



Conditional outcomes in ant–plant–herbivore interactions influenced by sequential flowering



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ABSTRACT

Mechanisms that affect a host plant's ability to face herbivory are subjects of ongoing interest. Plant reproductive phenology plays a key role in the dynamics of communities in many ways. In ant–plant–herbivore interactions, host–plant phenology affects traits of its herbivores which in turn determine what traits ants must have to benefit the host–plant. Diversity of plant phenological traits could influence the ecological diversity of coevolved ant–plant mutualisms.

In the Brazilian savanna, members of several plant families resprout and bloom simultaneously. However, some shrubs of the family Malpighiaceae exhibit sequential flowering, and four of these species also present extrafloral nectaries that attract ants. Here we determine whether their phenological patterns results in a shared herbivore guild and if this may be harmful to these plant species, making the association with ants critical to the plant optimal development and reproductive success. Plant phenology, herbivory, and the richness and abundance of ants and herbivores were recorded on control (with unrestricted ant access) and treatment (ant-excluded) shrubs. Floral-bud production and fruit set were also quantified. The plants flowered sequentially with brief periods of overlap, benefitting the guild of generalist herbivores. A cluster analysis indicated that 32 herbivore species were associated with these Malpighiaceae, with substantial species overlap. In all species, ants reduced leaf-area loss but not the damage to reproductive structures. Some floral herbivores presented adaptations to avoid or appease ants. We suggest that plant phenology directly influences the outcomes of these ant–plant–herbivore interactions and the related ecological networks.

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Introduction

As the base of terrestrial trophic chains, plants are consumed by a wide range of organisms, including microbes, invertebrates, and vertebrates. The pressure that herbivores exert over plant development and fitness has led plants to develop numerous defensive strategies (Marquis, 2012; Mortensen, 2013). While some defenses are constitutive, others are induced only upon the perception of an attack to allow for optimal resource allocation (Campbell and Kessler, 2013; Karban and Baldwin, 1997). One interesting plant trait to escape from herbivory is to resprout or bloom during a season when the main herbivores are less common in the field (Coley and Barone, 1996). Some plant families produce new leaves and flowers during the same season; others produce leaves and flowers at distinct times, such as during the dry and wet seasons (Raven et al., 2012). According to Staggemeier and

Morellato (2011), most tropical plant species rely upon animal vectors for pollination and seed dispersal, and temporal and spatial variations in flowering and fruiting phenology strongly affect animals that rely upon flowers or fruits as a food resource.

Plants present different patterns of flowering, such as aggregated, segregated (e.g., Gentry, 1974; Gotelli and Graves, 1996; Murali and Sukumar, 1994) or indistinguishable from what would be expected by chance (e.g., Rathcke, 1984). Several evolutionary hypotheses have been proposed to explain the distinct patterns observed in flowering times among species. Initially, Robertson (1895) suggested that plants with the same pollinators will avoid competition through staggered flowering and thus will increase their reproductive success. Another hypothesis states that staggered flowering could be a result of interaction between early-flowering and later-flowering species, wherein the first-flowering species facilitates the pollinators of the next species to flower (Waser and Real, 1979). The analysis of flowering strategies is a complex issue because they are the result of an interacting set of abiotic factors, plant traits, and plant–animal interactions (Armbruster, 1995). In a consumer–resource

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perspective, sequential flowering may represent a plant defensive strategy against floral herbivores (Coley and Barone, 1996; Marquis and Lill, 2010).

Biotic defenses, like the association with predators, most commonly ants, may also represent an important defensive strategy against action of herbivores in terrestrial ecosystems. Ant–plant relationships have made enormous contributions to our understanding of tropical communities (Rico-Gray and Oliveira, 2007; Rosumek et al., 2009), and these interactions are particularly pervasive in the Cerrado (the Brazilian tropical savanna) due to the high incidence of insect- and plant-derived exudates on foliage, which promotes intense ant activity on the vegetation (Rico-Gray and Oliveira, 2007, and references therein). The Cerrado is the most diverse tropical savanna in fauna and flora, and one remarkable characteristic of this ecosystem is its great seasonal variation (Oliveira-Filho and Ratter, 2002). The reproductive success of individual plant populations often depends on flowering phenology allowing plants to take advantage of temporally periods of favorable conditions (Mahoro, 2002). Studies comparing conditional outcomes in ant–plant–herbivore interactions mediated by temporal variation in host-plant phenology are of great relevance to the ecology of interactions and the conservation of natural communities. However, such studies are rare, especially in tropical America (Rosumek et al., 2009).

Experimental ant-exclusion studies have shown that the absence of ants can increase leaf-area loss in plants possessing extrafloral nectaries (Oliveira, 1997; Korndörfer and Del-Claro, 2006). The absence of ants can also reduce fruit set (Nascimento and Del-Claro, 2010; Oliveira et al., 1999), seed production (Vesprini et al., 2003) and viability (Sobrinho et al., 2002). However, data concerning the effectiveness of ant–plant mutualisms are sometimes controversial (see e.g., Holland et al., 2011; Nahas et al., 2012). Nevertheless, despite their importance to the study of mutualisms and to the structure and maintenance of natural communities (e.g., Bronstein, 2012; Rico-Gray and Oliveira, 2007), ant–plant interactions are most often studied in single plant species over a limited time period (Rosumek et al., 2009), ignoring sequential events. Recently, some researchers have shown the impact of ant–plant interactions on communities using diverse ecological network approaches (e.g., Blüthgen et al., 2007; Ings et al., 2009; Lange et al., 2013, and references therein) and have focused on the ecological factors that may cause a mutualism to vary in space and time, resulting in “conditional mutualism” (Alves-Silva and Del-Claro, 2013; Del-Claro and Oliveira, 2000; Herre et al., 1999).

In the Cerrado of central Brazil, shrubs of the family Malpighiaceae are diverse and abundant (Anderson, 1990; Gates, 1982). Several species exhibit sequential phenological development, in which individuals of different species resprout, bloom, and set fruit sequentially over time (Barros, 1992; Costa et al., 2006; Mendes et al., 2011; Torezan-Silingardi, 2007). These species also possess extrafloral nectaries (EFNs) and have close relationships with protective ants (Alves-Silva et al., 2013; Torezan-Silingardi, 2011). In Cerrado, the ant–plant–herbivore interactions occur within multitrophic systems whose outcomes are strongly influenced by plant phenology (Lange et al., 2013). Here we used a set of Malpighiaceae–ant–herbivore associations as model to determine the following: (a) whether herbivores shift among related host-plant species over time in response to variation in plant phenology; and (b) whether the outcomes of ant–plant interactions vary depending upon the associated herbivores and ants. Our major hypotheses are that the sequential flowering of related host plants results in a shared herbivore guild over time that may be quite harmful to these plant species, making the association with ants critical to the plants reproductive success.

Materials and methods

Study site and plant species

Fieldwork was carried out from May 2008 to June 2009 at the Reserva Ecológica do Clube Caça e Pesca Itororó de Uberlândia (CCPIU; 18°59'S, 48°18'W), Uberlândia, Minas Gerais State, Brazil. We used a 400 ha Cerrado site consisting of a dense scrub of shrubs and trees, known as Cerrado sensu stricto (Oliveira-Filho and Ratter, 2002). The climate is markedly seasonal, with a dry winter (April–September) and a rainy summer (October–March) – for additional details, see Réu and Del-Claro, 2005).

Four Malpighiaceae species were selected for the study: *Peixotoa tomentosa* A. Juss., *Banisteriopsis laevifolia* (A. Juss.) B. Gates, *Banisteriopsis campestris* (A. Juss.) Little, and *Banisteriopsis malifolia* (Ness and Mart.) B. Gates. These species were chosen because they are small shrubs with paired EFNs on the leaf base and are common in the Cerrado and abundant at the study site (Torezan-Silingardi, 2007).

Experiments

During the month in which each species sprouted (when the shrubs bore vegetative buds but not leaves), we tagged 30 individuals of similar size and architecture (1–2 m tall, with 5–7 stems) that were at least 3 m apart. Thus, the ant-exclusion experiments began in May 2008 for *P. tomentosa*, July 2008 for *B. laevifolia*, November 2008 for *B. campestris* and February 2009 for *B. malifolia*. For each species, by the flip of a coin, we designated tagged shrubs as control plants (with unrestricted ant access; $N=15$) or treatment plants (with ants excluded by applying Tanglefoot[®] resin on the main plant stem; $N=15$). In treatment plants, ants were manually removed and the trunk was covered with a 5 cm broad adhesive paper strap to which a layer of sticky resin was applied. We removed surrounding vegetation that ants could use as bridges to gain access to these plants. To be sure that the sticky resin did not interfere in the results, in control plants we also covered the trunk with a paper strap, but we applied the resin only on one side of the trunk.

Data collection

Each plant was monitored every two weeks during its four-month reproductive period. The plants were always inspected by the same observer, and the richness and abundance of herbivores on the reproductive and non-reproductive plant parts were recorded. We quantified herbivory (leaf area loss) monthly in the first week of each month. To determine the mean monthly herbivory, we recorded data from nine leaves per plant, three from the most apical stem, three from a middle stem and three from the most basal stem. This procedure was done without leaf removal. Measurements of herbivory rates on leaves were assessed by placing leaves on a transparent grid (divided into millimeters). An index of herbivory from each leaf was calculated as the proportion of points in the grid falling within damaged and undamaged areas of the leaf blade (Moreira and Del-Claro, 2005). Additionally, data about behavior of the animals at the time of observation were noted, including their topical position (on leaves, stems, buds, or flowers or feeding on EFNs). An animal was considered an herbivore if it was observed sucking, chewing, perforating or grasping the plant tissue. Voucher specimens were collected from non-experimental plants for identification. Plant phenology (developmental stage of leaves, buds, flowers, and fruits) was recorded by A. Vilela, following the practice of Torezan-Silingardi and Oliveira (2004) during May 2008–June 2009.

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