Review Article

THE IMPORTANCE OF NATURAL HISTORY STUDIES FOR A BETTER COMPREHENSION OF ANIMAL-PLANT INTERACTION NETWORKS

A IMPORTÂNCIA DE ESTUDOS SOBRE HISTÓRIA NATURAL PARA A MELHOR COMPREENSÃO DAS REDES DE INTERAÇÕES ANIMAL-PLANTA

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ABSTRACT: The central tendency in ecological studies to explain variations in the outcomes of biotic interactions is to suppose that the majority of meaningful functional diversity occurs at the species level. However, individuals are rarely identical and behavioral ecology shows that consistent individual differences alter the roles that individuals play within populations and possibly communities, but the intraspecific variation is commonly ignored in studies of species interactions. Here, throughout examples of field work studies, we discuss that the knowledge of individual aspects (including genetic variation) and natural history are basic tools and fundamental to a real and whole comprehension of species interaction networks in qualitative and quantitative terms.

KEYWORDS: Ant. Biodiversity. Cerrado. Fructification. Life history. Phenology.

INTRODUCTION

The success of life on Earth is directly associated to the success of biotic interactions. Everywhere, in the air, water, ground, over or inside organisms, whether big or small, biotic interactions are present. The richness of biotic interactions (“interaction biodiversity”, sensu THOMPSON, 1997) has been pointed out as the main force responsible for the biodiversity that maintain viable communities. In a more recent and realistic perspective biodiversity should be viewed and evaluated also in ways that embrace the extreme richness inherent in plant animal interactions, including not only trophic relationships, but also aspects of life histories, biology and behavior of related species (PRICE, 2002; DEL-CLARO, 2004). Despite ubiquitous the outcomes of each interaction vary depending on physical and biotic changes in the environment. Thus, there is no mutualism, for example, that will be ever and unconditionally a mutualism. Same parasitic or predatory relationships may suffer changes more slowly or quickly over evolutionary time that can drive the results of the interaction in a different direction (see DEL-CLARO; TOREZAN-SILINGARDI, 2012, for a review). The central tendency in ecological studies to explain these variations is to suppose that the majority of meaningful functional diversity occurs at the level of the species and intraspecific variation is commonly ignored (PRUITT; FERRARI, 2011). Nevertheless, individuals are rarely identical and behavioral ecology, for example, has showed that consistent individual differences in personality and/or temperament may alter the roles that individuals play within populations and possibly communities (e.g. SIH et al., 2004, 2012; PRUITT; FERRARI, 2011). Thus, the knowledge of individual aspects (including genetic variation) and natural history are fundamental to the study of biodiversity.

DEVELOPMENT

Discussing the importance of natural history studies on animal and plant interactions

Among all group of interactions, those between animals and plants have been pointed out as the main interactions responsible for the functioning and maintenance of trophic chains in all ecosystems and for the patterns and process that structure biodiversity on Earth (THOMPSON, 1994, 2005; DEL-CLARO; TOREZAN-SILINGARDI, 2009, 2012). In these systems, changes in the outcomes of interactions between seasons and/or years are common and represent a clear example of how important the study of natural history of related species to the real understanding of interactions is. For example, although greatly recognized as relevant, plant phenological variations are rarely considered in studies of plant-animal network interactions.

Recently Torezan-Silingardi (2007) and Vilela (2010) showed the relevance of phenological events to herbivores networks. Studying a group of Malpighiaceae species in the tropical savanna these

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authors showed that pollinators, herbivores and their predators, all may move on among host plants over the year. The change between plant species is influenced by which host species is offering itself as resource at that time (i.e. young leaves, blossoms, petals). In some cases, herbivores (more than 300 species), including florivores that can be generalists or specialists, were associated with one to six different plant species. Both authors showed that the sequential resprouting and flowering of Malpighiaceae species in the Cerrados provided food and shelter that sustain a great guild of herbivores in a very seasonal environment. Torezan-Silingardi (2007) also showed that several species of endophytic beetles (mainly Curculionidae, Figure 1a) that move on from one host plant to another, following the hosts plants species sequential resprouting and flowering, brings its predators together and influencing the fructification (TOREZAN-SILINGARDI, 2011a, Figure 1a). It emphasizes the importance of links between the natural history of related species to the comprehension of connections in trophic chains (TOREZAN-SILINGARDI, 2011b).

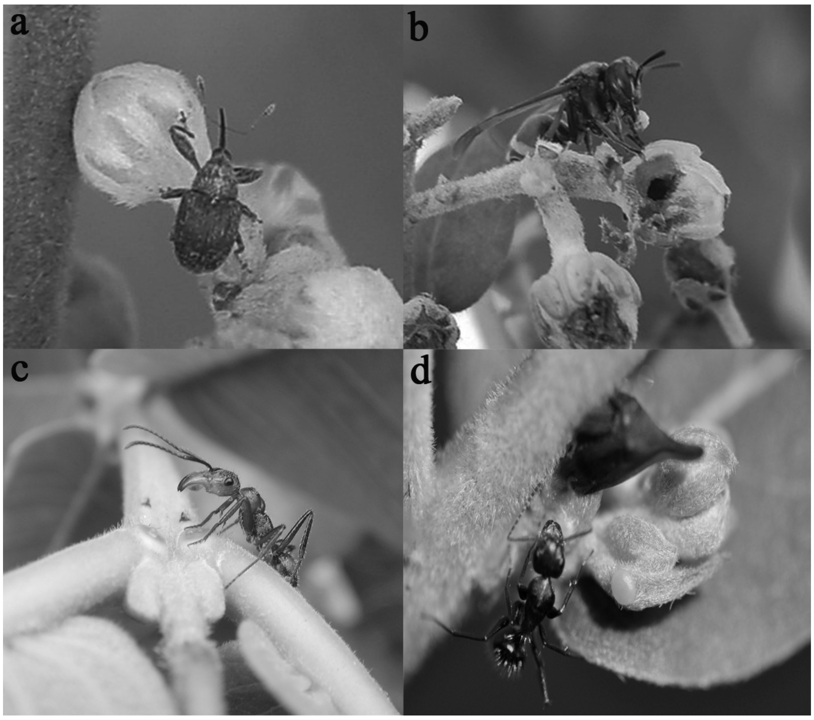

Figure 1. Herbivores (a – Curculionidae beetle – *Antonomus* sp.) can move on among host plants over time, attracting predators like wasps (b – *Brachygastra lecheguana* (Latreille, 1824) preying an endophytic beetle larva). Plants can offer resources, like extrafloral nectar (c – *Ectatomma tuberculatum* (Olivier, 1792) visiting EFNs in *Qualea multiflora*) or host trophobiont herbivores, like membracids (d – *Camponotus crassus* Mayr, 1862 tending a membracid in an EFN bearing Malpighiaceae) that also feed and attract ants that can prey on or chase herbivores.

Ant-plant-herbivore interactions

Literature on ant-plant-herbivore interactions is full of examples in which ecological studies overlooked the importance of individual variation and natural history studies. Myrmecophilous plants may offer as resources to ants: a) shelter (domatia and dead or hollow trunks) where they can build nests (RICO-GRAY; OLIVEIRA, 2007; SANTOS; DEL-CLARO , 2009); and b) food, mainly extrafloral nectar (LACH et al., 2009; BYK; DEL-CLARO, 2011, Figure 1c) and/or hemipteran (DEL-CLARO, 2004, Figure 1d) or lepidopteran exudates (FIEDLER; SAAM, 1995). In retribution, ants can benefit the plants mainly due to the removal of herbivores, reducing leaf are loss (KÖRNDORFER; DEL-CLARO, 2006) and increasing fruit set production (NASCIMENTO; DEL-CLARO, 2010). In the Brazilian tropical savanna, the membracid *Guayaquila xiphias* (Fabricius, 1803) (Hemiptera: Membracidae) has as host plant an Araliaceae, *Schefflera vinosa* (Cham and Schltdl.). In a series of publications (see DEL-CLARO; OLIVEIRA, 2000; OLIVEIRA et al., 2012, and citations therein) researchers showed that more than 21 different ant species tend the membracids providing them protection against natural enemies (mainly spiders and parasitoid wasps) increasing bug survivorship and reproduction. However, the benefits provided by ants vary over time depending on ant species behavior and the intensity and quality of enemy attack. In a similar system, Stefani and Del-Claro (2005) also showed that the benefit can be extended to the host plant, through the reduction of herbivory level, also dependent on the life history and behavior of associated ant species. Indeed, particular characteristics of ant species, like size (DEL-CLARO; MOUND, 1996), and/or behavioral aspects that vary intraspecifically, can interfere in the outcomes of these interactions. In the cited examples, the same interactions can have a mutualistic or parasitic character depending on a combination of associated natural histories. In both studies, authors needed one year of natural history studies in field to get to know the system and to elaborate a coherent protocol for experimental manipulations that answered their questions.

Ecosystem Engineers

The bottom-up forces in trophic chains, mainly herbivores, can alter plant architecture and influence on the whole chain that just one host plant sustains depending on species life histories and behavior. In natural environment some organisms can modify aspects of their niche making it more favorable to their existence. These transformations will affect other organisms and interactions during the life time and after the death of its creators. These animals are named "ecosystem engineers". Work to modify the environment is known for more than 150 years when Darwin firstly discussed the importance of worms in plant development (DARWIN, 1881). However, only recently the idea of ecosystem engineering was shaped, linking population ecology to ecosystem theory (JONES et al., 1994).

The first effect of ecosystem engineering is the modulation of available resources to other species, in a direct or indirect manner, which is caused by the modification produced by these animals in the physical state of biotic and abiotic materials (BERKE 2010). This interference in the habitat will influence the distribution and abundance of other organisms that use the same resource (LILL; MARQUIS 2007). In a recent research in the Brazilian Cerrado, Velasque (2011) showed the relevance of natural history and basic biology studies of ecosystem engineers to understand their impacts on the trophic chain they are involved in. During three years of field work, Velasque (2011) studied the interaction between the host plant *Byrsonima intermedia* A. Juss (Malpighiaceae) and its main herbivore, the larvae of the moth *Cerconota achatina* (Zeller, 1855) (Oecophoridae). The moth larvae is a concealed herbivore (Figure 2a) that attach host plant leaves, producing a shelter like a cigar, so called "cigar-moth shelter". In some cases more than 200 larvae are on the same plant and almost all stems of the plant present a cigar-moth shelter which greatly alters plant architecture (Figures 2b).

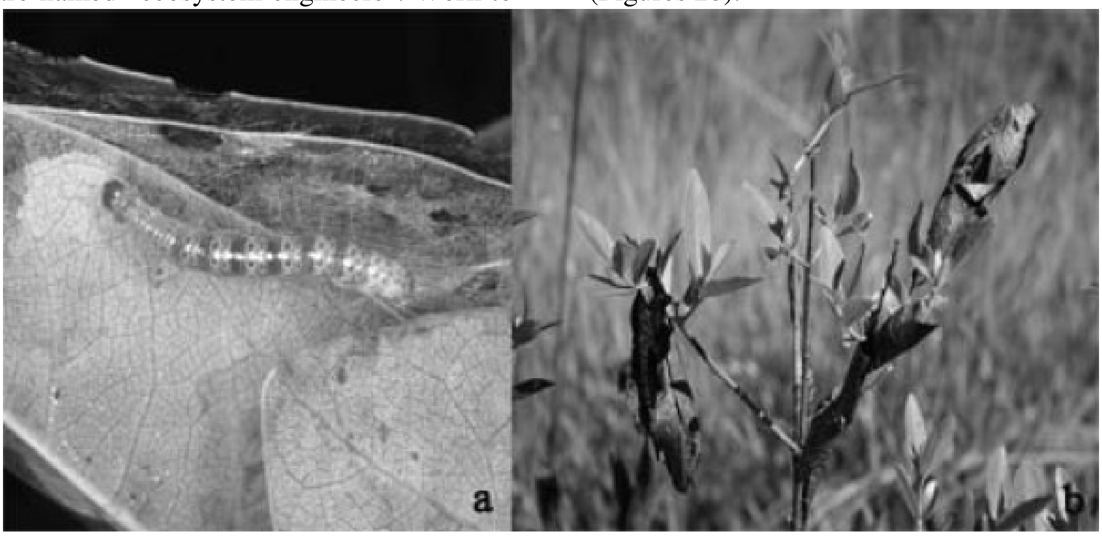

Figure 2. a) Moth larva, *Cerconota achatina* (Oecophoridae) in *Byrsonima intermedia* (Malpighiaceae). b) The moth larva is a concealed herbivore that attacks host plant leaves, which greatly alters plant architecture. Moth herbivore induces resprouting in the attacked plant stems.

Cigar-moth shelters can vary in size (length and thickness) depending on the position of steam (having small size in the apical meristem) and the number and behavior of larvae inside. The modification in plant architecture can directly benefit the larvae protecting them against adverse climatic conditions (excess of wind, sun, storms), natural enemies (i.e. ants; parasitoids; BÄCTHOLD et al., 2012) and also altering leaf chemistry, making it more palatable to the moth (see LILL; MARQUIS, 2007). In all phases the shelter can be used by a wide range of different animals including spiders, aphids and orthopterans, while larvae are still inside the cigar. When larvae leave the shelter, the structure now formed by dried leaves remains in the plant for several months and can be used by ants and same frogs and mice. The impact of this additional fauna on the host plants is unknown. However, the moth herbivore induced resprouting in the attacked plant stems (Figure 2b), and more infested plants produced more inflorescences and fruit. We suspect that specific plant individual characteristics (i.e. genetics, nutrition) will have a direct impact on resprouting and future flourishment. In a final analysis these impacts will also directly reflect on the next moth cycle. Furthermore, Velasque (2011) showed that the outcomes of this interaction vary strongly over time. Data like these can be obtained only with a consistent and permanent field work, taking into account the natural history of involved species and individual genetic analysis.

Spider-plant interactions

Turning our attention to the top-down forces in studies of multitrophic interactions it becomes still clearer how animal behavior and natural history of related species can produce strong variation in the results of interactions and in all levels of biodiversity. Spiders are among the most diverse animal taxa (more than 42.700 species according to PLATNICK, 2012) occurring in all terrestrial ecosystems (FOELIX, 2011). When foraging in vegetation spiders can positively interact with plants reducing herbivores abundance (ROMERO; VASCONCELLOS-NETO, 2004). Despite being known as an aggressive arthropod predator in some families (Anyphaenidae, Corinnidae, Clubionidae, Oxyopidae, Thomisidae and Salticidae) there are species that feed on plant resources, like nectar and pollen (SMITH; MOMMSEN, 1984; TAYLOR; FOSTER, 1996; TAYLOR; PFANNENSTIEL, 2008). Thomisidae is a family with several species that forage on flowers, and in a very interesting study of behavioral ecology and natural history. Pollard et al. (1995) showed that males of *Misumenoides formosipes* (Walckenaer, 1837) (Araneae: Thomisidae) also feed on floral nectar. The sugar obtained in nectar seems to be essential to the success of males to challenge rivals and to get access to females. Indeed, Jackson et al. (2001) showed that in laboratorial conditions more than 90 Salticidae species are able to feed on nectar, however, the histories behind each species and its interactions with plants are still not explored.

Colonial arachnids are in some circumstances treated as a superorganism due to the fact that grouped individuals share a strong genetic resemblance, have a common nest and feed and protect the colony in a cooperative manner (see DEL-CLARO; TIZO-PEDROSO, 2009; TIZO-PEDROSO; DEL-CLARO, 2011 and citations therein). In Australia, *Phryganoporus candidus* (L. Koch, 1872) (Desidae) is a subsocial spider whose individuals attach the leaves and stems of *Acacia ligulata* A. Cunn. ex Benth, 1842 (Fabaceae) with silk to build its nest (WHITNEY, 2004). Field experiments showed that larger colonies of *P. candidus* occur significantly more in *A. ligulata* than in other plants. In this interaction spiders benefit from the plant not only preying on herbivores, but also feeding on extrafloral nectaries (EFNs). On the other hand, plants are also benefitted by a reduction in fruit herbivory (WHITNEY, 2004).

Recently, Nahas et al. (2012) showed that also in Brazilian Cerrados spiders use EFNs as a resource. *Qualea multiflora* Mart. (Vochysiaceae) is a common Cerrado tree that has EFNs in the basis of leaves attracting ants that protect the plant against herbivores action, reducing leaf area loss and increasing fruit set production (DEL-CLARO et al., 1996). However, spiders are also abundant in leaves and flowers of this plant, preying on arthropods and feeding on EFNs (Figure 3). Multiple predators often have effects on their common prey populations that cannot be predicted by summing the effects of each predator at a time. When predators forage on the same vegetation substrate, intraguild interactions might cause emergent outcomes for the plants on which the predators co-occur. In field conditions, Nahas et al. (2012) experimentally evaluated the effects of spiders and ants on herbivory and reproduction of *Q. multiflora* dividing the trees in four experimental groups, depending on the presence or absence of ants and spiders. Results showed that the presence of ants reduced the abundance and richness of spiders, but spiders did not affect the abundance and richness of ants. Only the removal of ants resulted in a statistically significant increase in the abundance of herbivores and herbivore richness. In addition, authors found a significant interaction effect of ants and spiders on herbivory, indicating an emergent multiple predator effect. This study highlights the importance of evaluating the effect of the predator fauna as a whole and not only one specific group on herbivory.

Figure 3. The spider *Oxyopes macroscelides* Mello-Leitao, 1929 (Oxyopidae) feeding on extrafloral nectar (EFN) of *Qualea multiflora* (Vochysiaceae).

However, spiders can also prejudice plant-arthropod mutualistic relationships. Dukas and Morse (2003) showed that spiders can disturb pollinators that visit *Asclepias* shrubs (Apocynaceae). In the flowers of *Leucanthemum vulgare* Lamarck (Asteraceae), Suttle (2003) observed that the presence of spider *Misumenops schligeri* Schick, 1965 (Thomisidae) caused a significant reduction in pollinators visits (almost 40%) and seed production. Thomisidae family has species with a complete different life history than Salticidae, Clubionidae and Oxyopidae. Remaining more time on flowers and inflorescences, Thomisidae will interact and prey on pollinators more commonly. While Salticidae, Clubionidae and Oxyopidae hunt over or under leaves and stems, rarely interacting with pollinators, but commonly preying herbivores. Again, studies of natural history of each species involved in a multitrophic relationship are essential for a true comprehension of the role that each species play in a particular scenario.

Network of interactions

The scale of possible interactions among organisms is astonishingly diverse (e.g. BRONSTEIN, 2009; DEL-CLARO; TOREZAN-SILINGARDI, 2012) and the analysis of these relationships by means of interaction networks has been considered fundamental for the comprehension of specialization patterns in plants and animals (BASCOMPTE; JORDANO, 2007; LEWINSOHN; CAGNOLO, 2012). Technically, the structure of species interaction networks can have five distinct patterns: extremely generalist, nested, compartmented, combined or in gradient (see LEWINSOHN et al., 2006; BASCOMPTE; JORDANO, 2007, for details). Studies suggest that differences in network structure are related to the type of effective interactions, i.e. the connections (JORDANO et al., 2003). Thus, mutualistic interactions like plants-pollinators and ants-EFNs bearing plants have a nested pattern (BASCOMPTE et al., 2003; GUIMARÃES et al., 2006, 2007), while nets of antagonistic relationships like plants and herbivores have a compartmented structure (LEIBOLD; MIKKELSON, 2002). Notwithstanding, some recent papers also found trophic chains (predator-prey interactions) with nested patterns (SELVA; FORTUNA, 2007; JOPPA et al., 2010; KONDOH et al., 2010) and compartmented plant-pollinator systems (DICKS et al., 2002). Possible answers to these differences can be related to ecological and evolutionary processes that affected species over time (LEWINSOHN et al., 2006), including the coevolutionary changes directly influenced by the different ecological roles that species can play in communities in distant geographic areas or evolutionary times (THOMPSON, 2005; BLÜTHGEN; KLEIN, 2011; BLÜTHGEN, 2012). In this sense, networks have been also used in studies of niche specializations and generalization of interacting species (BLÜTHGEN; KLEIN, 2011). There is no doubt, that studies of species interaction networks are considered as an important tool in the understanding of patterns and process that maintain biodiversity in natural communities.

However, despite the extensive use of interaction network studies in the last decade trying to explain patterns and process of diversity in natural communities, studies involving interactions among animals are still rare (see STOUFFER et al., 2012). Zoological aspects of animal-animal and same animal-plant interactions, like individual behavioral and genetic variations, are extensively ignored. Indeed, most published papers using network analysis to study interactions only present records of species connections performed in basic matrixes of connect or not connected links represented by 0s and 1s (presence and absence). There is a clear lack of data quantifying these interactions and showing the real nature of each interaction, which can only be provided by complementary natural history studies. For these reason, network analysis is often disconnected from community ecology and is a long away from its purposes (see BLÜTHGEN, 2010).

We summarize our arguments in favor of increasing and encouraging natural history studies in the last figure of this manuscript (Figure 4): ecological studies recognize that plant-animal populations are integrated in evolutionary old interactions that were selected over geographic and evolutionary time, establishing communities and maintaining patterns of diversity in the ecosystems. However, intraspecific variation (genetics), natural history and phenological development, despite being basic tools for the comprehension of outcomes as to plant-animal interactions in all trophic levels are commonly ignored. We expect that the examples shown here have been sufficient to support our strong suggestion that natural history studies are basic tools and fundamental for the whole comprehension of species interaction networks in qualitative and quantitative terms. In a qualitative manner, as only through knowing the character and possible variations in each link (interaction) inside each node of a network will we be able to know the role of each species in a multitrophic system. Quantitative, because variation in total observation frequencies (that which is rare in species interaction network studies) may explain network patterns on their own (see BLÜTHGEN, 2010, 2012).

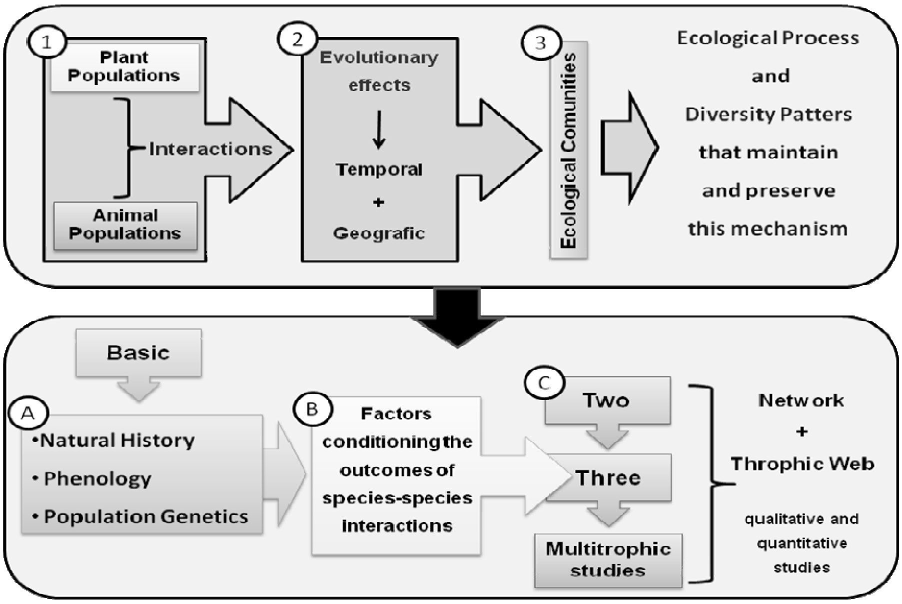

Figure 4. Ecological studies recognize that plant-animal populations are integrated in evolutionary old interactions (1) which have been selected over geographic and evolutionary time (2) establishing communities (3) and maintaining patterns of diversity in ecosystems. However, intraspecific variation (genetics), natural history and phenological development (A), despite being basic tools for the comprehension of outcomes in plant-animal interactions (B) in all trophic levels (C), they are commonly ignored. We strongly suggest that these basic tools are fundamental to a more accurate comprehension of species interactions network in qualitative and quantitative terms.

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RESUMO: A tendência central em estudos ecológicos para explicar as variações nos resultados das interações bióticas é supor que a maioria da diversidade funcional significativa ocorre em nível de espécie. No entanto, indivíduos raramente são idênticos e a ecologia comportamental mostra que as diferenças individuais alteram os papéis que cada um desempenha dentro das populações e possivelmente dentro em comunidades; e essa variação intraespecífica é comumente ignorada em estudos de interações entre espécies. Aqui, por meio de exemplos de estudos de trabalho de campo, discutimos que o conhecimento de aspectos individuais (incluindo a variação genética) e história natural são ferramentas básicas e fundamentais para uma compreensão real e mais ampla sobre redes de interação entre espécies, em termos qualitativos e quantitativos.

PALAVRAS-CHAVE: Biodiversidade. Cerrado. Fenologia. Formigas. Frutificação. História de vida.

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