



## Beta diversity of ant-plant interactions over day-night periods and plant physiognomies in a semiarid environment

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### ABSTRACT

Despite the growing knowledge regarding biotic interactions, the diversity and turnover of species interactions is one of the least understood and explored components in studies dealing with species interaction networks. Since the spatial and temporal distribution of animals and plants is unequal, their pairwise interactions are also expected to vary or rewire, generating dissimilarities among species interaction networks. In this study, we evaluated the structure of ant-plant interaction networks and described its dissimilarities by assessing species and the turnover of their interactions between day and night periods across two plant physiognomies in a semiarid Neotropical environment of central Mexico. We found that even though the emergent nested structure of networks remains invariant, the great majority of ant-plant interactions are reassembled in less than one day. Moreover, we observed that, between day-night periods, the interaction turnover was mainly driven by rewiring of interactions while, between plant physiognomies, this was generated by both interaction rewiring and species turnover. We postulate that interaction rewiring across the studied habitats could be influenced by the turnover of the central core of highly interacting species. Furthermore, we highlight that both interaction rewiring and species turnover shape ant-plant interactions turnover over day-night periods and plant physiognomies.

### 1. Introduction

The study of the distribution of biodiversity has provided important insights into many aspects regarding the function and structure of ecological communities (Andresen et al., 2018). In fact, most studies dealing with biodiversity have focused on how the composition of species varies along environmental gradients, revealing how species diversity responds to changes in the environment (e.g. Montaña and Valiente-Banuet, 1998; Whittaker, 1960). However, in recent years, the study of interactions between species under a network approach has changed our understanding about the mechanisms that generate and maintain biodiversity (Andresen et al., 2018; Bascompte and Jordano, 2007). Despite this, species interactions are rarely considered as important components of biodiversity (CaraDonna et al., 2017; Poisot et al., 2012) and implementing species interactions into diversity studies is therefore fundamental to the improvement of our understanding of how and why species and their interactions vary in nature (Poisot et al., 2015).

In the tropics, ant and plant communities interact in many different

ways, from mutualisms (e.g. protective ant-plant systems, pollination and seed dispersal) and antagonisms (e.g. leaf-cutter ants or seed predation), to commensalisms (i.e. ants using plants as substrate) and opportunisms (Rico-Gray and Oliveira, 2007). Thus, the great diversity of interactions between ants and plants can generate complex networks of ecological interactions, where species are represented by nodes and their interactions by links among them (Del-Claro et al., 2016; Guimarães et al., 2006). Many studies have demonstrated invariant patterns in the emergent nested structure of ant-plant networks across spatial (Dáttilo et al., 2013; Sugiura, 2010), and temporal (Díaz-Castelazo et al., 2013; Lange et al., 2013) scales, and even after environmental disturbances (e.g. tropical hurricanes) (Sánchez-Galván et al., 2012). However, this information has been produced from studying interaction networks as static entities, ignoring the fact that pairwise ant-plant interactions are very dynamic and can vary depending not only on spatial (e.g. local to regional) (Lange et al., 2013; Rico-Gray and García-Franco, 1998) and temporal (e.g. throughout the year, between day and night and through hours of a day) (Houadria et al., 2016; Lange et al., 2017; Rico-Gray et al., 1998) scales, but also

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according to the interaction type itself (e.g. mutualisms and antagonisms) (Rico-Gray and Oliveira, 2007). In fact, most of the variation of ant-plant interactions is associated with temperature, precipitation and temporal fluctuations of the availability of plant-derived resources (Lange et al., 2017; Rico-Gray et al., 2012). This leads us to the question of how the dynamic nature of pairwise ant-plant interactions generates variation in ant-plant interaction networks where many species are found together.

Despite the rapid development of knowledge about the key elements that regulate and maintain biodiversity, the beta diversity of interactions (hereafter turnover of interactions) is one of the least understood and studied components of ecological networks (Poisot et al., 2012). It has been proposed that the turnover of interactions arises from two additive components: i) species turnover, which can be understood as the changes in interactions realized in a community by the variable composition of species assemblages throughout the environment; and ii) interaction rewiring, generated by the reassembly of interactions between the same species under different scenarios (e.g., seasons or habitats). Both components can be used as a measure of the dynamics and variability of species interactions across ecological communities (Poisot et al., 2017, 2012). For example, recent studies have shown that the turnover of plant species is the main driver of the turnover of plant-pollinator interactions across geographical distances (Carstensen et al., 2014). In contrast, the rewiring of interactions was identified as a major component of the week-to-week turnover of plant-pollinator interactions (CaraDonna et al., 2017). While previous studies show that the turnover of species interactions may be driven by the turnover of species and the rewiring of interactions along temporal or spatial gradients, we still lack empirical evidence with which to understand how the turnover of interactions and the relative importance of their components shape ant-plant interaction networks.

The Neotropical semiarid valley of Zapotitlán in central Mexico harbors great floristic diversity, where at least 30% of vascular plants are endemic (Dávila et al., 2002). The plant diversity displays a high turnover of species among the spatial gradients in the region (Montaña and Valiente-Banuet, 1998), where we find a mosaic of diverse plant physiognomies formed by unique combinations of different life forms (e.g. annuals, trees and perennial shrubs, cacti and rosetophylls) (Valiente-Banuet et al., 2000). Moreover, similar ant communities can be found through the plant physiognomies of the region (Ríos-Casanova et al., 2006). In this region, ants and plants establish facultative interactions showing low levels of intimacy (Rico-Gray et al., 1998). Ranging from commensalisms (i.e., ants using plants as a substrate in which to escape from the soil heat) (e.g., Fitzpatrick et al., 2014; Luna et al., 2016), to mutualisms (i.e., dominant ants defending host plants against herbivores) (e.g., Dáttilo et al., 2015). Moreover, in this region ant-plant interactions are strongly affected by the highly variable climatic conditions that prevail in this environment (Rico-Gray et al., 1998). This remarkable seasonality seems to regulate the day-night turnover of ant species foraging on plants mainly due to the variation of microclimatic conditions and the availability of plant-derived resources (e.g., extrafloral nectar) (Dáttilo et al., 2015; Luna et al., 2016). Indeed, in this region, the foraging activity of dominant ants is temporally partitioned (one dominant species during the day and another at night) due to competitive interactions for extrafloral nectar and differences in thermal tolerance among species (Flores-Flores et al., 2018; Garcia-Robledo et al., 2017). The high beta diversity that the plant communities display in the Zapotitlán Valley and the daily turnover of ant species therefore offer an excellent benchmark for exploring the beta diversity of the interactions between ants and plants in different plant physiognomies in order to compare the relative importance of the components of the turnover of species in terms of its contribution to the variation of ant-plant interaction networks.

Here, we studied the beta diversity of ant-plant interactions by assessing the turnover of species (focusing on both the highly interactive core and peripheral species) and the rewiring of their interactions.

Specifically, we measured the structure and dissimilarities of ant-plant interaction networks between day-night periods in two widely distributed plant physiognomies of the Zapotitlán Valley (“Tetechera” and “Mezquitera”). Based on the empirical evidence and the natural history of the region, we propose the following predictions. Since it is known that the emergent nested structure of ant-plant networks does not change through space (Dáttilo et al., 2013; Sugiura, 2010), time (Díaz-Castelazo et al., 2013; Lange et al., 2013) and even events such as tropical hurricanes (Sánchez-Galván et al., 2012), we expect that the ant-plant networks from diurnal, nocturnal and different plant physiognomies would display an emergent nested structure. Considering that the two competitively superior ant species in our study area divide their foraging activities into day and night periods (Flores-Flores et al., 2018), we expect a day-night turnover in the core of highly interacting ant species of the networks. Furthermore, since the plant physiognomies of the region have a high turnover of plant species, we expect different highly interacting plant species between plant physiognomies. Finally, given that interactions between ants and plants are very dynamic and that we expect that the species with more interactions will change between day and night and among different plant physiognomies, we expect to find that rewiring of interactions is the main driver of the turnover of the studied ant-plant assemblage. That is, the turnover of interactions between local ant-plant networks will be generated to a greater extent by changes in pairwise ant-plant interactions than by changes in species composition.

## 2. Materials and methods

### 2.1. Study area

We conducted our study in the Neotropical semiarid valley of Zapotitlán, in the state of Puebla, Mexico, located in the Tehuacán-Cuicatlán Biosphere Reserve (18°19'42" N and 97°27'30" W). The elevation of this site varies from 1400 to 2500 m asl. Mean annual precipitation is 380 mm and mean annual temperature is 22 °C (Montaña and Valiente-Banuet, 1998 and references therein). The vegetation corresponds to semiarid scrubland (Rzedowski, 2006). This region exhibits strong seasonality, with a long dry season from October to May and a short rainy season from June to September.

### 2.2. Sampling ant-plant interactions

Field work was conducted in July 2016 in two plant physiognomies widely distributed in the Tehuacán-Cuicatlán Valley: the “Tetechera” and “Mezquitera” (*sensu* Zavala-Hurtado, 1982) (Fig. 1).

The “Tetechera” (18°19'39" N and 97°27'33" W) is a plant physiognomy dominated by the columnar cactus *Neobuxbaumia tetetzo* (Cactaceae), which may be accompanied by *Opuntia pillifera* (Cactaceae) and the thorny shrubs *Parkinsonia praecox* (Fabaceae), *Mimosa luisana* (Fabaceae), *Prosopis laevigata* (Fabaceae) and *Vachellia constricta* (Fabaceae). It is located on slopes at an elevation of approximately 1500 m asl (Fig. 1A). The “Mezquitera” (18°19'31" N and 97°27'16" W) is a plant physiognomy dominated by the shrub *P. laevigata* and the cacti *Myrtillocactus geometrizans* (Cactaceae), *O. decumbens*, *O. pillifera*, and *Pachycereus hollianus* (Cactaceae). The “Mezquitera” is located on flat areas at the bottom of the valley and has a greater vegetal cover than the “Tetechera” (Fig. 1B). In addition, both plant physiognomies display different temperatures and relative humidity between day and night cycles (Appendix A). The two plant physiognomies where we performed the sampling are located a distance of 140 m apart, and separated by 21 m in elevation.

Within each plant physiognomy (“Tetechera” and “Mezquitera”), we established two transects of different size (one of 300 m × 10 m and the other of 100 m × 10 m, separated by 100 m). At each transect, we searched for and collected all the ants we observed foraging on the plants (from 0.5 m to 3 m in height). In order to minimize the possibility

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