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# Differential pollination modes between distant populations of Unonopsis guatterioides (Annonaceae) in Minas Gerais and Amazonas, Brazil<sup>‡</sup>

Paulo Eugenio Oliveira<sup>a,\*</sup>, Carlos Eduardo R. Tomé<sup>a</sup>, Helena Maura Torezan-Silingardi<sup>a</sup>, Stefan Dötterl<sup>b</sup>, Ilse Silberbauer-Gottsberger<sup>c</sup>, Gerhard Gottsberger<sup>c</sup>

<sup>a</sup> Instituto de Biologia, Universidade Federal de Uberlândia, Brazil

<sup>b</sup> Department of Ecology and Evolution, University of Salzburg, Austria

<sup>c</sup> Botanischer Garten und Herbarium, Universität Ulm, Germany

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## ABSTRACT

Differentiation in angiosperms is often linked to small changes in floral features including morphology, but also phenology and floral resources, which select different arrays of pollinators and result in disassortative mating. Unonopsis is a bee-pollinated genus in the mostly beetle-pollinated tropical family Annonaceae. We studied Unonopsis guatterioides, a species widespread in South American forests, from the Amazon to São Paulo. A population in Uberlândia. Minas Gerais state. Central Brazil was investigated for its phenology and floral biology, including anthesis, floral scent, pollinator behavior, floral resources, and breeding system. The plants in Uberlândia were bee-pollinated and self-compatible. Its flowers were protogynous, and their anthesis lasted 30 h. Pistillate and staminate stage flowers mainly released monoterpenoids, among them 1,8-cineole and limonene. A comparison with the previously studied population of U. guatterioides in Amazonas state indicated remarkable differences between the two populations, with regard to flower characters, anthesis, and pollination process. There was a more diverse, unspecialized pollination by several small Halictidae and Apidae bee species in Uberlândia, while in Manaus there was a highly specialized pollination by perfume-collecting males of a single orchid bee species, Eulaema bombiformis (Apidae-Euglossini). The profound differences of floral biology in U. guatterioides in Uberlândia and Manaus indicate that these two populations eventually represent different species.

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1. Introduction

Pollination modes often differ among plant species and these differences have a central role in the radiation and evolution of the angiosperms (Barrett, 2010). However, differences or variations of pollination systems among individuals and populations within a species, although the starting points for the differentiation process, are less often considered (but see *e.g.*, Waser, 1983; Herrera, 1988; Gottsberger and Silberbauer-Gottsberger, 2006). It is important to keep in mind that flower-animal interactions are not constant and fixed, even at the level of communities. The interactions are rather part of a dynamic system with strong fluc-

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\* Corresponding author.

http://dx.doi.org/10.1016/j.flora.2016.07.014 0367-2530/© 2016 Elsevier GmbH. All rights reserved. tuations and modifications (Thompson, 2005). For example, the diversity, composition and abundance of pollinators of Lavandula latifolia (Lamiaceae) in southeastern Spain, vary markedly during the season or among years (Herrera, 1988). The elusive scent of flowers may attract different kinds of visitors, as sought by Stefan Vogel during his career (e.g., Vogel, 1963, 1966; Sazima et al., 1993). These factors might have an influence on the selective forces and on the evolution of flower-pollinator interactions (see e.g., Feinsinger and Tiebout, 1991; Feinsinger et al., 1991). The variability in interactions may be important for understanding how plants and pollinators adjust themselves in different environments, and for evaluating the resilience and flexibility of pollination systems in a changing world (Eckert et al., 2010; Valiente-Banuet et al., 2015). Ultimately, they can explain the building up of differences, which lead to speciation and radiation processes (e.g., Marques et al., 2016).







E-mail addresses: poliveira@ufu.br, poliveiragm@gmail.com (P.E. Oliveira).

Pollination systems are often highly specialized in tropical regions, where different plant species, even within a genus or family, interact with different pollinator species (e.g., Sazima et al., 1993). The pantropical and early-diverging Annonaceae is such a family in which pollination modes are largely specialized. As other early-diverging angiosperms, the Annonaceae lack self-incompatibility mechanisms and rely on their specialized protogynous flowers and synchronization mechanisms to attract biotic vectors and increase pollen flow among individuals (Pang and Saunders, 2014; Gottsberger, 2016). The majority of Annonaceae species are pollinated by different beetles, some by flies and thrips, a few by bees, and only one by cockroaches (Gottsberger, 2012). Although many Annonaceae have typically large and specialized flowers, some Neotropical forest species have small and relatively generalist flowers. The Unonopsis group is an alliance of three genera, Unonopsis, Bocageopsis and Onychopetalum, phylogenetically close to each other (Maas et al., 2007). It includes ca. 50 species of small-flowered trees, some pollinated by bees or other small insects (Webber and Gottsberger, 1996; Carvalho and Webber, 2000) but largely unstudied as vet.

Unonopsis is the largest genus in the alliance consisting of 48 species of understory trees or shrubs in tropical South and Central American forests (Maas et al., 2007; Chatrou et al., 2012). Some Unonopsis species form an important component of these forest habitats. The species Unonopsis guatterioides (A. DC.) R.E. Fries, studied in Manaus, Amazonas state, Brazil (Carvalho and Webber, 2000) and U. stipitata Diels, studied in Nouragues, French Guiana (Teichert et al., 2009), revealed to be pollinated by bees, a pollination mode which is rare in Annonaceae (Silberbauer-Gottsberger et al., 2003). Unonopsis guatterioides is a widely distributed species with somewhat morphologically distinct populations in Central Brazil, formerly described as U. lindmanii but included within U. guatterioides circumscription (Maas et al., 2007). We wondered if the reproductive biology of U. guatterioides close to Uberlândia, Minas Gerais state, almost 3000 km south of Manaus and under distinct environmental conditions, would reveal differences from the Amazonian population. In the present paper the notable differences found are presented and discussed, and additional data about anthesis and floral scent emissions are provided.

#### 2. Material and methods

#### 2.1. Study site

From March 1997 to March 1998 and from October to November 2012, U. guatterioides (A. DC.) R.E. Fries was studied in a semi-deciduous riparian forest at Panga Ecological Station (PES; 19°09'20"-19°11'10" S and 48°23'20"-48°24'35" W; alt. ca. 800 m), 30 km south of Uberlândia city, Minas Gerais state, a region which is part of the Brazilian Cerrado biome. The site presents 403.85 ha of a preserved natural area and an Aw climate, according to Köppen (1931) classification, with two well defined seasons, a warm and wet summer and a cooler and dry winter. The mean annual rainfall is 1550 mm and the mean annual temperature is 22 °C (Rosa et al., 1991). PES presents different plant formations characteristic of the Cerrado biome, including campo cerrado (physiognomy of low-tree and scrub savanna) and also gallery forests along the main streams (Cardoso et al., 2010). These gallery forests have a distinct stratification as found also in other tropical forests, with a rich understory layer of shrubs and small trees (Arantes, 2002).

#### 2.2. Plant characteristics and phenology

Unonopsis guatterioides is a very common, relatively small tree of up to 8–12 m height in the understory of gallery forests, in moist, often flooded areas near the streams. In an early study in 1997–1998, 15 individuals were marked for phenological 12month observations. The observations on leaf flush and leaf fall were recorded fortnightly and the development of floral buds, flowers and fruits were observed weekly. Quantitative data were analyzed but only general patterns are presented in the results.

#### 2.3. Floral biology

In 1997, the chronology of anthesis events, stigma receptivity, and pollen availability of 15 individuals was studied weekly during the whole flowering period from September to November. Floral visitors were observed and some were captured. In October 2012, anthesis and pollinator behavior were studied once more. Thirty flowers on four individuals were marked and flower development, odor production (as perceived to the human nose) and flower visitors were registered during four mornings (9 a.m.–11 a.m.), one afternoon (1 p.m.–5 p.m.), and also during two days from 7 a.m. to 3 p.m., comprising a total of 28 h.

The time of flower opening, duration of pistillate and staminate stages and the end of anthesis were registered. The pistillate stage was characterized by the production of sticky exudates on the stigmas, and the staminate stage by the opening of anthers and accessibility of pollen. The observations included insects visiting flowers in each sexual stage, and also non-pollinating insects on flowers and leaves. Several individuals of each insect species were pinned and sent to specialists for identification.

### 2.4. Scent sampling and analyses

Floral volatiles were collected during daytime from pistillate and staminate stage flowers in situ using dynamic headspace methods (Dötterl et al., 2005). Five samples were collected from two single pistillate stage and other three single staminate stage flowers, and one sample was collected from two pistillate stage flowers each (from overall four different individuals). With the exception of one pistillate stage flower, flowers were enclosed in a polyester oven bag (6 cm × 5 cm; Toppits<sup>®</sup>, Germany) for 10-65 min to allow accumulation of floral scent. Subsequently, volatiles were trapped by pulling the air from the bag (surrounding of the unbagged flower) through small adsorbent tubes (Varian Inc. ChromatoProbe quartz microvials) for 2 min using a membrane pump (G12/01 EB, Rietschle Thomas Inc., Puchheim, Germany; flow rate: 200 ml/min). The tubes contained 1.5 mg Tenax-TA (mesh 60-80) and 1.5 mg Carbotrap B (mesh 20-40; both Supelco) fixed by glass wool plugs. Samples of the surrounding air were collected as controls.

The volatiles trapped were analyzed by GC/MS using an automatic thermal desorption (TD) system (TD-20, Shimadzu, Japan) coupled to a Shimadzu GC/MS-QP2010 Ultra equipped with a ZB-5 fused silica column (5 % phenyl polysiloxane; 60 m, i.d. 0.25 mm, film thickness 0.25  $\mu$ m, Phenomenex), the same setup as used by Heiduk et al. (2015) and Mitchell et al. (2015). The samples were run with a split ratio of 1:1 (sample of one staminate flower) or 1:20 (remaining samples) and a constant helium carrier gas flow of 1.5 ml/min. The GC oven temperature started at 40 °C, then increased by 6 °C/min to 250 °C and held for 1 min. The MS interface worked at 250 °C. Mass spectra were taken at 70 eV (EI mode) from *m*/*z* 30 to 350. GC/MS data were processed using the GCMSolution package, Version 4.11 (Shimadzu Corporation 2013).

Identification of compounds was carried out using the NIST 11, Wiley 9, FFNSC 2, and Adams databases (Adams, 2007), and the database available in MassFinder 3. Structures of several com-

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