<i>X. gounellei</i>	Flowering	02/February	32.62°	113.59°	0.14	0.05
	Fruiting	23/March	81.35°	108.23°	0.26	0.01
<i>X. tuberculatus</i>	Flowering	02/October	272.37°	107.81°	0.17	0.19
	Fruiting	05/August	215.73°	93.40°	0.26	0.02



**Figure 5.** The reproductive phenology of the genus *Xiquexique* based on herbarium data. The flowering and fruiting of *Xiquexique* (A,B), *X. gounellei* (C,D), and *X. tuberculatus* (E,F).

The amplitude of reproductive phenology, using inverse distance weighting, showed that *Xiquexique* flowered and fruited throughout the year, with their highest intensities occurring from February to August and from March to August, respectively (Figure 6). The maps produced for *X. gounellei* (Figure 7A,B) and *X. tuberculatus* (Figure 7C,D) confirmed that the probability of finding plants in their reproductive phase between February and October was higher at sites with a mean annual rainfall rate between 500 and 1000 mm.





**Figure 7.** Probable flowering (A) and fruiting (B) months of *Xiquexique gounellei*, and the probable flowering (C) and fruiting (D) months of *Xiquexique tuberculatus*, according to IDW interpolation. The colors indicate the best months for field excursions. White dots represent herbarium specimens.

## 4. Discussion

This is the first study presenting data concerning the herbarium-based phenology of Cactaceae species, providing crucial insights into their life cycles, flowering, and fruiting. Our results demonstrate the importance of herbarium-based biological collections as resources for studying the reproductive phenophases of *X. gounellei* and *X. tuberculatus*, as well as other members of the genus (*X. frewenii* and *X. gounellei* subsp. *zehntneri*) containing only low numbers of herbarium collections. Furthermore, we highlight the relevance of herbarium data for understanding how *Xiquexique* species influence the resources available to pollinators and dispersers in arid regions.

### 4.1. Phenological Patterns and Resource Availability in *Xiquexique*

According to our results, fruits and flowers are present during almost every month of the year, which is consistent with field observations in Caatinga areas of Brazil that covered periods of one year [12], two years, or even up to four years [21]. The low seasonalities found in our study for the flowering and fruiting phases of *X. gounellei* and *X. tuberculatus* confirmed earlier studies within the genus in the Caatinga [12,21]. A central aspect of the reproductive phenology of columnar cacti in the Caatinga is the continuous availability of their flowers and fruits throughout the year [12–14,24]—a crucial feature for pollinators and dispersers, as it ensures a consistent food source and helps maintain ecological interactions in this challenging environment [12,21,24].

The diversity of columnar cactus species in the Caatinga, each with its distinct phenology, helps maintain crucial resource levels throughout the year [12,21]. Their morphological and physiological adaptations allow them to thrive in arid environments and regularly produce flowers and fruits [12,21]. An uninterrupted supply of Cactaceae flowers throughout the year is crucial for pollinators, especially bats and hummingbirds [13,14], and demonstrates the complexities of the relationships between plant phenology and the ecology of the Caatinga domain [21].

Several animals, such as bats, moths, hummingbirds, and lizards, play important roles in the reproductive ecology of Cactaceae species in the Caatinga [12–15,21]. They rely on these plants as primary sources of food resources, especially nectar, a substance rich in water, sugars, amino acids, vitamins, and minerals [13,15], and they play, in return, a critical role in promoting cross-pollination [13–15,25]. In addition to floral nectar, cactus fruits represent an important food source for a variety of animals, including birds, mammals, and reptiles [14,15,21]. These animals likewise play crucial roles in the dispersal of cactus seeds by transporting them through their digestive tracts and depositing them in distant locations, thus facilitating the colonization of semiarid environments [15,21].

Numerous studies have been conducted to document phenological patterns in tropical regions throughout the world [2,3,29–31], and have revealed complex interplays between environmental factors and phenological events [3,5,31]. Precipitation, solar radiation, and photoperiod stand out as key factors influencing plant phenology and, consequently, the ecologies of tropical organisms [30,31]. Understanding the relationships between these factors and phenological events is critical to understanding how climate change and seasonal variations will affect biodiversity and tropical ecosystems, and will provide valuable insights for the conservation and sustainable management of highly diverse regions [2,5,31].

In addition to the interaction with environmental factors, phenological patterns can influence different biological events, such as the formation of hybrids [32]. Our data revealed an overlap in the flowering periods of *X. gounellei* and *X. tuberculatus*, providing a partial explanation for potential hybrid formation, especially when these species are close geographically and genetically [22,23]. This flowering overlap presents favorable conditions for crossbreeding and the formation of hybrids [22,23].

#### 4.2. Challenges and Importance of Herbarium Data for Cactaceae Phenology

Our understanding of phenological variation can be significantly affected by restrictions on plant collections. Studies of newly discovered species will be directly affected by environmental regulations, conservation concerns, habitat degradation, and a lack of funding for fieldwork [2,3,6]. The limitations placed on specimen collections can affect the long-term continuity of phenological records and make it more difficult to detect long-term patterns [2,4]. It will therefore be important to search for a middle ground between the availability of specimens for phenological studies and conservation concerns [2–4,6].

The collection and conservation of herbarium specimens of Cactaceae are often challenging, which is exemplified by the recurrent lack of reproductive structures in material deposited in these biological collections. Due to their high water contents (a characteristic feature of Cactaceae), collecting often becomes a complicated task, and improper herborization attempts can have disastrous consequences [2]. Contact with their sharp spines can also inflict significant injuries on collectors, while the plant itself is susceptible to decay or fungal attacks if collected improperly [5]. The collection and handling of these plants therefore requires specialized techniques and careful attention to preserve both the integrity of the collector and the quality of the sample [2,3,5,8].

The compilation of useful phenological data is often complicated by encounters with specimens that were not collected with reproductive material, as we emphasize in the case of cacti. Even when a species is not reproducing, however, herbaria collections can provide permanent records [2,3], enabling studies of geographic distribution, morphology, and other biological facets [12,14,22,24]. These collections can therefore serve as rich sources of data that can fill in gaps in phenological research, increase our knowledge of flowering and fruiting cycles, and contribute to the conservation of Caatinga habitats [12–14].

Phenological studies in arid environments are essential for understanding plant adaptations to water scarcity conditions and the probable impacts of climate change on these sensitive ecosystems [2,4]. The Caatinga is a biodiverse environment, and phenological studies will be crucial for understanding its ecological dynamics [29–31].

It is essential, however, to approach this wealth of data with caution, as the quality of the samples and the accuracy of the accompanying information can vary considerably [3,4]. Data reliability can be affected by identification errors, problems with specimen preservation, and the lack of detailed information concerning the conditions under which the specimens were collected [2–4,6,7]. Therefore, although herbarium specimens are a potentially valuable tool for phenological research in the tropics, rigorous data assessments are imperative, as well as validation methods that can ensure robust results and reliable conclusions [2,6].

#### 5. Conclusions

It is important to emphasize the importance of herbarium collections and easily accessible scientific databases to increase our knowledge about poorly studied Caatinga species. These studies will be especially important for filling information gaps, such as this first phenological study of the reproductive ecology of Cactaceae, which demonstrated the continuous availability of flowers and fruits among Caatinga *Xiquexique* species, and *X. gounellei* and *X. tuberculatus* as essential resources for pollinators and fruit and seed dispersers.

The use of herbarium data for IDW interpolation proved to be extremely useful for extrapolating the reproductive phenologies of the species. The conservation of *Xiquexique* species will be important to ensure the sustainability and preservation of the Caatinga habitat and regional biodiversity.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/d16020079/s1>, Table S1: Herbarium records with reproductive material of *Xiquexique* genus species.

**Author Contributions:** A.B.-S., S.A.-L., A.C.d.A.F., M.T.D.G. and M.T.d.S. conceptualized the study and designed the methodology; A.B.-S. and S.A.-L. collected the data under the supervision of S.A.-L., V.G.N.G., I.C.M. and L.S.F.; A.B.-S. wrote the first draft of the manuscript, with contributions from S.A.-L., I.C.M. and L.S.F.; A.B.-S. led the writing of the final version of the manuscript, with contributions from S.A.-L., V.G.N.G., I.C.M. and L.S.F. All authors have read and agreed to the published version of the manuscript.

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