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Epiphytic bromeliads as key components for maintenance of ant diversity and ant–bromeliad interactions in agroforestry system canopies

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ABSTRACT

Cocoa is produced in a wide range of land use systems, with the traditional shaded systems in Bahia (Brazil) as the most forest-like and biodiverse. The aim of this study was to evaluate the role of different cocoa agroforestry systems (AFSs) in maintaining community structure and interactions between ants and epiphytic bromeliads. The study was conducted at four sites in the cocoa producing region of the southeastern of the state of Bahia, Brazil, and comprised a native forest and three different cocoa AFSs. We found a total of 103 ant species associated with epiphytic bromeliads, with 83% of the species occurring in native forest canopy bromeliads also occurring in cocoa AFSs. The Cocoa Cabruca System (CAB) and the Rustic-Planted Shade System (RPS) had ant community structural components of biodiversity similar to those found in the native forest environment. The alpha and gamma diversity of ants found in Monospecific-Shaded Cocoa Agroforestry System (MCA) associated with *Erythrina* spp. shade trees were significantly different from the diversity found in the other AFSs and native forest. The presence of epiphytic bromeliads, regardless of the system and scale, maintained ant diversity in agroforestry system canopies similar to that of native forest. Using metrics derived from graph theory, we found a high level of specialization regarding ant–bromeliad interactions in native forest, with a gradual decrease in specialization with environmental homogenization. Agroforestry systems thus represent an important strategy for maintaining the structure of canopy-associated ant communities by enabling the establishment of numerous bromeliad species, thus contributing to the maintenance of ant diversity and services in a mosaic landscape AFSs and native forest.

1. Introduction

Agroforestry systems (AFSs) have emerged as a good strategy for maintaining natural forest biodiversity while taking into account the economic needs of producers (Bhagwat et al., 2008; Falcão et al., 2015; Schroth et al., 2004; Steffan-Dewenter et al., 2007). Within this context, cocoa (*Theobroma cacao* L., Malvaceae) AFSs have been particularly successful in some tropical regions due to the exceptional potential of these systems to reconcile economic needs with conservation of biodiversity (Schroth et al., 2011, 2015). Cocoa AFSs are characterized by replacement of the original forest understory with cocoa crop, while maintaining or establishing a fraction of the canopy as shade for crops (Rice and Greenberg, 2000; Ruf and Schroth, 2004). Vascular epiphytes are among the plant types found in the canopy (Cruz-Angón and Greenberg, 2005; Hietz, 2005; Hylander and Nemomissa, 2008; Souza et al., 2015). Consisting mainly of bromeliads, cacti, ferns, and orchids, vascular epiphytes make up about 10% of the world's flora (Gentry and Dodson, 1987), with most species being typical of forest canopies (Benzing, 1995; Nieder et al., 2001). Tropical agroforestry canopies can have high structural complexity, including because of the frequent occurrence of epiphytes in tree crowns (Cruz-Angón and Greenberg, 2005; Hietz, 2005; Moffett, 2013). It follows that, since epiphytes increase microhabitat diversity in the agroforestry canopy, they play an important ecological role in community structure, and in the maintenance of diversity of ants and other arthropods that use epiphytes for foraging or nesting substrate (DaRocha et al., 2015; Rodgers and Kitching, 2011; Stuntz et al., 2003; Yanoviak et al., 2004).

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In tropical forest canopies, ants constitute the largest group of canopy-occupying organisms, representing between 20% and 40% of the total arthropod biomass present there (Davidson et al., 2003; Hunt, 2003; Tobin, 1995). Several different mechanisms have been suggested as pivotal in structuring the forest canopy invertebrate fauna, including epiphyte architectural morphometry and suspended soil formation associated with the roots of epiphytes that attach to tree branches and twigs (DaRocha et al., 2015; Paoletti et al., 1991; Yanoviak et al., 2004). Structural components of the canopy, such as tree crowns, vines, twigs, branches, and epiphytes increase habitat heterogeneity and complexity, and consequently shape the spatial and temporal diversity of species in these environments (Campos et al., 2006; Dáttilo and Dyer, 2014; Neves et al., 2013; Yanoviak et al., 2011). In this way, structural components are able to alter canopy community structure at different spatial scales.

Human land use and other anthropogenic changes can modify ant–plant interactions (Falcão et al., 2015) and may alter biodiversity at different spatial scales, including local (α-diversity) (Gibson et al., 2011; Newbold et al., 2015) and differences in species composition among sites (β-diversity) (Karp et al., 2012; Solar et al., 2015; Whittaker, 1972). Land use systems, such as AFSs, maintain a structured community of canopy epiphytes, and may be of especial interest for the maintenance of ant diversity and services, as well as ant–plant interactions (Gras et al., 2016). In AFSs, different species of ants and epiphytes interact with each other, creating complex interaction networks. Graph theory uses a unique set of metrics and tools to describe the structure of ecological interaction networks (Santos et al., 2014), which provide inferences about the ecological and evolutionary dynamics of a system (Bascompte et al., 2006). Despite the increasing number of studies using network theory to understand plant–animal interactions (i.e., especially mutualistic interactions: Bastolla et al., 2009; Dáttilo et al., 2014; Mello et al., 2011; Olesen et al., 2008), ant–epiphyte interactions have been neglected, possibly due to the difficulties associated with canopy sampling. Thus, general knowledge of community structure and ant–plant interactions in these environments are not well understood, nor are the effects of anthropogenic changes (i.e., in land use) upon these communities.

This study describes an ant community structure and ant–bromeliad interactions in a native forest and three different AFS types in an Atlantic forest region of Brazil. We tested the prediction that cocoa agroforestry systems with shading from native trees are more complex and heterogeneous than simpler (i.e., with monospecific shading) AFSs, and that these systems maintain ant community structure and ant–bromeliad interaction networks in ways similar to native forest.

2. Material and methods

2.1. Study sites

The study was carried out in one native forest area and three agroforestry cocoa systems in a cocoa region of the southeastern state of Bahia, Brazil from February 2009 to February 2010, in the months with higher temperatures and lower rainfall. The cocoa producing region of southeastern state of Bahia is defined here as the whole region standing between the Contas and Jequitinhonha Rivers (Fig. 1). The sampling areas were within Una and Ilhéus municipalities, distributed near the latitude 15°S close to the Atlantic coast where the dominant vegetation is South Bahiana humid forest (Gouvêa et al., 1976). This region falls within the Atlantic Forest biome, one of the priority biomes for the conservation of biodiversity (Myers et al., 2000). Atlantic forest is characterized by having tall, broadleaf, and evergreen trees with numerous vines and epiphytes. The climate is characterized as hot and humid, with the absence of a well-defined dry season (Type 'Af' on the Köppen's scale), with annual rainfall ranging between 1300 and 2000 mm. The annual average temperature is 24–25 °C, with warmer periods between October and April (max ~38 °C) and the coldest between June and August (min ~7 °C) (Mori, 1989). Average annual relative humidity is between 80% and 90%.

The Una Biological Reserve (15°11.230′S, 39°03.727′W) is covered by native forest (Saldarriaga and Uhl, 1991) in advanced succession with a closed canopy about 30–35 m in height, and with an understory largely devoid of underbrush and reaching about 18 m in height. The cocoa agroforestry systems were divided into three categories: rustic-planted shade system (RPS), cocoa cabruca system (CAB), and monospecific-shaded cocoa agroforestry system (MCA). The AFSs in this study differ from each other and from native forest in structural characteristics, and when compared to native forests. The RPS is cocoa plantations that keep different trees shading a combination of Rustic cocoa and Planted Shade system (see Rice and Greenberg, 2000). Therefore, here the RPS refers to the presence of shading by trees native forest remnants, primary and secondary naturally present intercropped with exotic trees planted for polycultures shading. The RPS were located in the Fazenda Ararauna (15°18.451′S, 39°09.773′W) and Fazenda Bonfim (14°39.606′S, 39°11.574′W). These two farms are shaded by trees characteristic of primary and secondary forest, such as: jequitibá-rosa (*Cariniana legalis* (Mart.) Kuntze), sapucaia (*Lecythis pisonis* Cambess. (Lecythidaceae)), *Cecropia* sp. (Urticaceae), *Inga* sp. (Mimosoideae), as well as numerous exotic species such as cajá (*Spondias mombin* L. (Anacardiaceae)), jackfruit (*Artocarpus heterophyllus* Lam. (Moraceae)), and eritrina (*Erythrina* spp. (Fabaceae)). Tree density is roughly 25–30 trees per hectare, and the canopy structure is discontinuous-open and reaches about 20–25 m in height. It has a heterogeneous landscape in terms of crop diversity, featuring next to cocoa plantations a variety of other cultivated plants such as açaí (*Euterpe oleracea* Mart (Arecaceae)), pupunha (*Bactris gasipaes* Kunth (Arecaceae)), cupuaçu (*Theobroma grandiflorum* (Willd. ex Spreng.) K. Schum. (Malvaceae)), banana (*Musa* sp. (Musaceae)), guaraná (*Paullinia cupana* Kunth (Sapindaceae)) and *Heliconia* sp. (Heliconiaceae). The CAB were located in the Fazenda Vera Cruz (15°18.327′S, 39°09.358′W) and Fazenda Santa Rita (14°41.889S, 39°11.786′W). Both farms have a cocoa agrosystem that involves retaining part of the primary native forest (trees at a density of 25–30 trees per hectare) for shading the cocoa plantation (Schroth et al., 2011). Examples of species retained are gindiba (*Sloanea obtusifolia* (Moric.) K. Schum. (Elaeocarpaceae)) are sapucaia (*Lecythis pisonis* Cambess. (Lecythidaceae)). The canopy structure is discontinuous to continuous, and reaches about 30–35 m in height. The canopy also features other crop types next to cocoa plantations, such as açaí, pupunha, and banana. The MCA, also known as "*derruba total*" or "total clearing", is located in the Cocoa Farming Research Center (CEPEC/CEPLAC) (45°44.114′S 39°14.011′W). The plants used for shading cocoa consist primarily of exotic tree species of the genus *Erythrina*, mainly *Erythrina fusca* Lour. (Fabaceae). This system has a discontinuous canopy at about 20–25 m height. Tree density for shading is 17.4 trees per hectare. The creation of the MCA system was a recommendation made by CEPLAC, which called in the 1960s (Gramacho et al., 1992).

2.1.1. Epiphyte sampling

We sampled the ant fauna associated with epiphytes by collecting bromeliads from the canopy of shade trees in cocoa agroforestry plantations and native forest canopy. As there is a high epiphyte diversity in the southeastern region of Bahia (Souza et al., 2015), sampling concentrated on bromeliad species in the genera *Hohenbergia* Schult. and Schult. F. and *Aechmea* Ruiz and Pav. (Bromeliaceae, subfamily Bromelioideae). *Hohenbergia*