



Sampling effort differences can lead to biased conclusions on the architecture of ant–plant interaction networks



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ARTICLE INFO

Article history:

Received 4 September 2015

Received in revised form 20 November 2015

Accepted 6 January 2016

Available online 29 January 2016

Keywords:

Ecological networks

Network structure

Scale dependence

Plant–animal interactions

Temporal variation

ABSTRACT

The study of plant–animal interactions using ecological networks as a tool has been intensified in recent years. However, one of the biggest criticisms of these studies is how sampling effort can affect the observed interaction patterns within these plant–animal networks. In this study we empirically evaluated how variation in sampling effort (comparing cumulative vs monthly sampled networks) influences the values of network descriptors more frequently used in the literature (i.e. number of links per species, network size, diversity of interactions, network specialization, robustness, nestedness, and modularity). For this, we studied interaction networks between ants and plants bearing extrafloral nectar sampled over 12 months in a tropical environment on the coast of Mexico. In general, all network descriptors used in this study were influenced by sampling effort via its effects on the record of new ant–plant interactions throughout the year. Interestingly, network specialization and the modularity tended to decrease with the increase of sampling effort, while all the other network descriptors tended to increase along with the sampling effort. Our study highlights the importance of standardizing data sampling in comparative studies to make sure that the results found in studies dealing with ecological networks are reliable, since the intensity of the sampling effort can directly affect the structure of plant–animal interaction networks.

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1. Introduction

In recent years ecological interactions involving animals and plants at the community level have become the focus of several studies in community ecology (reviewed by Vázquez et al., 2009). These studies have highlighted the importance of looking at species not as isolated entities, but also considering their interactions with each other in an environment. Interactions between species play an important role in maintaining the structure and stability of ecosystems (Janzen, 1974; Del-Claro and Torezan-Silingardi, 2009; Dyer et al., 2010). Indeed, the importance of studying species interactions has been widely recognized in the literature, from studies describing communities patterns (Rico-Gray et al., 1998), to studies focused on conservation and restoration of natural environments (Falcão et al., 2015; Tylianakis et al., 2010).

A new tool for studying the species interactions in species-rich communities is ecological networks, where species are represented by nodes and their interactions are represented by links (Bascompte and Jordano, 2013). This novel approach identifies the role of each species within a network based on the roles of all species, and it also provides a benchmark to test the patterns observed against random null models (Lewinsohn et al., 2006). The number of studies involving ecological networks (e.g. mutualism, neutralisms and antagonisms) are increasing in the literature. However, the lack of standardization in sampling effort, sampling methods, and metrics (i.e. network descriptors) could generate results that are not comparable between studies.

For example, in studies dealing with ecological networks, sampling effort can range from a few days (Nielsen and Bascompte, 2007; Dáttilo et al., 2014a) to decades (Díaz-Castelazo et al., 2013). However, we know that there is a temporal variation in interaction networks primarily due to the turnover of species and interactions (Alarcón et al., 2008; Díaz-Castelazo et al., 2010), often associated with species phenological differences (Moya-Raygoza and Larsen, 2001; Lange et al., 2013). Despite the importance of evaluating the fragility of ecological networks to differences in sampling effort,

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only a few studies have highlighted the effects of the sampling method (Gibson et al., 2011) and sampling effort (Nielsen and Bascompte, 2007; Chacoff et al., 2012; Rivera-Hutinel et al., 2012) on the structure of plant–animal interaction networks. Most of these studies state that the unique interactions can be undersampled and affect the network descriptors (Gibson et al., 2011; Rivera-Hutinel et al., 2012), even with a large sampling effort (Chacoff et al., 2012). However, these studies are limited to pollination networks, and other systems have been mostly neglected, possibly due to the limited number of research groups studying another study systems (e.g. ant–plant interaction networks). In fact, we are just beginning to understand how and why the sampling effects can affect the patterns of interaction networks.

Although knowledge about the architecture of ecological networks has increased in many study systems (e.g. plant–pollinator and plant–disperser) (Memmott et al., 2007; Santamaría and Rodríguez-Gironés, 2007), it is only in the last few years that studies have focused on the organization of interaction networks involving ants and plants with extrafloral nectaries (EFN-bearing plants) (e.g. Chamberlain et al., 2010; Dáttilo et al., 2013a and references therein). In this type of interaction, plants produce highly nutritious nectar to attract and reward ants that act as a biotic defense against herbivores (Rico-Gray and Oliveira, 2007). It is known that when we assemble a pool of monthly data, the structure of ant–plant networks remains stable over large spatial (Dáttilo et al., 2013b) and temporal scales (Díaz-Castelazo et al., 2013). However, this same structure is highly variable when compared using monthly periods, mainly due to the seasonal phenology of nectaries (Rico-Gray et al., 2012; Lange et al., 2013). Despite differences in sampling effort (days to years), collection time (day and night) and sampling method (manual collection and entomological umbrella) found in studies dealing with ant–plant networks, these studies are widely compared and discussed with one another (e.g. Dáttilo et al., 2014b; Cagnolo and Tavella, 2015). However, it is unknown how the structure of ant–plant networks is robust to temporal scaling of sampling effort. Therefore, this study system provides us an interesting proxy to investigate how sampling effort affects the structure of ant–plant interaction networks in natural environments.

Here we evaluate the structure of ant–plant networks using a series of cumulative networks consisting of an increasing in the number of monthly periods (every 1 month) resulting in a temporal series of 12 networks and, after, we compared these cumulative networks with monthly sampled networks (based on the approach used by Dupont and Olesen, 2012). We used these two different approaches (cumulative vs monthly sampled networks) in order to investigate how network properties changes in response to temporal and sampling effort scaling. Moreover, the use of these two categories provided a benchmark for studying how ant–plant interaction networks would be organized if the study design is balanced compared to increasing of a gradient of sampling effort. Specifically, we address the following questions: (1) Is the topological structure of cumulative ant–plant networks different from the monthly sampled networks? and, (2) How frequent are the pairwise interactions between ants and EFN-bearing plants throughout the year? In order to answer our questions we used a well-sampled and well-known community of ant–plant interactions sampled by the authors in a tropical environment in coastal Veracruz, Mexico.

2. Material and methods

2.1. Study site

The study was conducted at the Centro de Investigaciones Costeras La Mancha (CICOLMA), in the state of Veracruz, Mexico

(19°36'N, 96°22'W). The climate is warm and subhumid, the total annual precipitation is 1500 mm, mean annual temperature is 22–26 °C, and a rainy season occurs between June and September. The area has many vegetation types, including tropical deciduous forest, tropical dry forest, sand dune scrub, mangrove forest, freshwater marsh, and flooded deciduous forest (see Moreno-Casasola, 2006).

2.2. Data sampling

Fieldwork was carried out monthly from May 2010 to April 2011. These observations were made during two and four days per month along six arbitrarily selected 1 km trails (3 m wide) that sampled different vegetation associations: sand dune pioneer species, deciduous forest, deciduous forest–dry forest ecotone, dry forest and sand dune scrub, sand dune scrub, and sand dune–fresh water lagoon ecotone and mangrove forest. All transects were sampled within the same month in each sampling period (totaling 12 samples in each transect), and the differences between two and four days for data sampling was due only to difference in the number of plant species with active nectaries or weather conditions (i.e. when it started to rain). Note that this study design was balanced and we performed equal temporal repetitions of ant–plant interaction censuses within transects. We searched for ants collecting liquids from extrafloral nectaries and registered ant and plant species (between 08:00 and 13:00 h). Ants were considered to be feeding on nectar when they were immobile, with mouthparts in contact with nectar secreting tissues. Once an individual plant was marked as visited by ants, it was subsequently re-checked throughout the study (for more details see Rico-Gray, 1993). We sampled different habitats mainly due to low diversity of EFN-bearing plant species within each habitat (ranges from two to seven plant species). So, even though it is quite a small area, the variety of habitats found within the area is such that one 'needs' to sample all different habitats and pool the data.

2.3. Data analysis

We initially performed a direct ordination (i.e. species and their interactions by months) to evaluate if the occurrence of species and their number of interactions was stable over the 12-month sampling period. To assess if we had recorded enough species and interactions to describe our ant–plant network, we generated accumulation curves with the number of plants and ant species and distinct pairwise of interactions as a function of the number of sampled months (Donatti et al., 2011). For this, we performed a non-parametric bootstrapping based on resampling ($n = 1000$ repetitions) of presence/absence of a given pairwise interaction across 12 sampling months (Gotelli and Colwell, 2001).

To evaluate the effect of sampling differences on the structure of ant–plant networks we separated our networks in two different sampling categories: cumulative and monthly networks. Cumulative networks represent an increasing in the number of month periods (every 1 month) resulting in a series of 12 networks. For instance the first period represent only January, while the second period was the accumulation of species and interactions of January and February, and so on. Monthly networks represent species and interactions recorded only in a given sampling month. The resulting ant–plant networks were constructed from quantitative data (frequency of interactions) of each pairwise ant–plant interaction. Then, in order to describe the patterns of ant–plant interactions for both cumulative and monthly interaction networks, we calculated the following network descriptors for each ant–plant network: network size, number of links per species, diversity of interactions, network specialization, robustness, nestedness, and modularity. Network size was obtained by

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