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TESE DE DOUTORADO

Interações formiga-planta nos campos rupestres: diversidade, estrutura e dinâmica temporal

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BELO HORIZONTE

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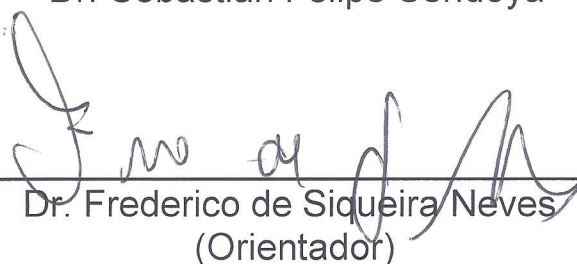
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"I am tempted to give one more instance showing how plants and animals, most remote in the

scale of nature, are bound together by a web of complex relations."

(Charles Darwin, 1860, On the Origin of Species)

A pedra

Pedra sendo.

Eu tenho gosto de jazer no chão.

Só privo com lagarto e borboletas.

Certas conchas se abrigam em mim.

De meus interstícios crescem musgos.

Passarinhos me usam para afiar seus bicos.

Às vezes uma garça me ocupa de dia.

Fico louvoso.

Há outros privilégios de ser pedra:

a - Eu irrito o silêncio dos insetos.

b - Sou batido de luar nas solitudes.

c - Tomo banho de orvalho de manhã.

d - E o sol me cumprimenta por primeiro.

(Manoel de Barros, Tratado geral das grandezas do ínfimo)

Sumário

Apresentação

Contexto geral

Nenhuma espécie vive isolada na natureza. Elas se associam de diferentes maneiras, formando interações que compõem o núcleo central da biodiversidade, especialmente dos ecossistemas tropicais (Jordano, 2016). Para entender o funcionamento destes ecossistemas, é necessário não somente avaliar a diversidade de espécies, mas também explorar como estas interagem umas com as outras (Jordano, 2016). Durante as últimas décadas, grandes esforços foram realizados para compreender a natureza das interações ecológicas, e como estas respondem a diferentes processos bióticos (e.g., tipo de interação - Kéfi *et al.*, 2016) e abióticos (e.g., tipo de solo - Dáttilo *et al.*, 2013). Ademais, o desenvolvimento da teoria de redes de interações ecológicas, permitiu uma melhor visualização e entendimento da estrutura de sistemas formados por múltiplas interações (Fig. 1A) (Bascompte & Jordano, 2014). Apesar dos avanços, a complexidade desses sistemas resulta em uma série de desafios e questões que permanecem inexploradas, como **em que medida a variabilidade ambiental no tempo e espaço afeta a estrutura e dinâmica das interações entre espécies?** (Sutherland *et al.*, 2013).

As interações bióticas compõem distintas funções ecossistêmicas como produção primária, ciclagem de nutrientes, controle de pragas, polinização e dispersão, dentre outros (Fontaine *et al.*, 2011). Estima-se que até 90% das espécies de angiospermas tropicais dependem de associações com animais para completar seus ciclos de vida (Jordano, 2000). Dentre estas, as associações entre formigas e angiospermas se destacam devido à sua grande prevalência nos ambientes terrestres (Rico-Gray & Oliveira, 2007) e por mediarem distintos serviços do ecossistema (Del Toro *et al.*, 2012). Interações formiga-planta são tradicionalmente classificadas de acordo com o tipo de função desempenhada (i.e,

polinização, dispersão, proteção), e/ou de acordo com os benefícios que geram para os parceiros envolvidos (i.e., mutualismo, parasitismo) (Bronstein, 1998). Entretanto, estudos recentes têm considerado a perspectiva de que interações ecológicas não são ecologicamente estáveis, e que seus resultados variam ao longo de um *continuum* positivo-negativo, o qual é dependente do contexto biótico e abiótico em que as espécies interagentes se encontram (Bronstein, 1994; Chamberlain & Holland, 2009).

Por exemplo, sabe-se que um tipo de interação, tradicionalmente classificado como positivo (e.g., dispersão de sementes), também pode ser negativo (e.g., predação de sementes) dependendo das espécies envolvidas e do contexto local (Genrich *et al.*, 2016). Determinadas espécies estão ligadas umas às outras por uma infinidade de associações positivas, neutras e negativas que se entrelaçam, formando uma rede intrincada de interações (Fig. 1B; Kéfi *et al.* 2016). O desenvolvimento teórico e analítico na teoria de redes (Kivelä *et al.*, 2014) abriu uma nova fronteira do conhecimento que tem propiciado a investigação de problemas que permaneciam no campo das ideias do estudo das interações (Fontaine *et al.*, 2011). Por exemplo, a complexidade das interações biológicas e o papel das diferentes espécies que realizam essas interações podem melhor compreendidos quando diferentes tipos se interações são consideradas simultaneamente.
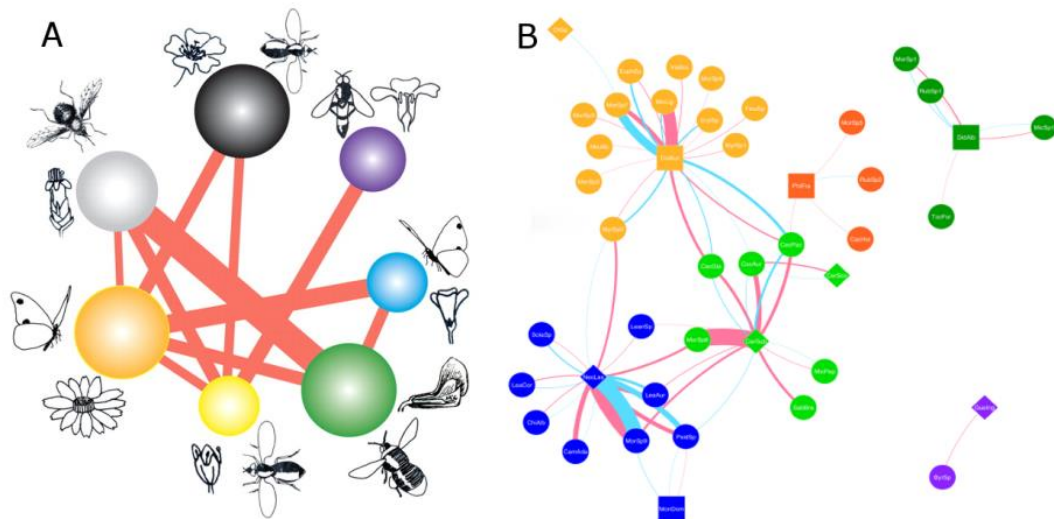
Figura 1. (A) Rede de interações representando como diferentes espécies de animais e de plantas interagem na natureza. A largura das linhas representa a frequência na qual a interação biológica ocorreu (Adaptado de Olesen *et al.* 2007); (B) Rede de interações representando como interações positivas (dispersão de sementes - linhas rosas) e negativas (predação de sementes - linhas azuis) ocorrem simultaneamente e são desempenhas pelas mesmas espécies em uma comunidade (Adaptado de Genrich *et al.* 2016).

Associações formiga-planta são ótimos modelos para o estudo dessas relações complexas, pois suas histórias evolutivas estão interligadas há pelo menos 100 milhões de anos, fato que gerou uma enorme diversidade de espécies e tipos de interações (Rico-Gray & Oliveira, 2007). Essas interações englobam funções ambientais como polinização, dispersão, mutualismos de proteção, herbivoria, nutrição, dentre outras (Bronstein, 1998; Del Toro *et al.*, 2012). A literatura sobre interações formiga-planta é vasta (revisado por Rosumek *et al.*, 2009), mas a maioria dos estudos considera somete um ou dois tipos de associações, frequentemente só entre poucos pares de espécies (e.g., Oliveira & Del-Claro 2005). Mesmo quando grandes revisões são realizadas (e.g., Mayer *et al.* 2014), dificilmente é explorado em que medida um tipo de interação pode afetar outro, ou como algumas espécies desempenham distintos papéis ecológicos na comunidade.

Uma vez que a história natural dessas interações é consideravelmente conhecida (Mayer *et al.*, 2014), novos estudos orientam-se a explorar como essas interações são estruturadas e como respondem a variações ambientais em grandes escalas. Por exemplo, sabe-se que as interações formiga-planta respondem a mudanças ambientais e distúrbios tais como, qualidade do solo (Dáttilo *et al.*, 2013), variações no clima (Rico-Gray *et al.*, 2012; Pringle *et al.*, 2013), fragmentação florestal (Emer *et al.*, 2013) e a presença do fogo (Paolucci *et al.*, 2016). Apesar dos avanços, tais abordagens consideram somente um ou dois tipos de interação (e.g., formiga-nectários extraflorais), e/ou não investiga como a dinâmica dessas interações pode ser afetada diante das atuais mudanças ambientais.

O ecossistema de estudo: os campos rupestres

Os campos rupestres são formações vegetais Neotropicais que em geral ocorrem entre 900 e 2000 m de altitude (a.n.m.), principalmente nas montanhas da Cadeia do Espinhaço (situada no sudoeste do Brasil), embora áreas isoladas também ocorram em montanhas do Brasil central (estado de Goiás) e serras do estado de Minas Gerais (Alves *et al.*, 2014; Fernandes, 2016) (Fig. 2). Abrangendo mais de 1200 km de extensão (norte-sul) e 50-100 km de largura (entre os estados de Minas Gerais e Bahia), o Espinhaço forma uma importante região biogeográfica do Brasil (Fig. 2). A cadeia tem complexas características topográficas que resultam de uma combinação de longos processos erosivos (~1.5 – 1.7 Ma) (Pedreira & de Waele, 2008) e recentes processos tectônicos (~500 - 600 Ma) (Abreu, 1995). Como resultado do processo erosivo da rocha matriz predominante (quartzito-arenito), os solos geralmente são superficiais e arenosos, altamente ácidos e extremamente pobres em nutrientes (Benites *et al.*, 2007). Devido à ausência de expansão geográfica significativa durante o Holoceno médio (~6.000 anos) e o último máximo glacial (~21.000 anos); Barbosa & Fernandes (2016) sugerem que os campos rupestres são ambientes evolutivamente estáveis

provavelmente em decorrência da alta especificidade de seus solos. Como paisagens antigas, climaticamente tamponadas e inférteis (Teoria *OCBIL – Old, Climatic Buffered and Infertile Landscapes* - Hopper, 2009), os campos rupestres são comparáveis aos *kwongkan* no sudoeste da Austrália, *fynbos* na África do Sul, e aos *tepuis* no Escudo das Guianas presentes na América do Sul (Silveira *et al.*, 2016).
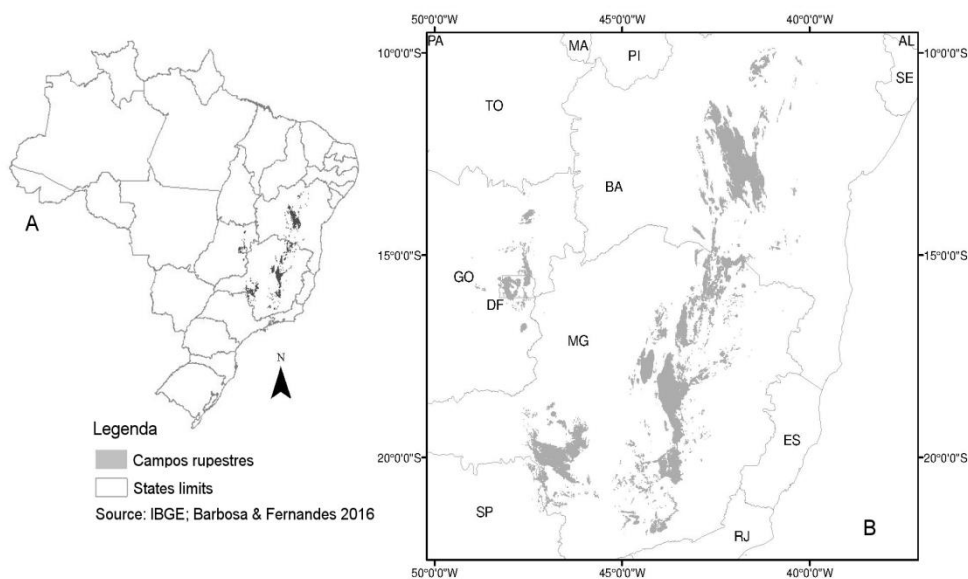
Figura 2. Projeção dos campos rupestres no território brasileiro (A), especificamente na Cadeia do Espinhaço, montanhas do Sul e Sudoeste do estado de Minas Gerais, e no Brasil Central no Estado de Goiás (B) (Fonte: IBGE; Barbosa & Fernandes, 2016).

Os campos rupestres são caracterizados por um mosaico vegetacional altamente diverso, formado principalmente por gramíneas, herbáceas e arbustos associados a afloramentos de quartzito, arenito ou minério de ferro (Fig. 3; Giulietti & Pirani 1997; Silveira *et al.* 2016). Sua elevada biodiversidade e taxa de endemismo vegetal são consequências das variações latitudinais e altitudinais, isolamento geográfico, topografia e antiga história geológica, que em conjunto, promovem em uma alta diversidade de solos e microclimas nos quais as condições abióticas variam extremamente. A alta diversidade desses ambientes também se

deve à influência dos domínios do Cerrado, Mata Atlântica e Caatinga, que foram fronteiras biogeográficas (Giulietti & Pirani, 1997). Além disso, sua vegetação é considerada inflamável, por ser composta por várias espécies com estratégias adaptativas que as permitem suportar determinados regimes de fogo, ou até mesmo se aproveitar dos recursos disponíveis no ambiente pós-queima; fatores que remetem à antiga história evolutiva do ambiente com as queimadas (Figueira *et al.*, 2016). Assim, condições edafo-climáticas e frequentes queimadas atuam como principais filtros ecológico-evolutivos que moldam a biodiversidade desses ecossistemas (Fernandes, 2016).
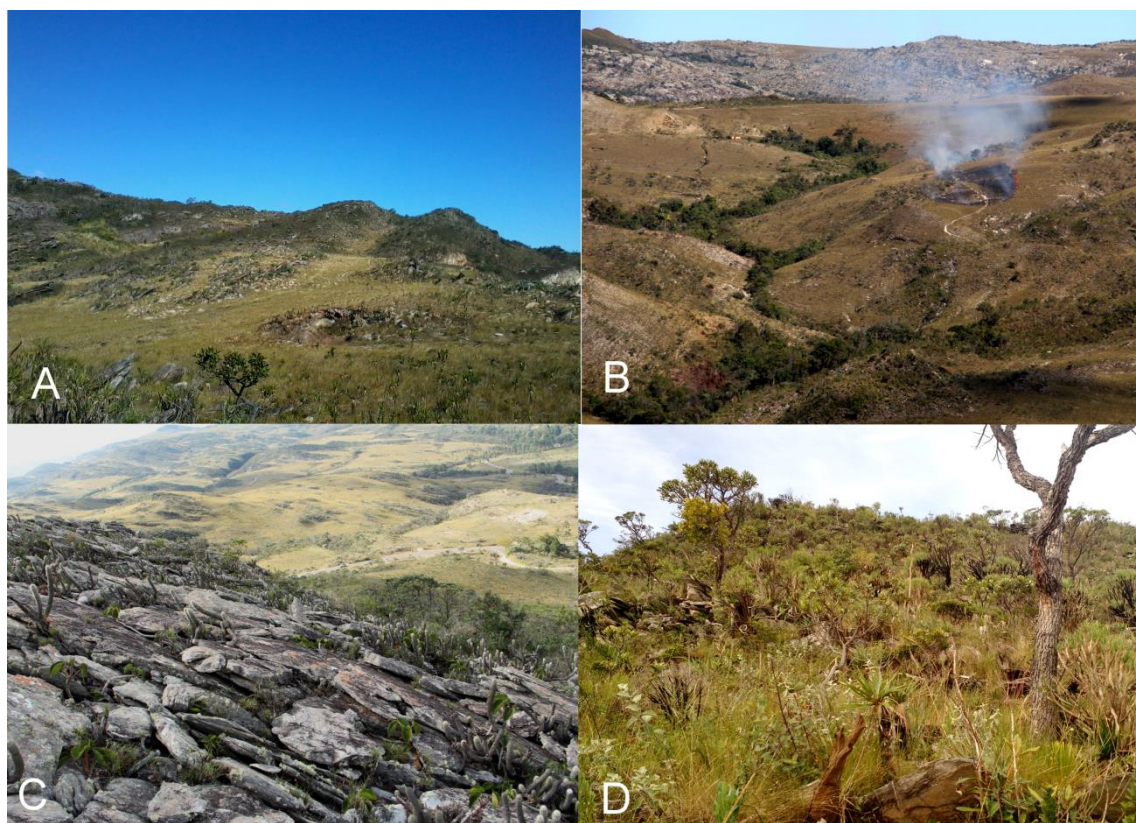
Figura 3. A) Visão geral dos campos rupestres, demonstrando os afloramentos quartzíticos circundados por uma matriz com vegetação predominantemente graminóide; B) Visão geral da paisagem com evidência em foco de queimada; C) Afloramento rochoso dominado por plantas herbáceas e cactáceas; D) Vegetação densa com presença de arbustos e pequenas árvores sobre afloramento rochoso (Local: Serra do Cipó - MG; Fotos: Fernanda V. Costa).

Estima-se a existência de mais de 5000 espécies vasculares de plantas, que correspondem a quase 15% da flora vascular brasileira, em uma área geográfica muito restrita (inferior a 1% da superfície do país) (Rapini *et al.*, 2008; Silveira *et al.*, 2016). De forma similar, há uma considerável diversidade faunística de vertebrados tais como, anuros (Leite, 2012), aves (Vasconcelos & Rodrigues, 2010) e mamíferos (Lessa *et al.*, 2008). Entretanto, alguns grupos como microrganismos (mas veja Oki *et al.*, 2016) e invertebrados (Callisto *et al.*, 2016) são mais negligenciados. O conhecimento da mirmecofauna dos campos rupestres, um dos grupos focos desse estudo, até poucos anos atrás provinha de estudos restritos a pequenas escalas geográficas e/ou táxons (e.g., Guerra *et al.* 2011; Viana-Silva & Jacobi 2012; Fagundes *et al.* 2013). Como objetivo de preencher essa lacuna do conhecimento sobre a fauna de formigas, nós compilamos registros bibliográficos e observações de campo, de modo que estimamos uma riqueza de ao menos 300 espécies de formigas nos campos rupestres (Costa *et al.*, 2015 - Anexo I). Apesar dessa riqueza considerável, a mesma está subestimada devido aos grandes vazios amostrais. De fato, a maior parte da diversidade de formigas documentada (~90% das espécies) está concentrada na região da Serra do Cipó (porção sul do Espinhaço), demonstrado o quão esse ecossistema ainda é inexplorado (Costa *et al.*, 2015).

Interação animal-planta nos campos rupestres

Grande parte dos estudos envolvendo interações antagonistas entre plantas e animais nos campos rupestres envolve herbivoria, especialmente a investigação de como a abundância e distribuição dos insetos herbívoros são afetadas pela qualidade das plantas e pressões exercidas por inimigos naturais (revisado por Neves *et al.*, 2016). As interações mutualistas (*a priori* positivas) mais exploradas envolvem polinização, dispersão e mutualismos de proteção (revisado por Guerra *et al.*, 2016).

Polinização é o principal mecanismo de fluxo gênico das plantas nesse ambiente, especialmente quando realizadas por animais com dispersões mais amplas como morcegos e aves. Levantamentos bibliográficos e observações de campo indicam que as síndromes de polinização predominantes nos campos rupestres do sudeste do Brasil são entomofilia, anemofilia e ornitofilia, respectivamente (Jacobi & Carmo, 2011; Carstensen *et al.*, 2014). De fato, o único estudo empírico realizado na escala da comunidade observou que dentre os animais, as abelhas são o grupo predominante de polinizadores (34% das espécies registradas), seguidas pelas moscas, borboletas, vespas e besouros (~15% para cada grupo), e por fim, beija-flores e formigas (6% para cada grupo) (Carstensen *et al.*, 2014).

As síndromes de dispersão de sementes dominantes nos campos rupestres são anemocoria e autocoria, embora a zoocoria aconteça em determinados grupos de plantas das famílias Melastomataceae, Myrtaceae e Cactaceae (Conceição *et al.*, 2007; Jacobi & Carmo, 2011; Silveira *et al.*, 2016). Dispersões zoocóricas em longa distância são majoritariamente realizadas por aves frugívoras não especializadas, enquanto que em curtas distâncias são mediadas por lagartos e formigas (revisado por Guerra *et al.*, 2016). Sugere-se que a mirmecocoria é uma predominante estratégia de dispersão de sementes que evoluiu em similares paisagens inférteis da África do Sul e Austrália (i.e., OCBIL) (Milewski & Bond, 1982). Todavia, somente dois estudos registraram dispersão por formigas nos campos rupestres (Fonseca *et al.*, 2012; Lima *et al.*, 2013).

Os mutualismos de proteção envolvem principalmente o sistema multitróficos entre formigas, insetos trofobiontes (normalmente hemípteros) e plantas que possuem recursos alimentares, como nectários extraflorais (NEFs) (Rico-Gray & Oliveira, 2007). Nos campos rupestres, o conhecimento sobre mutualismos entre formigas e hemípteros trofobiontes (e.g., Guerra *et al.*, 2011; Fagundes *et al.*, 2012) e entre formigas e plantas com NEFs (e.g., Dáttilo *et al.*, 2014a; Fagundes *et al.*, 2016) não é abrangente, pois deriva de estudos com táxons e

escalas geográficas locais. Esse cenário nos estimulou a investigar a diversidade de interações formiga-planta nesse ambiente (Fig. 4) e entender como diferentes tipos de interações são estruturados (Guerra *et al.*, 2016 - Anexo II). O atual conhecimento sobre a diversidade de espécies, interações e funções ecossistêmicas documentadas para os campos rupestres só reafirmam a megadiversidade e o alto potencial desse ambiente para conservação e manutenção da biodiversidade.

Figura 4. Exemplos de interações entre formigas e insetos trofobiontes (A- *Cephalotes pusillus* e *Aphis spiraecola* – Foto: Tadeu Guerra), flores (B – *Camponotus rufipes* e *Bionia coriaceae* – Foto: Marco Mello), nectários extraflorais (C – *Ectatomma tuberculatum* e *Peixotoa tomentosa* – Foto: Fernanda Costa), e frutos (D – *Ectatomma tuberculatum* e *Byrsonima* sp1 – Foto: Fernanda Costa).

Atuais ameaças aos campos rupestres

Apesar dos avanços, frequentes pressões antrópicas (Kolbek & Alves, 2008), a baixa capacidade de recuperação após distúrbios antrópicos (e.g. mineração) (Le Stradic *et al.*, 2014) e alta susceptibilidade às futuras mudanças climáticas (Barbosa & Fernandes, 2016), advertem sobre a necessidade de enquadramento desse ecossistema como área prioritária para conservação. Neste sentido, a Convenção Sobre a Diversidade Biológica (CDB) reconheceu a fragilidade dos ecossistemas de montanha, bem como a sua vulnerabilidade a distúrbios naturais e antrópicos, particularmente no atual contexto de uso da terra e alterações climáticas (CBB 2016).

Modelos climáticos preveem um futuro pessimista diante de distintos cenários, onde até o final do século XXI, os campos rupestres do Espinhaço poderão perder grande parte da sua área atual adequada (~77% - ~96%) (Barbosa & Fernandes, 2016). Esse cenário negativo, associado à intensificação dos distúrbios ambientais, torna a situação ainda mais alarmante. Por décadas essas montanhas vêm sofrendo impactos antrópicos tais como, pecuária, intensas e frequentes queimadas (Figueira *et al.*, 2016), mineração, turismo descontrolado, assentamento humano, dentre outros (Madeira, 2009; Fernandes *et al.*, 2014; Figueira *et al.*, 2016). Portanto, a prevenção e mitigação desses impactos sobre a biodiversidade exigem grandes esforços para ampliar o conhecimento sobre a ecologia e funcionamento desses ecossistemas.

Áreas estudadas: campos rupestres da Serra do Cipó

As áreas de estudo estão localizadas na parte sul da Cadeia do Espinhaço, especificamente dentro da Área de Proteção Ambiental Morro da Pedreira, que corresponde à Zona Tampão do Parque Nacional Serra do Cipó (Fig. 5). A APA foi criada em 1990 e,

juntamente com o PARNA Cipó, protegem uma área de 100.000 hectares onde são encontradas feições do bioma Cerrado e da Mata Atlântica, associados às bacias do rio São Francisco e do Rio Doce que drenam o território (ICMBio, 2014).

Elementos topográficos, vegetacionais e climáticos foram considerados na escolha das áreas de estudo. Assim, selecionamos sete áreas que fossem similares umas às outras em altitude (~1100 – 1200 m) e estrutura da vegetação (campos rupestres sobre afloramento quartizítco), além de estarem distantes umas das outras em pelo menos 1 km e com uma estação meteorológica nesse mesmo raio de alcance (Fig. 5, Tabela 1).
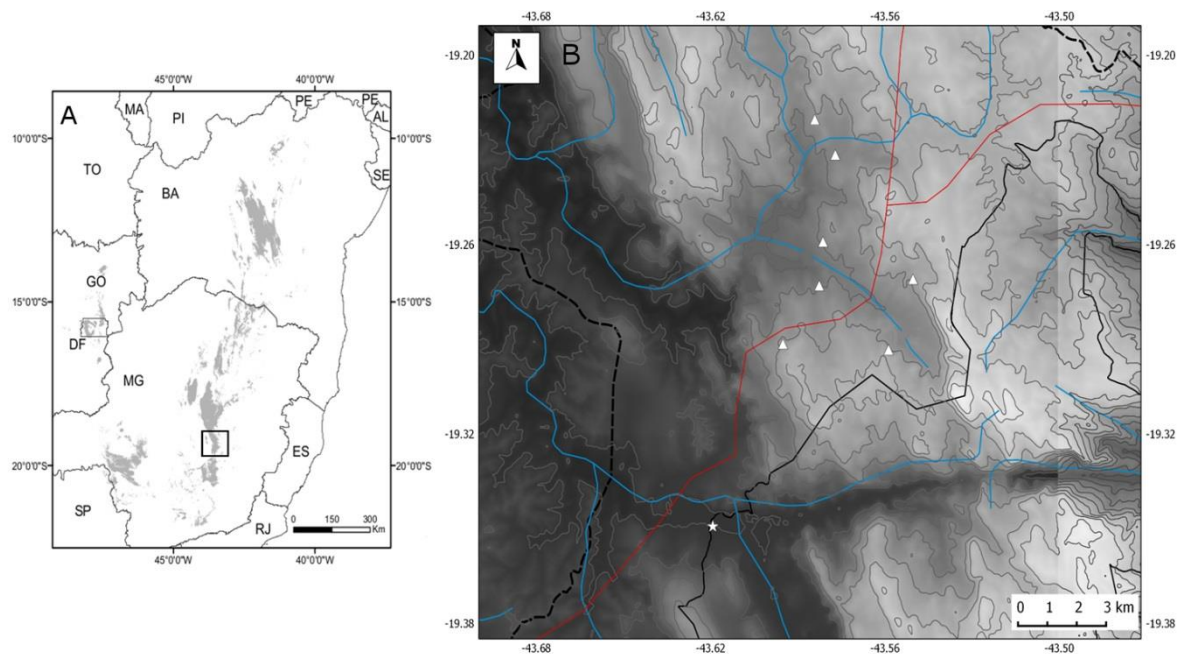
Figura 5. Localização da APA Morro da Pedreira e PARNA Serra do Cipó na parte sul da Cadeia do Espinhaço (A); Mapa topográfico das áreas de estudo representadas pelos triângulos (B). As linhas cinzas indicam a curva do nível do terreno, a linha preta tracejada indica o limite da APA, a linha preta sólida indica o limite do parque, com a entrada principal simbolizada pela estrela. As linhas azuis são referências aos rios e a linha vermelha à rodovia

MG-010. Cores mais claras indicam altitudes mais elevadas (B) (Fonte: IBGE; Barbosa & Fernandes, 2016).

Tabela 1. Descrição das sete áreas de campo rupestre selecionadas para o presente estudo (d = distância ao site mais próximo).

Área	Coordenadas geográficas	Altitude media (m)	Riqueza de plantas	Abundância de plantas	Mínima d (km)
Cedro	S19°13'51.5" W43°34'35.9"	1119	37	167	1,44
Midway	S19°16'13.4" W43°32'59.7"	1212	35	140	2,71
Pedra do Elefante	S19°17'33.9" W43°33'29.9"	1232	30	119	2,67
Paulino	S19°15'30.8" W43°34'51.2"	1108	34	124	1,58
Q16	S19°17'27.3" W43°35'40.8"	1212	39	207	2,48
Soizig	S19°16'20.7" W43°34'55.8"	1095	45	137	1,58
Tinkerbell	S19°13'11.3" W43°35'01.3"	1177	49	219	1,44

Objetivos e apresentação dos capítulos

O primeiro objetivo da tese explora a necessidade de considerarmos, simultaneamente, diferentes tipos de interações ecológicas para entendermos a estrutura e o funcionamento dos ecossistemas. Portanto, o primeiro capítulo tem como pergunta central: **os atuais padrões estruturais descritos para interações formiga-planta se mantêm quando vários tipos de interações são considerados?** Neste estudo, publicado na revista *PLOS ONE*, mostramos que diferentes tipos de interações são estruturalmente diferentes, apesar de serem conectadas por um pequeno grupo de formigas que é comum. Dessa forma, essas poucas espécies de formigas atuam como componentes-chave nos campos rupestres, pois mediam distintas funções ecossistêmicas e têm grande influência na organização dessas interações.

No segundo capítulo questionamos se **variações sazonais nas condições abióticas e o distúrbio causado pelo fogo não manejado são importantes filtros ambientais que influenciam a dinâmica temporal das interações formiga-planta.** Por meio de dois anos observações de campo, mostramos que a dinâmica temporal das interações é sazonal e altamente dependente da variação temporal das condições abióticas, especialmente temperatura. Além disso, encontramos que o efeito do fogo sobre diversidade e frequência de interações é negativo, mas transitório, indicando que as interações formiga-planta nos campos rupestres são resilientes ao fogo. Esse estudo não está publicado e encontra-se nas normas do manuscrito pretendido.

Portanto, essa tese contribui para o conhecimento sobre a diversidade e estrutura das interações formiga-planta e o entendimento de como as variações climáticas e distúrbios causados pelo fogo afetam a dinâmica temporal dessas interações nos campos rupestres. A seguir, encontram-se os dois capítulos, escritos em inglês e no formato do periódico publicado ou pretendido. Ademais, incluímos dois estudos com resultados que proporcionam um maior

entendimento sobre o sistema formiga-planta dos campos rupestres. O primeiro (anexo I) contém um compilado sobre a riqueza e distribuição da fauna de formigas dos campos rupestres, enquanto que o segundo (anexo II) explora de forma abrangente o atual conhecimento sobre interações as interações entre animais e plantas nos campos rupestres.

Boa leitura!

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Capítulo 1

Few ant species play a central role linking different plant resources in a network in rupestrian grasslands

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Few ant species play a central role linking different plant resources in a network in rupestrian grasslands

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Abstract

Ant-plant associations are an outstanding model to study the entangled ecological interactions that structure communities. However, most studies of plant-animal networks focus on only one type of resource that mediates these interactions (e.g, nectar or fruits), leading to a biased understanding of community structure. New approaches, however, have made possible to study several interaction types simultaneously through multilayer networks models. Here, we use this approach to ask whether the structural patterns described to date for ant-plant networks hold when multiple interactions with plant-derived food rewards are considered. We tested whether networks characterized by different resource types differ in specialization and resource partitioning among ants, and whether the identity of the core ant species is similar among resource types. We monitored ant interactions with extrafloral nectaries, flowers, and fruits, as well as trophobiont hemipterans feeding on plants, for one year, in seven rupestrian grassland (*campo rupestre*) sites in southeastern Brazil. We found a highly tangled ant-plant network in which plants offering different resource types are connected by a few central ant species. The multilayer network had low modularity and specialization, but ant specialization and niche overlap differed according to the type of resource used. Beyond detecting structural differences across networks, our study demonstrates empirically that the core of most central ant species is similar across them. We suggest that foraging strategies of ant species, such as massive recruitment, may determine specialization and resource partitioning in ant-plant interactions. As this core of ant species is involved in multiple ecosystem functions, it may drive the diversity and evolution of the entire *campo rupestre* community.

Introduction

Animals and plants live in a "tangled bank" of interactions [1], a network formed by different types of positive, negative, and neutral associations [2]. The nature of these multispecies systems has been illuminated by theoretical advances in community ecology [3]. Network analytical tools have allowed the operationalization of ecological concepts such as specialization [4], functional groups [5], and keystone species [6]. However, despite this boom in the field, studies of most plant-animal networks focus on a single interaction type at a time, or interactions mediated only by a single type of resource. A very few studies have attempted to model antagonistic and mutualistic interactions in the same network, but most of them without empirical data [7], and using simulation models to understand interactions structure [8,9]. To our knowledge, only one empirical study has explored how certain species have dual roles, acting both as seed dispersers, as seed predators in a network [10]. This dominant approach hinders further developments [11], especially considering that individual species are involved in many kinds of interactions at the same time [12].

Ant-plant associations are an outstanding model to study complex ecological interactions, as ants can play distinct functional roles simultaneously [13]. Many ants are considered herbivorous, with most of their food coming directly or indirectly from plants [14]. Most well-studied interactions between ants and plants are putatively mutualistic, with plants providing shelter (e.g., nesting cavities) and food (e.g., extrafloral and floral nectar, pollen, food bodies, and fruit pulp and exudates), and ants providing diverse benefits in return, including protection against natural enemies [15], seed dispersal [16], and even pollination [17]. Another widespread resource indirectly provided by plants is honeydew, an exudate rich in carbohydrates and amino acids, which is excreted by certain hemipteran insects that feed upon the phloem of several plant families [18]. In this association, the ants feed on honeydew, while the hemipterans, termed trophobionts, gain protection from their

natural enemies [18]. Although ant-trophobiont interactions are antagonistic to the plants on

which they occur, when ants tend trophobionts, they might have ecological and evolutionary

impacts on plant fitness [19]. Ants in turn might gain some benefits from these interactions, as

has been demonstrated by higher abundance of pupae in ant colonies supplemented with

elaiosomes [20] and higher growth and survivorship when workers fed upon EFNs [21] or

trophobiont secretions [22].

Ant-plant interactions are mediated by plant-derived food rewards that vary in quality

[23], predictability, and availability in the environment [24]. These factors may influence ant

behavior and foraging strategies, leading to differences in the structure of interaction networks

according to resource type. In fact, recent findings have shown that ant dominance over

resource usage is the main mechanism responsible for differences in specialization of

networks formed by interactions between ants and extrafloral nectary (EFN)-bearing plants,

and between ants and honeydew-producing hemipterans [25]. Likewise, results from

compiled datasets suggest that ant-flower networks are more specialized (i.e., more modular)

than ant–Hemiptera and ant-EFN networks [26].

More broadly, evidence indicates that mutualistic networks have in common a

fundamental property: the presence of a core formed by the most influential species, which

reach high scores of centrality [27]. In ant-plant networks specifically, is known that a few

central ant species form a core that strongly influences the structure of the entire community

[28]; this is especially true in generalized ant-EFN networks compared to those involving

specialized myrmecophytic plants [29]. This core of central ant species is consistent in space

[28] and time [30], and consists mostly of dominant species displaying high recruitment rates

and strong territoriality [31].

94   These findings have brought important insights to the understanding of ant-plant

95   networks. However, any one ant species uses multiple kinds of plant-derived resources at a

96   single time [14]. It is not known whether a single ant species plays a different role in the

97   community according to the type of resource it collects. Thus, we need empirical studies that

98   integrate different interactions into a complete ant-plant network, in order to understand plant

99   resouce use by foliage-dwelling ants. New models of multilayer networks have recently

100   opened the possibility of studying several interaction types simultaneously. In multilayer

101   networks, interactions between species may be of two or more types, creating interconnected

102   layers [32]. This breakthrough allows us to address a new question: do the structural patterns

103   described to date for ant-plant networks hold when interactions with different resource types

104   are considered? To investigate this issue, we studied one multilayer network formed by

105   interactions between ants and a set of plants that provide different food rewards (EFNs,

106   flowers, fruits), and that also host trophobionts, another food source. We tested whether

107   networks formed by interactions between ants and different food types differ from one

108   another in specialization and resource partitioning among ants. In addition, we tested whether

109   the core of central ant species is similar among resource types.

110

111   **Materials and Methods**

112

113   **Study area**

114   The study was carried out in Morro da Pedreira Environmental Protection Area, the buffer

115   zone of Serra do Cipó National Park, in the southern region of the Espinhaço Mountain

116   Range, southeastern Brazil (19°17'27.3" S, 43°35'40.8" W). We studied ant-plant interactions

117   in rupestrian grasslands, or *campo rupestre*, a megadiverse mountainous ecosystem composed

118   of grasslands and rocky outcrops occurring mainly from 900 to over 2000 m asl. in Brazil

119 [33,34]. It is characterized by a species-rich vegetation, high levels of plant endemism, and a

120 large number of threatened plant species [35]. *Campo rupestre* are also characterized by high

121 ant species richness (288 species), with the highest diversity found in the Cipó Mountains

122 [36]. The vegetation is comprised mostly of small sclerophyllous evergreen shrubs and herbs

123 associated with rock outcrops within quartzitic and sandstone soils with high levels of

124 aluminum and low concentration of nutrients [35]. The climatic regime of this region is

125 characterized as tropical altitudinal (Cwb) according to Köppen's classification [37],

126 comprising markedly dry and cold winters and hot and wet summers, with mean temperature

127 around 22º C and mean annual rainfall of 1,500 mm [33]. All permissions to visit and collect

128 biological data were authorized by ICMBio of the Brazilian Ministry of Environment

129 (SISBIO authorization number 38952-6). Data collection in sites located at private lands was

130 authorized by the owners and ICMBio.

131

132 **Sampling design**

133

134 We selected seven sites similar to one another in altitudinal range (from 1100 to 1200

135 m asl.), climate regime, and plant species richness, but distant by at least 1.44 km from one

136 another. We chose these sites not for comparative purposes but in order to capture a

137 representative sample of the area. At each site, we delimited one transect 200 m in length and

138 1 m in width, which was divided into 20 plots (10 x 1 m). We randomly sampled five plots at

139 least 30 m away from one another. In each plot, we marked all trees, shrubs, subshrubs,

140 rosettes and herbs that were fully accessible to us, those 50-200 cm in height.

141

Assessment of ant-plant interactions

We monitored the marked plants quarterly in 2014, at the peak and at the end of the rainy and dry seasons (respectively, January, April, July, and October). Between 0800–1200 and 1400-1700, each plant was observed for approximately 3 min. The interaction event was recorded only when the ant was observed feeding upon the food source [38,39]. We computed interaction frequency when we observed the same pair of species interacting in a different event. We also recorded the number of worker ants using the resource at the time of monitoring to estimate the recruitment rate of each ant species.

We classified interaction events according to the type of resource used by ants: extrafloral nectar and similar secretions (EFNs), floral nectar or pollen (flowers), glands and fleshy pulp of fruits (fruits), and honeydew droplets from trophobiont hemipterans (trophobionts). When we observed an ant on an individual plant that did not provide any resource, or an ant that left a plant without making contact with resources of any type, we defined the interaction as a "visit".

We collected vouchers of plants and insects for taxonomic identification. To identify ants we used the key by Baccaro et al. [40] and also consulted a specialist. We deposited ant vouchers in the entomological collection Padre Jesus Santiago Moure at the Federal University of Paraná (UFPR). Trophobiont insects were identified using the key by Rafael et al. [41], and also by consulting experts. Vouchers are deposited in the collection of the Insect Ecology Lab at the Federal University of Minas Gerais (UFMG). We identified plants with the support of botanists from UFMG, and deposited vouchers in the herbarium of the Botanical Department (UFMG).

Network structure

168

169   We built a multilayer network formed by ants and their interactions with EFNs,

170 flowers, fruits, trophobionts, as well as visit events, from five weighted matrices, with plant

171 species as rows and ant species as columns, and cells filled with the number of interaction

172 events of that type observed between a *i* plant species and a *j* ant species. We built one matrix

173 for each food type incorporating interactions recorded over the entire year across the seven

174 sites, each representing one layer of the network. Trophobiont associations with ants were

175 analyzed from an ant-plant perspective, so the respective matrix was built only with ant and

176 plant species connected to one another through trophobionts. Since most studies have

177 explored trophobiosis from the trophobiont-ant viewpoint, we choose this approach in order

178 to bring insights for indirect effects of ants on plants (see [42] for a similar approach).

179 Moreover, in the focal habitat, plant-trophobiont interactions are very specialized and modular

180 (S3 Table), making this approach useful to compare ways in which ants are associated with

181 plants. Thus, the multilayer network comprised all types of events recorded in the seven sites

182 during one year of sampling. For some analyses, we assessed the interactions as a multilayer

183 network, while for other analyses, the data were divided by food type into five layers.

184   To test whether different resource types are associated with different patterns of

185 specialization and resource partitioning by ants, we chose four network metrics frequently

186 used for this purpose: nestedness, modularity, complementary specialization, and niche

187 overlap. Those metrics have the additional advantage of being insensitive or only moderately

188 sensitive to sampling completeness and network size [43]. We computed those metrics for the

189 multilayer network and for each layer separately. Nestedness may provide additional insights

190 into feeding preferences, as in a nested network, interactions involving the least-connected

191 species are a subset of the interactions made by species in the core [44]. We evaluate

192 nestedness using the WNODF metric, which is based on overlap and decreasing fill in the

193 weighted matrix [45].

194   Network modularity is used to assess whether some groups of species are more

195 densely connected to one another than to other species within the same network [46].

196 Modularity is positively correlated to network specificity, because distinct modules require a

197 certain degree of specificity in the community, and thus can be used as a proxy of

198 specialization [47,48]. We calculated modularity using the QuanBiMo algorithm, which was

199 developed specifically for weighted bipartite networks [48] and is based on a simulated

200 annealing approach. The level of modularity (Q) measures the extent to which species interact

201 mainly with other species of its own or other modules, and ranges from 0 to 1. Since the

202 algorithm is stochastic, module arrangement can vary between iterations. For this reason, we

203 retained the optimum Q value as being the highest value after 1,000 iterations. Values of Q

204 were standardized (standardized Q), considering the number of standard deviations above the

205 average value recorded in 1,000 iterations. Thus, values of standardized Q indicate significant

206 values of modularity, since they represent how many standard deviations the real Q-value is

207 far from the mean of 1,000 Q-values generated from randomized networks using the

208 QuanBiMo algorithm [48]. Therefore, instead of P-values, we used standardized Q-values to

209 estimate the significance of modularity.

210   Complementary specialization (H_2') was derived from Shannon entropy and describes

211 interaction diversity, i.e., how evenly distributed the weighted interactions are in a network.

212 This index is very robust to differences in sampling effort and network size [43]. Values

213 closer to 0 indicate high generalization or redundancy of interactions, and values closer to 1

214 indicate high specialization [29,49].

215   Niche overlap among ant species was also calculated using the Morisita-Horn index,

216 which varies from 0 to 1 [50]. We used the Patefield null model to estimate the significance of

217   the observed network metrics and expectations from 999 randomized networks [51]. All

218   network metrics and their significances were calculated in the bipartite (Dormann et al. 2008)

219   and vegan [52] packages for R [53].

220

221   **Differences among resource types**

222

223   To test whether network metrics vary with food type, we compared network metrics

224   between pairs of resource layers: ant-EFN *vs*. ant-trophobiont, ant-EFN *vs*. ant-flower, and

225   ant-trophobiont *vs*. ant-flower. Ant-fruit interactions were removed from the statistical

226   analysis because the networks formed by them were too small (S1 Table). For this reason,

227   several metrics could not be reliably compared, as they are strongly biased by network size

228   [43]. In this analysis, we pooled the seven sites in order to increase the robustness of the

229   network analysis. We calculated the pairwise differences between layers, then tested whether

230   the observed differences were lower or higher than expected by chance using a Monte Carlo

231   procedure with 999 randomizations of pairwise differences ($\alpha = 5\%$).

232   To explore differences in general descriptors of network structure among resource

233   types, we computed network size (i.e., number of interacting species), frequency of

234   interactions, and richness of interactions for each layer considering the site as a sampling unit

235   (n = 7 sites). We calculated generalized linear models (GLMs) in which network descriptors

236   (size, richness and frequency of interactions) were the dependent variables and resource type

237   (EFNs, trophobionts and flowers) was the predictor variable. GLMs were compared with null

238   models, and the residuals were analyzed to verify the suitability of the models based on the

239   Poisson distribution of errors.

240

241   **The core formed by central species**

242   The concept of centrality is useful to assess the relative importance of a species to the

243   structure of the whole network [54]. There are several centrality indices proposed in the

244   literature [28,55], most of which can be used to determine a core/periphery structure in a

245   network. Degree centrality is the simplest, as it is measured as the number of connections

246   (links) made by each species (nodes) [6,56]. We chose degree centrality to identify the core of

247   central species in each resource layer so that we could test whether this core is similar across

248   them. For each resource type, within each sampling site (n = 7) we selected the ant and plant

249   species with degree centrality above the network average. We then calculated a permutational

250   multivariate analysis of variance (PERMANOVA, [57]) to test whether this core of central ant

251   and plant species is similar across resource types, and ordered the layers with nonmetric

252   multidimensional scaling (NMDS). These analyses were made in the package vegan for R

253   [53].

254   All statistical analyses were performed in R 3.2.3 [53], and network drawings were

255   prepared in Pajek 4.09 [58].

256

257   **Results**

258
259   **Species and their interactions**

260   We monitored a total of 1,114 individual plants from 108 species and 32 families. The

261   most represented families were Asteraceae (28% of sampled plants), Velloziaceae (12%),

262   Malpighiaceae and Melastomataceae (8% each), Lythraceae (6%) and Fabaceae (5%). In

263   general, the sampled vegetation was 80 ± 29 cm in height (mean ± SD) and was composed

264   mainly of subshrubs (46% of plants), shrubs (36%), rosettes (12%), trees (5%), and herbs

265   (1%).

266   The multilayer network comprised 795 interaction events between 78 plant species

267   and 30 ant species (Fig 1). Hence, 30 plant species were either not visited by ants or else

268   lacked EFNs and other food sources used by ants (S1 Table). Sixty-six percent of all events

269   were considered visits (i.e., ants were observed on a plant but were not seen feeding on it),

270   20% involved ants feeding on EFNs and similar secretory structures, 8% involved ants

271   feeding on flowers (nectar or pollen), 5% involved ants tending trophobionts, and 1%

272   involved ants feeding on fruits (eating pulp or feeding on fruit secretory structures) (Fig 1).

273

274   **Fig 1.** Multilayer network formed by interactions between ants and plants that provide

275   different food types. Circles represent plant species and diamonds represent ant species. Lines

276   represent interactions and line thickness is proportional to interaction frequency. Line color

277   represents the type of resource used. See ant and plant species names in S1 and S2 Table,

278   respectively.

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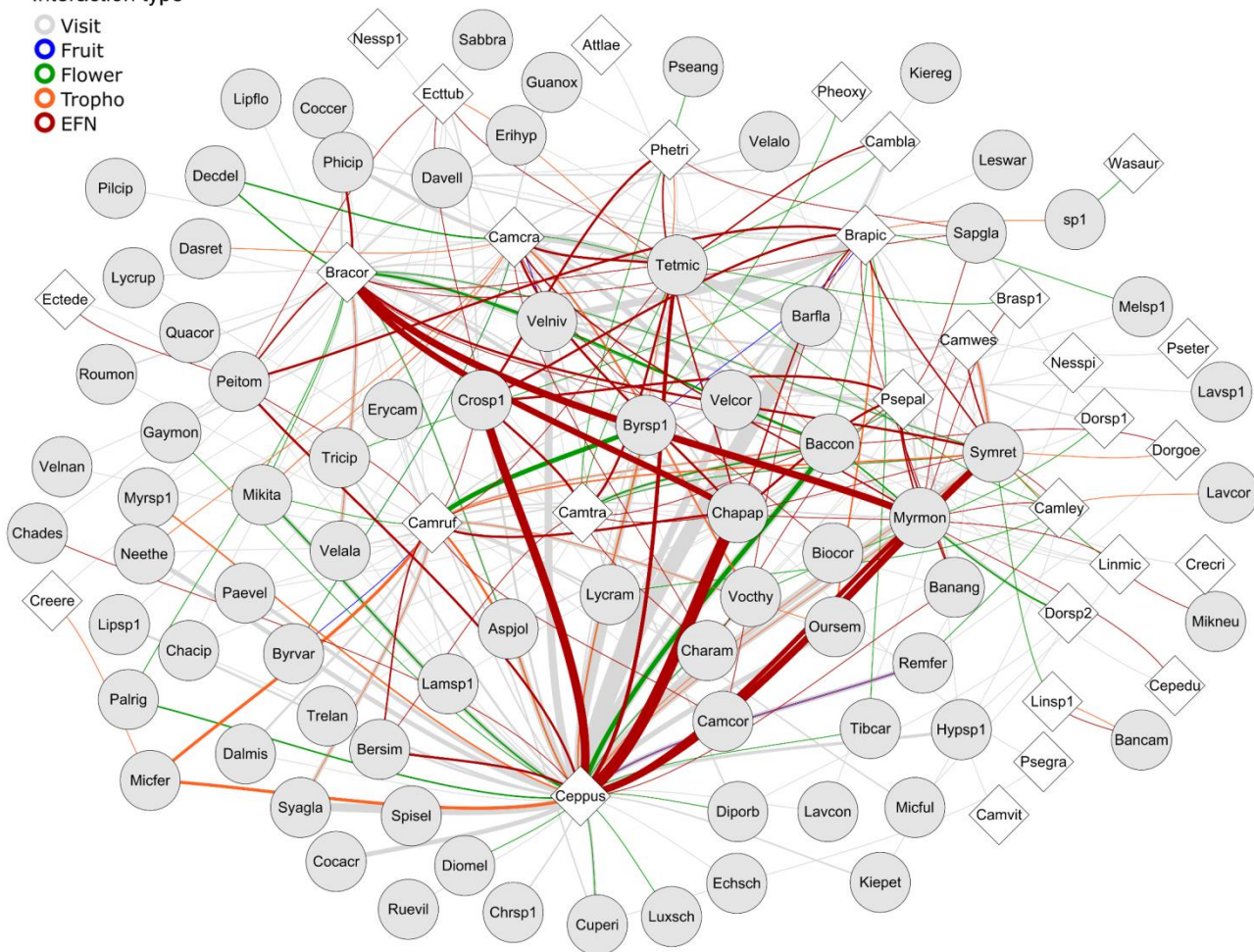
280   We observed 1,770 ant workers of five subfamilies and 30 species. Of these, 18

281   species fed on EFNs, 17 species fed on flowers, 12 species fed on trophobionts, and four

282   species fed on fruits. *Cephalotes pusillus* (37% of all records), *Brachymyrmex cordemoyi*

283   (12%) *Camponotus rufipes* (10%), *Camponotus crassus* (10%), and *Brachymyrmex pictus*

284   (6%) together made up 75% of all records and were observed interacting with the most types

285   of food (except fruits). The ant-EFN and ant-flower layers shared 12 ant species, the ant-EFN

286   and ant-trophobiont layers shared 11, and the ant-flower and ant-trophobiont layers shared

287   eight ant species. All ant species in the ant-fruit layer were found on additional resource

288   layers as well.

289   Visits were made to 71 plant species, among which the most important species were

290   those that provided nesting sites (e.g., *Vellozia* spp.) and EFNs (when this structure was not

291   active). Plant species with EFNs were the most represented in the multilayer network (18%, n

292   = 14, S1 Table). The families with EFN-bearing species were Fabaceae (5 spp.),

293   Malpighiaceae (3 spp.), Euphorbiaceae (3 spp.), Myrsinaceae (1 spp.), Araceae (1 sp.), and

294   Polygonaceae (1 sp.). Three Asteraceae species (*Baccharis concinna*, *Symphyopappus*

295   *reticulatus*, and *Mikania neurocaula*) secreted other substances within their leaf blades,

296   probably resins, which the ants collected. Since ant behavior when attending these structures

297   was similar as in the case of EFNs, we pooled these interaction types for a total of 17 species

298   with secretory structures in the multilayer network (22%, 11 exclusive species, S1 Table).

299   Ants used flower resources on 23% of plant species (23 spp., S1 Table). Of those species, 14

300   were exclusive to the flower layer. Interactions with fruits were observed only between four

301   plant species (5% of all species) and four ant species (S1 and S2 Table).

302   Twenty-three percent of all plant species (18 spp, see S1 Table) had hemipterans

303   feeding on them (13 spp., S3 Table), leading to networks with high specialization, high

304   modularity, and low niche overlap among hemipterans (S4 Table). Those hemipteran species

305 were tended by 12 ant species, but specialization and modularity were low in this layer (S4

306 Table). The most represented trophobionts were Aphididae (*Aphis spiraecola* and *Aphis*

307 *fabae*) and Coccidae (*Parasaissetia nigra* and Coccidae sp 2), which together made up 77%

308 of all interactions in the ant-trophobiont layer (S3 Table). The five most represented plant

309 species in the ant-trophobiont layer lacked EFNs (S1 Table).

310

311 **Structure of the multilayer network**

312 The multilayer network formed by the five interaction types had low but significant

313 modularity, complementary specialization, weighted nestedness, and niche overlap among

314 ants (Fig 1, Table 1). The structure of the ant-visit layer was similar to that of the complete

315 network: low but significant modularity, complementary specialization, weighted nestedness,

316 and low and non-significant niche overlap among ants (Table 1).

317 Considering the layers formed by different food sources, the ant-EFN layer had the

318 lowest modularity and specialization, but the highest weighted nestedness and niche overlap

319 among resource layers. The ant-flower layer had intermediate values for modularity,

320 complementary specialization, weighted nestedness and niche overlap. The ant-trophobiont

321 layer had the highest modularity and complementary specialization, but lower weighted

322 nestedness and niche overlap among resource layers (Fig 2, Table 1).

323

324

325

326   **Fig 2.** Network layers formed by interactions between ants and plants with extrafloral

327   nectaries, trophobionts, and flowers. Circles represent plant species and diamonds represent

328   ant species. Lines represent interactions between species and line thickness is proportional to

329   interaction frequency. See ant and plant species codes in S1 and S2 Table, respectively.

330

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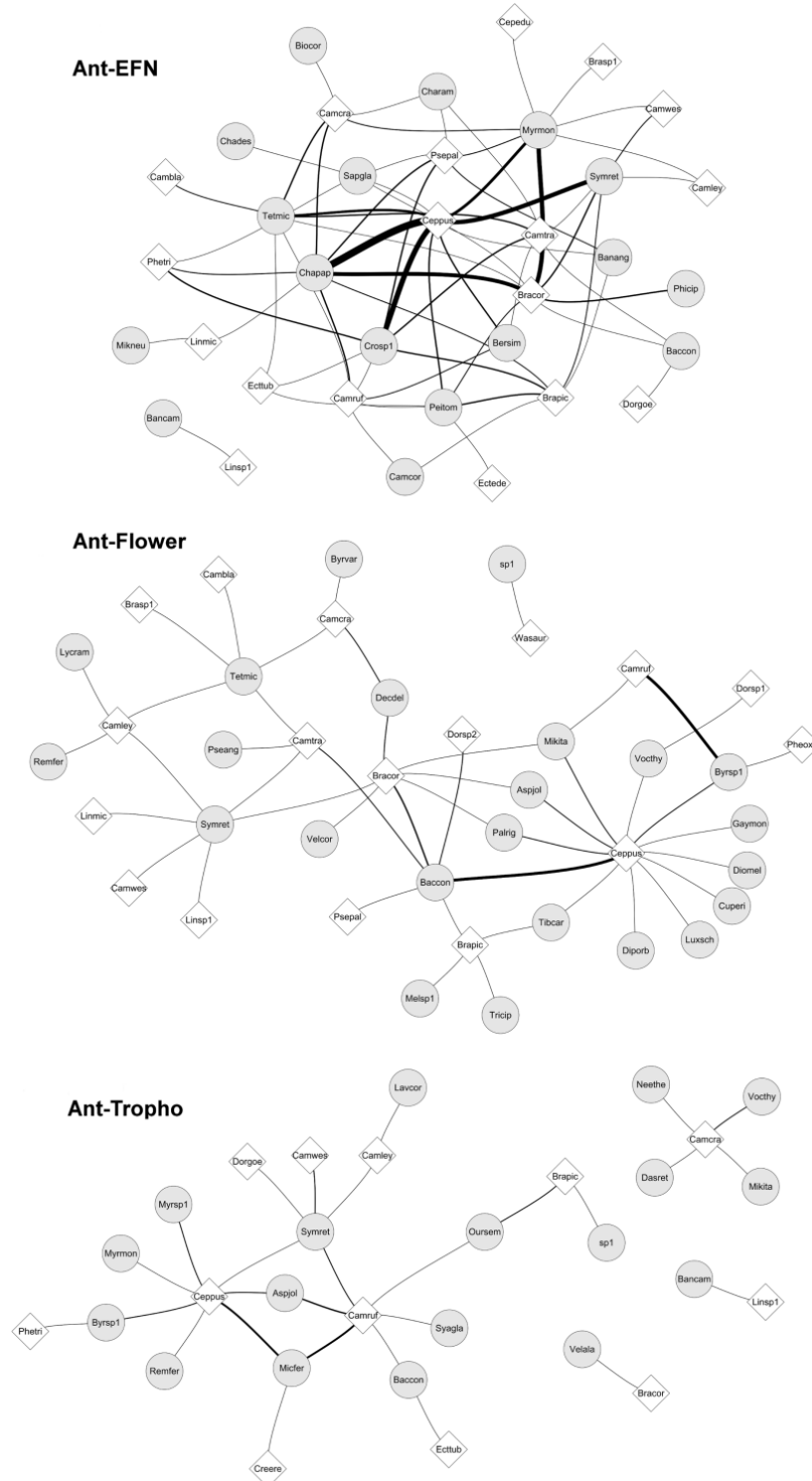
Table 1. Values for complementary specialization (H_2'), modularity (Q), weighted nestedness (WNODF), niche overlap for ants (Horn), and their respective significances (P) for different layers in a multilayer ant-plant network (symbol "*" indicates significant differences, N = 999 randomizations, St. Q = standardized Q, Visit = ant-visit, EFN = ant-extrafloral nectar, Tropho = ant-trophobiont, Flower = ant-flower).

Network	H_2'	P (H_2')	Q	St. Q	WNODF	P (WNODF)	Horn	P (Horn)
Multilayer	0.27	0.001*	0.27	15.82*	27.12	0.001*	0.13	0.001*
Visit	0.26	0.001*	0.29	7.61*	22.01	0.004*	0.14	0.312
EFN	0.27	0.001*	0.30	4.37*	22.72	0.019*	0.26	0.002*
Flower	0.34	0.006*	0.51	2.80*	11.29	0.687	0.13	0.144
Tropho	0.45	0.001*	0.57	1.64	6.46	0.456	0.05	0.001*

Differences among resource types

Consistent with our first expectation, the resource layers differed in network structure. The ant-EFN layer was the largest (GLM: deviance = 189.08, df = 2, p = 0.02, n = 7 sites), and had higher interaction richness (GLM: deviance = 23.94, df = 2, p = 0.001, n = 7 sites) and higher interaction frequency (GLM: deviance = 79.34, df = 2, p = 0.0003, n = 7 sites) than the ant-flower and ant-trophobiont layers, which were similar to one another (S5 Table). Similarly, the ant-flower and ant-trophobiont layers were similar in terms of network metrics (Table 2). The ant-flower layer was also similar to the ant-EFN layer in terms of specialization and niche partition metrics, but the ant-EFN layer exhibited lower complementary specialization than did the ant-trophobiont layer (Table 2).

348 **Table 2.** Structural comparison between resource types in the ant-plant multilayer network

349 (symbol "*" indicates significant differences, N = 999 randomizations, EFN = ant-extrafloral

350 nectar layer, Tropho = ant-trophobiont layer, Flower = ant-flower layer).

351

Structural metrics	Observed values for each layer		Differences among layers
	EFN	Tropho	P-value
Q	0.30	0.57	0.853
WNODF	22.72	6.46	0.974
H_2'	0.27	0.45	0.032*
Horn	0.26	0.05	0.245
	EFN	Flower	P-value
Q	0.30	0.51	0.391
WNODF	22.72	11.29	0.984
H_2'	0.27	0.34	0.571
Horn	0.26	0.13	0.083
	Tropho	Flower	P-value
Q	0.57	0.51	0.842
WNODF	6.46	11.29	0.688
H_2'	0.45	0.34	0.839
Horn	0.05	0.13	0.803

352

The core formed by central species

354   The core of most central ant species in the ant-EFN layer was formed by eight ant

355 species, followed by the ant-flower layer with five ant species, and the ant-trophobiont layer

356 with four ant species. In total, the cores of resource layers were made up of nine ant species.

357 Consistent with our second expectation, the species composition in these cores was similar

358 (PERMANOVA: R^2 = 0.145, p = 0.264, n = 7 sites, Fig 3A). Only *Cephalotes pusillus*,

359 *Camponotus rufipes*, and *Camponotus crassus* occurred in the core of all resource layers.

360   Together they made up 57% of all interactions in the multilayer network. In contrast to the

361   high overlap in ant composition, the composition of the most central plant species in the cores

362   of the resource layers were distinctly different (PERMANOVA: $R^2 = 0.226$, p = 0.001; n = 7

363   sites, Fig 3B). Nineteen plant species formed the resource layer cores, with no species in

364   common among them.

365

366

367

368

369 **Fig 3.** Nonmetric multidimensional scaling ordination (NMDS) showing the similarity of

370 most central ant species (A), and central plant species (B) among resource layers in the

371 multilayer ant-plant network. Points represent sampling sites and the polygons indicate

372 significant differences (EFN = ant-extrafloral nectar, Flower = ant-flower, Tropho = ant-

373 trophobiont).

374

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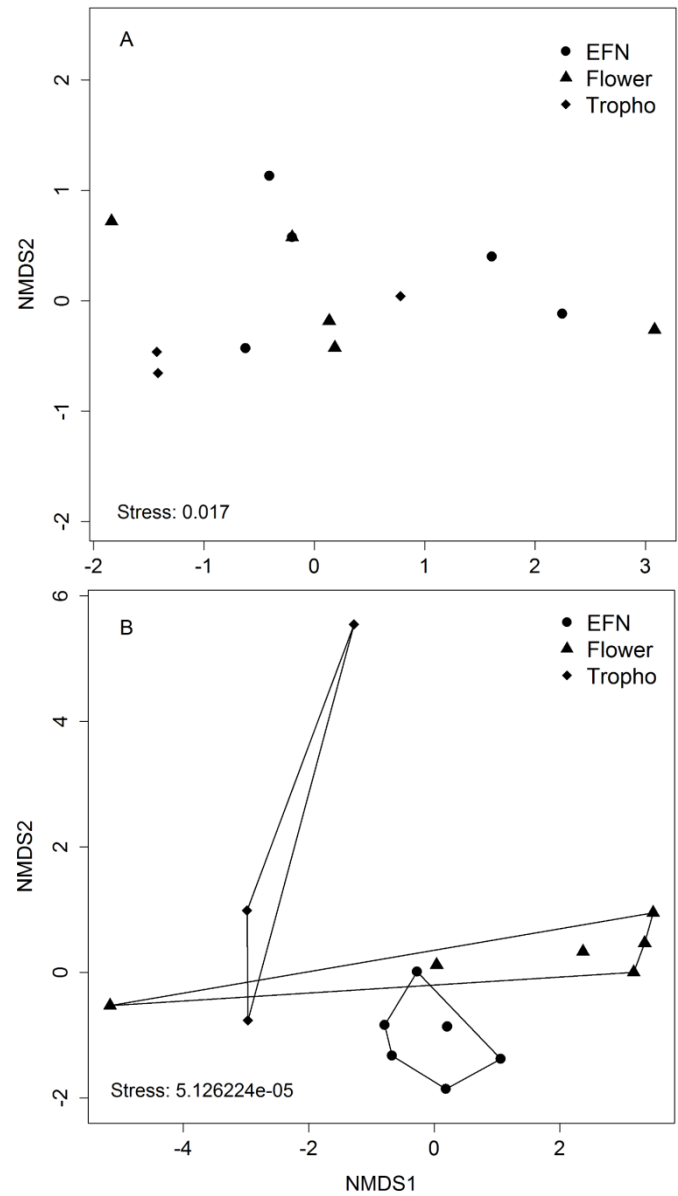
Discussion

This study is the first to assess a multilayer network formed by ants feeding upon different food types in plants. The structure of this multilayer network follows no clear topological pattern corresponding to resource types, but when it is disentangled, interactions with distinct food sources can be seen to differ from one another in terms of specialization and resource partitioning among ants. Despite differing in structure, a core of a few ant species made up most of the interactions with resources provided by different plant species. Those findings suggest that the structural proprieties of interactions between ants and food rewards do not hold when different resource types are considered simultaneously. These results suggest a clear need to move from one single interaction to multiple types to understand communities. On the other hand, we show that the plant community is bound together by a few highly central ant species that could provide different ecological functions to plants. Below, we first discuss possible mechanisms underlying these findings, then conjecture how ant-food reward relationships can be understood from a network perspective.

Consistent with our first expectation, distinct resource types formed structurally different networks. EFN was the most common resource consumed by foliage-dwelling ants, followed by flower resources (pollen and/or nectar), and then hemipteran honeydew. Fruit, however, does not seem to be a common food source for ants in *campo rupestre* vegetation. In fact, EFNs attracted a larger number of ant species, promoted higher recruitment, and frequency of interactions than other food types (S2 and S5 Table). EFNs also formed networks with the highest nestedness, highest niche overlap among ants, and largest ant core among resources, suggesting more interspecific co-occurrences in comparison to other resources. A nested pattern in ecological networks indicates the presence of a core in which frequent species interact with less frequent species in the network, leading to higher

401   persistence and stability of the mutualism [59]. The ecological and evolutionary importance of

402   EFNs for ant-plant community has been heavily discussed in literature [19,60]. Our results

403   support the idea that EFNs are a key resource promoting ant diversity and driving the

404   structure of the ant-plant community not only in savannas [61,62] and rainforests [23], but

405   also in *campo rupestre*.

406   The higher specialization and non-nested pattern found in the ant-trophobiont layer

407   would be expected if we consider that honeydew availability in *campo rupestre* is apparently

408   more limited than nectar [25] and that honeydew, especially from Aphididae and Coccidae, is

409   nitrogen-enriched and more nutritious than plant nectars [63]. As a consequence, it is likely

410   that honeydew is a more valuable and rare resource for ants [23]. This seems likely to

411   promote interspecific segregation, with superior competitors species dominating better quality

412   resources [61]. In addition, the ant-trophobiont layer also had the lowest niche overlap among

413   ants and the smallest core (four ant species) among food types, supporting the idea that

414   honeydew promotes segregated patterns of ant species co-occurrence in *campo rupestre* [25].

415   Territorial competition among ants are well-known in tropical vegetation, where dominant

416   ants organize interspecific interactions and drive community assembly [64].

417   Foraging on flowers involved similar ant diversity and frequency of interactions as did

418   feeding on honeydew. Likewise, the structure of the ant-flower layer was very similar to the

419   ant-trophobiont layer, both forming more specialized networks than found in the ant-EFN

420   layer. Honeydew, floral nectar and pollen are resources of high quality and nutritional value

421   for ants [65,66]. Since ants consume food rewards in opportunistic ways, it seems probable

422   that resource availability and predictability across the year determine their foraging strategies:

423   flowers normally are prevalent in the dry season, a period when trophobionts are less

424   abundant [24,62]. This same phenological pattern might be taking place at our study site,

425   where several plant species exhibit a flowering peak during the dry season [67]. Thus, is

likely that ants switch food sources during the year, leading to a similar structure of interactions. On flowers, ants are typically considered robbers and thieves [68], although evidence that ants can also act as pollinators does exist [17]. Trophobionts are plant herbivores that reduce plant fitness, but when attended by ants might lead to indirect positive effects for plants (reviewed by [18]). Although we have not quantified interaction outcomes, our results illustrate how interactions that likely range from negative to positive effects are tied together in the community.

The core plant species belonged to different families and life forms [35], covering a wide spectrum of flower types, fruit types and secretory structure types. In contrast, a core of relatively few ant species made up most of the interactions with resources provided by different plant species, in line with our expectation. Three ant species stand out in the *campo rupestre*, since they were present in the cores of all resource networks. Although they encompass only 1% of the ant species recorded in the region [36], they are over-represented in the multilayer network (> 50% of records). Previous studies carried out in distinct habitats suggest that the cores of ant-EFN and ant-honeydew networks are composed by competitively superior ant species [25,31]. In fact, *Camponotus crassus* and *Camponotus rufipes* are numerically dominant and aggressive ants, which are considered truly trophobiont and plant mutualists in cerrado [69] and *campo rupestre* [70]. *Cephalotes pusillus* is a sub-dominant ant that has evolved some traits that favor its success on vegetation, such as a diet based largely on plant resources and a body morphology and a caste of soldiers specialized for nest defense [71]. We might expect that these species prevalence would reflect mostly their abundance. However, we verified that ant species centrality in this study is not influenced by their local abundance, but rather their recruitment rate (S6 Table). These evidence indicate that traits related to foraging strategies, such as massive recruitment and defense behavior, might explain the consistence of this core in different resource types.

In conclusion, we suggest that the structural patterns described so far for ant-plant networks are not consistent when interactions with multiple resources are considered. Ant interactions with EFNs, flowers and trophobionts formed networks that differed in ant diversity, specialization and niche overlap. However, a common core of a few ant species feed on these plant-derived food rewards, leading to a generalized multilayer network. This generalized structure mediated by a small core of ants may be a consequence of the opportunistic nature of ant-plant interactions [24]. On the other hand, foraging strategies of ant species appear to underlie the differences in specialization and niche partitioning in ant-plant interactions. These findings point to the importance of incorporating different types of interactions in order to unveil the complexity of communities. Whether the core species function as mutualists, antagonists or a combination is an open question that needs further investigation. These ant species might play a major ecological role in *campo rupestre*, as they appear to be involved in a diversity of ecosystem functions.

Acknowledgments

482

483   **References**

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Supporting information

S1 Table. Data on plant species and their interactions in the multilayer network (Species code = plant species code in the multilayer

network; E = extrafloral nectaries, FL = flowers, FR = fruits, T = trophobionts, V = visits, Recruit = ant workers recruitment, symbol "-

" indicates the absence of interaction with ants and absence of food resource).

Plant taxa	Species code	Plant abundance	Portion of individuals which interacted (%)	Interaction frequency	Resource type					Ant richness/ species	Ant recruit/ species
Acanthaceae											
Ruellia vilosa	Ruevil	17	5.9	1	-	-	-	-	V	1	1
Apocynaceae											
Oxypetalum sp1	-	2	0	-	-	-	-	-	-	-	-
Araceae											
Philodendron cipoense	Phicip	3	100.0	14	E	-	-	-	V	4	29
Arecaceae											
Syagrus glaucescens	Syagla	8	87.5	18	-	-	-	T	V	2	46
Syagrus pleioclada	-	4	0	-	-	-	-	-	-	-	-
Asteraceae											
Acritopappus confertus	-	4	0	-	-	-	-	-	-	-	-
Aspilia jolyana	Aspjol	91	19.8	22	-	FL	-	T	V	5	46
Asteraceae sp1	-	1	0	-	-	-	-	-	-	-	-
Baccharis concinna	Baccon	44	40.9	47	E	FL	-	T	V	12	96

Plant taxa	Species code	Plant abundance	Portion of individuals which interacted (%)	Interaction frequency	Resource type					Ant richness/ species	Ant recruit/ species
Chromolaena sp1	Chrsp1	7	28.6	2	-	-	-	-	V	1	2
Dasyphyllum reticulatum	Dasret	18	11.1	2	-	-	-	T	V	2	21
Echinocoryne schwenkiifolia	Echsch	9	11.1	1	-	-	-	-	V	1	1
Lessingianthus warmingianum	Leswar	2	50.0	1	-	-	-	-	V	1	7
Lychnophora ramosissima	Lycpas	46	30.4	18	-	FL	-	-	V	7	26
Lychnophora rupestris	Lyctri	4	50.0	2	-	-	-	-	V	2	6
Mikania itambana	Mikita	28	35.7	14	-	FL	-	T	V	4	46
Mikania neurocaula	Mikneu	2	50.0	1	E	-	-	-	-	1	1
Porophyllum angustissimum	-	7	-	-	-	-	-	-	-	-	-
Pseudobrickellia angustissima	Pseang	2	50	1	-	FL	-	-	-	1	1
Symphyopappus reticulatus	Symret	53	47.2	60	E	FL	-	T	V	11	111
Aquifoliaceae											
Ilex theezans	-	2	0	-	-	-	-	-	-	-	-
Cactaceae											
Pilosocereus cipoense	Pilcip	2	50.0	1	-	-	-	-	V	1	1
Clusiaceae											
Kielmeyera petiolaris	Kiepet	3	100.0	3	-	-	-	-	V	2	3
Kielmeyera regalis	Kiereg	4	25.0	1	-	-	-	-	V	1	1
Dilleniaceae											
Davila elliptica	Davell	3	100.0	6	-	-	-	-	V	5	15
Ericaceae											

Plant taxa	Species code	Plant abundance	Portion of individuals which interacted (%)	Interaction frequency	Resource type					Ant richness/ species	Ant recruit/ species
Gaylussacia montana	Gaymon	10	50.0	5	-	FL	-	-	V	3	8
Eriocaulaceae											
Paepalanthus vellozioides	Paevel	4	75.0	8	-	-	-	-	V	4	13
Erythroxylaceae											
Erythroxylum campestris	Erycam	16	25.0	5	-	-	-	-	V	4	6
Euphorbiaceae											
Bernardia similis	Bersim	1	100.0	6	E	-	-	-	-	3	14
Croton sp1	Crosp1	14	57.1	31	E	-	-	-	V	7	49
Euphorbiaceae sp1	-	2	0	-	-	-	-	-	-	-	-
Sapium glandulatum	Sapgla	3	66.7	7	E	-	-	-	V	5	19
Fabaceae											
Bionia coriacea	Biocor	12	50.0	6	E	-	-	-	V	5	16
Chamaecrista cipoana	Chacip	11	27.3	3	-	-	-	-	V	3	3
Chamaecrista desvauxii	Chades	2	50.0	2	E	-	-	-	V	2	2
Chamaecrista papillata	Chapap	12	108.3	58	E	-	-	-	V	10	58
Chamaecrista ramosa	Charam	11	54.5	11	E	-	-	-	V	6	11
Dalbergia miscolobuim	Dalmis	6	66.7	4	-	-	-	-	V	2	4
Mimosa maguirei	-	1	0	-	-	-	-	-	-	-	-
Lamiaceae											
Eriope hypoleuca	Erihyp	8	25.0	3	-	-	-	-	V	2	3
Hypenia macrantha	-	3	0	-	-	-	-	-	-	-	-

Plant taxa	Species code	Plant abundance	Portion of individuals which interacted (%)	Interaction frequency	Resource type					Ant richness/ species	Ant recruit/ species
Hyptis proteoides	-	7	0	-	-	-	-	-	-	-	-
Hyptis sp1	Hypsp1	30	16.7	7	-	-	-	-	V	4	8
Lamiaceae sp1	Lamsp1	3	100.0	3	-	-	-	-	V	3	3
Lamiaceae sp2	-	1	0	-	-	-	-	-	-	-	-
Lamiaceae sp3	-	2	0	-	-	-	-	-	-	-	-
Lauraceae											
Ocotea langsdorffii	-	1	0	-	-	-	-	-	-	-	-
Loganiaceae											
Antonia ovata	-	1	0	-	-	-	-	-	-	-	-
Spigelia sellowiana	Spisel	5	20.0	1	-	-	-	-	V	1	1
Lythraceae											
Cuphea ericoides	Cuperi	29	20.7	8	-	FL	-	-	V	3	10
Diplusodon hirsutus	-	5	0	-	-	-	-	-	-	-	-
Diplusodon orbicularis	Diporb	32	12.5	4	-	FL	-	-	V	3	4
Malpighiaceae											
Banisteriopsis angustifolia	Banang	9	55.6	9	E	-	-	-	V	5	19
Banisteriopsis campestris	Bancam	1	100.0	2	E	-	-	T	-	1	10
Byrsonima sp1	Byrsp1	19	78.9	31	-	FL	FR	T	V	9	51
Byrsonima vacciniifolia	Byrvar	12	41.7	7	-	FL	FR	-	V	4	14
Malpighiaceae sp1	-	1	0	-	-	-	-	-	-	-	-
Peixotoa tomentosa	Peitom	12	66.7	15	E	-	-	-	V	6	71

Plant taxa	Species code	Plant abundance	Portion of individuals which interacted (%)	Interaction frequency	Resource type					Ant richness/ species	Ant recruit/ species
Tetrapterys microphylla	Tetmic	36	50.0	26	E	FL	-	-	V	10	33
Malvaceae											
Ayenia angustifolia	-	3	0	-	-	-	-	-	-	-	-
Melastomataceae											
Lavoisiera confertiflora	Lavcon	1	100.0	2	-	-	-	-	V	2	2
Lavoisiera cordata	Lavcor	14	7.1	1	-	-	-	T	-	1	4
Lavoisiera sp1	Melsp2	8	12.5	1	-	-	-	-	V	1	1
Marcetia taxifolia	-	15	0	-	-	-	-	-	-	-	-
Melastomataceae sp1	Melsp1	3	66.7	2	-	FL	-	-	V	2	2
Melastomataceae sp2	-	1	0	-	-	-	-	-	-	-	-
Melastomataceae sp3	-	5	0	-	-	-	-	-	-	-	-
Miconia ferruginata	Micfer	2	100.0	9	-	-	-	T	-	3	98
Microlicia fulva	Micful	16	18.8	3	-	-	-	-	V	2	3
Microlicia sp1	-	3	0	-	-	-	-	-	-	-	-
Microlicia tetrasticha	-	1	0	-	-	-	-	-	-	-	-
Tibouchina cardinalis	Tibcar	5	20.0	2	-	FL	-	-	-	2	2
Tibouchina heteromalla	-	1	0	-	-	-	-	-	-	-	-
Trembleya glandulosa	-	1	0	-	-	-	-	-	-	-	-
Trembleya laniflora	Trelan	11	45.5	5	-	-	-	-	V	3	5
Myrsinaceae											
Myrsine monticola	Myrmon	11	100.0	46	E	-	-	T	V	11	100

Plant taxa	Species code	Plant abundance	Portion of individuals which interacted (%)	Interaction frequency	Resource type					Ant richness/ species	Ant recruit/ species
Myrtaceae											
Campomanesia pubescens	-	1	0	-	-	-	-	-	-	-	-
Myrcia sp1	Myrsp1	31	16.1	6	-	-	-	T	V	3	8
Nyctaginaceae											
Guapira areolata	-	1	0	-	-	-	-	-	-	-	-
Guapira noxia	Guanox	3	66.7	3	-	-	-	-	V	2	3
Neea theifera	Neethe	10	50.0	9	-	-	-	T	V	3	13
Ochnaceae											
Luxemburgia schwackeana	Luxsch	1	100.0	1	-	FL	-	-	-	1	7
Luxemburgia villosa	-	3	0	-	-	-	-	-	-	-	-
Ouratea semiserrata	Oursem	13	46.2	13	-	-	-	T	V	4	15
Polygonaceae											
Coccoloba acrostichoides	Cocacr	6	83.3	6	-	-	-	-	V	1	7
Coccoloba cereifera	Coccer	1	100.0	1	-	-	-	-	V	1	3
Proteaceae											
Roupala montana	Roumon	3	33.3	3	-	-	-	-	V	2	3
Rubiaceae											
Declieuxia deltoidea	Decdel	3	66.7	4	-	FL	-	-	-	2	8
Declieuxia fruticosa	-	4	0	-	-	-	-	-	-	-	-
Dioidia mello-barretoi	Diomel	1	200.0	2	-	FL	-	-	V	1	2
Palicourea rigida	Palrig	8	37.5	5	-	FL	-	-	V	2	12

Plant taxa	Species code	Plant abundance	Portion of individuals which interacted (%)	Interaction frequency	Resource type					Ant richness/ species	Ant recruit/ species
Remijia ferruginea	Remfer	9	77.8	14	-	FL	FR	T	V	5	26
Rubiaceae sp1	-	1	0	-	-	-	-	-	-	-	-
Sabiceae brasiliensis	Sabbra	2	50.0	1	-	-	-	-	V	1	2
Trigoniaceae											
Trigonia cipoensis	Tricip	49	10.2	6	-	FL	-	-	V	4	11
Unidentified											
sp1	sp1	2	50.0	3	-	FL	-	T	V	2	6
Velloziaceae											
Barbacenia flava	Barfla	39	59.0	46	-	-	-	-	V	12	60
Vellozia alata	Velala	12	50.0	12	-	-	-	T	V	5	95
Vellozia cf. aloifolia	Velniv	5	60.0	3	-	-	-	-	V	2	3
Vellozia nanuzae	Velcor	2	50.0	2	-	-	-	-	V	2	2
Vellozia nivea	Velnan	43	55.8	47	-	-	FR	-	V	13	146
Vellozia varabilillis	Velsp1	31	64.5	33	-	FL	-	-	V	11	76
Verbenaceae											
Lippia florida	Lipflo	15	6.7	1	-	-	-	-	V	1	1
Lippia sp1	Lipsp1	6	50.0	4	-	-	-	-	V	2	4
Vochysiaceae											
Qualea cordata	Quacor	1	100.0	2	-	-	-	-	V	2	2
Vochysia elliptica	-	5	0	-	-	-	-	-	-	-	-
Vochysia thyrsoidea	Vocthy	14	64.3	19	-	FL	-	T	V	6	57

S2 Table. Data on ant species and their interactions with different resource types in the multilayer network (Code = species code in

696 the network, E = extrafloral nectaries, FL = flowers, FR = fruits, T = trophobionts, V = visits, Recruitment = ant workers recruitment).

Ant taxa	Species code	Interaction frequency					Recruitment	Recruitment / plant (mean ± SD)	Partner richness
		E	FL	FR	T	V			
Formicidae									
Dolichoderinae									
Dorymyrmex goeldii	Dorgoe	1	-	-	1	1	3	1	3
Dorymyrmex sp1	Dorsp1	-	1	-	-	4	6	1.5 ± 1	4
Dorymyrmex sp2	Dorsp2	-	2	-	-	6	14	2 ± 0.8	5
Linepithema micans	Linmic	2	1	-	-	5	15	1.9 ± 2.1	7
Linepithema sp1	Linsp1	1	1	-	1	-	11	5.5 ± 6.4	2
Ectatomminae									
Ectatomma edentatum	Ectede	1	-	-	-	1	2	2	1
Ectatomma tuberculatum	Ecttub	3	-	-	1	6	27	3.9 ± 4.2	7
Formicinae									
Brachymyrmex cordemoyi	Bracor	28	10	-	1	55	388	5.7 ± 11.0	30
Brachymyrmex pictus	Brapic	12	4	1	3	25	154	3.9 ± 8.0	21
Brachymyrmex sp1	Brasp1	1	1	-	-	2	5	1.3 ± 0.5	3
Camponotus blandus	Cambla	2	1	-	-	8	19	2.4 ± 1.6	5
Camponotus crassus	Camcra	10	4	2	5	59	150	2.6 ± 3.5	29
Camponotus leydigi	Camley	2	4	-	2	4	24	2 ± 1.2	9
Camponotus rufipes	Camruf	9	7	3	12	50	205	3.1 ± 8.4	36

Ant taxa	Species code	Interaction frequency					Recruitment	Recruitment / plant (mean ± SD)	Partner richness
		E	FL	FR	T	V			
Camponotus trapeziceps	Camtra	10	5	-	-	23	44	1.3 ± 0.8	19
Camponotus vitatus	Camvit	-	-	-	-	1	1	1	1
Camponotus westermanni	Camwes	3	1	-	2	17	42	2.3 ± 2.5	10
Myrmicinae									
Atta laevigata	Attlae	-	-	-	-	1	9	9	1
Cephalotes eduarduli	Cepedu	1	-	-	-	1	5	5	1
Cephalotes pusillus	Ceppus	54	21	2	13	204	544	2.8 ± 3.3	51
Crematogaster crinosa	Crecri	-	-	-	-	1	1	1	1
Crematogaster erecta	Creere	-	-	-	1	1	10	5	2
Nesomyrmex sp1	Nessp1	-	-	-	-	1	1	1	1
Nesomyrmex spininodis	Nesspi	-	-	-	-	3	7	2.3 ± 2.3	3
Pheidole oxyops	Pheoxy	-	1	-	-	1	2	1	2
Pheidole triconstricta	Phetri	6	-	-	1	8	32	2.3 ± 2.1	9
Wasmannia auropunctata	Wasaur	-	1	-	-	-	4	4	1
Pseudomyrmecinae									
Pseudomyrmex gracilis	Psegra	-	-	-	-	2	2	1	2
Pseudomyrmex pallidus	Psepal	12	1	-	-	28	42	1.2 ± 0.6	19
Pseudomyrmex termitarius	Pseter	-	-	-	-	1	1	1	1
Total		**158**	**66**	**8**	**43**	**519**	**1770**		

697 **S3 Table.** Data on trophobionts and their interactions with plants and ants in the multilayer

698 network.

Trophobiont taxa	Frequency in plants	Ant species interacting	Ant workers/ plant	Total ants recruitment
Aphididae				
Aphis fabae	3	3	12 ± 8.5	36
Aphis spiraecola	5	4	17.2 ± 29	103
Coccidae				
Coccidae sp1	1	1	1	1
Coccidae sp2	6	4	4.5 ± 8.1	27
Parasaissetia nigra	7	5	3.4 ± 2.7	24
Margarodidae				
Margarodidae sp1	2	2	3.5 ± 0.5	7
Unidentified family				
Hemiptera sp1	1	1	1	1
Hemiptera sp2	1	2	1	2
Hemiptera sp3	1	1	7	7
Hemiptera sp4	1	1	1	1
Hemiptera sp5	1	1	2	2
Hemiptera sp6	1	1	1	1

S4 Table. Structural metrics performed for networks formed by interactions between plant species and trophobiont species ("Plant-Tropho"), and interactions between trophobiont species and ant species ("Tropho-Ant") (symbol "*" indicates significant differences between observed value and Monte Carlo randomizations, n=999, St. Q = standardized Q value).

Network type	Metric	Real value	Significance
Plant-Tropho	WNODF	2.21	p = 0.001*
	H2'	0.73	p = 0.001*
	Niche overlap	0.09	p = 0.001*
	Modularity	0.70	St. Q = 22.162*
Tropho-Ant	WNODF	15.34	p = 0.142
	H2'	0.28	p = 0.929
	Niche overlap	0.17	p = 0.049*
	Modularity	0.38	St. Q = 0.635

S5 Table. General properties of the networks formed by interactions between ants and different food types in the multilayer network. Values are presented as average ± standard deviation for each layer (EFN = extrafloral nectar, Tropho = trophobiont).

Layers	Size	Richness	Frequency
Ant-EFN	69.71 ± 40.89	11.85 ± 4.33	22.57 ± 14.16
Ant-Flower	41.28 ± 34.65	7.28 ± 3.86	9.42 ± 5.62
Ant-Tropho	21.57 ± 24.01	4.57 ± 2.76	6.14 ± 4.25

706   **S6 Table.** Generalized linear model (GLM) analysis showing the relationship between

707   centrality degree of ant species (n = 30) and their abundance and recruitment. Abundance data

708   was recorded by pitfall traps installed in the same seven studied sites (symbol "*" represents

709   significant differences, Df = degrees of freedom).

Response variable	Explanatory variable	Df	Deviance	P-value	Error distribution
Centrality degree	Ant recruitment	28	55.358	< 0,001*	Negative binomial
Centrality degree	Ant abundance	28	0.10802	0.7424	Poisson

710

Capítulo 2

Fire disturbance and climate conditions drive the temporal dynamic of ant-plant interactions in Brazilian rupestrian grasslands

Fernanda V. Costa, Nico Blüthgen, Arleu B. Viana-Junior, Tadeu J. Guerra & Frederico S. Neves

1 **Fire disturbance and climate conditions drive the temporal dynamic of ant-plant**

2 **interactions in Brazilian rupestrian grasslands**

3

4 Running title: Environmental drivers of ant-plant interactions

5

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20 **Suggested journal: Functional Ecology**

21

Summary

1. Flammable ecosystems have been shaped by edapho-climatic filters that regulate plant growth, distribution, and its associated biota. Thus, the temporal dynamic of biotic interactions in these environments is very likely dependent on the effects of seasonal climate conditions and fire disturbance.

2. Here, we tested whether the temporal dynamic of ant-plant interactions in Brazilian rupestrian grasslands is determined by temporal variation in climatic conditions, and whether fire disturbance may alter this dynamic. For two years, from 2014 to 2016, we monitored ant-plant interactions in 35 plots, out of which 26 were burned and 9 remained unburned, and assessed if abiotic conditions and fire affect the temporal variation of interaction diversity and frequency.

3. We found that diversity and frequency of ant-plant interactions are highly seasonal and positively influenced by temperature, humidity and rainfall. Temperature was the most important abiotic predictor of ant and interaction activities. We also observed that fire negatively affected ant-plant interactions up to one month after burning, up to four months on ant community, and up to a year post fire on plant community. Thus, its overall effects on interactions were negative, but transitory.

4. We observed that abiotic conditions, especially temperature, predict the temporal variation of interactions, mainly determining changes in resource availability and ant foraging activity. Fire has led to negative short-term impacts on interactions, ant community and plant community in rupestrian grasslands, suggesting their resilience to fire disturbance.

5. Our study shows that ant-plant interactions in Brazilian grasslands are strongly dependent on climate and resilient to fire. We suggest that long-term experimental studies including assisted burnings are needed to forecast how fire impacts and its synergy with weather conditions would affect biodiversity as a whole. For rupestrian grasslands, further efforts are necessary to assess which fire regimes are suitable to maintain biodiversity and ecosystem functioning, as well which fire management policies would prevent damaging fires.

Key-words: *campos rupestres*, climate changes, fire management, fire-prone ecosystems, resilience, thermal niche, tropical savanna.

Introduction

Despite community ecology has made great progress in understanding the assembly rules of multispecies interaction systems (Bascompte & Jordano 2014), to what extent environmental variability in space and time affects those systems still is an open question (Sutherland *et al.* 2013). Since interspecific interactions have a profound influence on biodiversity and ecosystem functions (Chapin *et al.* 2000), we need to be able to predict their temporal dynamic as a function of the major drivers that operate in a changing world. Severe climatic conditions and disturbances (e.g., fire) stand out among the environmental filters that might control species occurrence and interactions (Gibb *et al.* 2015; Leal & Peixoto 2016), particularly in flammable and seasonally-dry ecosystems (Fernandes 2016).

The dynamic of communities in flammable ecosystems might be dependent on fire disturbance (Gibb *et al.* 2015), as it plays a crucial role in determining system structure and functioning (Bond & Keeley 2005). Usually, the biotas in these environments are highly resilient to fire as a result of their association over evolutionary time (Whelan 1995). Indeed, recent evidence have shown that ant community from tropical and temperate flammable environments, such as deserts, grasslands, and savannas are resilient to fire (reviwed by Vasconcelos, Maravalhas & Cornelissen 2016). Likewise, their flora has a good capacity of regeneration in post-fire environment (Maurin *et al.* 2014), where some species even re-sprout and bloom in response to burning (Figueira *et al.* 2016). Alternatively, fire promotes negative impacts on communities by simplifying vegetation structure (Kimuyu *et al.* 2014), decreasing the availability of nesting sites for ants, and causing direct mortality of colonies, features that together negatively impact ant-plant interactions (Fagundes *et al.* 2015).

79   Ant-plant interactions are a good model to study those effects, as ants interact with a

80   large diversity of plants mediating many ecosystem functions (Costa *et al.* 2016). Besides, it

81   is known that humidity positively affects ant activity (Kaspari 1993), as well as ant diversity

82   is positively related to rainfall (Gibb *et al.* 2015) and temperature (Dunn, Parker & Sanders

83   2007). In fact, temperature is taken to be the main abiotic predictor of insect distribution and

84   abundance (Damos & Savopoulou-Soultani 2012), specially thermally constrained groups that

85   display specific thermic responses, such as ants (Diamond *et al.* 2012; Arnan *et al.* 2015). On

86   vegetation, the proximal climate effect is on plant phenology that mediates food availability

87   for ants (Belchior, Sendoya & Del-Claro 2016). Thus, it is expected that the temporal

88   dynamic of ant-plant interactions is very likely regulated by climate.

89   Brazilian rupestrian grasslands (locally known as *campos rupestres*) are old-growth

90   tropical vegetation that occurs in mountaintops of Espinhaço Range in Brazil (Silveira *et al.*

91   2016). This ecosystem is characterized by a grassy-shrubby and fire-prone vegetation that has

92   been shaped by edapho-climatic filters and frequent fires that regulate plant growth and

93   distribution (Figueira *et al.* 2016). Its complex topography, associated with considerable

94   geographical isolation and antiquity, resulted in a variety of strong abiotic filters (e.g.

95   radiation incidence and microclimate conditions) that vary enormously promoting the high

96   biodiversity and plant endemism (Silveira *et al.* 2016). Besides the environmental harshness,

97   grassy ecosystems are under severe anthropogenic threats, such as frequent fires (Veldman *et*

98   *al.* 2015), which can act synergistically with climate, causing unpredictable impacts on

99   biodiversity (Gibb *et al.* 2015) and vegetation structure (Lehmann *et al.* 2014).

100   Despite the considerable literature on the effects of climate and fire on plant (e.g.,

101   Veldman *et al.* 2015) and animal (e.g., Gibb *et al.* 2015) communities in fire-prone

102   ecosystems, little is known about how these filters influence ecological interactions. Few

103   studies in literature evaluated the effect of abiotic conditions (Rico-Gray *et al.* 2012; Leal &

104 Peixoto 2016) and fire (Parr *et al.* 2007; Paolucci *et al.* 2016) on ant-plant interactions.

105 Moreover, no study to date has addressed to what extent both environmental drivers may

106 affect ant-plant interaction dynamic. Here, we tested whether the temporal dynamic of these

107 interactions in Brazilian rupestrian grasslands is determined by climate, and whether a single

108 fire event may alter this dynamic. This study was conducted in a fire-prone ecosystem

109 featured by strong seasonality and recurrent events of human made fires (Fernandes 2016).

110 We have four expectations: first, we expect to find higher interaction diversity and interaction

111 frequency when temperature, rainfall, and humidity are higher, as those are assumed to be

112 better conditions for ant activity (Gibb *et al.* 2015) and resource availability (Chollet *et al.*

113 2014); second, we expect a low overlap in ant species thermal responses, since ants thermic

114 physiological constraints are species-specific (Arnan & Blüthgen 2015), and most tropical-

115 seasonal communities display narrow thermal tolerances (Kaspari *et al.* 2015); third, we

116 predict that fire effects on interaction diversity and frequency to be negative, but temporary,

117 as plant and ant communities are supposed to be resilient to fire (Andersen *et al.* 2014;

118 Figueira *et al.* 2016); and finally, we predict that fire will lead to transitory changes in the

119 composition of interacting species, as this disturbance is supposed to affect the structure of

120 ant and plant communities (Hoffmann 1999; Maravalhas & Vasconcelos 2014).

121

122 **Materials and Methods**

123
124 STUDY AREA

125   The study was carried out in seven sites at Morro da Pedreira Protection Area, a buffer

126 zone of Serra do Cipó National Park, in the southern region of the Espinhaço Mountain

127 Range, southeastern Brazil (19º17'49" S, 43º35"28" W). At higher altitudes (upper to 900 m

128 asl.) the region is featured by rupestrian grasslands, a rocky montane savanna composed by

129 species-rich vegetation, high levels of plant endemism, large number of threatened plant

130 species (Silveira *et al.* 2016), and high ant richness (Costa *et al.* 2015). Fire events in this

131 region are mainly anthropogenic and superficial, which in most cases consume fine fuels of

132 herbaceous layer (Figueira *et al.* 2016). The climatic regime is characterized as tropical

133 altitudinal (Cwb) according to Köppen's classification (Alvares *et al.* 2013), comprising

134 markedly dry and cold winters and hot and wet summers, with mean temperature around 22°

135 C and mean annual rainfall of 1,500 mm (Fernandes 2016).

136

137 SAMPLING DESIGN

138 We selected seven sites similar to one another in terms altitude (from 1100 to 1200 m

139 a.s.l.), climatic conditions, and vegetation structure, but distant by at least 1.44 km from one

140 another. At each site, we delimited one transect 200 m in length and 1 m in width, which was

141 divided into 20 plots (10 x 1 m). Five plots in each site were drawn, in a way that they were at

142 least 30 m away apart from one another, totaling 35 plots. In each plot, we recorded ant-plant

143 interactions on all herbs, rosettes, subshrubs, shrubs and trees that were fully accessible to us,

144 those with 50 - 200 cm in height. We monitored the marked plants quarterly, at the peak and

145 at the end of the rainy and dry seasons (respectively, January, May, July and October), from

146 January 2014 to October 2015, plus one sampling during the peak for rainy season (February)

147 of 2016, totaling nine sampling periods.

148

149 CLIMATIC VARIABLES

150 Close to each site there is a weather station (equipped with data logger Onset HOBO®

151 U30) which records several climatic variables every five minutes. Here, we choose three

152 variables that very likely affect ant activity and diversity (Kaspari & Valone 2002; Kaspari *et*

153   *al.* 2015): air temperature (ºC), air humidity (%) and rainfall (mm). Temperature and humidity

154   values correspond to the mean values for the precise moment in which each plot was

155   monitored, while rainfall values correspond to the accumulated rain of the sampling month.

156

157   FIRE DISTURBANCE

158   For at least five years, these study sites have not been burned by frequent fires that

159   take place in the region of Morro da Pedreira Environmental Protection Area. Approximately

160   after one year of monitoring (in September 2014) an extensive unmanaged fire started in this

161   region and persisted all over two months, affecting a wide geographical area (~ 7.300 ha)

162   (ICMBio 2014). At the end of the burning events, 26 of the 35 plots have burned and 9 plots

163   remained unburned. For most of plots we could conclude one year of sampling before the fire

164   has started (see at Table S1). Thus, we continued the monitoring for one more year after fire

165   in order to assess whether fire would affect the temporal dynamic of interactions.

166

167   ASSESSING ANT-PLANT INTERACTIONS

168   We observed each plant for approximately 3 min between 08:00–12:00 and 14:00-

169   17:00, avoiding samples during rainy periods. To get a better representativity of ant activity

170   on plants, we recorded every type association taking place in each host plant: ants feeding

171   upon extrafloral nectary, floral nectar or pollen, glands and fruit secretions, and honeydew

172   droplets from trophobiont hemipterans. When we observed an ant on an individual plant that

173   did not provide any food source, or when an ant left a plant without making contact with

174   resources of any type, we defined the interaction as a "visit" (see (Costa *et al.* 2016 in press

175   for more details). We also recorded the number of worker ants in each plant to estimate the

176   recruitment rate of each species.

177   We collected vouchers of plants and insects for taxonomic identification. To identify

178   ants we used the key by Baccaro *et al.* (2015) and also consulted a specialist from Federal

179   University of Paraná (UFPR). We deposited ant vouchers in the entomological collection

180   *Padre Jesus Santiago Moure* at UFPR. We identified plants with the support of many

181   botanists from Federal University of Minas Gerais (UFMG) and deposited vouchers in the

182   herbarium of the Botanical Department (UFMG).

183

184   DATA ANALYSIS

185   *Climatic effects* - To test whether the temporal dynamic of ant-plant interactions is affected by

186   climatic conditions we built generalized linear mixed effects models (GLMMs, *lmer* function

187   for data with normal distribution and *glmer* for non-normal ones, with *lme4* package in R)

188   with fixed and random effects which account for data temporal autocorrelation (Crawley

189   2013). Sampling plots within sites were grouped as random effects following a structure

190   where the intercept vary among sites and plots are nested within it (1|sites/plots) (Bates *et al.*

191   2014). As fixed effects we used all climatic variables, as they were not correlated (see Table

192   S2): dependent variable ~ mean temperature + mean humidity + accumulated rainfall. Since

193   those variables have distinct units and ranges they were scaled in order to standardize for

194   those differences.

195   As dependent variables, we used total interaction frequency per plot and Shannon

196   interaction diversity per plot (H_2 - Bersier *et al.* 2002; Blüthgen *et al.* 2008). Interaction

197   frequency represents a quantitative component that is computed when the same pair of species

198   is observed interacting in distinct plants. Thus, we included all observations from all

199   interactions types that occurred between ants and plants within each plot. From those, we built

weighted matrices with plant species as rows and ant species as columns, and filled cells with the number of events observed between one plant species i and one ant species j. Each matrix was standardized and used to compute the frequency and diversity of interactions. In total, we had 315 matrices/networks that correspond to each plot (n=5 per site), within each site (n=7 sites), for each sampling period (n=9 for each plot).

To test whether ant fauna thermal responses are predicted by temperature variation during seasons, we performed a thermal niche model that is based on abundance-weighted temperature conditions of each species activity (see Kühsel & Blüthgen 2015). This weighted approach considers the relative temperature preferences (rates) as well as the reliability (number of observations per temperature) to characterize a species' niche. Thus, we used the temperature during the period in which each plot was monitored and defined the abundance-weighted mean temperature for each ant species across all sites as its thermal optimum. As a proxy for a species niche breadth, we calculated the abundance-weighted standard deviation of mean temperature. To test if patterns along the temperature gradient could have been produced by a random occurrence we looped a null distribution of expected thermal niche for each species, in which a species can occur on every plot with the same likelihood and describes the most probable condition (plot temperature) for that species. We performed 1000 randomizations to calculate how often the expected thermal niche is higher or smaller than observed temperature for each species (α = 5%) (Kühsel & Blüthgen 2015; Chisté *et al.* 2016).

Fire effects - To evaluate to what extent fire affects the temporal dynamic of interactions and remains in the community, we fitted mixed models where fire (two levels variable with burned and unburned plots) and the interaction with sampling period (nine levels variable corresponding to sampling periods) were fixed effects: dependent variable ~ fire x sampling

225 period. Sites and plots were grouped as random effects following a structure were the

226 intercept vary among sites and the plots are nested within sites (1|sites/plots) (Bates *et al.*

227 2014). We built one model for interaction frequency and one for interaction diversity (H_2).

228   To test if fire leads to transitory changes in plant and ant community composition, we

229 performed a permutational multivariate analysis of variance using Bray-Curtis dissimilarity

230 index as distance matrix (PERMANOVA, Anderson 2001) and *vegan* package for R

231 (Oksanen *et al.* 2016). For each sampling period, we used weighted and standardized matrices

232 based on interaction frequency made by each species and tested whether burned and unburned

233 plots differ in species composition. Burned plots were defined as "pre-burning" in periods

234 before fire, in order to control its effects before disturbance.

235   The residuals of all GLMMs models were evaluated, as well as the suitability of error

236 distribution chosen. The complete models were simplified until minimum suitable models by

237 backward selection based on P-value. All statistical analyses were performed in R (R

238 Development Team 2015).

239

240 **Results**

241

242   We monitored a total of 1,113 individual plants of 106 species. Among these, 873

243 plants of 98 species of 32 families provided food or were used as foraging substrate by 3859

244 ants of 43 species, 16 genera, and 6 subfamilies. Those 141 species made up a total of 1,905

245 interaction events in two years of sampling. Ants foraged on plants to consume nectar from

246 extrafloral nectaries (23% of the records), nectar or pollen from flowers (7%), honeydew from

247 trophobiont hemipterans (6%), and pulp or secretions from fruits (2%). The most

248 representative plant families that provided ants with resources were Malpighiaceae (e.g.,

249 EFNs in *Tetrapterys microphylla* with 7% of all records), Fabaceae (e.g., EFNs in

250   *Chamaecrista papillata* with 6%), Velloziaceae (e.g., shelter in *Barbacenia flava* with 6% and

251   *Vellozia nivea* with 5%), Myrsinaceae (e.g., EFNs in *Myrsine monticola* with 5%), and

252   Asteraceae (e.g., secretory structures in *Symphyopappus reticulatus* with 5%). The most

253   common ant subfamily that foraged on plants was Formicinae (50% of records) and

254   Myrmicinae (39%), and the most common species were *Cephalotes pusillus* (35% of

255   interaction events), *Camponotus crassus* (12%), *Camponotus rufipes* (10%), *Brachymyrmex*

256   *cordemoyi* (9%), and *Camponotus trapeziceps* (6%). *C. pusillus, C. rufipes*, and *C. crassus*

257   were the only species that occurred in all sampling periods, and had the highest interaction

258   frequencies in all networks.

259

260   RESPONSE OF ANT-PLANT INTERACTIONS TO CLIMATE

261   There was marked seasonality in all climate variables studied (Fig. 1). Interaction

262   diversity increased with temperature (22 ± 3.55 ºC, mean ± SD) and humidity (67 ± 12.6 %),

263   and interactions frequency increased with temperature and rainfall (40 ± 30.33 mm) (Fig. 2,

264   Table S3). All over the seasons, ant species thermal optima ranged from 14ºC (*Nesomyrmex*

265   sp1) to 28ºC (*Cephalotes eduarduli*), and species thermal breadth varied from 0,10ºC (e.g.

266   *Cephalotes eduarduli*) to 13,0ºC degrees of extend (*Linepithema* sp1). This thermic response

267   to seasonality mostly corresponds to the mean thermal optimum and mean thermal breadth of

268   the whole community (i.e., 22ºC ± 2,27ºC; mean ± SD) (Fig. 3). Only a few species had their

269   optimal thermal response and niche breadth significantly out of this range, being able to

270   forage at colder or warmer temperatures (Fig 3).

271

272   Figure 1. Monthly values of rainfall, temperature and humidity in Brazilian rupestrian

273   grasslands monitored for two years.
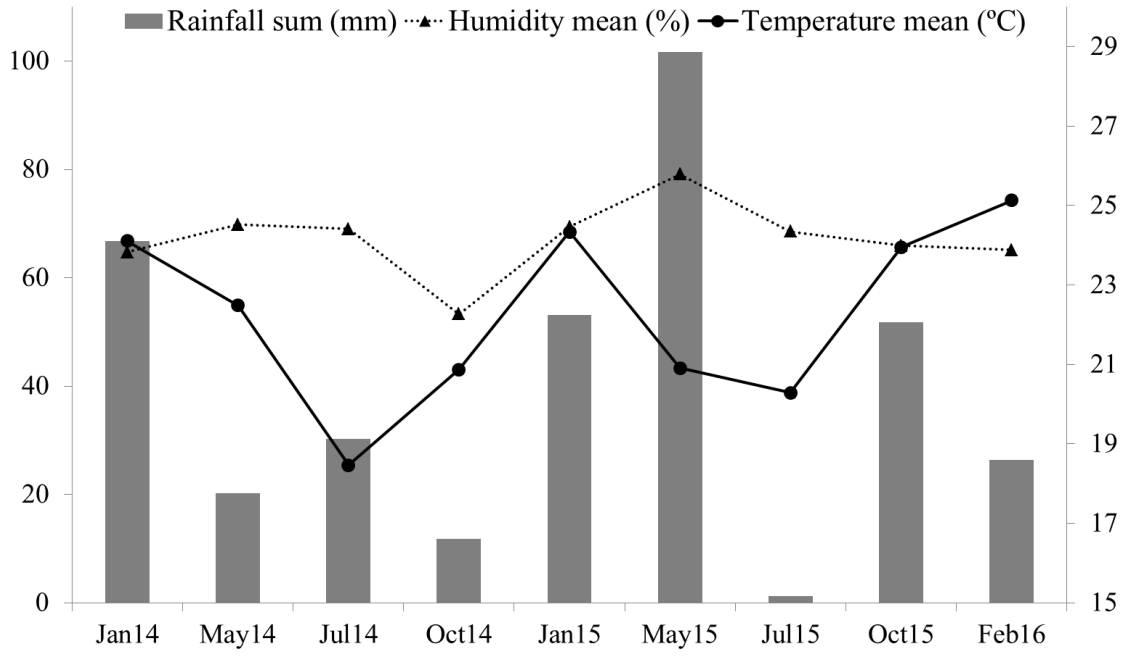
274

275

276 Figure 2. Relationship between climate and ant-plant interactions monitored for two years in

277 Brazilian rupestrian grasslands. Values in *x*-axis are minimum, medium and maximum values

278 of climatic variables. Points in temperature and humidity illustrations are mean values for

279 each site in each sampling period. Points in rainfall illustration are mean values for each

280 sampling period, considering all sites together. Vertical and horizontal gray lines are the

281 standard errors of dependent and predictor variables, correspondingly. Curves were fitted with

282 parameters from GLMM models.
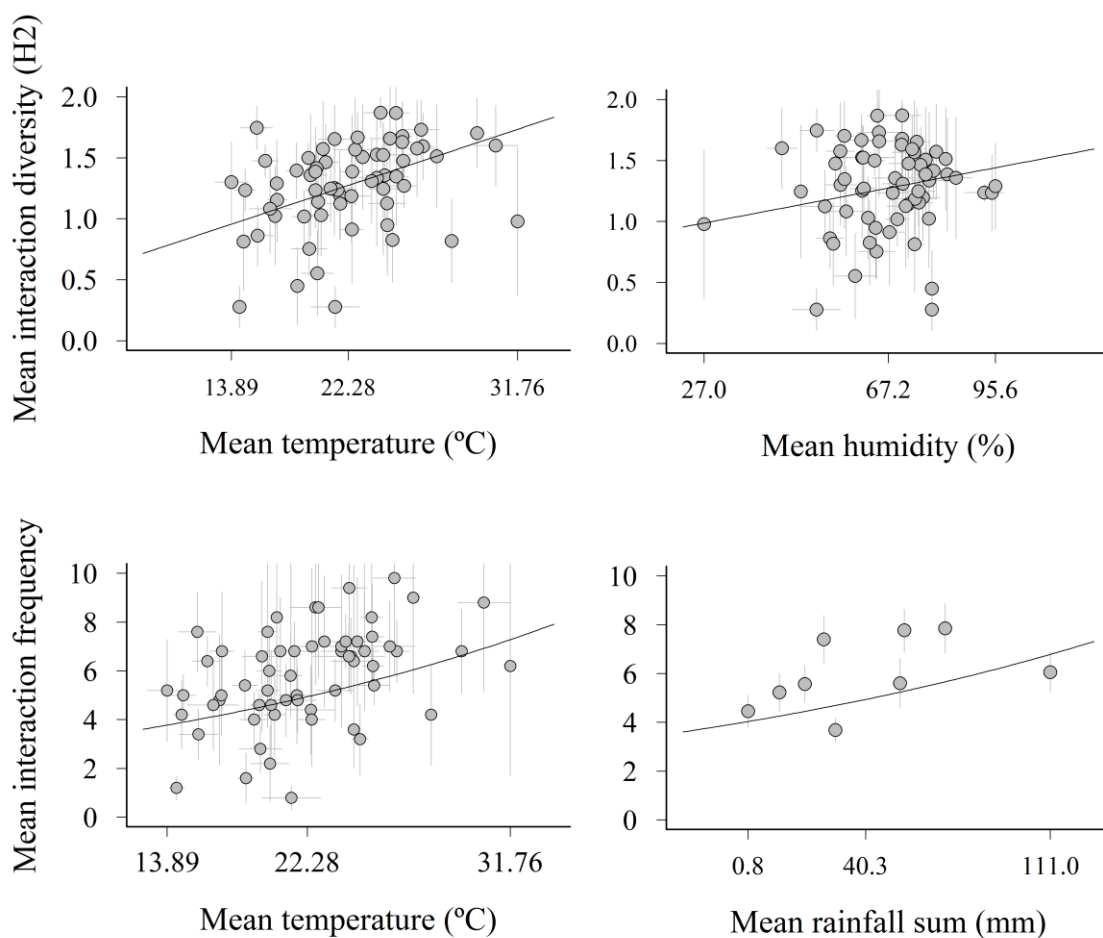
Figure 3. Thermal characterization of ant community showing the mean temperature of plots where each species occurred (weighted by abundance) with weighted standard deviations (corresponding to niche breadth). Stars mean that ant species occurrence is significantly different from the expected by null model. Species in the right side of the red line are more heat tolerant, while species in the left side prefer cooler conditions. Numbers inside parenthesis represent species occurrence in different plots. Complete ant species name are on Table S4.
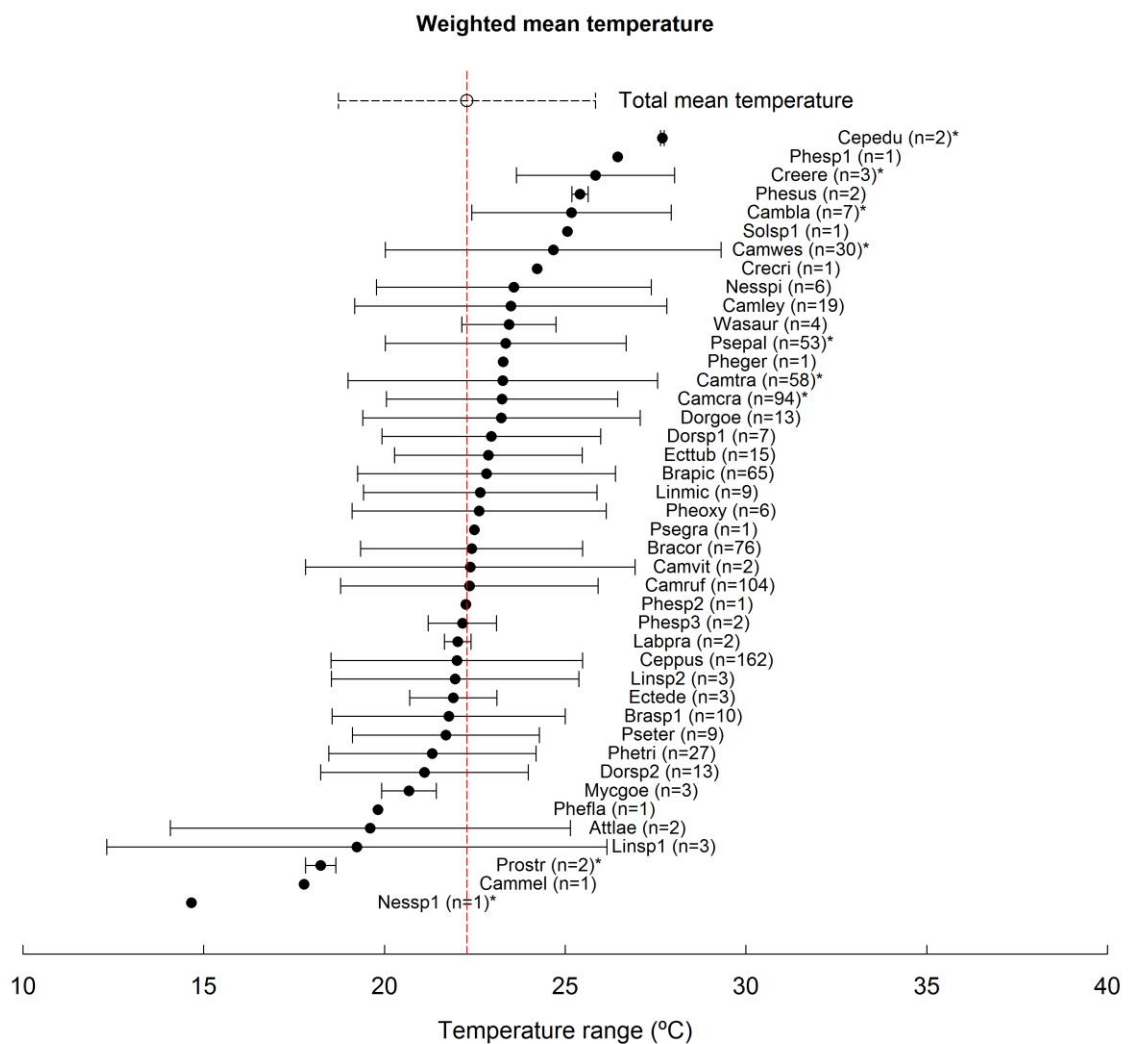
291   FIRE EFFECTS ON THE TEMPORAL DYNAMIC OF INTERACTIONS

292   Fire effects on the temporal dynamic of ant-plant interactions were evident only one

293   month after the fire event (Oct 2014), period in which burned plots had less diversity and

294   frequency of interactions than unburned plots (Table S5, Fig. 4). Likewise, fire affected ant

295   species composition until four months after burning (Jan 2015), while in plant composition it

296   persisted up to 10 months (July 2015) (Table 1). Thus, fire overall effects on species and their

297   interactions were transient, since differences were no longer observed between burned and

298   unburned plots after 10 months post-fire.

299

300   Figure 4. Fire effects on the temporal dynamic of interaction diversity (A) and interaction

301   frequency (B), both represented by mean (points) and standard deviation (vertical bars)

302   measured for the plots in each sampling period. Stars indicate periods when burned and

303   unburned plots differed from one another.
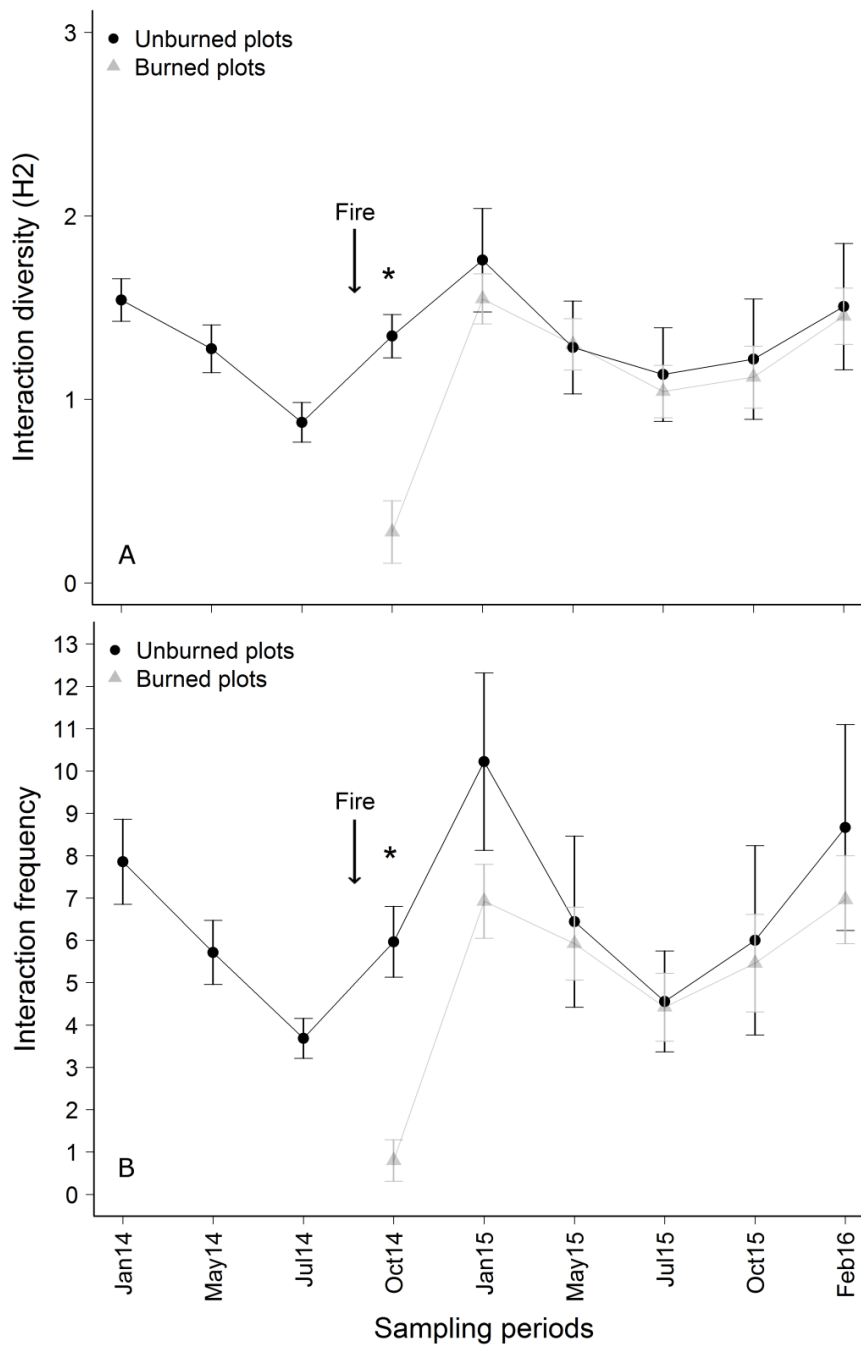
304

305 Table 1. Fire effects on the composition of interacting ant and plant species. Stars represent

306 periods in which we observed significant differences in species composition between burned

307 and unburned plots (Bray-Curtis index – PERMANOVA, n=999).

Sampling period	F-value ants	P-value ants	F-value plants	P-value plants
Jan14	2,46	0,080	1,72	0,090
May14	2,46	0,070	1,14	0,274
Jul14	1,54	0,167	1,35	0,132
Oct14	2,32	0,022*	1,73	0,021*
Jan15	1,94	0,023*	2,14	0,001*
May15	1,47	0,190	2,10	0,004*
Jul15	1,41	0,200	1,88	0,007*
Oct15	2,07	0,062	1,19	0,196
Feb16	1,44	0,200	1,62	0,060

308

309

Discussion

We found that the temporal activity of ant-plant interactions is highly seasonal and positively influenced by temperature, humidity and rainfall. Temperature was the most important abiotic predictor of temporal changes in interactions and species activities, although ant community exhibited high overlap in thermal niche response and no clear pattern of species constraint according to seasonal temperature variation. We also observed that fire overall effects on interactions were negative, but very transitory, suggesting the resilience of interactions under fire impacts. Indeed, the dynamic of interactions and species occurrence were affected by fire, whose effects remained less than a year on the community. These results pinpoint how climate and fire disturbance affects the temporal dynamic of ecological interactions in Brazilian rupestrian grasslands. Below, we first discuss which biological mechanisms are involved in interaction responses to these environmental filters. Then, we move forward drawing a parallel with other savanna-like environments and raise future perspectives for studies.

We observed that weather conditions varied seasonally and positively affected interactions diversity and frequency, whose activity peaks matched periods of higher temperature, humidity, and rainfall (i.e., rainy seasons). It seems that at local scale, climate conditions positively influence ant activity (Kaspari & Valone 2002) and ant-plant interactions (Belchior *et al.* 2016), while at global scales its effects are contrasting, ranging from positive (e.g., Dunn *et al.* 2009) to negative (e.g., Pringle *et al.* 2013; Leal & Peixoto 2016). In fact, local-scale studies carried out in cerrado observed that ants feeding upon EFNs (Belchior *et al.* 2016) and the structure of ant-EFN networks (Lange *et al.* 2013) are mainly determined by nectar availability, which is related to seasonality. Likewise, we found that ant recruitment is highly correlated to the abundance of plants providing resources (see Table S6) that varied temporally according to climatic conditions (see Table S7). Moreover, ants interactions with

EFNs, which are the main plant-derived source in rupestrian grasslands (Costa *et al.* 2016),

were higher at the onset and peak of rainy seasons, when plants are flushing new leaves and

nectar availability is greater (Alves-Silva & Del-Claro 2014). These results point that resource

availability and ants foraging on them are the main mechanisms that trigger climate effects on

interactions dynamic.

Positive effects of temperature on ecosystem productivity (Kaspari, Ward & Yuan

2004), ant species distribution (Sanders *et al.* 2007), and ant biodiversity (Kaspari *et al.* 2004)

are well known. Despite its positive influence on interactions, ant community exhibited low

thermal complementarity, which is characterized by high overlap of species-specific thermal

responses. Ants in seasonal environments are supposed to have high complementarity and low

overlap in thermal responses, because temperature variability provides available thermal

niches for species with different thermal optima (Arnan *et al.* 2015). Our results though,

indicate that temperature range across seasons is not constraining species occurrence. In fact,

ant recruitment on plants seems to be the main mechanism that prompts the positive

relationship between climate and interactions (Table S8), indicating that temperature is

triggering ant foraging activity, rather than constraining species occurrence. Communities

with low thermal complementarities are likely to be more sensitive to climatic variability

(Arnan *et al.* 2015). Also, mountainous ecosystems are more subjected to suffer shifts in their

temperature ranges in response to climate changes (IPCC 2013). Thus, we might expect that

future climatic changes in rupestrian grasslands will lead to shifts in species activity and

community structure.

Fire did promote negative and temporary impacts on species and their interactions, in

line with our predictions. Interaction diversity and frequency were lower in burned plots, but

they quickly recovered after four months after fire. The earliest fire impacts in fire-prone

ecosystems may include the simplification of vegetation structure (Maravalhas & Vasconcelos

2014) and limitation of cavities to be used as nest (Fagundes *et al.* 2015). However, many

plant species in rupestrian grasslands are adapted and even resistant to fire, as vegetation

structure promptly recover after burning (Figueira *et al.* 2016; Le Stradic *et al.* 2016).

Actually, we verified that the abundance of plants providing resource for ants is very

associated with interaction activity (Table S6), and that fire did affect plant abundance in a

similar temporal pattern as it did with ant-plant interactions (Table S7). Thus, it seems that

fire is likely affecting resource availability that consequently prompts to changes in

interactions dynamic.

Changes in species composition persisted up to four months after fire in ant

community and up to 10 months in plant community (Fig. 5). Short-term responses to fire are

well documented for ground-dwelling ant composition in rupestrian grasslands (Anjos,

Campos & Ribeiro 2015; Neves *et al.* 2016), cerrado (Maravalhas & Vasconcelos 2014),

African (Parr *et al.* 2004), and Australian (Andersen, Hertog & Woinarski 2006) savannas.

The most remarkable direct and transient effect of a single fire event on ants is the increasing

of colony mortality, mainly for species that nest in twigs and small branches (Kimuyu *et al.*

2014). Actually, rupestrian grasslands vegetation is mostly composed by herbs and small

shrubs (Giulietti & Pirani 1997) that may not support shelter structure for most species. Thus,

it appears that most ants nest on natural cavities in the ground and cavities of fire-adapted

plants (e.g. *Vellozia* genus) that act offering protection against superficial burning. Changes in

plant community are also expected since species vary in their tolerance to fire (Bond & Parr

2010). Indeed, compositional and demographic responses of flora may vary extremely from

few days to more than three years, depending on plant life-form and adaptive strategies

(Figueira *et al.* 2016). These findings, associated with the evident evolutionary history of fire

and savanna-like environments (Bond & Keeley 2005), support the view that ant-plant

385   interactions in grassy environments are very likely resilient to fire, as do ants (Parr *et al.*

386   2004) and plants (Figueira *et al.* 2016).

387   To our knowledge, this is the first comprehensive study that shows how climate drives

388   the temporal dynamic of ant-plant interactions and to what extend an unmanaged fire event

389   alters this dynamic. In summary, our results point out that weather conditions, especially

390   temperature, predict the temporal variation of interactions mainly due to changes in resource

391   availability and ant activity. Fire has led to short-term, though negative impacts on

392   interactions and communities structure, which exhibited a good resilience to it. Long-term

393   experimental studies including assisted burnings are needed to forecast fire impacts and how

394   its synergy with weather conditions would affect biodiversity as a whole. However, studies on

395   long-term effects of fire on rupestrian grasslands community's dynamic is challenging (see Le

396   Stradic *et al.* 2016). In this environment, the highly- heterogeneous landscape associated with

397   fire patchiness in space and time clearly difficult to disentangle burning effects from other

398   abiotic drivers as climate. Many studies have shown the role of prescribed fire as a

399   fundamental management component that maintain long-term community structure and

400   biodiversity in Brazilian, African and Australian savannas (e.g., Andersen *et al.* 2014; Levick,

401   Baldeck & Asner 2015; Durigan & Ratter 2016). For rupestrian grasslands, though, additional

402   effort are needed to assess which fire regimes are suitable to maintain biodiversity and

403   ecosystem functioning, as well which management policies prevent fire damaging effects (but

404   see some considerations in Figueira *et al.* 2016).

405

Acknowledgments

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615

Supporting Information

618 Table S1. Description of the seven rupestrian grasslands sites monitored over two years in

619 southern Brazil (nearest d = nearest distance to the next site; # Sampling = number of

620 samplings carried out before fire has started).

Sites	Geographical coordinates	Mean altitude (m)	Nearest d (km)	# Burned plots/total	Fire date	# Sampling
Cedro	S19°13'51.5" W43°34'35.9"	1119	1,44	5/5	October 2014	4
Midway	S19°16'13.4" W43°32'59.7"	1212	2,71	5/5	October 2014	4
Pedra do Elefante	S19°17'33.9" W43°33'29.9"	1232	2,67	5/5	October 2014	4
Paulino	S19°15'30.8" W43°34'51.2"	1108	1,58	5/5	October 2014	4
Q16	S19°17'27.3" W43°35'40.8"	1212	2,48	1/5	October 2014	4
Soizig	S19°16'20.7" W43°34'55.8"	1095	1,58	5/5	September 2014	3
Tinkerbell	S19°13'11.3" W43°35'01.3"	1177	1,44	0/5	October 2014	4

621

622 Table S2. Climatic variables have low and significant correlation.

Person's correlation	Effect size (r)	p-value
Temperature x Humidity	-0,574	< 0,001
Temperature x Rainfall	0,124	0,027
Humidity x Rainfall	0,273	< 0,001

623

Table S3. Suitable minimum models (GLMMs) results showing the effects of climatic
variables on ant-plant interactions. Error distribution fitted for each model is inside
parentheses.

Dependent variable	Coefficients of fixed effects

Interaction diversity (Gaussian)	Parameters	Estimate	Std. Error	t-value	p. z
	Intercept	1,273	0,089	14,280	0,001
	Temperature	0,186	0,041	4,522	< 0,001
	Humidity	0,091	0,041	2,216	0,026
Interaction frequency (Negative binomial)	Parameters	Estimate	Std. Error	z-value	Pr (>|z|)
	Intercept	1,596	0,107	14,85	< 0,001
	Temperature	0,157	0,039	4,009	< 0,001
	Rainfall	0,090	0,035	2,540	0,011

624

625 Table S4. Ant species code and complete scientific name.

Species code	Scientific name
Attlae	*Atta laevigata*
Bracor	*Brachymyrmex* pr. *cordemoyi*
Brapic	*Brachymyrmex pictus*
Brasp1	*Brachymyrmex* sp1
Cambla	*Camponotus blandus*
Camcra	*Camponotus crassus*
Camley	*Camponotus* pr. *leydigi*
Cammel	*Camponotus melanoticus*
Camruf	*Camponotus rufipes*
Camtra	*Camponotus trapeziceps*
Camvit	*Camponotus vitatus*
Camwes	*Camponotus westermanni*
Cepedu	*Cephalotes eduarduli*
Ceppus	*Cephalotes pusillus*
Crecri	*Crematogaster crinosa*
Creere	*Crematogaster* pr. *erecta*
Dorgoe	*Dorymyrmex goeldii*
Dorsp1	*Dorymyrmex* sp1
Dorsp2	*Dorymyrmex* sp2
Ectede	*Ectatomma edentatum*
Ecttub	*Ectatomma tuberculatum*
Labpra	*Labidus praedator*
Linmic	*Linepithema micans*
Linsp1	*Linepihtema* sp1
Linsp2	*Linepithema* sp2
Mycgoe	*Mycocepurus goeldii*
Nessp1	*Nesomyrmex* sp1
Nesspi	*Nesomyrmex spinoidis*
Phefla	*Pheidole (Flavens)* sp1
Pheger	*Pheidole gertrude*
Pheoxy	*Pheidole oxyops*
Phesp1	*Pheidole* sp1
Phesp2	*Pheidole* sp2
Phesp3	*Pheidole* sp3
Phesus	*Pheidole susannae*
Phetri	*Pheidole triconstricta*
Prostr	*Procryptocerus striatus*
Psegra	*Pseudomyrmex gracilis*
Psepal	*Pseudomyrmex pallidus*
Pseter	*Pseudomyrmex termitarius*
Solsp1	*Solenopsis* sp1

Wasaur	*Wasmannia auropunctata*

626

627 Table S5. Suitable minimum models (GLMMs) used to test whether fire affects the temporal

628 dynamic of ant-plant interactions. Error distribution fitted for each model is inside

629 parentheses.

Dependent variable	Coefficients of fixed effects				
Interaction diversity (Gaussian)	Parameters	Estimate	Std. Error	t. value	p. z
	Intercept	1.623	0.258	6.285	< 0.0018
	Fire	-0.081	0.227	-0.357	0.721
	May 2014	-0.265	0.128	-2.069	0.0385
	Jul 2014	-0.666	0.128	-5.190	< 0.001
	Oct 2014	-1.377	0.344	-4.002	< 0.001
	Jan 2015	-0.041	0.259	-0.158	0.874
	May 2015	-0.289	0.259	-1.115	0.265
	Jul 2015	-0.545	0.259	-2.106	0.035
	Oct 2015	-0.467	0.259	-1.803	0.0713
	Feb 2016	-0.135	0.212	-0.637	0.523
	Fire x Oct 2014	1.185	0.348	3.407	< 0.001
	Fire x Jan 2015	0.159	0.293	0.541	0.588
	Fire x May 2015	-0.068	0.293	-0.234	0. 815
	Fire x Jul 2015	0.040	0.293	0.136	0.891
	Fire x Oct 2015	0.045	0.293	0.155	0. 876
Interaction frequency (Negative binomial)	Parameters	Estimate	Std. Error	z-value	Pr(>|z|)
	Intercept	1.962	0.264	7.419	< 0.001
	Fire	-0.051	0.228	-0.224	0.822
	May 2014	-0.358	0.133	-2.684	0.007
	Jul 2014	-0.759	0.143	-5.283	< 0.001
	Oct 2014	-2.209	0.582	-3.792	0.0001
	Jan 2015	-0.100	0.259	-0.388	0.697
	May 2015	-0.290	0.260	-1.114	0.265
	Jul 2015	-0.598	0.265	-2.255	0.0241
	Oct 2015	-0.434	0.262	-1.655	0.098
	Feb 2016	-0.137	0.210	-0.656	0.511
	Fire x Oct 2014	1.917	0.586	3.268	0.001
	Fire x Jan 2015	0.201	0.286	0.702	0.482
	Fire x May 2015	-0.124	0.300	-0.416	0.677
	Fire x Jul 2015	-0.140	0.315	-0.445	0.655
	Fire x Oct 2015	-0.113	0.303	-0.376	0.707

630

631   Table S6. Correlations involving ant recruitment, abundance of plants providing resources,

632   interaction diversity, and interaction frequency.

Spearman's correlation	Effect size (rho)	p-value
Ant recruitment x Plant abundance	0,84	< 0,001
Ant recruitment x Interaction diversity	0,79	< 0,001
Ant recruitment x Interaction frequency	0,85	< 0,001
Plant abundance x Interaction diversity	0,92	< 0,001
Plant abundance x Interaction frequency	0,98	< 0,001

633

634

635 Table S7. Suitable minimum models (GLMMs) showing that climatic conditions (upper part)

636 and fire (lower part) affect the dynamic of plants providing resources for ants. Inside

637 parentheses are error distributions fitted for each model.

638

Explanatory variable	Parameters	Estimate	Std. Error	z-value	Pr(>|z|)
Plant abundance	Intercept	1,626	0,098	16,578	< 0,001
(Poisson)	Temperature	0,200	0,030	6,589	< 0,001
	Humidity	0,058	0,028	2,010	0,044
	Rainfall	0,064	0,024	2,623	0,008
Plant abundance	Intercept	1,911	0,186	10,259	< 0,001
(Poisson)	Fire	-0,013	0,152	-0,088	0,930
	May 2014	-0,329	0,093	3,518	< 0,001
	Jul 2014	-0,711	0,105	-6,748	< 0,001
	Oct 2014	-1,701	0,438	-3,878	< 0,001
	Jan 2015	-0,042	0,171	-0,249	0,803
	May 2015	-0,197	0,174	-1,131	0,258
	Jul 2015	-0,484	0,180	-2,688	0,007
	Oct 2015	-0,277	0,175	-1,576	0,115
	Feb 2016	-0,042	0,136	-0,315	0,752
	Fire x Oct 2014	1,419	0,441	3,215	0,001
	Fire x Jan 2015	0,150	0,184	0,816	0,414
	Fire x May 2015	-0,150	0,202	-0,742	0,458
	Fire x Jul 2015	-0,202	0,22359	-0,907	0,364
	Fire x Oct 2015	-0,122	0,206	-0,595	0,551

639

640 Table S8. Suitable minimum models (GLMMs) showing that ant recruitment is the main

641 biological mechanism that mediates climatic influence on interaction frequency and diversity.

642 When we include ant recruitment in the climatic models (i.e. $= y \sim$ temperature + humidity +

643 rainfall + ant recruitment) it takes most of explanation that previously were partitioned

644 amongst climatic variables (see result without ant recruitment on Table S3). Inside

645 parentheses is the error distribution fitted for each model.

646

Explanatory variable	Parameters	Estimate	Std, Error	z-value	Pr(>|z|)
Interaction frequency	Intercept	1,121	0,077	14,512	< 0,001
(Negative binomial)	Recruitment	0,036	0,002	12,695	< 0,001
	Temperature	0,084	0,032	2,595	0,009
Interaction diversity	Intercept	-0,144	0,075	-1,925	0,054
(Gaussian)	Recruitment	0,026	0,003	8,124	< 0,001

Considerações finais e perspectivas

Concluímos que os padrões estruturais das interações formiga-planta são, de certa forma, dependentes da escala de investigação, uma vez que diferentes estruturas emergem quando um ou vários tipos de interações são considerados, Diferentes recursos alimentares promoveram dissimilares níveis de especialização e sobreposição de nicho, que provavelmente são consequências das diferenças biológicas existentes nas estratégias de forrageamento das espécies de formigas envolvidas, Apesar dessas discrepâncias, todas as interações foram conectadas por um núcleo comum formado por poucas espécies de formigas generalista, A atuação dessas formigas centrais como "mutualistas-chave", ou seja, realizando funções ecossistêmicas, como polinização, dispersão de sementes e mutualismos de proteção, é uma questão aberta que necessita de maiores investigações,

Também encontramos que as condições climáticas nos campos rupestres, especialmente a temperatura, influenciam positivamente a diversidade e frequência de interações formiga-planta, A dinâmica sazonal dessas interações é mediada pela disponibilidade de recursos vegetais e atividade de forrageamento das formigas que, da mesma forma, são dependentes pela sazonalidade climática, O fogo não manejado afetou essa dinâmica temporal de forma negativa, mas seus efeitos foram temporários indicando que as interações formiga-planta são resilientes ao fogo, Sugerimos que outros aspectos da interação clima *vs,* fogo tais como, frequência e intensidade dos incêndios (por exemplo, época da queimada), precisam ser mais explorados, a fim de se determinar os efeitos em longo prazo desses filtros ambientais na manutenção da biodiversidade dos campos rupestres,

Portanto, essa tese traz duas principais contribuições: (1) amplia o conhecimento sobre a diversidade de interações formiga-planta nos campos rupestres e aponta os mecanismos

biológicos envolvidos na estruturação de interações mediadas por distintos recursos alimentares; e (2) mostra que a dinâmica temporal dessas interações é dependente da sazonalidade climática e que essas interações são resilientes ao efeito do fogo não manejado,

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Ant fauna in megadiverse mountains: a checklist for the rocky grasslands

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Abstract

The rocky grasslands, environments locally known as *campo rupestre*, occur mainly along the Espinhaço Mountains and are considered local centers of biodiversity and endemism in Brazil. However, knowledge of ant species richness (Hymenoptera: Formicidae) in this kind of environment is still poor. Aiming at filling this gap, we compiled information from empirical studies and literature records. We found a total of 288 species of 53 genera and eight subfamilies recorded in rocky grasslands. Myrmicinae and Formicinae were the most representative subfamilies, with 53% and 18% of the total species richness, respectively. The genera with the largest number of species were *Pheidole* (41) and *Camponotus* (40). This large number of ant species recorded for the rocky grasslands surpasses those found in other studies conducted in several different places. Ant species richness decreased with altitude; most species occur below 800 m a.s.l. (171), and only a few species occur above 1600 m a.s.l. (17). Some genera occur only at a specific altitude (e.g., *Azteca* and *Dolichoderus* at 800/900 m a.s.l.; *Leptogenys* and *Labidus* at 1400 m a.s.l.), which points out to the potential use of ants as biological indicators. Our results suggest that the rocky grasslands favor high ant diversity. The patterns of ant richness associated with the altitudinal gradient reinforce the idea of considering the rocky grasslands as priority areas for biological conservation. Moreover, we observed a lack of records on the occurrence of most ant species considered in the present study (93%), which shows that Brazilian myrmecologists need to invest more in taxonomy, management, and data sharing.

Introduction

The rocky grasslands, locally known as *campo rupestre*, are an ecosystem characterized by a montane, fire-prone vegetation mosaic, with rocky outcrops on quartzite, sandstone, or ironstone soils. They are inserted in a matrix of sandy and stony grasslands, and other vegetation types, such as Cerrado (Brazilian savanna), Atlantic Forest, and Caatinga (Giulietti & Pirani, 1997; Alves et al., 2014; Fernandes et al., 2014). Rocky grasslands occur mainly along the Espinhaço Mountains, a vast mountain range that has its southern limit in the state of Minas Gerais, southeastern Brazil, encompass important smaller ranges, such as Serra do Caraça and Serra do Cipó, and ends in Chapada Diamantina, state of Bahia, northeastern Brazil (Giulietti & Pirani, 1997). Rocky grasslands are also found in the mountains of central (e.g., Serra da Canastra) and southeastern Brazil (e.g., Serra da Mantiqueira), whose geology and flora resemble those of the Espinhaço Mountains (Giulietti & Pirani, 1997; Rapini et al., 2008; Vasconcelos,

2011). This complex geographic mosaic associated with a long evolutionary time turned this environment into a local biodiversity center, with high endemism (approximately one-third of its plant species are endemic) and several endangered species (Giulietti & Pirani 1997; Rapini et al., 2008).

Tropical grasslands have been under severe threat and are consistently overlooked by conservation policies (Parr et al., 2014). These ecosystems are subjected to several human pressures, such as mining, livestock raising, agriculture, road construction, tourism, and frequent fires (Barbosa et al., 2010; Fernandes et al., 2014). In addition to their large number of endangered species and human threats, montane ecosystems are also subjected to global changes (IPCC, 2013). Climatic models predict a catastrophic future in which, by the end of this century, the rocky grasslands may lose up to 95% of their current area (Fernandes et al., 2014). In this scenario, the development of effective conservation strategies is crucial. Fauna and flora inventories are of fundamental importance, as describing the biodiversity of rocky grasslands is the first step towards their conservation (Pearson, 1994).

Despite the information on the flora and fauna of rocky grasslands (Giulietti et al., 1987; Lessa et al., 2008; Rapini et al., 2008; Rodrigues et al., 2011), sampling in those environments has been heterogeneous and large areas remain unexplored (Madeira et al., 2008). In addition, most of the literature on the biodiversity of rocky grasslands focus on plants and vertebrates (Silveira et al., unpublished data). Therefore other groups, such as invertebrates, remain unknown. Some of the challenges to invertebrate conservation are a scarce and underfunded basic research, and the overlooking of invertebrates in most conservation policies (Cardoso et al., 2011).

Conversely, invertebrates dominate most terrestrial environments and deliver several ecosystem services (Cardoso et al., 2011). Among invertebrates, ants (Hymenoptera: Formicidae) represent one of the most important and abundant terrestrial groups (Hölldobler & Wilson, 1990). Well known for their functional roles, ants have been used as bioindicators due to their sensitivity to environmental and climate changes (Lach et al., 2010). Previous studies reported changes in ant diversity along altitudinal gradients (Fisher, 1996; Bharti & Sharma, 2013; Bishop et al., 2014). Altitudinal gradients are excellent to model species distribution, due to differences in abiotic conditions. However, as most literature records came from temperate mountains, the lack of information on tropical mountains makes it difficult to elaborate conservation plans.

What we know about ants from rocky grasslands comes from case studies on ant species associated with a particular plant or area (e.g., Guerra et al., 2011; Viana-Silva & Jacobi, 2012; Fagundes et al., 2013). However, a complete record that comprises the whole diversity and distribution of ants is still missing. In order

to fill this gap of knowledge and support invertebrate conservation in the rocky grasslands, we need a more thorough biodiversity survey. In the present study, we compiled a checklist of ant species and their occurrence from original data and published information.

Material and Methods

Data sampling and database

We searched for studies carried out in areas of rocky grasslands that informed the geographic coordinates of their sampling sites and identified ants to the species. We compiled records from a total of eight datasets, most of which original and collected in Serra do Cipó (Lana, 2015). Seven other datasets were found through an online survey in the Web of Knowledge, other academic search engines such as Google Scholar, and Brazilian academic libraries. Among those sources is one unpublished dataset from Serra do Cipó (hereafter "Cipó") (Soares, 2003) and six published datasets from Cipó (n = 1), Serra do Rola Moça State Park (hereafter "Rola Moça") (n = 1), Itacolomi State Park (hereafter "Itacolomi") (n = 3), and Ibitipoca State Park (hereafter "Ibitipoca") (n = 1). All studied sites are located in the Espinhaço Mountains, except for Ibitipoca.

As we aimed at providing a broad inventory of the ant fauna, we used studies carried out with different sampling efforts and methods. Table 1 describes the samples collected from the literature, including information on sampling method, environment, and location. Details on species identification are given for each study.

Table 1. Sites where ants were sampled in the Brazilian rocky grasslands.

Sampling sites	Reference	Sampling method	Environment	Altitudinal Range (m)	Geographic coordinates provided in the study
Serra do Cipó region	Lana, 2015[1]	pitfalls, Winkler, beating and sweep net	cerrado ecotones, rocky grasslands	800 – 1400	19°21'36.2'' S, 43°36'25.2'' W 19°16'17.8'' S, 43°36'18.1'' W 19°15'50.6'' S, 43°35'10.3'' W 19°13'56.5'' S, 43°34'34.8'' W 19°17'43.0'' S, 43°33'17.4'' W 19°17'49.6'' S, 43°35'28.2'' W 19°16'59.3'' S, 43°32'08.9'' W
Itacolomi State Park region	Almeida et al., 2014*[2]	active capture	Rocky grasslands, *canga* outcrops	1200 – 1500	20°22'30'' S, 43°32'30'' W 20°27'55.4'' S, 43°35'59'' W 20°21'47'' S, 43°30'10'' W 20°22'27'' S, 43°32'22'' W
Itacolomi State Park	Fagundes et al., 2013*[3]	observations and active capture	Rocky grasslands	1400	20°26'26'' S, 43°30'52'' W
Serra do Rola Moça State Park	Viana-Silva & Jacobi, 2012*[4]	ground baits	*canga* outcrops	1400 – 1500	20°03'35.19' S, 44°00'41.9'' W 20°03'33.57''S, 44°01'52.01'' W
Itacolomi State Park	Rosumek, 2009*[5]	baits, observations and active capture	*canga* outcrops	1320 - 1400	20°26'18'' S, 43°30'35'' W
Serra do Cipó region	Soares, 2003*[6]	baited pitfalls	Rocky grasslands, Cerrado ecotone	800 - 1600	19°10'00'' to 19°40'00'' S, 43°30'00'' to 43° 55'00'' W
Serra do Cipó region	Araújo & Fernandes, 2003*[7]	baits and active capture	Rocky grasslands, Cerrado ecotone	800 – 1400	19°10'00'' to 19°40'00'' S, 43°30'00'' to 43°55'00'' W
Ibitipoca State Park	Sales et al., 2014*[8]	active capture	Rocky grasslands	1400	21°42'00'' S, 43°53'00'' W

*Studies found through an online survey; Superscript numbers provide reference for sources in the full list of species (Table 2).

In the original dataset (Lana, 2015) ants were sampled in seven sites during the Long Term Ecological Research of the Rocky Grasslands of Serra do Cipó (PELD-CRSC, in the Portuguese acronym). Those seven sites were chosen along an altitudinal gradient in Cipó, from 800 to 1,400 m a.s.l. In each site, three transects of 200 m were set up and five sampling points were established at 50 m from each other. In 2011 and 2012, ants were sampled quarterly, mainly with pitfalls traps, but also with beating, sweep nets, and Winkler traps. Ants were identified using a taxonomic key (Fernández, 2003), by comparison with specimens deposited in the Laboratório de Mirmecologia do Centro de Pesquisas do Cacau (CEPEC/CEPLAC), and by consulting specialists (Jacques H. C. Delabie). Nomenclature followed Bolton et al. (2005), with posterior improvements made available on the Online Catalog of the Ants of the World (AntCat).

We built a complete species checklist (Appendix) with information on several ant species organized by study, sampling locality, and altitude. As it was not possible to match the morphospecies hosted in different institutions and collections, we included in the analysis only one record for each morphospecies, regardless of its potential presence in more than one study, area, or altitude. Each morphospecies (e.g., *Pheidole* sp.1) probably represents more than one species, as the same nomenclature was established by different authors. However, excluding those records or trying to tell them apart could interfere with the estimation of the real diversity. Although we are aware of this taxonomic limitation, in face of the difficulty of assigning names to several Neotropical ant species (e.g., *Camponotus* and *Pheidole*) and the lack of current taxonomic revisions for many species-rich genera (e.g., *Brachymyrmex*, *Cyphomyrmex*, and *Solenopsis*) (Lach et al., 2010), this is the most parsimonious option for a study that aimed at estimating ant species diversity on a broad scale.

Study sites

The Espinhaço Mountains are 50-100 km wide and 1,200 km long, and encompass several mountains (up to approximately 2,000 m a.s.l.) (Giulietti & Pirani, 1997). Rocky grasslands occur mostly from 900 to 2,033 m a.s.l. In the basal part of the range, at altitudes between 800-1,000 m a.s.l., we found ecotones between savanna and rocky grassland. Trees and shrubs are the most common life forms at lower altitudes, but their predominance decreases with altitude, as the soil profile also changes, and they gradually give way to outcrops and grasslands (Giulietti & Pirani, 1997; Alves et al., 2014). Similarly, together with the altitudinal gradient there is also a climate gradient, in which the mountaintop is colder and moister than the base (Giulietti & Pirani, 1988).

Serra do Cipó is located in the southeastern part of the Espinhaço Mountains, state of Minas Gerais, southeastern Brazil (Fig 1). This region has a diversified mosaic of vegetations, which varies with soil type and altitude (from 800 to 1.600 m a.s.l.). This environment is covered by a low vegetation composed of shrubs and small trees and abundant grasses and sedges. There are also several watercourses, along which gallery evergreen forests grow (Giulietti et al., 1987).

Itacolomi State Park and Serra do Rola Moça State Park are characterized by rocky grasslands that grow on ironstone, locally known as *canga*. Both areas are located in the Iron Quadrangle of Minas Gerais, a 7,200 km² region in the southern part of the Espinhaço Mountains (Fig 1). The Iron Quadrangle is geologically dominated by ironstone and represents one of the world's main mineral provinces (Jacobi et al., 2011). Itacolomi comprises an altitudinal range varying from 700 to 1,772 m a.s.l. and a mosaic of rocky grasslands, *canga*, semi-deciduous montane forest, and associated vegetation types (Gastauer et al., 2012). Rola

Legend
★ Sampling sites
▨ Campos Rupestres
▢ States limits

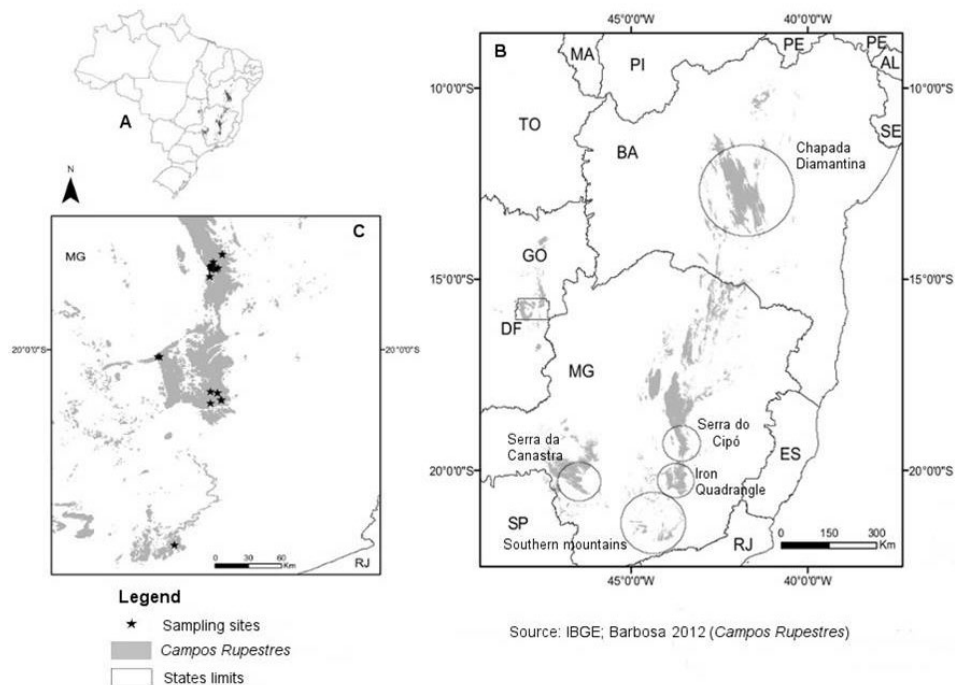Source: IBGE; Barbosa 2012 (*Campos Rupestres*)

Fig 1. The location of rocky grasslands in Brazil (A). Rocky grasslands along the Espinhaço Mountains and other Brazilian mountain ranges (circumscribed) (B). Sampling sites in the southern part of the Espinhaço Mountains and the southern mountains of Minas Gerais (C).

Moça is located in an ecotone between the Cerrado and Atlantic Forest biomes, which comprises several vegetation types, such as Cerrado, semi-deciduous forest, riparian forest, and prominent rocky grasslands developing on *canga* on the mountaintops (1,200 –1,500 m a.s.l.) (Jacobi et al., 2008).

Ibitipoca State Park is a protected area located in Serra da Mantiqueira, southern Minas Gerais (Fig 1). This site is characterized by a vegetation type composed of grasses, herbs, and shrubs on outcrops of quartzite rocks associated with shallow soils and high sun incidence (Dias et al., 2002).

Results and Discussion

We recorded 288 ant species of 53 genera and eight subfamilies (Appendix). Myrmicinae was the most speciose subfamily, with 53% of the recorded species, followed by Formicinae (18%), Dolichoderinae (11%), Ponerinae (6%), and Ectatomminae (5%). The richest genus was *Pheidole* (41 species), followed by *Camponotus* (40), *Crematogaster* (22), *Dorymyrmex* (14), and *Solenopsis* (13). The largest number of ant species was found in Cipó (n = 265), followed by Itacolomi (48), Ibitipoca (20), and Rola Moça (14). Similarly, Cipó was the locality with the largest proportion of exclusive species (83%), which indicates that this site was the best sampled and the faunas of other sites are nested within it. The proportion of exclusive ant species in each site and ant species shared between at least two sites is shown in Fig 2.

Among the identified species, only *Camponotus crassus* (Mayr 1862) occurred in all sites. Only morphospecies of *Pheidole* exhibited similar distribution. Thus, *Camponotus* and *Pheidole* emerged as the most widespread genera currently recorded for rocky grasslands. The dominance of those genera is consistent with the patterns suggested for other Neotropical ants (Fernández & Sendoya, 2004) and similar ecosystems, such as open Cerrado (Ribas et al., 2003; Campos et al., 2011; Pacheco & Vasconcelos, 2012). Likewise, Myrmicinae and Formicinae were also the most prominent subfamilies in ant inventories conducted in different environments, such as Cerrado

(Ribas et al., 2003; Campos et al., 2011), Amazon (Miranda et al., 2012), and Caatinga (Ulysséa & Brandão, 2013).

The large number of ant species recorded for rocky grasslands (288) deserves attention, as other studies carried out in wider geographical ranges found a smaller or similar number. For example, checklists made for the Caatinga (Ulysséa & Brandão, 2013) and Amazon (Miranda et al., 2012) found 173 and 276 species, respectively. Although we did not find a comprehensive inventory for the Cerrado that could be used for comparison, studies carried out over large areas revealed about 150 species (Ribas et al., 2003; Campos et al., 2011; Pacheco & Vasconcelos, 2012). Actually, it is hard to compare number of species among studies or environments, as different studies used different sampling efforts and methods.

Nevertheless, by analyzing the map in Fig 1, we infer that the rocky grasslands have several sampling gaps (e.g., Chapada Diamantina, Serra da Canastra, northern and southern Minas Gerais). Considering this gap of knowledge, high endemism, and complex environmental mosaic found on those mountains, we expect ant diversity in the rocky grasslands to be even higher than observed in the present study (288). Moreover, the large number of unidentified species together with the inclusion of only one record per morphospecies point out to an underestimation of the number of ant species in the rocky grasslands.

We observed a decrease in ant richness along the altitudinal range (Appendix). The lowest altitudes, 800 and 900 m a.s.l., contributed with 171 and 127 ant species, respectively, whereas the highest altitude (1,600 m a.s.l.) had a smaller number of species (17). Only *Solenopis* occurred at all altitudes. Those findings corroborate the general diversity pattern of ants that live on mountains, in which the number of species decreases with altitude (Fisher, 1996; Brühl et al., 1999; Longino & Colwell, 2011; Bharti & Sharma, 2013). Nonetheless, very few studies have documented the altitudinal trends of ant biodiversity in Brazilian montane ecosystems (but see Araújo & Fernandes, 2003).

At 800 m a.s.l., there were 18 exclusive species, whereas at 1,400, 1,500, and 1,600 m a.s.l. there were 21, five, and two, respectively. We found some genera of dominant arboreal ants (*Azteca* and *Dolichoderus*) restricted to the mountain base (800/900 m a.s.l.), which indicates that altitude may restrict ant occurrences. Similarly, at 1,400 m a.s.l., we recorded some unique genera, such as specialized predators (*Leptogenys*) and legionary ants (*Labidus*) (Brandão et al., 2012). Those findings corroborate the potential of ants as bioindicators, especially of climate change. Similar patterns of restriction of functional groups to particular altitudes have already been observed for tropical (Brühl et al., 1999) and temperate regions (Bharti & Sharma, 2013). However, those findings may have been biased by the sampling effort used in each site. Ant responses to altitude, associated with the high richness found in a small geographic area, point to the importance of conserving the rocky grasslands. This conclusion is consistent with the strategies recommended for ant conservation, which state that efforts should be targeted to high biodiversity, high endemism, and extremely threatened areas (Alonso, 2010).
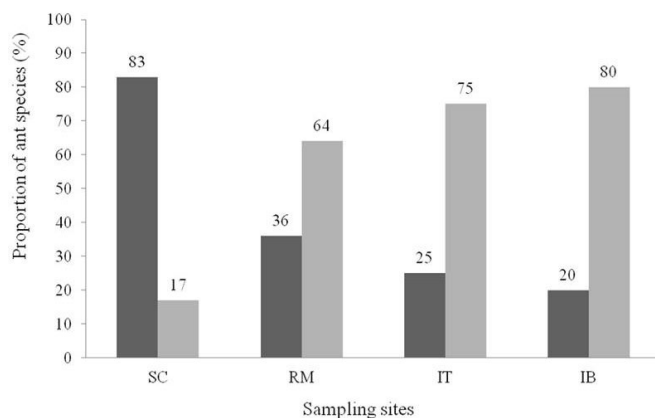

Fig 2. Proportion of ant species exclusive to each site and shared between at least two sites. Sampling site abbreviations: Serra do Cipó (SC), Itacolomi State Park (IT), Ibitipoca State Park (IB), and Serra do Rola Moça State Park (RM). Dark bars represent exclusive proportion and light bars correspond to the shared proportion of species.

We also bring to light the need for investing in ant taxonomy, database management, and data sharing, which are essential tools for biodiversity conservation, though they are neglected in most Brazilian research institutions. Those gaps of knowledge became clear when we searched for information on ant species occurrence and distribution (only those with complete taxonomic identification) in online databases (Antwiki, AntWeb, CRIA speciesLink) and specialized catalogues (Kempf, 1972; Brandão, 1991). We noticed that most ant records (94%) neither were followed by a formal record for the rocky grasslands nor were hosted in databases (Appendix, symbol*). Approximately 5% of the records contained no information on geographic distribution and only 1% accounted this kind of information for the rocky grasslands. Therefore, myrmecology in Brazil needs to invest strongly in taxonomy and species inventories. Despite some recent advances, rocky grasslands still have many sampling gaps for ants, and, therefore, they need more efforts in conservation.

Acknowledgments

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Appendix. Occurrence and distribution of ant species along the altitudinal gradient, localities, and studies carried out in the Brazilian rocky grasslands. Sampling sites: Serra do Cipó (SC), Itacolomi State Park (IT), Ibitipoca State Park (IB), and Serra do Rola Moça State Park (RM). Numbers in columns indicate the literature sources described in Table 1.

TÁXON	800 SC 1	800 SC 6	800 SC 7	900 SC 1	900 SC 6	900 SC 7	1000 SC 1	1000 SC 7	1000 SC 7	1100 SC 1	1100 SC 6	1100 SC 7	1100 IT 2	1200 SC 1	1200 SC 7	1200 SC 8	1200 IT 2	1300 SC 1	1300 SC 6	1300 SC 7	1300 IB 8	1300 IT 3	1300 IT 5	1400 SC 1	1400 SC 6	1400 SC 7	1400 RM 4	1500 IT 2	1500 SC 6	1500 SC 7	1600 SC 6
Formicidae																															
Amblyoponinae																															
Prionopelta sp														x				x													
Dolichoderinae																															
Azteca sp		x	x			x																									
*Dolichoderus diversus (Emery, 1894)**	x																														
*Dolichoderus lutosus (Smith, 1858)**	x																														
*Dorymyrmex brunneus (Forel, 1908)**	x				x		x			x															x						
*Dorymyrmex goeldii (Forel, 1904)**	x				x		x			x				x				x							x						
*Dorymyrmex iheringi (Forel, 1912)**								x																							
*Dorymyrmex pyramicus (Roger, 1863)**	x				x		x			x				x				x													
Dorymyrmex sp										x																					
Dorymyrmex sp1								x			x				x					x											
Dorymyrmex sp2					x			x			x				x																
Dorymyrmex sp3					x		x								x					x											
Dorymyrmex sp4	x				x																										
Dorymyrmex sp5	x																														
Dorymyrmex sp6						x																									
Dorymyrmex sp7												x																			
Dorymyrmex sp8																x															
Dorymyrmex sp9																													x		
*Forelius brasiliensis (Forel, 1908)**	x																														
*Forelius maranhaoensis (Cuezzo, 2000)**	x						x			x								x													
Forelius sp	x				x										x																
*Linepithema cerradense (Wild, 2007)**																					x										
*Linepithema humile (Mayr, 1868)**	x									x				x				x							x	x					
Linepithema micans (Forel, 1908)†																										x					
Linepithema prox. humile sp																x															

*Species with no occurrence in the sampling area; † Species with no information on distribution; ‡ Species with occurrence recorded for the sampling site.

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TÁXON	\<ALTITUDES (m)\> 800	800	900	900	900	1000	1000	1000	1100	1100	1100	1100	1200	1200	1200	1200	1300	1300	1300	1300	1300	1300	1400	1400	1400	1400	1400	1500	1500	1500	1600
	SC	SC	SC	SC	SC	SC	SC	SC	SC	SC	SC	SC	IT	SC	SC	SC	IT	SC	SC	SC	IB	IT	IT	SC	SC	SC	RM	IT	SC	SC	SC
	1	6	7	1	6	7	1	7	7	1	6	7	2	1	7	8	2	1	6	7	8	3	5	1	6	7	4	2	6	7	6
Dolichoderinae (Continuation)																															
Linepithema sp1	x	x	x	x	x	x	x	x		x		x		x	x			x		x				x		x					
Linepithema sp2	x		x	x		x	x			x	x			x				x	x					x							
Linepithema sp3	x		x	x		x	x	x		x	x	x		x		x		x	x	x						x				x	
Linepithema sp4	x	x		x										x	x			x		x											
Linepithema sp5	x	x		x										x				x													
Linepithema sp6														x	x			x						x	x				x		x
Tapinoma sp1	x	x	x	x			x			x	x			x	x			x									x				
Tapinoma sp2	x	x	x	x			x				x					x															
Dorylinae																															
Labidus coecus (Latreille, 1802)*										x																					
Labidus praedator (Smith, 1858)*																							x								
Leptogenys prox. *linda* sp																								x							
Neivamyrmex diana (Forel, 1912)*																										x					
Neivamyrmex pseudops (Forel, 1909)*								x																							
Neivamyrmex sp1	x		x															x													
Neivamyrmex sp2			x				x							x						x											
Ectatomminae																															
Ectatomma brunneum (Smith, 1858)*	x	x		x																											
Ectatomma edentatum (Roger, 1863)*	x	x	x	x		x	x			x	x			x	x			x		x	x										
Ectatomma muticum (Mayr, 1870)*								x				x																			
Ectatomma opaciventre (Roger, 1861)*	x	x		x			x																								
Ectatomma permagnum (Forel, 1908)*	x			x														x													
Ectatomma planidens (Borgmeier, 1939)*	x			x			x	x																							
Ectatomma sp1		x	x					x				x									x										
Ectatomma sp2		x	x			x					x					x															
Ectatomma suzanae (Almeida, 1986)‡	x																	x													
Ectatomma tuberculatum (Olivier, 1792)*	x	x	x																												

*Species with no occurrence in the sampling area; ‡ Species with no information on distribution; †Species with occurrence recorded for the sampling site.

Appendix. Occurrence and distribution of ant species along the altitudinal gradient, localities, and studies carried out in the Brazilian rocky grasslands. Sampling sites: Serra do Cipó (SC), Itacolomi State Park (IT), Ibitipoca State Park (IB), and Serra do Rola Moça State Park (RM). Numbers in columns indicate the literature sources described in Table 1 (Continuation).

ALTITUDES (m)

TÁXON	800		900			1000		1100				1200				1300							1400				1500			1600
(locality)	SC	SC	SC	SC	SC	SC	SC	SC	SC	SC	IT	SC	SC	SC	IT	SC	SC	SC	IT	IB	IT	IT	SC	SC	SC	RM	IT	SC	SC	SC
(source)	1	6	1	6	7	7	7	1	6	7	2	1	7	8	2	1	6	7	2	8	3	5	1	6	7	4	2	6	7	6
Ectatomminae (Continuation)																														
Gnamptogenys sp1								x																						
Gnamptogenys striatula (Mayr, 1884)*								x																						
Gnamptogenys sulcata (Smith, 1858)*					x					x						x														
Formicinae																														
Brachymyrmex patagonicus (Mayr, 1868)*			x			x						x				x							x			x				
Brachymyrmex sp		x			x					x				x				x												
Brachymyrmex sp1	x	x	x	x		x	x	x	x			x	x			x	x	x					x					x		
Brachymyrmex sp2	x			x		x						x						x										x		x
Brachymyrmex sp3		x		x						x																				
Camponotus (Hypercolobopsis) sp1	x		x							x		x				x														
Camponotus (Hypercolobopsis) sp2	x																													
Camponotus (Hypercolobopsis) sp3								x								x														
Camponotus (Myrmaphaenus) sp1	x	x	x	x		x		x	x					x																
Camponotus (Myrmaphaenus) sp2	x	x	x	x		x		x	x			x		x									x					x		
Camponotus (Myrmaphaenus) sp3	x	x	x	x		x		x	x			x																		
Camponotus (Myrmaphaenus) sp4		x		x		x				x		x													x					
Camponotus (Myrmaphaenus) sp5						x				x				x																
Camponotus (Myrmaphaenus) sp6	x		x			x				x																				
Camponotus (Myrmaphaenus) sp7	x									x																				
Camponotus (Myrmaphaenus) sp8	x																													
Camponotus (Myrmaphaenus) sp9	x																													
Camponotus (Myrmaphaenus) sp10						x		x																						
Camponotus (Myrmaphaenus) sp11				x														x							x				x	
Camponotus (Tanaemyrmex) sp1	x	x	x					x																						
Camponotus (Tanaemyrmex) sp2	x	x	x	x		x	x			x		x	x																	
Camponotus (Tanaemyrmex) sp3	x	x	x	x		x		x	x			x	x																	x
Camponotus (Tanaemyrmex) sp4	x	x		x		x				x			x	x		x		x							x				x	

Appendix. Occurrence and distribution of ant species along the altitudinal gradient, localities, and studies carried out in the Brazilian rocky grasslands. Sampling sites: Serra do Cipó (SC), Itacolomi State Park (IT), Ibitipoca State Park (IB), and Serra do Rola Moça State Park (RM). Numbers in columns indicate the literature sources described in Table 1 (Continuation).

ALTITUDES (m)

TÁXON	800 SC 1	800 SC 6	800 SC 7	900 SC 1	900 SC 6	900 SC 6	1000 SC 1	1000 SC 7	1000 SC 7	1100 SC 1	1100 SC 6	1100 SC 6	1100 SC 7	1100 IT 2	1200 SC 1	1200 SC 7	1200 SC 8	1200 IT 2	1300 SC 1	1300 SC 6	1300 SC 6	1300 SC 7	1300 IT 2	1300 IB 8	1300 IT 3	1300 IT 5	1300 SC 1	1300 SC 6	1300 SC 7	1400 SC 1	1400 SC 6	1400 SC 7	1400 SC 6	1400 SC 7	1400 RM 4	1500 IT 2	1500 SC 6	1500 SC 7	1600 SC 6
Formicinae (Continuation)																																							
Camponotus (Tanaemyrmex) sp5																				X																			
Camponotus atriceps (Smith, 1858)*	X																																						
Camponotus blandus (Smith, 1858)*	X			X			X								X				X												X								
Camponotus cingulatus (Mayr, 1862)*	X																																						
Camponotus crassus (Mayr, 1862)*	X	X		X	X		X	X		X		X	X		X	X			X	X		X					X	X			X		X	X	X		X		
Camponotus fastigatus (Roger, 1863)*	X									X											X																		
Camponotus genatus (Santschi, 1922)*																					X													X					
Camponotus leydigi (Forel, 1886)*	X			X	X	X																																	
Camponotus melanoticus (Emery, 1894)*	X			X			X			X					X				X										X				X				X		
Camponotus novogranadensis (Mayr, 1870)*	X			X			X			X					X				X						X				X				X				X		
Camponotus punctulatus (Mayr, 1867)*		X							X			X																					X						
Camponotus renggeri (Emery, 1894)*	X			X	X		X	X		X		X			X	X			X			X		X					X				X				X		
Camponotus rufipes (Fabricius, 1775)*	X	X		X	X		X	X		X		X	X		X	X			X		X	X			X	X	X	X	X		X		X	X	X		X		
Camponotus senex (Smith, 1858)*	X			X			X			X		X			X				X			X			X	X	X	X	X		X		X						
Camponotus sericeiventris (Guérin-Méneville, 1838)*			X				X																																
Camponotus sp1										X									X														X						
Camponotus sp2															X										X	X							X						
Camponotus sp3	X			X					X	X									X						X	X			X				X	X					
Camponotus sp4	X																								X	X			X				X	X					
Camponotus sp5	X			X								X					X		X			X				X			X				X	X					
Camponotus sp6																													X										
Camponotus vittatus (Forel, 1904)‡	X									X					X				X														X						
Myrmelachista nodigera (Mayr, 1887)*														X				X					X													X			
Myrmelachista sp														X									X													X			
Myrmelachista sp1	X									X									X					X						X									
Myrmelachista sp2										X														X														X	X
Myrmelachista sp3										X									X														X						
Nylanderia sp	X																																						
Paratrechina sp									X		X																												

*Species with no occurrence in the sampling area; ‡ Species with no information on distribution; †Species with occurrence recorded for the sampling site.

Appendix. Occurrence and distribution of ant species along the altitudinal gradient, localities, and studies carried out in the Brazilian rocky grasslands. Sampling sites: Serra do Cipó (SC), Itacolomi State Park (IT), Ibitipoca State Park (IB), and Serra do Rola Moça State Park (RM). Numbers in columns indicate the literature sources described in Table 1 (Continuation).

TÁXON	800 SC 1	800 SC 6	900 SC 1	900 SC 6	1000 SC 1	1000 SC 7	1100 SC 1	1100 SC 6	1100 SC 7	1200 IT 2	1200 SC 1	1200 SC 7	1200 SC 8	1300 IT 2	1300 SC 1	1300 SC 6	1300 SC 7	1400 IB 8	1400 IT 3	1400 IT 5	1400 SC 1	1400 SC 6	1400 SC 7	1400 RM 4	1500 IT 2	1500 SC 6	1500 SC 7	1600 SC 6
Myrmicinae																												
Acromyrmex balzani (Emery, 1890)*	x	x	x		x						x				x											x		
Acromyrmex crassispinus (Forel, 1909)*	x		x																									
Acromyrmex fracticornis (Forel, 1909)*	x		x																									
Acromyrmex sp1	x	x		x											x							x				x		
Acromyrmex sp2	x	x	x			x		x				x									x							
Acromyrmex sp3	x	x	x	x													x						x				x	
Acromyrmex sp4																x						x						
Acromyrmex subterraneus subterraneus (Forel, 1893)*	x		x		x						x				x													
Apterostigma (gr.Pillosum) sp1	x								x							x												
Apterostigma sp1		x		x																								
Apterostigma sp2				x																								
Atta sexdens (Linnaeus, 1758)*	x							x			x					x												
Atta sexdens rubropilosa (Forel, 1908)*	x			x																								
Octostruma iheringi (Emery, 1888)‡	x																											
Carebara sp	x	x	x		x																							
Cephalotes atratus (Linnaeus, 1758)*	x	x																						x				
Cephalotes maculatus (Smith, 1876)*	x	x																										
Cephalotes minutus (Fabricius, 1804)*	x											x			x			x										
Cephalotes pavonii (Latreille, 1809)*	x																											
Cephalotes prox. pallidoides sp	x	x	x		x		x	x	x		x		x		x		x					x						
Cephalotes pusillus (Klug, 1824)*	x	x																		x								
Cephalotes sp1	x		x		x															x								
Cephalotes sp2				x																								
Cephalotes sp3	x				x						x				x													
Crematogaster acuta (Fabricius, 1804)*	x		x		x				x			x				x												
Crematogaster arcuata (Forel, 1899)*																					x							
Crematogaster brasiliensis (Mayr, 1878)*										x															x			

*Species with no occurrence in the sampling area; ‡ Species with no occurrence in the sampling site; †Species with no information on distribution; ‡ Species with occurrence recorded for the sampling site.

Appendix. Occurrence and distribution of ant species along the altitudinal gradient, localities, and studies carried out in the Brazilian rocky grasslands. Sampling sites: Serra do Cipó (SC), Itacolomi State Park (IT), Ibitipoca State Park (IB), and Serra do Rola Moça State Park (RM). Numbers in columns indicate the literature sources described in Table 1 (Continuation).

TÁXON	800 SC 1	800 SC 6	800 SC 7	900 SC 1	900 SC 6	900 SC 7	1000 SC 1	1000 SC 7	1000 SC 7	1100 SC 1	1100 SC 6	1100 SC 7	1200 IT 2	1200 SC 1	1200 SC 7	1200 SC 8	1300 IT 2	1300 IT 1	1300 SC 1	1300 SC 6	1300 SC 7	1300 IB 8	1400 IT 3	1400 IT 5	1400 SC 1	1400 SC 6	1400 SC 7	1400 RM 4	1500 IT 2	1500 SC 6	1500 SC 7	1600 SC 6
Myrmicinae (Continuation)																																
Crematogaster complex. *crinosa* sp1													x																			
Crematogaster complex. *crinosa* sp2																												x				
Crematogaster erecta (Mayr, 1866)*													x				x															
Crematogaster goeldii (Forel, 1903)*																												x				
Crematogaster moelleri (Forel, 1912)*	x			x			x																									
Crematogaster prox. *erecta* sp1	x			x			x			x																						
Crematogaster prox. *obscurata* sp1																						x										
Crematogaster prox. *sericea* (Forel, 1912)*																	x															
Crematogaster sp	x						x				x	x					x															
Crematogaster sp1	x						x	x		x				x			x						x									
Crematogaster sp2					x										x									x								
Crematogaster sp3															x																	
Crematogaster sp4															x																	
Crematogaster sp5	x			x						x									x													
Crematogaster sp6	x																															
Crematogaster sp7								x												x												
Crematogaster sp8																				x												
Crematogaster sp9																				x										x		
Crematogaster sp10		x						x																								
Cyphomyrmex (gr.Rimosus) sp1	x							x		x				x					x						x							
Cyphomyrmex (gr.Rimosus) sp2	x													x																		
Cyphomyrmex (gr.Strigatus) sp1														x					x													
Cyphomyrmex (gr.Strigatus) sp2																			x													
Cyphomyrmex (gr.Strigatus) sp3	x			x						x				x					x													
Cyphomyrmex lectus (Forel, 1911)*																x																
Cyphomyrmex peltatus (Kempf, 1966)*																x											x					
Cyphomyrmex sp1																											x					

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TÁXON	800 SC 1	800 SC 6	900 SC 1	900 SC 6	1000 SC 1	1000 SC 7	1100 SC 1	1100 SC 6	1100 SC 7	1200 IT 2	1200 SC 1	1200 SC 7	1200 SC 8	1300 IT 2	1300 SC 1	1300 SC 6	1300 SC 7	1300 IB 8	1400 IT 3	1400 IT 5	1400 SC 1	1400 SC 6	1400 SC 7	1400 RM 4	1500 IT 2	1500 SC 6	1500 SC 7	1600 SC 6
Myrmicinae (Continuation)																												
Cyphomyrmex sp2	x				x										x						x						x	
Cyphomyrmex transversus (Emery, 1894)*							x								x						x							
Hylomyrma balzani (Emery, 1894)*																	x						x				x	x
Hylomyrma sp			x												x													
Kalathomyrmex emeryi (Forel, 1907)*									x				x															
Leptothorax sp1		x				x		x	x				x															
Leptothorax sp2													x				x											
Leptothorax sp3											x																	
Megalomyrmex sp								x								x												x
Monomorium pharaonis (Linnaeus, 1758)*											x																	
Mycetarotes sp					x							x																
Mycetophylax emeryi (Forel, 1907)*	x		x		x		x					x									x							
Mycocepurus goeldii (Forel, 1893)*	x		x		x																							
Mycocepurus smithi (Forel, 1893)*	x	x																										
Myrmicocrypta sp														x														
Nesomyrmex prox. echinatinodis (Forel, 1886)										x																		
Nesomyrmex spininodis (Mayr, 1887)*	x				x																							
Ochetomyrmex semipolitus (Mayr, 1878)*	x				x						x				x													
Ochetomyrmex sp															x													
Oxyepoecus prox. bruschi sp1															x						x							
Oxyepoecus prox. bruschi sp2							x								x						x							
Oxyepoecus sp1							x								x		x						x			x		
Oxyepoecus sp2																										x		
Oxyepoecus sp3																											x	
Pheidole gertrudae (Forel, 1886)*	x		x		x		x																					
Pheidole obscurithorax (Naves, 1985)*																		x						x				
Pheidole oxyops (Forel, 1908)*	x	x			x		x				x				x						x							

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TÁXON	*ALTITUDES (m)																															
	800			900			1000			1100				1200				1300						1400				1500			1600
	SC	SC	SC	SC	SC	SC	SC	SC	SC	SC	SC	SC	IT	SC	SC	SC	IT	SC	SC	SC	IB	IT	IT	SC	SC	SC	RM	IT	SC	SC	SC
	1	6	7	1	6	7	1	7	7	1	6	7	2	1	7	8	2	1	6	7	8	3	5	1	6	7	4	2	6	7	6
Myrmicinae (Continuation)																															
Pheidole radoszkowskii (Mayr, 1884)*																					x										
Pheidole sp																						x									
Pheidole sp1	x	x	x			x		x	x			x			x			x		x				x	x		x		x		
Pheidole sp2	x	x	x			x	x	x	x		x	x			x	x		x	x					x	x				x		
Pheidole sp3	x	x	x		x	x	x	x	x		x	x			x	x		x						x							
Pheidole sp4			x		x	x		x	x		x	x			x			x	x	x											
Pheidole sp5	x	x	x			x	x		x		x				x			x		x					x				x		
Pheidole sp6	x	x	x		x	x	x	x	x		x							x						x							
Pheidole sp7	x	x			x									x								x		x							
Pheidole sp8	x	x			x													x				x		x							
Pheidole sp9	x				x			x				x			x			x	x	x				x		x			x		
Pheidole sp10	x	x			x	x	x	x	x		x	x				x			x		x			x			x		x		
Pheidole sp11	x				x			x				x			x			x						x							
Pheidole sp12	x				x			x				x			x			x	x												
Pheidole sp13	x				x			x							x			x							x						
Pheidole sp14			x												x			x	x												
Pheidole sp15	x							x				x			x			x													
Pheidole sp16	x	x			x										x										x						
Pheidole sp17	x				x													x													
Pheidole sp18	x	x					x											x													
Pheidole sp19	x	x						x	x			x			x	x		x		x											
Pheidole sp20	x			x	x	x	x	x																							
Pheidole sp21	x				x						x																				
Pheidole sp22	x			x																											
Pheidole sp23	x							x																							
Pheidole sp24	x							x																							
Pheidole sp25	x							x					x	x	x																

*Species with no occurrence in the sampling area; ‡ Species with no information on distribution; †Species with occurrence recorded for the sampling site.

Appendix. Occurrence and distribution of ant species along the altitudinal gradient, localities, and studies carried out in the Brazilian rocky grasslands. Sampling sites: Serra do Cipó (SC), Itacolomi State Park (IT), Ibitipoca State Park (IB), and Serra do Rola Moça State Park (RM). Numbers in columns indicate the literature sources described in Table 1 (Continuation).

ALTITUDES (m)

TÁXON	800 SC 1	800 SC 6	800 SC 7	900 SC 1	900 SC 6	900 SC 7	1000 SC 1	1000 SC 7	1000 SC 7	1100 SC 1	1100 SC 6	1100 SC 7	1100 IT 2	1200 SC 1	1200 SC 7	1200 SC 8	1200 IT 2	1300 SC 1	1300 SC 6	1300 SC 7	1300 IB 8	1300 IT 3	1300 IT 5	1400 SC 1	1400 SC 6	1400 SC 7	1400 RM 4	1500 IT 2	1500 SC 6	1500 SC 7	1600 SC 6
Myrmicinae (Continuation)																															
Pheidole sp26								x			x													x					x		
Pheidole sp27										x	x																				x
Pheidole sp28	x															x				x						x			x		x
Pheidole sp29	x																			x											
Pheidole sp30	x																			x						x			x		
Pheidole sp31							x													x											
Pheidole sp32	x																									x					
Pheidole sp33																										x			x		
Pheidole sp34																													x		
Pheidole sp35		x			x																										
Pheidole sp36								x												x											
Pogonomyrmex abdominalis (Santschi, 1929)*	x				x			x				x								x					x				x		
Pogonomyrmex naegelii (Emery, 1878)*	x			x			x			x				x				x									x		x		
Pogonomyrmex sp1												x																			
Procryptocerus sp													x				x														
Sericomyrmex sp	x	x				x		x		x								x													
Solenopsis (Diplorhoptrum) sp																					x					x			x		
Solenopsis bondari (Santschi, 1925)‡		x				x						x									x								x		
Solenopsis globularia (Smith, 1858)*	x				x		x			x				x				x													
Solenopsis saevissima (Smith, 1855)*		x				x	x	x		x	x					x			x	x				x		x			x		
Solenopsis sp1	x				x		x			x	x			x					x	x				x	x				x		x
Solenopsis sp2	x	x		x	x		x	x		x	x			x					x				x								
Solenopsis sp3	x	x		x	x		x	x		x				x				x					x						x		
Solenopsis sp4						x		x				x						x					x	x	x					x	
Solenopsis sp5	x				x		x			x				x				x	x												
Solenopsis sp6						x		x		x								x	x					x							
Solenopsis sp7																										x					

*Species with no occurrence in the sampling area; ‡ Species with no information on distribution; †Species with occurrence recorded for the sampling site.

Appendix. Occurrence and distribution of ant species along the altitudinal gradient, localities, and studies carried out in the Brazilian rocky grasslands. Sampling sites: Serra do Cipó (SC), Itacolomi State Park (IT), Ibitipoca State Park (IB), and Serra do Rola Moça State Park (RM). Numbers in columns indicate the literature sources described in Table 1 (Continuation).

ALTITUDES (m)

TÁXON	800			900			1000			1100			1200				1300					1400						1500			1600
	SC	SC	SC	SC	SC	SC	SC	SC	SC	SC	SC	SC	IT	SC	SC	SC	IT	SC	SC	SC	IB	IT	IT	SC	SC	SC	RM	IT	SC	SC	SC
	1	6	7	1	6	7	1	7	7	1	6	7	2	1	7	8	2	1	6	7	8	3	5	1	6	7	4	2	6	7	6
Myrmicinae (Continuation)																															
Solenopsis sp8																													x		
Solenopsis sp9																													x		x
Strumigenys crassicornis (Mayr, 1887)*	x																														
Strumigenys eggersi (Emery, 1890)*														x																	
Strumigenys elongata (Emery, 1890)*														x																	
Strumigenys louisianae (Roger, 1863)*	x																	x						x							
Strumigenys schulzi (Emery, 1894)*	x																														
Strumigenys sp																															x
Trachymyrmex sp1	x				x		x			x	x		x	x			x	x	x					x	x						
Trachymyrmex sp2	x	x			x		x											x	x						x				x		
Trachymyrmex sp3	x	x																x													
Trachymyrmex sp4	x				x		x									x															
Trachymyrmex sp5																		x													
Trachymyrmex sp6	x																														
Trachymyrmex sp7										x								x							x						
Trachymyrmex sp8	x				x									x					x												
Trachymyrmex sp9	x				x					x																					
Tranopelta gilva (Mayr, 1866)*	x				x					x																					
Wasmannia auropunctata (Roger, 1863)*	x	x			x		x			x				x				x					x	x			x				
Wasmannia sp																															x
Ponerinae																															
Anochetus diegensis (Forel, 1912)*							x																								
Anochetus inermis (André, 1889)*	x				x					x																					
Hypoponera sp									x																	x					
Hypoponera sp1	x				x		x			x								x						x							
Hypoponera sp2	x	x			x		x			x				x																	
Neoponera bucki (Borgmeier, 1927)‡																														x	x

*Species with no occurrence in the sampling area; † Species with no information on distribution; ‡Species with occurrence recorded for the sampling site.

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TÁXON	800			900			1000		1100			1200				1300				1400							1500			1600
	SC	SC	SC	SC	SC	SC	SC	SC	SC	SC	SC	IT	SC	SC	SC	IT	SC	SC	SC	IT	IT	IB	SC	SC	SC	RM	IT	SC	SC	SC
	1	6	7	1	6	7	1	7	1	6	7	2	1	7	8	2	1	6	7	3	5	8	1	6	7	4	2	6	7	6
Ponerinae (Continuation)																														
Neoponera villosa (Fabricius, 1804)*	x			x																										
Odontomachus bauri (Emery, 1892)*					x													x												
Odontomachus brunneus (Patton, 1894)*	x				x																									
Odontomachus chelifer (Latreille, 1802)*	x	x			x																									
Odontomachus haematodus (Linnaeus, 1758)*																										x				
Odontomachus insularis (Guérin-Méneville, 1844)*	x																													
Odontomachus meinerti (Forel, 1905)*				x																										
Odontomachus sp1																						x								
Pachycondyla sp1	x	x				x																								
Pachycondyla sp2	x													x																
Pachycondyla striata (Smith, 1858)*	x										x								x					x	x				x	x
Ponera sp1								x																						
Pseudomyrmicinae																														
Pseudomyrmex (gr. Pallidus) sp2																										x				
Pseudomyrmex (gr.Pallidus) sp	x			x										x				x				x		x						
Pseudomyrmex cf. flavidulus	x							x																						
Pseudomyrmex elongatus (Mayr, 1870)*	x																													
Pseudomyrmex gracilis (Fabricius, 1804)*	x	x					x	x															x							
Pseudomyrmex pupa (Forel, 1911)*					x																									
Pseudomyrmex sp1										x							x					x					x	x		
Pseudomyrmex sp2			x							x					x				x								x			
Pseudomyrmex termitarius (Smith, 1855)*	x	x		x	x		x	x	x	x			x	x			x							x						
Total number of species per altitude	171			127			111		116			117				121				112							45			17

*Species with no occurrence in the sampling area; †Species with no information on distribution; ‡ Species with occurrence recorded for the sampling site.

ANEXO II

Chapter 13
Mutualistic Interactions Among Free-Living Species in Rupestrian Grasslands

Tadeu J. Guerra, Daniel W. Carstensen,
Leonor Patricia Cerdeira Morellato, Fernando A.O. Silveira
and Fernanda V. Costa

Abstract Mutualisms such as animal pollination and seed dispersal, and protection of plants and insects by ants are ubiquitous in terrestrial ecosystems. Currently, mutualistic interactions among plants and animals are recognized for their paramount importance in biodiversity maintenance, especially in tropical ecosystems. In this chapter, we review the literature and present unpublished data on the ecology of mutualistic interactions among free-living species in Brazilian megadiverse montane Rupestrian Grasslands, the *Campo Rupestre*. We focus on interactions between plants and their pollinators and seed dispersers, and also interactions between ants, myrmecophilous plants and trophobiont insects. We provide basic information on mutualistic interactions, including data on natural history in addition to more advanced studies using network-based approaches. Only in the past decade mutualistic interactions have become intensively studied in *Campo Rupestre*, but information is still scattered and concentrated for a few localities. Pollination is an important process for reproduction of most plant species studied so far, with bees

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and hummingbirds acting as the main pollinators. Seemingly, animal pollination is more important than seed dispersal for gene flow across plant populations. Most vertebrate seed dispersal is carried out by non-specialized avian frugivorous, but also by short-distance seed dispersers such as ants and lizards. Moreover, ants are diversified and abundant group that seem to play a major role in these ecosystems, acting as secondary seed dispersers, as nectar thieves, and as bodyguards of plants and insects. We conclude this chapter by pointing out some gaps in our knowledge and proposing avenues for future research.

Contents

13.1   Introduction

Throughout the history of life, natural selection has repeatedly favored the evolution of traits that allow individuals to exploit the whole genomes of other species to survive and reproduce (Thompson 2010). In fact, coevolved interactions comprise the foundations of all species-rich ecosystems of the Earth and without such coevolved partnerships, highly diverse ecosystems would simply collapse (Thompson 2005). Organisms from all kingdoms are involved in mutually beneficial interactions among species, or mutualisms, which may take different forms in nature and vary from obligate to facultative (Bronstein 2009). The most well-known mutualistic interactions involving free-living species in terrestrial ecosystems are plant pollination and seed dispersal by animals and plant and insect protection, mostly by ants (Herrera and Pellmyr 2002). However, obligate and intimate relationships such as symbiotic mutualisms that include vertebrate and invertebrate gut symbionts, lichens, rhizobia and mycorrhizae are also important in ecosystems (Douglas 1994).

Mutualisms typically involve conflict of interests among interacting species and rise from mutual exploitation between selfish individuals (Axelrod and Hamilton 1981). Indeed, mutualistic systems are usually exploited by cheater species (Bronstein 2001). Even supposed mutualisms can be conditional, or context dependent, and they are usually contingent on the balance between costs and benefits for those individuals that interact, with the outcomes varying from positive to negative according to biotic and abiotic conditions (Bronstein 1994; Bronstein

et al. 2003). Furthermore, other kinds of mutualisms may be observed when we consider the complexity of natural communities where species are also linked to each other by indirect interactions (van Ommeren and Whitham 2002; Romero and Vascocelos-Neto 2004; Verdú and Valiente-Banuet 2008).

In his classic book on orchid pollination, Charles Darwin established a naturalistic approach that led to the field of mutualism ecology (Darwin 1862). This mostly adaptive agenda were focused on understanding how traits of animals and plants favored survival and reproduction of interacting species. After the publication of a seminal paper by Janzen (1966), the mutualistic relationships among animals and plants became more intensively studied and the first landmark publications regarding mutualisms appeared in the 80s (Beattie 1985; Boucher 1985; Estrada and Fleming 1986). The knowledge accumulated over the past 50 years paved the current view that mutualistic interactions among plants and animals play a central role in the generation and maintenance of biodiversity (Bascompte and Jordano 2007). Moreover, mutualistic interactions such as pollination and seed dispersal are now recognized as important services providing processes that are essential for sustaining natural and agricultural ecosystems (Valiente-Banuet et al. 2015).

Understanding the identity of interacting species, what adaptations are involved in these interactions and the outcomes for the interacting partners is still of paramount importance in basic and applied ecology. Nevertheless, new ideas and approaches have emerged in the past years. For instance, network theory has played a major role in the understanding of mutualistic interactions among free-living species (Bascompte and Jordano 2014). The use of network metrics and structural properties such as nestedness, modularity, centrality, and link asymmetry allows the exploration, and comparison of patterns in structure and organization of ecological interactions within and between communities (Bascompte and Joradno 2007; Olesen et al. 2007; Gonzalez et al. 2010). Jordano et al. (2003) identified invariant properties of mutualistic networks that reveals some major ecological patterns of community organization. First, there is always a core of generalists in communities, those species that interact among themselves and with a set of more specialized species that consistently interact with that generalist core. Second, interactions are generally weak in terms of reciprocal dependence, but the few of them that are stronger tend to be quite asymmetric, which means that one partner is more dependent upon the interaction than the other (Bascompte et al. 2006). Finally, most networks show distinct modules or compartments, meaning that distinct subsets of species interact more strongly among themselves than with species form other modules (Olesen et al. 2007).

The Rupestrian Grasslands or *Campo Rupestre* comprise megadiverse montane fire-prone vegetation that occur on Brazilian ancient landscape mosaics (Fig. 13.1a), which include rocky outcrops of quartzite, sandstone or ironstone along with sandy, stony and waterlogged grasslands. *Campo Rupestre* ecosystems predominate in those areas above 900 m and up to 2000 m a.s.l. in disjoint areas, mostly within Espinhaço Mountain Range in Brazilian States of Minas Gerais and Bahia (Giulietti et al. 1997; Alves et al. 2014) and are recognized as an important center of biological diversity and endemism of flora (Giulietti et al. 1997; Rapini
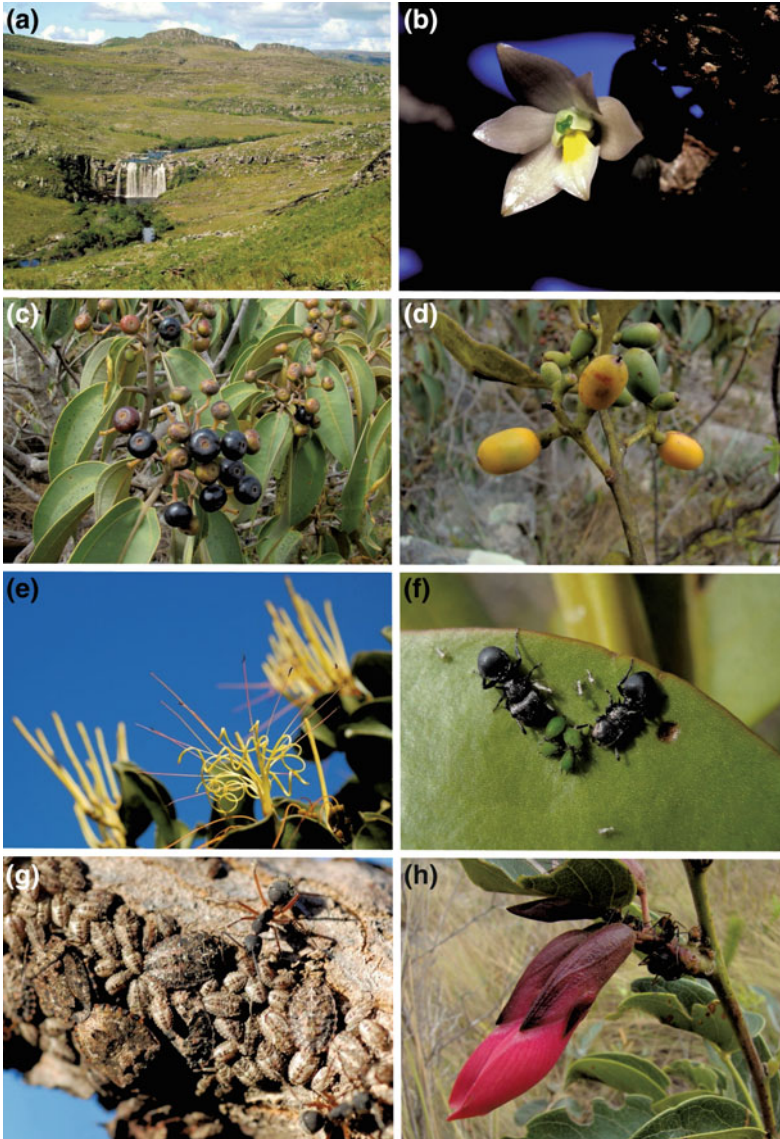
Fig. 13.1 **a** A typical landscape encompassing *Campo Rupestre* ecosystems in Lapinha da Serra, southern Espinhaço Range. **b** The endemic bee-pollinated orchid *Constantia cipoensis*. The ornithocorich fruits of (**c**) *Miconia irwinii* and (**d**) *Struthanthus flexicaulis*. **e** The flowers of the hummingbird-pollinated mistletoe *Psittacanthus robustus*. **f** The aphid *Aphis spiraecola* attended by the ant *Cephalotes pusillus*. **g** The trophobiont stinkbug *Eurystethus microlobatus* attended by the ant *Camponotus rufipes*. **h** *Bionia coriaceum* with ant bodyguards associated to its extra-floral nectaries. (Photos by T.J. Guerra)

et al. 2008; Echternacht et al. 2011) and fauna (Alves et al. 2008; Leite et al. 2008; Chaves et al. 2015). Despite the relevance of *Campo Rupestre* for biodiversity conservation in Brazil (Fernandes et al. 2014; Silveira et al. in press), currently, there is no published compilation of studies concerning mutualistic interactions for these unique ecosystems.

13.2   Scope

In this chapter, we review the literature and present unpublished information on ecology of mutualistic interactions among free-living species in the *Campo Rupestre* (CR hereafter) ecosystems. We focus on interactions among plants and their pollinators and seed dispersers, and on interactions between ants, myrme-cophilous plants and trophobiont insects, i.e. those that produce sugar- and amino acid-rich honeydew as rewards for their bodyguards. Our aim is to provide basic information on mutualistic interactions in CR, presenting data from those more naturalistic studies as well more advanced studies using network-based approaches. We conclude this chapter by pointing out some major gaps in the study of mutu-alisms in CR and propose avenues for future research.

13.3   Linking Plants to Their Pollinators

Biotic pollination, i.e., animals harvesting resources from flowers and in return providing pollination services, is ubiquitous to all terrestrial ecosystems. On average in tropical communities 94 % of the plant species are estimated to be pollinated by animals (Ollerton et al. 2011). There are few studies of animal and abiotic polli-nation mechanisms for the CR flora, but existing information are congruent with a predominance of biotic pollination. Jacobi and Carmo (2011) showed that insect pollinated species, mostly those pollinated by bees, comprise nearly 70 % of the plant species in the community, whereas bird pollinated plants represent almost 13 % and wind pollination 16 % in ironstone outcrop site in southern Espinhaço Range. In addition, Conceição et al. (2007) found that animal pollinated species also outweigh abiotic mechanisms of pollinationin Chapada Diamantina, northern Espinhaço Range. However, the authors observed a marked seasonal pattern, with entomophily occurring mostly from summer through autumn, ornithophily pre-dominating during winter, whereas anemophily prevailed in the spring.

Existing work on pollination is sparse and restricted mostly to studies on the reproductive biology of a single or few species (e.g., Sazima 1977; Jacobi et al. 2000; Guerra et al. 2014). However, those studies offer valuable insight into the natural history of CR vegetation, including some extraordinary cases of mutu-alisms. For instance, the epiphytic orchid *Constantia cipoensis* (Fig. 13.1b), which grows only on two species of *Vellozia* (*V. piresisana* and *V. compacta*), is

exclusively pollinated by the carpenter bee *Xylocopa artifex*, which also build its nests inside the branches of *V. piresiana* and *V. compacta* (Matias et al. 1996). This endemic and threatened orchid is restricted to growing on *Vellozia* trunks and several other poorly known orchids are found in connection with *Vellozia*, such as, *Cattleya brevipedunculata*, which grows on *V. gigantea*, which itself has a narrow geographical distribution (Lousada et al. 2011). Such highly specific requirements for growth and reproduction constrain gene flow and dispersal of individuals across populations and likely contribute to the strong heterogeneity in species distributions across CR landscapes.

Pollination systems of endemic species vary from highly specialized (e.g. few pollinator species within an animal group) to more generalized (e.g. many species from distinct taxonomic groups) and include both invertebrates and vertebrates as pollinators. For example, some endemic orchids are highly specific regarding their fly pollinator species and this specialization is consistent among populations (Borba and Semir 2001; Melo et al. 2011), with fly-pollination as the main mechanism favoring maintenance of high genetic variability in the populations studied by Borba et al. (2001). In contrast, the endemic bromeliad *Echolirium glaziovii* is pollinated by the nectarivorous bat *Lochophylla bokermani* in Serra do Cipó, but the authors also recorded visits by two hummingbird species during the day and noctuid and sphingid moths during the night (Sazima et al. 1989). Other CR species, *Paliavana sericiflora* (Gesneriaceae), represent an interesting case of transition between bat and hummingbird pollination. This species has features related to attraction of both groups, but in the field hummingbirds were observed as the main pollinators (San Martin-Gajardo and Sazima 2005). Some endemic species are pollinated exclusively by bees (Matias et al. 1996; Jacobi et al. 2000; Franco and Gimenes 2011), while other species have generalized systems involving bees and hummingbirds as pollinators (Sazima and Sazima 1990; Jacobi and del Sarto 2007; Jacobi and Antonini 2008; Ferreira and Viana 2010; Hipólito et al. 2013).

Interactions among hummingbirds and flowers are fairly common in CR and occur in plants from several families, including many endemic genera (Vasconcelos and Lombardi 2001; Machado et al. 2007; Santana and Machado 2010; Rodrigues and Rodrigues 2014). Nevertheless, the studies mentioned above raised two remarkable points related to interactions among plants and hummingbirds in CR. First, hummingbird species are more commonly reported as visitors of non-ornithophilous than ornithophilous species, e.g. plants with red, orange or yellow flowers that are tubular shaped and produce nectar as reward (Vasconcelos and Lombardi 2001; Machado et al. 2007; Santana and Machado 2010; Rodrigues and Rodrigues 2014). For example, the Espinhaço Range endemic hummingbird *Augastes scutatus* was commonly observed visiting species in the primarily insect pollinated family Asteraceae (Vasconcelos and Lombardi 2001; Rodrigues and Rodrigues 2014). Although only a subset of CR plants are considered ornithophilous, hummingbirds could play a major role in reproduction of some species, as thieves or pollinators. Second, nectar rich species in CR along the Espinhaço Region seem to concentrate some highly territorial hummingbird species that defend flower resources against other visitors (Sazima 1977; Sazima and Sazima 1990;

Vasconcelos and Lombardi 2001; Machado et al. 2007; Jacobi and Antonini 2008; Guerra et al. 2014). This common behavioral pattern of hummingbirds could result in restriction of gene flow to plants within some rock outcrop patches and, thus, reducing the variability in some hummingbird pollinated species. In fact, the bee pollinated *Vellozia epidendroides* has higher genetic variability than hummingbird pollinated *V. leptopetala* (Franceschinelli et al. 2006), suggesting that bees could be more effective in long distance dispersal of pollen than territorial hummingbirds.

The open, high altitude vegetation that characterizes the CR could be connected to an expectation of higher proportion of wind-pollinated plants (Culley et al. 2002). However, the spatial heterogeneity of the landscape, a mosaic of rocky outcrops embedded in a matrix of sandy or rocky soils, is another typical characteristic of CR. This causes patchy distribution patterns in most plant species, and has likely selected for animal pollination as an essential means to obtain gene flow between populations that are spatially constrained by environmental heterogeneity, reflected in substrate, hydrology, and local climate (see Giulietti et al. 1997; Silveira et al. in press). Even so, species confined to rocky outcrops seem to show lower genetic diversity than species associated with sandy soils (Franceschinelli et al. 2006; Lousada et al. 2011). The patchy distribution of populations translates into a high turnover of plants and pollinator species across space; this spatial variation being larger for plants than pollinators (Carstensen et al. 2014). Plant phenology patterns across the year are complex and likely affected by both regional and local climatic factors as well as occasional fires (Chap. 12). Pollinators, in turn, likely track this variation in flower resources in space and time, resulting in complex dynamics of local plant-pollinator interactions.

Plant-pollinator interactions within communities are analyzed and visualized using networks, in which plant and pollinator species (the network nodes) are connected (or linked) to each other if they are observed interacting (Jordano et al. 2003). While network-scale properties, such as nestedness and modularity, seem to be conserved, it has also been shown that detailed network structures, such as species and interaction composition (Dupont and Olesen 2009; Carstensen et al. 2014) and functional roles (Gonzalez et al. 2010), can change dramatically in both time and space (Trøjelsgaard et al. 2015). In Serra do Cipó rocky outcrops, communities seem to abide by the generalities of plant-pollinator networks found elsewhere (Fig. 13.2). The only existing community-scale dataset on plant-pollinator interactions from CR consists of seven sampled networks across rocky outcrop vegetation sites within CR landscape in Serra do Cipó (Carstensen et al. 2014). While network properties seem to be relatively constant across space (Carstensen et al. in prep) species and interaction turnover are large even across small distances (Carstensen et al. 2014). All sites combined showed a rich community with 101 flowering species visited by 199 pollinator species. In this dataset gathered in the beginning of the rainy season (from October to December), bees were dominant in terms of species richness and overall number of interactions, comprising 34 % of all species and 60 % of all interactions observed. Flies, butterflies, wasps, and beetles all had a strong presence in the data set, each group accounting for 13–18 % of the species observed. Hummingbirds and

Fig. 13.2 The local plant-pollinator network sampled in the *Campo Rupestre* of Serra do Cipó, southeastern Brazil. *Black boxes* on the *left* represent plant species; *boxes* on the *right* represent pollinator species. The size of the boxes represents the total degree of the species in the network, that is, the number of interactions observed for a given species. Species are connected with lines if they were observed interacting, the thickness of the line representing the frequency of interaction. Notice the nested organization of interactions, where species with few interaction partners tend to interact with species with many interaction partners
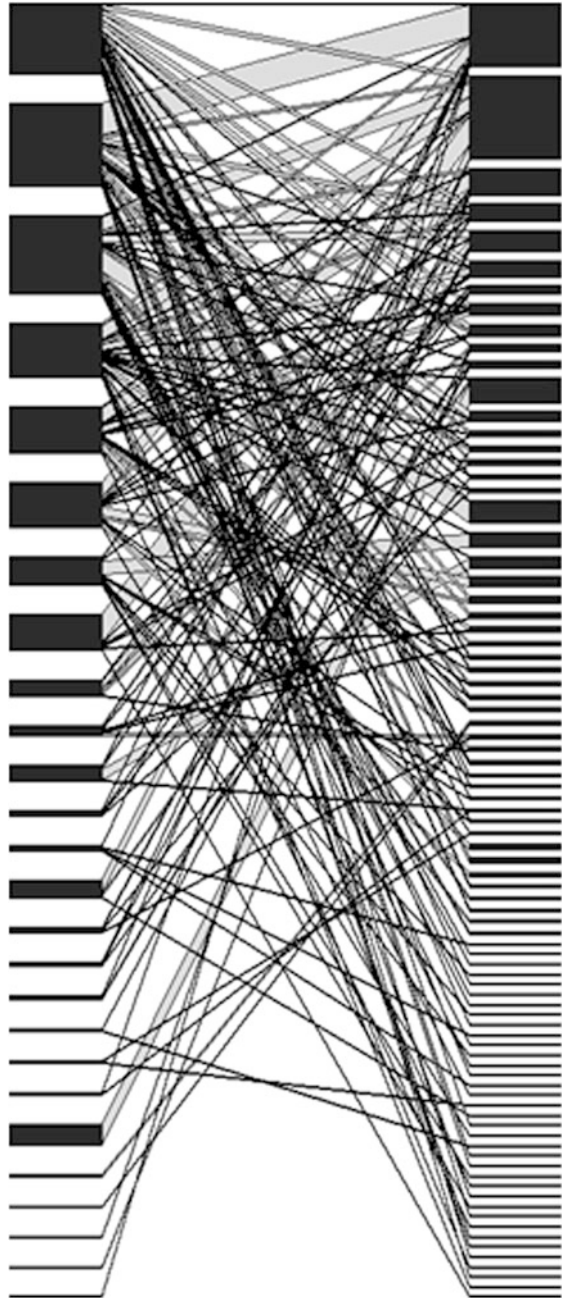
ants were less diverse, only each comprising 6 % of the total species richness of the flower visitors. Only one plant species was found in all sites, *Cuphea ericoides* (Lythraceae), while others such as *Paepalanthus bromelioides* (Eriocaulaceae) and *Aspilia jolyana* (Asteraceae) were widely common as well. On the other hand, several pollinators were found in all sites, e.g. *Apis mellifera*, *Bombus pauloensis* as well as six of other bee species, and hummingbirds such as *Chlorostilbon lucidus* and *Heliactin bilophus* were both observed in five out the seven sites.

In that unique dataset from Carstensen et al. (2014), flower visitors were regarded as pollinators if they touch the reproductive organs of the flowers, but not all flower visitors "follow the rules". Some can be classified as illegitimate visitors, that is, they visit the flower and harvest floral resources but do not return any immediate service in the form of pollination. This can be a result of either morphological mismatches or because they circumvent the floral system by puncturing the corolla and accessing nectar directly, without getting into contact with the reproductive organs of the plant. This puncturing, or an otherwise destructive behavior to access floral nectar, is termed nectar robbing (Inouye 1980) and can be observed in several types of flower visitors, but especially bees and hummingbirds. However, the role of flower visitors as pollinators and robbers or thieves in CR remains poorly known.

13.4 Frugivory and Seed Dispersal

To understand the ecology of seed dispersal in CR, first we need to understand the natural history and ecology of their fruits and frugivores. According to Silveira et al. (2016), the CR can be classified as a geologically old, climatically stable, infertile landscapes of the Earth (Hopper 2009). In those landscapes, reduced dispersal ability should be favored by natural selection, because recruitment is strongly controlled by soil conditions and the safe sites for establishment are usually near the parent-plants (Hopper 2009). As expected, most species from the CR have no conspicuous mechanism for seed dispersal. Unassisted dispersal is the prevalent dispersal mode among dominant (e.g. Poaceae, Cyperaceae, and Fabaceae) and herb families with many endemic species (e.g. Xyridaceae, Eriocaulaceae, and Velloziaceae). In fact, Conceição et al. (2007) observed that few species in CR site in Chapada Diamantina produce fleshy fruits, with those individuals representing 21 % of vegetation cover.

The production of fleshy fruits by CR plants seems to be restricted to a few Neotropical clades that are typically vertebrate-dispersed (e.g. Melastomataceae, Myrtaceae and Cactaceae), most of them which occur in woody vegetation, such as gallery forests and natural forest patches (locally known as *capões* de mata, see Chap. 7). However, plant species from at least 16 families that produce fleshy fruits were reported to occur in CR sites, mostly bird dispersed berries (Faustino and Machado 2006; Conceição et al. 2007; Silveira et al. 2012; Guerra and Pizo 2014).

In fact, even some endemic species (e.g. *Coccoloba cereifera*) typical from CR rocky outcrops produce fleshy fruits. Most of those fruits are small, and have dark-crimson or red color, but yellow, rose, brown, orange, and purple fruits are not uncommon (Faustino and Machado 2006; Guerra and Pizo 2014).

Birds and mammals are the predominant vertebrate seed dispersers worldwide (Fleming and Kress 2011). In CR, primates are virtually absent in the open vegetation areas, so seed dispersal by mammals is probably mostly carried out by bats, yet there is no study to support this idea. Although there are records of carnivorous species such as the maned wolf (*Chrysocyon brachyurus*) and the crab-eating fox (*Dusicyon thous*) serving as seed dispersers, the role of large mammals in seed dispersal is also unexplored. The scarce available evidence suggests that in CR birds are the main seed dispersers among vertebrates. However, the avifauna present in these ecosystems is characterized by the dominance of generalist species and the lack of specialized avian frugivores (Faustino and Machado 2006; Guerra and Pizo 2014). Seed dispersal by lizards is considered a predominantly oceanic island phenomenon (Olesen and Valido 2004). However, it has been recently observed in a CR site, where two cactus species are dispersed by two lizard species, but also by ants (Fonseca et al. 2012).

A useful starting point to unveil the complexity of seed dispersal in CR is the seminal paper by McKey (1975). He defined two opposing seed dispersal strategies that, rather than representing mutually exclusive categories, are best viewed as extremes of a continuum. The specialist plant syndrome comprises species that produce few, lipid rich fruits that contain a few (or a single) large seeds. The generalist syndrome, in turn, is observed in species with massive production of small-sized fruits with high sugar and low nutrient content, which often have several tiny seeds. The former are dispersed by effective, reliable and specialized frugivores, while the latter are dispersed by a wider range of non-specialized frugivorous species (Howe 1993). Studies focused on the Miconieae (Melastomataceae) species, plants which are the archetype of the generalist syndrome, have been the primary study model of seed dispersal in CR.

Studies on frugivory and seed dispersal in CR have focused on Miconieae not only because of their dominance and diversity, but also because of their key role in providing resources to several disperser groups (Silveira et al. 2013a). This combination offers the unique opportunity to compare seed dispersal effectiveness (sensu Schupp et al. 2010) among different taxonomic groups of frugivores. Miconieae is a species-rich Neotropical tribe of Melastomataceae that comprises nearly 2200 species (Goldenberg et al. 2008), which are commonly found in most Neotropical vegetation (Silveira et al. 2013a). Fruit morphology in Miconieae is extraordinarily diverse, with species showing marked differences in crop size, fruit size, color, water and sugar content, seed number, pulp/seed ratio, and contrasting displays. All those traits have been shown to directly influence removal rates (Blendinger et al. 2008; Christianini and Oliveira 2009; Camargo et al. 2013).

The primary seed consumers of those berries are a taxonomically diverse community of small-to-medium-sized birds (Silveira et al. 2013a) that include thrushes, tangers, and *Elaenia.* The number of birds foraging on fruits of each

Miconia species ranges from two to ten (Guerra and Pizo 2014), which suggests a reduced number of seed dispersers for CR plants when compared to those of lowland tropical forests (Ellison et al. 1993). For instance, in tropical forest up to 36 bird species may feed on *Miconia* fruits (Galletti and Stotz 1996). Data on frugivory of two *Miconia* species in ironstone rocky outcrops in southern Espinhaço Range, indicate a reduced number of seed dispersers. The thrusher *Mimus saturninus* and the tanager *Schystoclamys ruficapillus* as the most effective dispersers of *M. ligustroides*, tough, most interestingly, the rufous-collared sparrow *Zonotrichia capensis*is an effective seed disperser of *M. pepericarpa* (Silveira, F.A.O. unpublished data). This result suggests that even typically granivorous birds may be important to the dispersal of small-sized seeds in CR vegetation, as suggested by Faustino and Machado (2006).

The probability that a dispersed seed will grow into a new reproductive individual depends on the site of seed deposition and on the quality of handling in the mouth and gut of the frugivore (Schupp et al. 2010). Therefore, we should disentangle the effects of seed cleaning (pulp removal), seed coat scarification, and fertilization effects (Samuels and Levey 2005). Seeds within berries of Miconieae cannot germinate because of the inhibition effect, i.e., the presence of germination inhibitors in the fleshy placentas and the dark pigmentation that prevents light from reaching the positively photoblastic seeds (Silveira et al. 2013b). It has been experimentally demonstrated that gut-passed seeds have similar germination percentages and germination time than hand-extracted seeds. Those results led to the conclusion that germination enhancement deriving from gut scarification does not play a role in recruitment of Miconieae. However, seed cleaning is an important service delivered by birds, and varies according plant and bird species involved in these mutualistic interactions (Silveira et al. 2012).

The large crop produced by Miconieae plants is usually not consumed by their primary seed dispersers. As a consequence, the fruits that fall to the ground become available for consumption by secondary seed dispersers (Christianini and Oliveira 2009). Myrmecochory (dispersal by ants) is a common phenomenon in sclerophyllous, fire-prone, nutrient-poor shrublands such as CR (Milewski and Bond 1982). Primary myrmecochory is rare in the Neotropics, with no reports for CR. However, a study on secondary seed dispersal by ants of *Miconia irwinii* (Fig. 13.1c), a primarily bird-dispersed commonly found in CR areas, suggests that ants in several genera could play an important role in seed fate (Lima et al. 2013). The ants transport fallen fruits to their nests, clean the seeds, and discard them outside the refuse piles, thereby rescuing many seeds that were not primarily dispersed by birds (Lima et al. 2013).

In CR, fallen fruits of Miconieae can also be exploited by marsupials, rodents (Lessa et al. 2013), and lizards. Marsupials could also provide important benefits to plants, since many of the small seeds can pass unharmed through their guts (Lessa et al. 2013). However, more work is necessary to evaluate the role of small mammals in Miconieae seed dispersal.

13.5 Mutualistic Interactions Between Birds and Mistletoes

Mistletoes comprise a polyphyletic group of parasitic plants that infect the aerial parts of their hosts, mostly trees and shrubs (Nickrent et al. 2010). Those plants are mostly hemiparasites, as they attach themselves to the host's shoots via haustorial roots, in order to obtain water and minerals, but are able to photosynthesize their own carbohydrates (Ehleringer et al. 1985). Mistletoes are important elements of natural communities, because they provide structural and nutritional resources within the canopy (Watson 2001), and their positive influence on diversity led to their recognition as keystone resources for animals (Watson and Herring 2013). Loranthaceae is the largest family among parasitic angiosperms with nearly 900 species distributed in approximately 70 genera, which occur in most terrestrial ecosystems of the world, including tropical and temperate forests, mangroves, savannas, semi-arid vegetation, and deserts (Calder and Bernhardt 1983). Most species produce nectar as a reward to pollinating birds (Kuijt 1969). The effectiveness of mistletoe pollinators, the quality of the floral reward, and the consequences of their interactions for plant reproduction are still poorly known (Aizen 2003). For example, plant breeding system, nectar availability and secretion dynamics are key traits to understand the behavior of pollinators, and may help us to determine costs and benefits of such interactions (Gill and Wolf 1975).

The mistletoe *Psittacanthus robustus* (Loranthaceae) has tubular and colorful flowers (Fig. 13.1e), which produce copious dilute nectar as the main reward for pollinators throughout the rainy season in the CR areas of Serra do Cipó (Guerra et al. 2014). Indeed, nectar of *P. robustus* represented an exceptional resource for birds. The local guild of nectarivorous birds that feed on *P. robustus* include eight hummingbirds and two passerines, which represents the largest guild reported for an ornithophilous plant species in the CR sites.

Mistletoe flowers secrete most of their nectar right after flower opening, with little sugar replenishment after experimental removal. The experiments with exclusion of flower visitors revealed that flowers quickly reabsorbed the nectar, which is evidence of the high costs of nectar secretion (Guerra et al. 2014). Surprisingly, flowers naturally exposed to pollinators produced less seeds than hand-, self-, and cross-pollinated flowers, which suggests some degree of pollination limitation. However, hummingbird-pollinated flowers still produce significantly more seeds than flowers excluded from pollinators. Because *P. robustus* cannot produce seeds spontaneously without pollinators, hummingbirds seem to be crucial for seed production. In effect, the low values of nectar recorded in open flowers are consistent the high hummingbird visitation rates reported. Thus, reproductive limitation in this mistletoe does not seem to be related to pollinator scarcity. Indeed, the high frequency of visitation by hummingbird pollinators seem to be costly, because they leave almost no nectar for reabsorption and the subsequent use of sugars to produce seeds in the plants. The pollination system involving the mistletoe *P. robustus* and hummingbirds in rocky outcrops illustrates that the

costs and benefits of pollination mutualisms are influenced by the strength of the interaction among flowers and their pollinators (Guerra et al. 2014).

Mistletoes are known for their particular mutualistic associations with narrow bird guilds that disperse their seeds worldwide (Reid 1991). Birds obtain nutrients from mistletoe fruits, which in turn receive the service of directional seed dispersal onto the host twigs, which are safe sites for establishment (Roxburgh and Nicolson 2005). Seeds require pericarp removal by birds to germinate, as well as deposition on branches with specific diameters on live compatible host species (Sargent 1995). Thus, interaction with seed dispersers is obligate for mistletoes. Nevertheless, mutualism strength among mistletoes and their avian seed dispersers is still poorly known (Watson and Rawsthorne 2013). In this context, Guerra and Pizo (2014) evaluated simultaneously the effectiveness of the avian seed dispersers of the mistletoe *Struthanthus flexicaulis* (Loranthaceae) and the contribution of its fruits to their diets in a CR site at Serra do Cipó.

Fruits are yellow, small, lipid-rich pseudo-berries (Fig. 13.1d) produced asynchronously among individual plants and available throughout the year. Although four bird species were observed feeding on mistletoe fruits, the plain-crested elaenia *Elaenia cristata* (Tyrannidae) was the most effective disperser, responsible for more than 96 % of the seeds dispersed. This bird swallowed fruits whole, expelling and depositing undamaged seeds by regurgitation and bill wiping on perches. Seeds can be dispersed up to 100 m, but most were dispersed within 30 m from the parent-plants, because seed retention time in the disperser's gut is short ($\sim$6 min on average). Fifty-six percent of the dispersed seed land on safe sites: the thin live twigs of 38 potential host species. The avian seed dispersers were predominantly frugivorous, and feed on typically ornithocoric fruits of at least 12 species, but also on arthropods on the foliage. In fact, fruits represented 75 % of the plain-crested elaenia´s diet throughout the year, but the fruits of *S. flexicaulis* represented nearly 34 % of its diet. Those results, published by Guerra and Pizo (2014) corroborated predictions from network studies (Bascompte et al. 2006) highlighting the asymmetrical nature of seed dispersal mutualisms, with the mistletoe life cycle locally linked to one highly effective seed disperser that is weakly dependent on mistletoe fruits.

13.6   Linking Ant Bodyguards to Their Plant and Animal Partners

Ant-plant mutualisms have played a major role in shaping our broad understanding of mutualism (Bronstein et al. 2006). In the tropics, several ant species use plants as a foraging substrate to search for prey and food resources, such as extrafloral nectar and honeydew from trophobiont insects (Blüthgen et al. 2000; Rico-Gray and Oliveira 2007; Rosumek et al. 2009). Those associations between ants and plants can result in obligate or facultative mutualisms, whose mutual benefits will depend on the nature of the interacting species (Bronstein et al. 2006; Rico-Gray and

Oliveira 2007). Moreover, the outcomes of interactions between ants and plants bearing extrafloral nectaries (EFNs hereafter) or trophobiont insects are controversial, and most of them are facultative and dependent on biotic and abiotic conditions (Bronstein 1994).

Two main factors contribute to the high ant abundances found in tropical vegetation. First, the high availability of nesting sites, which are provided by galleries in trunks built by bark beetles and by unoccupied galls after the emergence of insects (Oliveira and Freitas 2004), and second, the high food availability provided by EFNs and insect trophobionts (Blüthgen et al. 2000, 2004). Studies carried out in the Cerrado (Brazilian savanna) showed that plants with EFNs (of at least 15 families) may represent up to 25 % of the species and individual trees in some vegetation (Oliveira and Leitão-Filho 1987; Oliveira and Freitas 2004) and around 30 % of the plants with insect trophobionts (Lopes 1995). Such conditions have made it possible to gather a large amount of information on multitrophic interactions involving ants in this biome (see Del-Claro et al. 2006; Rico-Gray and Oliveira 2007), although some vegetation within the Cerrado domain, such as CR, remain poorly studied. The first survey of extra-floral nectarines is the study from Morellato and Oliveira (1991) for iron-stone outcrops on North Brazil (Serra dos Carajás, Pará). They report 53 % of species (7 out of 13) bearing extrafloral nectaries. However the role of these plant resources on ant community organization still is in the beginning for CR.

The current knowledge on the ant-trophobiont mutualisms in CR is limited to a few studies (Fagundes et al. 2012; Guerra et al. 2011). The sap-feeding stinkbug *Eurystethus microlobatus* (Heteroptera: Pentatomidae) is exclusively associated with woody mistletoes in Serra do Cipó. These stinkbugs have cryptic coloration and maternal care, are gregarious, and produce allomone volatiles, but their most conspicuous defense strategy is ant protection (Guerra et al. 2011). In their study, stinkbugs produced honeydew and four ant species attended to their aggregations. However, *Camponotus rufipes* was the most frequent and aggressive ant species, and the only species that protected stinkbugs by night and day (Fig. 13.1 g). Other ants such *Cephalotes pusillus* and *Camponotus crassus* were less aggressive and mostly diurnal, whereas *Camponotus melanoticus* were was mostly nocturnal. The authors observed that aggregation size positively affect the number of ant attending stinkbugs, but per capita attendance were actually reduced in those very large aggregations. This remarkable interaction represents the only known case of trophobiosis between ants and stinkbugs, and it is the first report of such an association between heteropterans and ants in the American continent (Guerra et al. 2011).

Fagundes et al. (2012) found the trophobiont treehopper *Calloconophora pugionata* (Hemiptera: Membracidae) feeding on *Myrcia obovata* (Myrtaceae) in CR site. They observed that an increase in the number of trophobionts positively affected ant abundance, but negatively affected ant richness. They observed 10 ant species interacting with trophobionts, but *C. rufipes* and *C. crassus* were the most frequent and dominant, and had a negative influence on the occurrence of other species. In another study (Fagundes et al. 2013), the authors evaluated experimentally the role of ant protection against predators and showed that ants increased

the survivorship and reproductive success of the trophobiont *C. pugionata*. Such case studies are highly important, as they describe a new and uncommon ant-hemipteran association and reveal a new kind of mutualism, although the benefits for ants are seldom evaluated (but see an example from the Cerrado, Byk and Del-Claro 2011).

Ants are assumed to be nectar robbers and have limited potential as pollinators (Hölldobler and Wilson 1990; Peakall et al. 1991). However, floral nectar is an essential food for many ant species (Davidson et al. 2003; Blüthgen et al. 2004), and studies on the relationship between ant activities and consumption of floral nectar in CR are scarce. Romero (2002) using termite baits to simulate herbivores on *Vochysia elliptica* (Vochysiaceae) found higher rates of removal by ants in leaves and inflorescences compared to plants without ant access, suggesting that even ant nectar thieves could protect those shrubs from herbivores. Flower-visiting ants may have positive or negative effects on the reproductive success of plants, depending on the context in which the interactions take place (Willmer et al. 2009).

Dáttilo et al. (2014) recorded 20 ant species associated with two plants with EFNs that occur in CR: *Chamaecrista mucronata* (Fabaceae) and *Stachytarpheta glabra* (Verbenaceae). The authors utilized a network approach to show how different ant species are linked to individuals of these two plant species and observed that the core of highly interacting species changed significantly between day and night. These results are important as they demonstrate daily partition of resources by ants, and highlight the need of nocturnal observations to understand the ecological dynamics of ant-plant interactions.

During ongoing studies on ant-plant interactions in CR sites in Serra do Cipó, Costa et al. (in prep.) recorded a multi-relation network formed by 5 types of interaction (subnetworks), 992 interaction events, 79 plant species, and 29 ant species. Seventy percent of those interaction events are neutral visits (ants foraging on the plant), whereas 15 % of interactions involve ants and EFNs, 7 % of interactions are between ants and nectar or pollen, 6 % of interactions are among ants and trophobiont insects, and 1 % of interactions is with fruits(frugivory or visit to extrafloral nectaries on fruits). This myriad of interaction types indicates that ants foraging on vegetation is a common phenomena and that ants could play a major role in interaction networks in CR.

A recent study carried out by Costa et al. (in prep.) in CR of Serra do Cipó indicates a total of 20 % of plants species with secretory structures considered extrafloral nectaries (16 out of 79-species), a result consistent with surveys from Cerrado, which indicate a total of 25 % of plants with have EFNs (Oliveira and Leitão-Filho 1987; Oliveira and Freitas 2004). Six plant families stand out due to the predominance of EFNs at CR: Fabaceae (5 species—e.g., *Bionia coriaceum* Fig. 13.1h), Malpighiaceae (4 species—e.g., *Peixotoa tomentosa* and *Banisteriopsis angustifolia*), Euphorbiaceae (3 species—e.g., *Sebastiania* sp), Asteraceae (2 species—*Symphyopapus reticulatus* and *Baccharis concinna*), Araceae (1 species—*Philodendron cipoense*), and Myrsinaceae (1 species—*Myrsine* sp.). The most common plant families utilized by ants, including all types of resources and neutral interactions were Asteraceae, Velloziaceae, Malpighiaceae, Fabaceae and Myrsinaceae.

At present, most studies focused in the organization of ant trophobiont inter-
actions at the community level in tropical forests (Blüthgen et al. 2000), with no
data available for CR sites. In areas of CR, 26 % of the plant species have estab-
lished aggregations of hemipteran trophobionts (Costa et al. in prep), most of them
members of the families Aphididae (e.g., *Aphis spiraecola* Fig. 13.1f) and Coccidae
(e.g., *Parasaissetia nigra*). Considering together the ant fauna associated with
EFNs and honeydew, a total of five subfamilies in which the most frequent ant
species were *C. pusillus*, *C. crassus*, *C. rufipes* and two species of *Brachymyrmex*
genus (unidentified). Together these five species were responsible for 73 % of the
observed interactions during daily samplings, with *C. pusillus* and *C. crassus* being
the most frequent species (29 and 13 % respectively) (Costa et al. in prep).

Structural organization of ant-EFNs interactions in CR (Fig. 13.3), suggest that
network topology is not modular with low level of specialization. In the contrary,
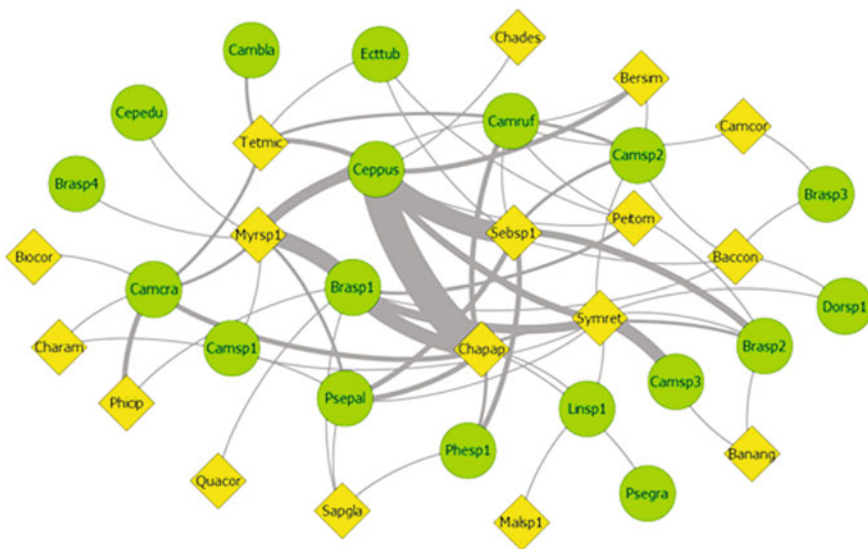

Fig. 13.3 The network formed between ants (*circles*) and plants with extrafloral nectaries
(*diamonds*) in *Campo Rupestre* site at Serra do Cipó, southeastern Brazil. *Lines* represent
interactions, and line thickness is proportional to interaction frequency. Plant species—Baccon:
Baccharis concinna; Banaug: *Banisteriopsis angustifolia*; Bersim: *Bernardia similis*; Biocor:
Bionia coriacea; Camcor: *Camptosema coriaceum*; Chades: *Chamaecrista desvauxii*; Chapap:
Chamaecrista papillata; Charam: *Chamaecrista ramosa*; Malsp1: Malpiguiaceae sp1; Myrsp1:
Myrsine sp1; Peitom: *Peixotoa tomentosa*; Phicip: *Philodendron cipoensis*; Quacor: *Qualea
cordata*; Sapgla: *Sapium glandulatum*; Sebsp1: *Sebastiania* sp1; Symret: *Symphyopapus reticu-
latus*; Ant species—Brasp1: *Brachymyrmex* sp1; Brasp2: *Brachymyrmex* sp2; Brasp3:
Brachymyrmex sp3; Brasp4: *Brachymyrmex* sp4; Camcra: *Camponotus crassus*; Camruf:
Camponotus rufipes; Camsp1: *Camponotus*(*Tanaemyrmex*) sp1; Camsp2: *Camponotus*
(*Myrmaphaenus*) sp2; Camsp3: *Camponotus*(Myrmaphaenus) sp3; Cepedu: *Cephalotes eduarduli*;
Ceppus: *Cephalotes pusillus*; Dorsp1: *Dorymyrmex* sp1; Ecttub: *Ectatomma tuberculatum*; Linsp1:
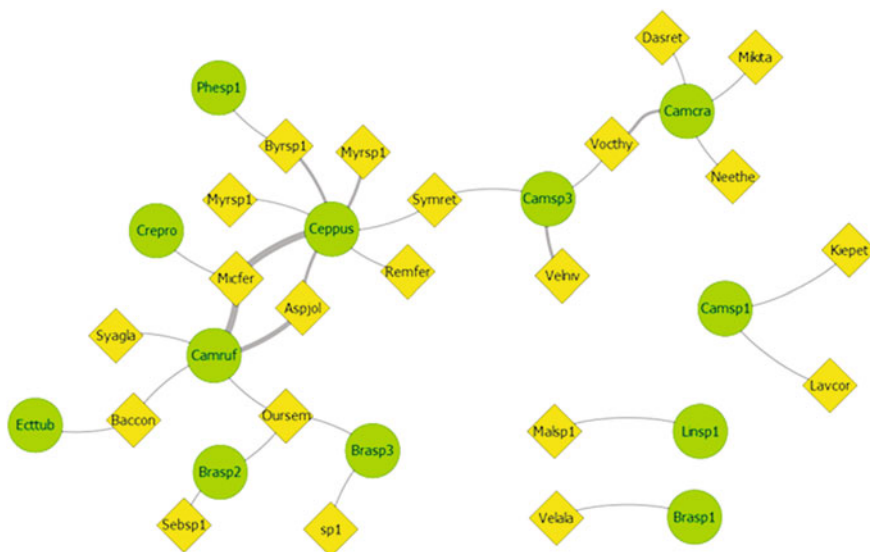*Linepithema* sp1; Phesp1: *Pheidole* sp1; Psesp1: *Pseudomyrmex* sp1; Psesp2: *Pseudomyrmex* sp2

Fig. 13.4 The network formed between ants (*circles*) and plants with trophobiont insects (*diamonds*) in *Campo Rupestre* vegetation of Serra do Cipó, southeastern Brazil. *Lines* represent interactions, and line thickness is proportional to interaction frequency. Plant species—Aspjol: *Aspilia jolyana*; Baccon: *Baccharis concinna*; Byrsp1: *Byrsonima* sp1; Dasret: *Dasyphyllum reticulatum*; Kiepet: *Kielmeyera petiolaris*; Lavcor: *Lavoisiera cordata*; Malsp1: *Malpighiaceae* sp1; Micfer: *Miconia ferruginata*; Mikita: *Mikania itambana*; Mycsp1: *Myrcia* sp1; Myssp1: *Myrsine* sp1; Neethe: *Neeatheifera*; Oursem: *Ouratea semiserrata*; Remfer: *Remijia ferruginea*; Sebsp1: *Sebastiania* sp1; Sp1: unidentified; Syagla: *Syagrus glaucescens*; Symret: *Symphyopapus reticulatus*; Velala: *Vellozia alata*; Velniv: *Vellozia nivea*; Vocthy: *Vochysia thyrsoidea*; Ant species—Brasp1: *Brachymyrmex* sp1; Brasp2: *Brachymyrmex* sp2; Brasp3: *Brachymyrmex* sp3; Camcra: *Camponotus crassus*; Camruf: *Camponotus rufipes*; Camsp1: *Camponotus*(*Tanaemyrmex*) sp1; Camsp3: *Camponotus* (*Myrmaphaenus*) sp3; Ceppus: *Cephalotes pusillus*; Crepro: *Crematogaster*prox. *erecta*; Ecttub: *Ectatomma tuberculatum*; Linsp1: *Linepithema* sp1; Phesp1: *Pheidole* sp1

ant-trophobiosis subnetwork (Fig. 13.4) are modular and have higher specialization values. Through network structure it is possible to visualize that ant-trophobiont interactions, in opposition to ant-EFNs, forms distinct modules or groups of interactions, which suggest certain resource partitioning by ants. In fact, some field observations at Serra do Cipó, as well as previous studies performed in other ecosystems (Del-Claro and Oliveira 1993; Blüthgen et al. 2000), suggest that amino acid-rich honeydew is a more valuable resource than extrafloral nectar, being frequently monopolized by colonies of dominant ants.

Despite structural differences between EFN and trophobionts subnetworks, they share the five most central ant species (measured by number of interactions made by the species): *C. pusillus*, *C. rufipes*, *C. crassus*, and two unidentified species of *Brachymyrmex* genus. It seems that relatively few ant species are involved in those interactions with EFN-producing plants and trophobionts insects in CR sites, especially when we consider the huge richness recently proposed for these

environments—around 288 species (Costa et al. 2015). In fact, the same ant species, *C. rufipes*, *C. crassus* and *C. pusillus* have consistently been associated to different liquid resources in different localities in CR and Cerrado sites, suggesting that they can be considered keystone species for ant-plant interactions, mainly mutualisms involving extrafloral nectar and honeydew. However, the role of these ants as bodyguards of plants and insect trophobionts, the benefits provided by these liquid sources for ant colony fitness as well the degree of interactions intimacy need further investigations in CR.

13.7 Concluding Remarks

The investigations regarding mutualisms among free-living species in CR started with pollination studies in the 70s, but only in the past decade have these interactions received more attention by ecologists. Despite an increase in the number of studies, the information remains scattered and concentrated for few localities, such Serra do Cipó and Chapada Diamantina mountains. The compilation presented in this chapter clearly indicates that the ecology of mutualisms in CR is still in its infancy and that there is lot of work ahead. However, some patterns have emerged and could serve as starting points for further investigations.

Despite the relatively crescent number of studies regarding interactions between flowers and theirs visitors in CR, the role of animals as effective pollinators or cheaters (e.g. thieves or robbers) remain poorly known. Bees and hummingbirds have been reported as the main flower visitors of CR plants, but pollination by other groups such, butterflies, moths, and bats need better evaluation in the future. Breeding biology of few species have been studied in detail so far, the available data indicate that pollination systems are diverse varying form highly specialized to more generalized. In the future it would be very important to determine the degree of specialization in pollination systems and the degree of plant dependence on their pollinators, especially for those endemic and threatened species.

Seed dispersal of CR plants is virtually unknown, as there is information available for too few species. For now we can only conclude that most vertebrate seed dispersal is carried out by birds, and to a lesser extent by ants and lizards. Because bird communities encompasses mostly non specialized frugivorous species, with few species relying only partially on fruits, we could expect a weak degree of interdependence among CR plants and avian frugivores, or at best, highly asymmetric degrees of interdependence among them. Nevertheless, the role of birds, lizards, mammals and ants as primary and secondary seed dispersers, or predators, remain poorly investigated. Additional studies determining structure of plant-frugivore networks in CR are deeply needed.

Ants seem to play a major hole in CR ecosystems, due their abundance and the diversity of interactions in which they are involved. Ants may act as seed dispersers, as nectar thieves, as bodyguards of myrmecophilous plants and trophobiont insects in CR. The studies encompassing a network approach applied to ant-plant

and ant-insect interactions at the community level, associated with knowledge of natural history of these interactions, could bring insights on the ecology and evolution of protective mutualisms, particularly in megadiverse environments such as the CR. The next step is to extend the studies of ant-plant mutualisms to larger scales along the Espinhaço range and experimentally explore the possible outcomes of these interactions subjected to context-dependent variations.

The results of Carstensen et al. (2014) have provided important insight into the ecology of mutualisms in CR. The authors observed that even in small spatial scales there is a high site turnover in plant-pollinator interactions and this pattern could be a pervasive feature of all mutualistic interactions reported in this chapter, not only pollination. Many CR species have restricted distribution, while other species are more widespread. Besides, species distribution in CR are subject to high variation due the altitudinal and latitudinal gradients (Chap. 15). The matches and mismatches in partners` distributions could generate selection mosaics of interactions, thus CR could be a natural laboratory to explore predictions from the theory of coevolutionary mosaics proposed by Thompson (2005). To understand how coevolutionary processes shape the mutualistic interactions in CR is important to start long term studies of mutualistic interactions on broader spatial and temporal scales.

The study of community organization using mutualistic networks in CR is just at the beginning. Now is the time to start applying these ecological tools for biodiversity conservation. *Campo Rupestre* ecosystems are subject to intensification of fire regimes, mining, road construction and biological invasion (Fernandes et al. 2014). The way these negative impacts affect community organization and structure of mutualistic networks will require further investigations. Besides, mountain tops all around the world figure amongst the most threatened ecosystems by the global warming predicted for the next century (Colwell et al. 2008). Therefore, we suggest that standardized protocols for assessment and long term monitoring of mutualistic networks involving animals and plants in *Campo Rupestre* could be a useful tool for the evaluation of global warming effects on the biodiversity of tropical mountain tops.

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