



## Original research

# Reproductive phenology and floral visitors of a *Langsdorffia hypogaea* (Balanophoraceae) population in Brazil



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## ARTICLE INFO

## Article history:

Received 18 July 2016

Received in revised form 11 February 2017

Accepted 20 February 2017

Edited by Stefan Dötterl

Available online 24 February 2017

## Keywords:

Floral visitors

Floral morphology

High montane seasonal forests

Nitidulidae beetles

Phenology

## ABSTRACT

The floral biology and reproductive phenology of *Langsdorffia hypogaea* were investigated. Flowering is annual and high synchronicity was observed along two years, with significant correlation with rainfall. The post-reproductive death of rhizomes suggests monocarpy. Flowers have anthers with extrorse dehiscence and a stigma exposed above the perigonium, and are arranged in dense inflorescences which produce extrafloral nectar. A total of 259 floral visitors were observed, mostly Hymenoptera/Formicidae (149 individuals, 17 ant species), and eight species of Araneae. Although ants were frequent floral visitors, a Coleoptera (Nitidulidae, Stelidota; 28% of total visits) species was the most abundant pollinator. In consequence of herbivory only 12.5% of all inflorescence clusters fruited, and we could not evaluate the percentage of pollinated plants due to insect damage. By being a rich resource in a season of scarcity, activity on inflorescences of *L. hypogaea* of both pollinators and herbivores was high.

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## 1. Introduction

Parasitic plants are an exceptional guild due to their sophisticated and little studied strategies to obtain nutrients and water from host plants. These plants find their host through chemical signals (Runyon et al., 2006), use structures known as haustoria to access the xylem (Falcão, 1975; Vega et al., 2009) and most parasitic plants exploit a broad host range (Press and Phoenix, 2005). This system, widespread in flowering plants, has been recorded in more than 4.000 species of different angiosperm families (Bellot and Renner, 2013). Balanophoraceae are almost exclusively tropical and present 18 genera (approximately 50 species) (Hansen, 1980) with seven species occurring in Brazil (Cardoso et al., 2011). Balanophoraceae species are characterized by an herbaceous life form, dioecy (rarely monoecy) and root holoparasitic behavior (Hansen, 1972). The achlorophyllous inflorescences are fleshy, unisexual or

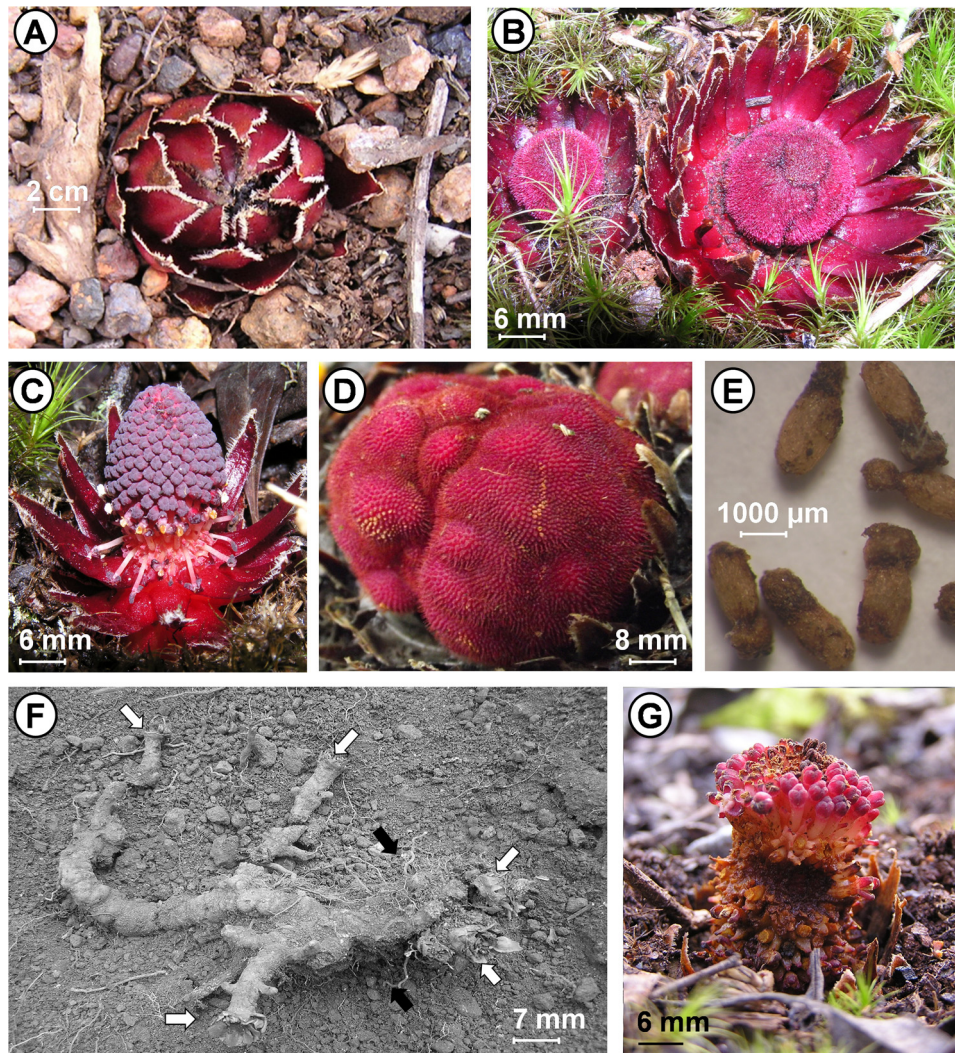
hermaphrodite, and are surrounded by bracts of leathery appearance (Falcão, 1975).

However, data about ecological interactions, pollination biology and breeding system in Balanophoraceae are scarce in the literature. Few studies listed both extremely specialized and more generalist floral visitors (Bellot and Renner, 2013). Mammals (Ecroyd, 1996), birds (Heide-Jørgensen, 2008) and several insect orders have been recorded as floral visitors. Some insects use the reproductive structures as food resource and oviposition sites, which might involve a critical trade-off between the reproductive gains by pollinating adults and losses for herbivorous larvae (Borchsenius and Olesen, 1990; Kawakita and Kato, 2002).

*Langsdorffia hypogaea* Mart. (Fig. 1) is a neotropical species, commonly found in Southeastern Brazilian montane savanna and forests. Previous observations by the authors (unpublished data) point out flowering in the dry winter period in this region. In consequence, a seasonal phenology produces flowers and fruits in expected periods of time, which may result in predictable resources for predators as well as pollinators (Develey and Peres, 2000; Barea and Watson, 2007). However, as the species flowers in the dry sea-

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**Fig. 1.** *Langsdorffia hypogaea* reproductive and vegetative structures. (A) Inflorescence bud with coriaceous bracts and serrated edges. (B) Female inflorescences. (C) Male inflorescence. (D) Unripe multiple fruit. (E) Achene (credit photo E. Leandro Cardoso). (F) Underground vegetative parts of the plant, senescent in the 2010 post-reproductive period, with intact epidermis, vestigial bracts and scapes (white arrows) and dead host roots (black arrows). (G) Male inflorescence with flowers partially eaten by *Acromyrmex* ants.

son, when other flesh plant tissues are scarce, the most important food resources for herbivore animals might be their fruits, flowers and other floral tissues, thus causing a critical trade-off between the benefits of pollination and the costs of floral and fruit herbivory. The selection of flowering timing may have evolved under the influence of a complex set of pollinators and herbivores.

Recently, [Felestrino et al. \(2017\)](#) found an intricate bacteria-dependent link between *L. hypogaea* and its host plant, but the ecology and evolution of subterranean parasitic plants still is a neglected subject. To investigate this parasitic plant adaptation to the biotic landscape one first need to understand the basics of reproductive biology of the species. Therefore, the present study describes the flower morphology, reproductive phenology and the fauna associated to *L. hypogaea*.

## 2. Materials and methods

### 2.1. Study sites and sampling design

Itacolomi State Park is located in the municipalities of Ouro Preto and Mariana, Minas Gerais State, Brazil. The area is characterized by two defined seasons: dry winter and wet summer,

and the latter concentrates 90% of the annual precipitation, from 1100 mm to 1800 mm. Annual average temperature is between 17.4 °C and 19.8 °C. The Park is within the Espinhaço mountain range and comprises the so-called “ferriferous quadrangle”, a region of approximately 7200 km<sup>2</sup> with high biological diversity and plant endemism ([Jacobi and Carmo, 2008](#)).

The sampling area was a secondary forest in high Montane Seasonal Forest, often with shallow soils ([Pedreira and Sousa, 2011](#)). The occurrence of *Langsdorffia hypogaea* population happened in a very binomial negative fashion, thus, many individuals clumped together here and there. These population clusters (hereafter only clusters) were recorded in two areas both at an altitude of 1350 m and 370 m distant from each other, precisely at 20°25'59.34" S and 43°30'23.26" W. To estimate how many clusters may exist, a thorough survey along two 1000 × 5 m transects, parallel and around access paths (road and track, respectively) was performed in each area, as the species is usually found close to pathways. No new population clusters were found in this 20,000 m<sup>2</sup> survey other than these here studied. To verify vegetative propagation, 21 clusters were excavated and uprooted, seven of them in 2009 and the remaining in 2010. The measurement of the length, number of ram-



ifications as well as a description of the epidermis in the central cylinder was carried out.

The hypogeic habit makes the delimitation of an individual plant difficult. In this sense, we assumed as individual units any cluster of inflorescences at a minimum distance of 0.20 m from the outer inflorescence, regardless organism identity. Thus, a cluster unit may consist of many individuals with male and female inflorescences.

## 2.2. Study plant species

A *Langsdorffia hypogaea* plant is divided into two parts: an elongated, hypogeic, and irregularly cylindrical vegetative body of fleshy and tomentose rhizome, from which emerges the haustoria (Hansen, 1980) (Fig. 1F); and the reproductive organs. The unisexual succulent inflorescence burst open from the scapes, surrounded at the base by a sheath of bracts (Fig. 1A–C). The inflorescences have highly active extrafloral nectaries: the male inflorescences have them between the flowers, scattered all over the inflorescence body, while the female ones have them mainly on the bracts, but also on the inflorescence basis. However, the floral morphology of this family is poorly known (Souza and Lorenzi, 2008; Erberwein et al., 2009). *Langsdorffia hypogaea* lives at altitudes ranging from 60 to 3100 m and it has been found parasitizing *Geonoma* sp. (Arecaceae), *Iriarteia* sp. (Arecaceae), *Mimosa* sp. (Mimosoideae), *Byrsonima* sp. (Malpighiaceae), *Trichilia* sp. (Meliaceae), and *Ficus* sp. (Moraceae) (Hansen, 1980).

## 2.3. Floral morphology

Morphological examination of flowers was performed with material fixed in FAA (Johansen, 1940) using a stereomicroscope and a scanning electron microscope. Both male and female flowers were isolated, dehydrated in a graded ethanol series, dried using the critical point method, mounted and coated with gold. The observations and image recording were performed in a Zeiss DSM 940 scanning electron microscope at 10 kV coupled to a digital camera.

## 2.4. Reproductive phenology

We carried out weekly phenological observations in 2010 and 2011, when 22 and 10 inflorescence clusters, respectively, were marked (109 inflorescences in total). To investigate the occurrence of apomixis, three female clusters (eight inflorescences) were isolated from visitors with fine nylon mesh bags from bud stage (emergence) to the end of flowering.

The time length of each phenophase in the population was investigated and the phenological pattern described according to the classification proposed by Newstrom et al. (1994). We observed the following phenophases: flower bud formation, flowering, unripe fruits and ripe fruits. Phenograms were made based on the following: for values lower than 20%, the population was considered asynchronous; for values between 20% and 60% it had low synchronicity; and for values higher than 60% we assumed the population had high phenological synchronicity (Bencke and Morellato, 2002). To determine whether there was correlation between phenology and rainfall we conducted a Spearman correlation (Sc) analysis (alpha-level of 0.05), focusing on flowering. Then, we correlated monthly rainfall and the frequency of individuals exhibiting this particular monthly phenophase in both study years.

## 2.5. Flower visitors

Data were collected during four nights by two observers between 19 h00 min and 07 h00 min and during seven days by one observer between 07 h00 min and 19 h00 min, totaling 180 observation hours and 45 inflorescences analyzed, belonging to 15

population clusters. A red light was used to minimize the impact of the lighting on nocturnal visitors, as recommended by Peitsch et al. (1992). Specimens were classified and identified with the assistance of specialists.

To identify potential pollinators, individuals of the same (morpho) species had to visit flowers of both sexes, touching the anthers and stigmas. Common non-pollinating floral visitors were categorized based on percentage occurrence of visitation event in relation to total number of visitors and percentage of flowers visited.

To determine whether there were any differences in the number of visits between day and night we used the Mann-Whitney *U* test with the data collected on the different days being the replicates. We applied a Chi-square test using visitor counts per taxonomic group to analyze whether the main visitor groups responded differently to the day period of foraging. To differentiate between predation by mammals and insect herbivores, five inflorescences (three male and two female) were isolated with wire grids, limiting the access to the inflorescence by mammals. All statistical analysis were performed with a significance level of 0.05.

## 3. Results

### 3.1. Floral morphology

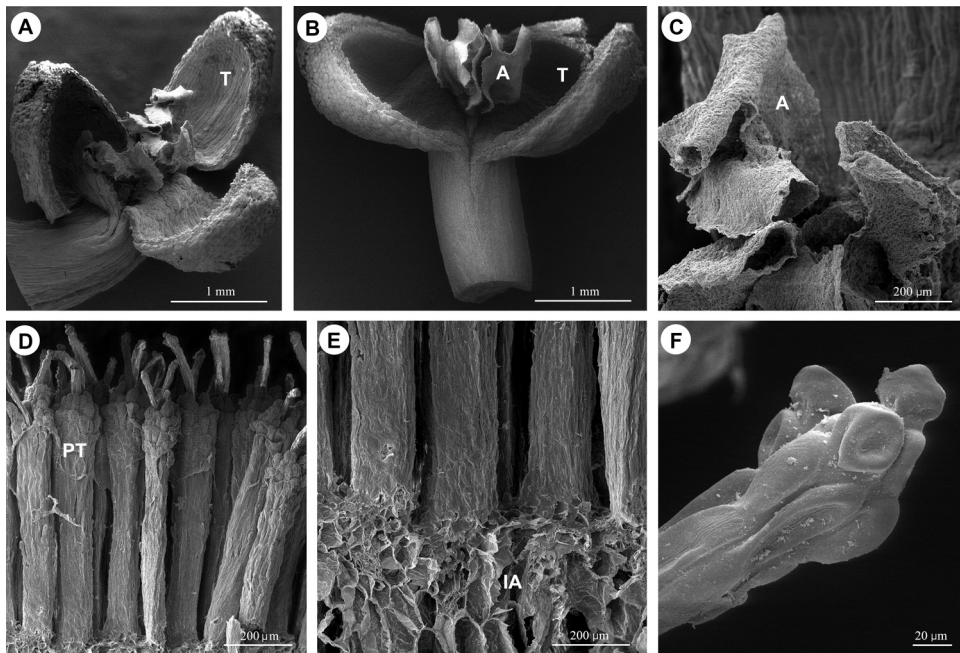
Male and female inflorescences of *Langsdorffia hypogaea* differ in several aspects (Fig. 1). The male inflorescence is a raceme surrounded by a uniform ring of bracts above its base (Fig. 1C) and other bracts scattered throughout the scape. Male flowers are pedicellate (Figs. 1C, 2A–C), monochlamydeous, trimerous (sometimes with two or four tepals), dialytpalous, isostemonous, with monadelphous stamens (Figs. 1C, 2A–C). Anthers have extrorse dehiscence (Fig. 2C). Flowers of both genders emit a sweet odor during anthesis, mainly at dawn and the following few hours, and extrafloral nectar droplets were observed on the surface of the entire inflorescence.

Female inflorescence resembles a spadix on the apex of the scape with a ring of bracts above its base (Fig. 1B). Both inflorescences are congested and have a succulent axis, but female flowers are sessile, monochlamydeous, gamotepalous, tubular (Fig. 2D–E) irregularly lobed, with a syncarpous gynoeceum. There is only one style and a stigma minutely capitate (Fig. 2F) projected above the perigone tube (Fig. 2D). Extrafloral nectar was observed only on the inflorescence base, above the bracts.

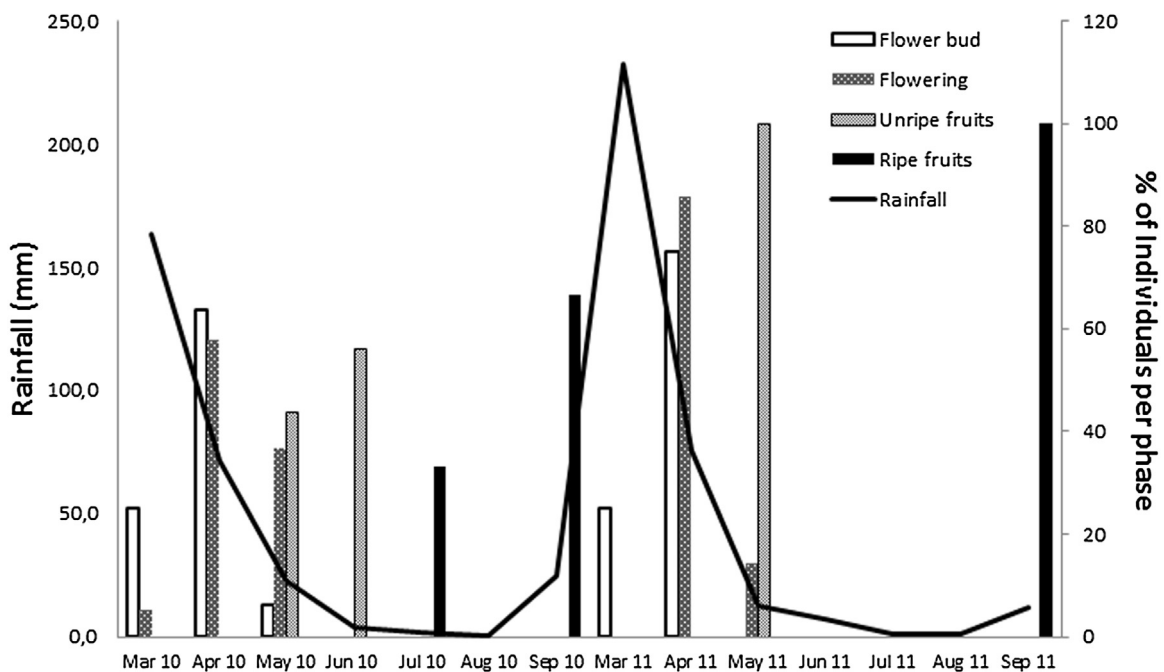
### 3.2. Reproductive phenology

Inflorescence clusters had a 2:1 sex ratio in 2010 (15 female clusters and seven male clusters) and 1:1 in 2011 (five female and five male clusters). In 2010, *L. hypogaea* exhibited an annual flowering that lasted continuously from March to May, with a peak of buds as well as opened flowers in April. In 2011, flowering events began also in March, with a peak of flower buds and opened flowers in April, and few last flowers appearing in May (Fig. 3).

In 2010, the flower bud phenophase lasted 38 days. After 35 days 58% of clusters were flowering (ie., the maximum number of individuals in that phase;  $N = 11$  individuals) and by the end of May all clusters ( $N = 73$  inflorescences) had flowered ( $N = 19$  clusters,  $3.8 \pm 3.0$ ). In 2011, flower buds ( $N = 19$ ) were also recorded in March ( $N = 7$  clusters,  $4.7 \pm 4.1$  flower buds/cluster) and April, when there was the peak activity with 13 flower buds ( $N = 6$  clusters,  $4.3 \pm 4.9$  flower buds/cluster) (Fig. 3). High population synchronicity was observed in 2010 (63.6% of individuals at the same time in a same phase) and 2011 (60%). Flower bud phenophase was positively correlated with rainfall in 2010 ( $r_s = 0.77$ ;  $p = 0.044$ ) and 2011 ( $r_s = 0.76$ ;  $p = 0.046$ ) (Fig. 3).



**Fig. 2.** Scanning electron microscopy of *Langsdorffia hypogaea* flowers. (A–C) Pedicellate diallytepalous male flowers. (A) Trimerous flower. (B) Diallytepalous flower. (C). Detail of the three open free anthers. (D–F). Tubular gamotepalous female flowers. (E) Detail of the base of sessile flowers. (F). Detail of stigma. Abbreviations: A = anther; IA = inflorescence axis; PT = perigonal tube; T = tepal.



**Fig. 3.** Reproductive phenology (flowering and fruiting) of *Langsdorffia hypogaea* in 2010 (n = 22) and 2011 (n = 10). Mean values of rainfall are represented by the line.

In May 2010, the first unripe fruits were recorded in seven clusters, and a set of ripe fruits appeared in July and again in September, when 54 multiple fruits were observed over 36 days (N = 16 clusters,  $3.3 \pm 2.0$  multiple fruits/cluster). In 2011, unripe fruits appeared in also in May, and in September they were ripe. There was no evidence of apomixis, and no significant correlation between fruiting phenophase and rainfall ( $r_s = 0.17$ ;  $p = 0.072$ ). Moreover, 26% of all clusters had their fruits removed near the peak of fruiting activity, and seven days later six clusters with 17

multiple fruits (89%) had disappeared (prior to fruit ripeness). The synchronicity in this phenophase in 2011 could not be determined, because all but one of the 19 inflorescences had been eaten by rodents.

The multiple fruits started to being dispersed and/or being foraged in average 22 days after ripening. After the first multiple fruit of a cluster reached the ripeness, it took 26 days on average for all fruits to disappear. This figure was estimated for 2010, when a huge number of fruits were recorded. The disappearance of fruits

**Table 1**  
Arthropod visitors of *Langsdorffia hypogaea* flowers in studied area between 2010 and 2011.

	Species	Total visits per species	Consumed items (floral tissues/reward or others)
<b>Insecta</b>			
Hymenoptera – Formicidae			
	<i>Acromyrmex</i> sp.	11	Flowers, floral and inflorescence axes
	<i>Acromyrmex</i> cf. <i>subterraneus</i> Forel, 1893	1	Flowers, floral and inflorescence axes
	<i>Brachymyrmex heeri</i>	4	Nectar
	<i>Brachymyrmex</i> sp.1	17	Nectar
	<i>Brachymyrmex</i> sp.2	2	Nectar
	<i>Camponotus melanoticus</i> Emery, 1894	4	Nectar
	<i>Crematogaster</i> sp.	16	Hemiptera honey dew
	<i>Hypoponera</i> sp.	2	Prey
	<i>Linepithema</i> cf. <i>pulex</i> Wild, 2007	1	Nectar, Hemiptera honey dew
	<i>Linepithema</i> sp.1	15	Nectar, Hemiptera honey dew
	<i>Pheidole</i> cf. <i>flavens</i> Roger, 1863	4	Nectar
	<i>Pheidole</i> sp.1	2	Nectar
	<i>Pheidole</i> sp.2	3	Nectar
	<i>Pheidole</i> sp.3	4	Nectar
	<i>Pheidole</i> sp.4	2	Nectar
	<i>Solenopsis</i> sp.	2	Nectar
	<i>Wasmannia</i> sp.	1	Hemiptera honey dew
Coleoptera			
	<i>Stelidota</i> sp. (adults)	55	Flowers, floral and inflorescence axes
	<i>Stelidota</i> sp. (larvae)	13	Flowers, floral and inflorescence axes
Dermaptera			
	Dermaptera sp.	4	Ants
Blattodea			
	Blattodea sp.	4	Nectar
Hemiptera			
	Hemiptera sp.	18	Plant sap
<b>Araneae</b>			
Salticidae			
	Salticidae sp.	1	Prey
Theridiidae			
	Theridiidae sp.	1	Prey
Lycosidae			
	Lycosidae sp.	3	Prey
Gnaphosidae			
	<i>Camillina</i> sp.	1	Prey
	<i>Eilica</i> aff. <i>modesta</i> Keyserling, 1891	2	Prey
Thomisidae			
	Thomisidae sp.	3	Prey
Linyphiidae			
	<i>Sphecozone castanea</i>	2	Prey
	Linyphiidae sp.	3	Prey

was followed by the apparent death of the plant, suggesting that the species is semelparous. Additionally, we observed few seedlings in some clusters, which allow the settling of new generations at the same site.

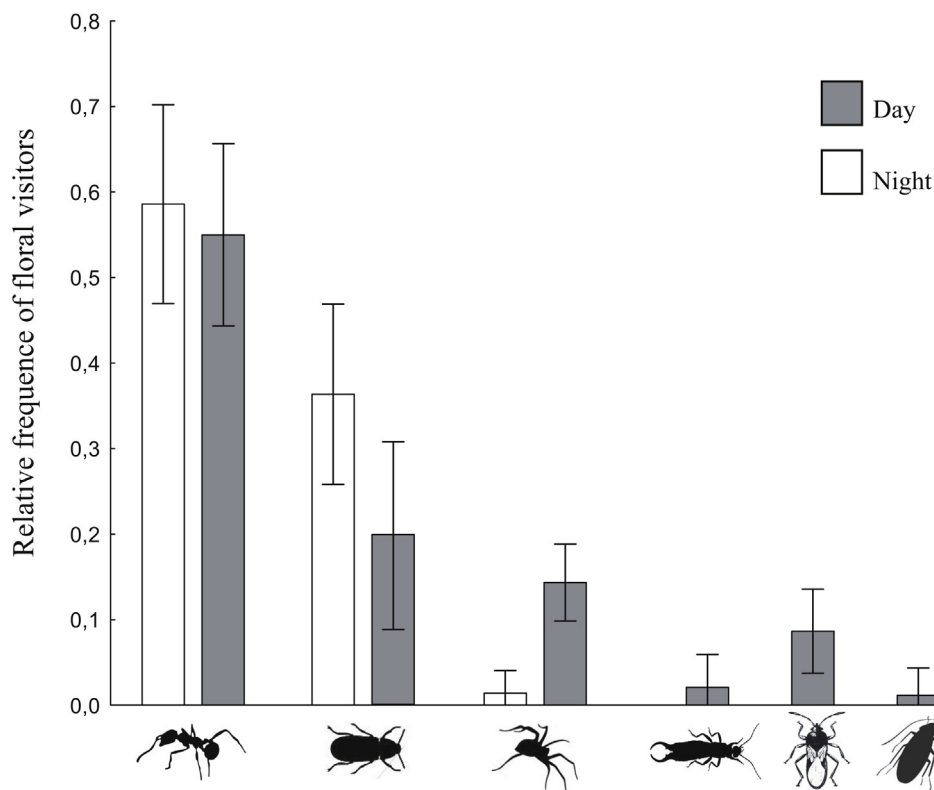
Rhizomes from the 21 excavated clusters had approximately 11.8 cm in length and five ramifications (10.3–13.7 cm), and all rhizomes were in different stages of decomposition according to the time of reproduction. The epidermis was grayish and necrosis spots were detected in plants that had reproduced one year before the study. Regarding the morphology, both the epidermis and the coating hairs were intact in all plants. The ramifications of plants that reproduced in 2009 were brittle, which hindered excavation. However, plant architecture was preserved in most samples of plants that reproduced in 2010.

The inner parts of the rhizomes were rotten and dark-colored. We did not find any evidence of parasitic or herbivory attacks in these tissues. In addition to the vegetative region, the scape with inflorescence bracts remained attached to rhizomes in most cases, facilitating the localization of individuals in the field. In the 11 individuals that reproduced in 2010, decomposing roots were found unattached from their hosts but still connected to *Langsdorffia hypogaea* flowers (Fig. 1F).

### 3.3. Flower visitors

A total of 259 visits of different arthropods species (Hymenoptera, Hemiptera, Dermaptera, Blattodea, Araneae and Coleoptera) were recorded. Moreover, evidences found on plants (e.g. teeth marks and excavations) suggest the action of them acting as accidental pollinators, a part of a sole observation of a line of fruits in the edge of a partially rodent eaten inflorescence. A Nitidulidae (Coleoptera) species was the most frequent pollinator. We observed different floral visitor taxa. 17 ant species belonging to the subfamilies Myrmicinae, Formicinae, Dolichoderinae and Ponerinae were identified. Blattodea, Hemiptera, and Dermaptera were represented by one species each. In addition to insects, eight species of Araneae belonging to the families Salticidae, Theridiidae, Lycosidae, Gnaphosidae, Thomisidae and Linyphiidae were also observed (Table 1).

The most frequent floral visitor was *Brachymyrmex* sp.1, an ant species with 149 visits recorded (57% of all individuals observed; an average of three ants per inflorescence monitored). Ant occurrence in inflorescences was not significantly different between day and night (Mann Whitney  $Z = 1.88$ ;  $p = 0.058$ ; Fig. 4). Ant species were observed using sugar sources (honeydew from hemipterans feeding on the plant and extrafloral nectar), cutting floral tissues and the



**Fig. 4.** Frequency of floral visitors during day and night periods in *Langsdorffia hypogaea* inflorescences. Left to right: Formicidae, Coleoptera, Araneae, Dermaptera, Hemiptera and Blattodea. Data represent mean  $\pm$  s.d.

floral axis, and preying on other ants. Although ants visited a large number of flowers of both sexes, they were not observed touching the stigma, therefore the possibility that they act as pollinators was not taken into account.

Nitidulidae (genus *Stelidota*, Coleoptera) composed 28% of overall visits observed (73 visits), with highest occurrence at night (Mann Whitney  $Z = -2.07$ ;  $p = 0.037$ ; Fig. 4). These insects were observed foraging nectar in 86.3% of the visits, while mating behavior was recorded in 13.7% of visits, followed by piercing of flowers with their ovipositor along to the inflorescence axis, for oviposition. Our additional haphazard sample of 13 inflorescences of both sexes presented 68 larvae feeding on the scape and axis of these structures. These adult insects, that visited 55% of all flowers sampled ( $N = 25$ ), were considered the only potential pollinators of *L. hypogaea*. When visiting flowers during day and night (Fig. 4) they touched both the male and female reproductive structures while collecting extrafloral nectar and copulating.

Spiders were observed using *L. hypogaea* inflorescences as foraging sites. No significant differences in number of spider visits were observed between day and night (Mann Whitney  $Z = 1.79$ ;  $p = 0.072$ ; Fig. 4). Two Dermaptera specimens were also observed using inflorescences to forage for prey during the day. They were found in 4% of visitation events, and two unidentified cockroach morphospecies were observed collecting extrafloral nectar during the day. Although Nitidulidae and Formicidae present differences in relative frequency of visits, no significant difference was observed in these values between day and night ( $\chi^2 = 1.77$ ;  $df = 1$ ;  $p = 0.18$ ).

Only 12.5% out the 32 *L. hypogaea* clusters monitored completed their life cycle, mostly as consequence of herbivory. Teeth marks on flowers/inflorescences suggest foraging by small rodents or marsupials (C. Schindwein, pers. comm.). In some cases, such animals fed only on the scape, inflorescence axis and flowers, avoiding bracts

and the aerial part of the rhizome; in others, the soil surface was excavated and parts of the rhizome were also eaten.

#### 4. Discussion

Synchronization of plant reproduction has evolved in many different plant species to optimize reproductive success and seed dispersal, being also influenced by climatic factors (Janzen, 1976; Howe and Westley, 1997; Lambert et al., 2010). Our data for *L. hypogaea* showed that all reproductive phenophases are in the dry season, with the exception of flower bud emergence, making succulent flower, extrafloral nectar and fruit resources available in dry season. Flowering synchronicity could result from several ecological factors (Ollerton and Lack, 1998) as well as to represent a phylogenetically constrained trait of the taxon (Kochmer and Handell, 1986). In the case of *L. hypogaea* it was not possible to associate the advantage of synchronicity of bud and flowering to reproductive success. The flower bud phenophase was not only synchronized but also correlated positively with rainfall. At this stage, flower buds developed a cover with coriaceous bracts lined with rigid bristles (Fig. 1A), until flowering occurred in early dry season.

In this sense, *L. hypogaea* contribute to the maintenance of a food supply during its reproductive season. It produces patchily, both in time as in space, succulent inflorescences with attractive color and rich in nectar, followed by fruits. The evolutionary trade-off between reproduction and predation could have “designed” floral morphology and neat seasonality that presently optimize and favour such life history. Male and female flowers of *Langsdorffia* species differ in the tepal fusion pattern and presence of pedicel (Erberwein et al., 2009). Male flowers keep the anthers exposed with nectar droplets in several places, suggesting the occurrence of generalist pollinators which could forage on the entire inflorescence. Likewise, the scent of flowers by late day and evening likely



attracts pollinators such as the Hymenoptera, Coleoptera and Blattodea listed here. Female flowers are gamotepalous with reduced exerted stigma, and due to the flowers proximity, the receptive area of the inflorescence becomes increased, which also suggests that this inflorescence may favour a wide range of pollinators.

An entomophilous pollination system, also found in most other holoparasitic species (Bellot and Renner, 2013), is confirmed in this study. Diverse invertebrate groups were recorded in another Balanophoraceae, *ksuch as Dactylanthus taylorii*, with presence of pollen on their bodies (Ecroyd, 1996), but the main effective pollinators were not observed. Different from other Brazilian Balanophoraceae species that present flies as pollinators (Kinoshita et al., 2006), however, *L. hypogaea* has an unusual pollination strategy with Nitidulidae beetles as pollinators. These insects are important pollinators of other plant species, such as Annonaceae (Teichert et al., 2011) and Thymelaeaceae (Alonso 2004). The frequent oviposition behavior observed in the *L. hypogaea* inflorescence axes could be associated with an interesting trade-off between the gain in seed set promoted by adults and loss by larval floral herbivory (Pellmyr, 1989) as observed in two others Balanophoraceae species (Borchsenius and Olesen, 1990; Ecroyd, 1996; Goto et al., 2012). Chemical compounds of floral volatiles are associated with attraction of Coleoptera in other pollination systems (Pereira et al., 2014), and in *L. hypogaea* this trait should be evaluated in future studies.

The range of floral visitors followed an extremely generalist pattern, contrasting with the very specialized pollination system. However, the fauna species richness associated with *L. hypogaea* is suggestive of its importance as a food resource along the dry season. The present work is the first record about ecological features and natural history of *L. hypogaea* in Brazil and more studies are needed to improve our understanding about the effectiveness of this pollination system and the effects of the oviposition by Nitidulidae on reproductive success.

### Conflict of interest

The authors declare that they have no conflict of interest.

### Acknowledgements

The authors thank L. Cardoso (Escola Nacional de Botânica Tropical, Instituto de Pesquisas Jardim Botânico do Rio de Janeiro) for clarification and photography, R. Fagundes for help with statistical analysis, E. Rangel for field support, F. Siqueira (DEBIO-UFOP), I. Fiorini (UFMG) and P. Audisio (Sapienza Università di Roma, Italy) for ant, spider and beetle identification.

This work was supported by the National Council for Scientific and Technological Development – CNPq (Project 481226/2013-3) and UFOP scientific grants granted to LMM.

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