



Assessing the impacts of tramp and invasive species on the structure and dynamic of ant-plant interaction networks



Jéssica C.F. Falcão^{a,1}, Wesley Dáttilo^{b,*}, Cecilia Díaz-Castelazo^c, Victor Rico-Gray^a

^a Instituto de Neuroetología, Universidad Veracruzana, Av. Dr. Luís Castelazo s/n, 91190 Xalapa, Veracruz, Mexico

^b Red de Ecoetología, Instituto de Ecología A.C., Carretera antigua a Coatepec 351, CP 91070 Xalapa, Veracruz, Mexico

^c Red de Interacciones Multitróficas, Instituto de Ecología A.C., Carretera antigua a Coatepec 351, CP 91070 Xalapa, Veracruz, Mexico

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ABSTRACT

Ants are among the most widespread and damaging of introduced organisms. In the last decade, many studies have documented the negative impact of tramp and invasive ant species (TIS) on native ant species mainly through competitive displacement and behavior. However, despite the great advances in the knowledge of TIS, still little is known about the impacts of these ants on the trophic cascade. In this study we used an approach based on network theory to explore the impact of TIS on the structure and ecological dynamic of a well-sampled and well-known community of ant-plant interactions in a tropical environment in coastal Veracruz, Mexico. We observed that of all the ant-plant interactions recorded, only 15% involved TIS and the ant *Paratrechina longicornis* (Formicinae) was the unique tramp species to be part of the central core of highly interacting species. We also found that TIS had little impact on the structure and dynamic ant-plant interactions in our study area, although possible indirect effects for specific TIS are also discussed. This study represents a valuable tool to conservation planners, mainly because we show the vulnerability and robustness of a tropical system rich in species and interactions to biological invasions.

1. Introduction

Ants are among the most widespread and damaging of introduced organisms (Holway et al., 2002). Worldwide, approximately 150 ant species are reported as introduced into new environments by humans (McGlynn, 1999). Most of these ants are associated to human-modified habitats and because of that are often referred as tramp and invasive ant species (hereafter TIS) (Passera, 1994). In general, TIS are polygynous and have omnivorous supercolonies that can reach up to billions of workers, which allows them to explore different types of environments under different conditions (Moffett, 2012). Many studies have documented the disappearance of native ant species from areas invaded by TIS mainly through competitive displacement (e.g., TIS can raid nests of other species, show physical and chemical aggression, and forage both during day and night) (reviewed by Holway et al., 2002). Negative effects of TIS on the growth and/or survival of organisms are not limited to native ant species, but also to other animal and plant species in an environment (Holway et al., 2002; Pignati et al., 2011).

Although much is known about the effects of TIS on native ant species, still little is known about the impacts of these ants on the trophic cascade at the community level (but see Lach, 2003; Ness and

Bronstein, 2004). Due to their high diversity and abundance, ants interact with many organisms in different ways and, therefore, play an important role in the structure and stability of biological communities (Rico-Gray and Oliveira, 2007). One of the most remarkable ecological interactions in tropical environments occurs between extrafloral nectar-bearing plants and ants. In this interaction, plants provide nectar, a highly nutritious food resource, while ants protect them against potential herbivores (Del-Claro et al., 2016). Over space and time, these ant-plant interactions generate complex networks composed of several species that interact among them, generating new properties in the collective behavior. An excellent tool used to study these complex ant-plant interactions is derived from graph theory, which uses a set of mathematical abstractions to identify and connect links that represent interactions between species. Despite the recent advances in the knowledge about the structure and dynamic of ant-plant networks (see Cagnolo and Tavella, 2015; Del-Claro et al., 2016), little is known about the impacts that invasive species can have on those networks. To the best of our knowledge, only one study considered the impact of exotic species on ant-plant networks. In this case, the author shows that ecological interactions involving exotic species (including both ants and/or plants) can represent up to 82.5% from all ant-plant interactions

* Corresponding author.

E-mail addresses: wdattilo@hotmail.com, wesley.dattilo@inecol.mx (W. Dáttilo).

¹ Present address: Red de Estudios Moleculares Avanzados, Instituto de Ecología A.C., Carretera antigua a Coatepec 351, CP 91070 Xalapa, Veracruz, Mexico.

observed on islands in the Pacific Ocean (Sugiura, 2010). Indeed, the effect of invasive species on the trophic cascades and the structure of interactive communities have only recently begun to engage attention of ecologists (Aizen et al., 2008; Abe et al., 2011; Heleno et al., 2013; Stouffer et al., 2014).

In a rich system of both species and ant-plant interactions located in a coastal environment in the Gulf of Mexico, the introduction of the longhorn crazy ant has been reported since 1990 (*Paratrechina longicornis*) (Díaz-Castelazo et al., 2010). *P. longicornis* is apparently native to Southeast Asia and Melanesia (Wetterer, 2008). Surprisingly, in a little over ten years, the TIS species already represented about 17% of the total ant richness in that environment (Díaz-Castelazo et al., 2013). However, despite the knowledge about the introduction and fast establishment of TIS in the area, its effects on the structure of ant-plant interactions remains yet to be determined. In this study we used an approach based on network theory to explore the impact of TIS on the structure and ecological dynamic of a well-sampled and well-known community of ant-plant interactions in a tropical environment in coastal Veracruz, Mexico. Specifically, we evaluated the strength and contribution of TIS to the structure of the ant-plant networks. Additionally, because ant-plant interactions in the study site are highly dynamic over time (Falcão et al., 2016), we also evaluated how the variation in the presence of TIS species over a year of sampling could affect the dynamic of the ant-plant networks.

2. Materials and methods

2.1. Study area

The study was conducted at Centro de Investigaciones Costeras La Mancha (CICOLMA), located on the coast of the state of Veracruz, Mexico (19°36' N, 96°22' W, elevation < 100 m). The climate is warm and subhumid, with annual means of rainfall and temperature of approximately 1500 mm and 25 °C, respectively. Our study area experiences three well-defined seasons: dry season from February to May, rainy season from June to September, and a cold front season from October to January (Moreno-Casasola, 2006). The major vegetation types at CICOLMA are tropical deciduous forest, tropical dry forest, sand dune scrub, mangrove forest, freshwater marsh, and flooded deciduous forest (surrounding a freshwater lagoon) (Rico-Gray, 1993).

2.2. Field observations and data collection

We sampled ant-plant interactions biweekly between May 2010 and April 2011, always between 08:00 and 13:00 h. Field observations were conducted along six arbitrarily selected but representative 1-km trails that sampled different vegetation associations within the field station: Trail 1, sand dune pioneer species; Trail 2, deciduous forest; Trail 3, limits of deciduous and dry forest; Trail 4, dry forest and sand dune scrub; Trail 5, sand dune scrub; and Trail 6, limits among sand dune, fresh water lagoon, and mangrove forest. Distance between trails varied depending on how clustered the habitats were (approximately 100 and 800 m). Each trail was covered twice per month, in which two researchers walked the trails and recorded all ant species collecting nectar from EFN-bearing plants that were accessible to the collector (from 0.5 m to 3 m high). Ants were considered to be feeding on nectar when they were immobile, with mouthparts in contact with EFNs, and in some cases exhibiting distended gasters (based on Rico-Gray, 1993). In this study we recorded ant species feeding on EFNs present on the spike, pedicel, bud, calyx, leaves, shoots, petioles, bracts or stems. Representative samples of ants and plants were collected for later identification.

2.3. Data analysis

Initially, we built an adjacency matrix A , in which $a_{ij} = 1$ represent

an interaction between the animal species i and the plant species j , and zero for no observed interaction (Bascompte et al., 2003), considering all sampled ant-plant interactions between May 2010 and April 2011. Then, we classified ant species as generalist core (those with the most interactions) or peripheral components (those with fewer interactions) according to Dáttilo et al. (2013): $G = \left(\frac{A_i - A_{mean}}{\sigma_A} \right)$, where A_i = mean number of links for a given ant species i , A_{mean} = mean number of links for all ant species in the network, and σ_A = standard deviation of the number of links for ant species. $G > 1$ are ant species included in the central core, and $G < 1$ are peripheral ant species.

The strength of each ant species in the network is the sum of level of dependencies of plants on each particular ant species (Bascompte et al., 2006). In this case, the dependence D_{ij} of plant species j on ant species i is the fraction of all visits by a particular ant species to a particular plant, and is calculated as $D_{ij} = V_{ij}/V_i$; where V_{ij} is the number of visits of ant i to plant j and V_i is the total number of visits of ant j to all plant species in the environment (Bascompte et al., 2006). Then, we tested for differences in the number of interactions and the values of strength between TIS and NAS using a Generalized Linear Model (GLM) with a quasi-Poisson error distribution and a log-link function. In this study, we used the categorization proposed by Schultz and McGlynn (2000) and Suarez et al. (2010) to classified ant species into TIS and NAS.

To evaluate if selective ant species would visit only a subset of plant individuals visited by the generalist ant species (i.e., nested pattern of ant-plant interactions), we estimated nestedness using a metric less prone to Type I statistical error when compared to other nestedness indices called Nestedness metric based on Overlap and Decreasing Fill (NODF) (Almeida-Neto et al., 2008). This metric is calculated as: $NODF = \frac{\sum N_{paired}}{\left[\frac{P(P-1)}{2} \right] = \left[\frac{A(A-1)}{2} \right]}$, where N_{paired} is a measure of nestedness among pairwise animals and plant species; P is the number of plant species; and A is the number of animal species in the interaction network (Almeida-Neto et al., 2008). We generated 1000 random matrices to test the significance of nestedness using a null model where the probability of occurrence of an interaction is proportional to the number of interactions of both ant species and plant individuals, and can be calculated as follows: $\frac{P_i}{T} = \frac{P_j}{A}/2$ where P_i is the number of interactions of plant species i , P_j is the number of interactions of ant j , and T and A are the number of plant and ant species. P -value was defined as the probability of a null model replicate being equally or more nested than the observed networks (Bascompte et al., 2003).

Because the ant-plant network was significantly nested (see Results), we explored whether TIS and NAS contribute equally to the structuring of this non-random pattern of species interactions. For this, we estimated the degree to which the interactions of plant or ant species increase or decrease the network's overall nestedness and compared it to our random expectations, according to Saavedra et al. (2011). This metric is a z-score relative to null models and is defined as follows: $cn_i = \left(\frac{N - N_i}{\sigma_{N_i}} \right)$ where N is the observed nestedness (NODF) of the network, N_i is the average of nestedness when randomizing just the interactions of the species i , and σ_{N_i} is the standard deviation of nestedness when randomizing just the interactions of the species i ($n = 100$ randomizations). Positive values of cn_i indicate a higher contribution of species (i) to the nested structure. We then used a Generalized Linear Model (GLM) with a Gaussian error distribution and a log-link function to compare the values of cn_i between TIS and NAS.

In order to evaluate the impacts of invasion by TIS on the structure of ant-plant networks over time, we used an invasion index (I_{TIS}) (Aizen et al., 2008), which is defined as the average proportion of all ant-plant interactions that were made only by these TIS. For each month and the total network (between May 2010 and April 2011), we calculated I_{TIS} and correlated (using Simple Linear Regression) with the values of some network descriptor also calculated for each ant-plant network: nestedness (described above), diversity of interactions, and network specialization (ranges from extreme generalization when $H_2' = 0$ to extreme

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