

# Abiotic factors shape temporal variation in the structure of an ant–plant network

Victor Rico-Gray · Cecilia Díaz-Castelazo ·  
Alfredo Ramírez-Hernández · Paulo R. Guimarães Jr. ·  
J. Nathaniel Holland

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**Abstract** Despite recognition of key biotic processes in shaping the structure of biological communities, few empirical studies have explored the influences of abiotic factors on the structural properties of mutualistic networks. We tested whether temperature and precipitation contribute to temporal variation in the nestedness of mutualistic ant–plant networks. While maintaining their nested structure, nestedness increased with mean monthly precipitation and, particularly, with monthly temperature. Moreover, some species changed their role in network structure, shifting from peripheral to core species within the nested network. We could summarize that abiotic factors affect plant species in the vegetation (e.g., phenology), meaning presence/absence of food sources, consequently an increase/decrease

of associations with ants, and finally, these variations to fluctuations in nestedness. While biotic factors are certainly important, greater attention needs to be given to abiotic factors as underlying determinants of the structures of ecological networks.

**Keywords** Mutualistic networks · Effect of abiotic factors · México · Veracruz

## Introduction

Beginning nearly a century ago with Clements-Gleasonian debates over the superorganism and individualistic concepts of community organization, both biotic and abiotic factors have been recognized to shape spatiotemporal variation in the structure of biological communities (Kingsland 2005). Nonetheless, influences of abiotic factors on the patterns of species interactions within communities and emergent structural properties have been relatively neglected compared to biotic factors (Dunson and Travis 1991). Over the past two decades, much progress has been made in understanding how various abiotic factors affect the roles of competition and predation for species niches, species sorting, and community organization (Chase and Leibold 2003). In a strict sense, it has only been in recent years through the application of network theory that we have begun to recognize non-random structure in mutualistic communities (Bascompte 2009). However, the study of communities and species interactions has been analyzed over the years using a variety of approaches. For example, using different approaches and at different times, several authors have addressed the structure of plant–pollinator communities (e.g., Schemske et al. 1978; Thomson 1980, 1981; Tepedino and Stanton 1981;

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V. Rico-Gray · C. Díaz-Castelazo · A. Ramírez-Hernández  
Instituto de Ecología, A.C. Xalapa, 91070 Veracruz, Mexico

*Present Address:*

V. Rico-Gray (✉)  
Instituto de Neuroetología, Universidad Veracruzana,  
Calle Dr. Luis Castelazo s/n, Col. Industrial Ánimas, Xalapa,  
Veracruz 91190, Mexico  
e-mail: vricogray@yahoo.com; vrico@uv.mx

*Present Address:*

A. Ramírez-Hernández  
Instituto de Biodiversidad CIBIO, Universidad de Alicante,  
San Vicente del Raspeig, 03080 Alicante, Spain

P. R. Guimarães Jr.  
Departamento de Ecologia, Universidade de São Paulo,  
São Paulo, SP 05422-970, Brazil

J. Nathaniel Holland  
Department of Ecology and Evolutionary Biology,  
Rice University, Houston, TX 77005, USA

Waser 2006; Memmott et al. 2004; Alarcón et al. 2008; Dupont et al. 2009; Alarcón 2010; Lázaro et al. 2010; Ramos-Jiliberto et al. 2010; Waser et al. 2010; Burkle and Alarcón 2011). Additionally, several biotic factors are being explored to explain the structural properties of mutualistic networks, such as trait matching, phenological synchrony, relative abundances of species, and body size (e.g., Stang et al. 2006; Rezende et al. 2009; Bascompte 2009; Chamberlain and Holland 2009a; Vázquez et al. 2009). Despite the need to consider multiple determinants of the organization of mutualistic communities (Vázquez et al. 2009), there has been little consideration of the influences of abiotic factors on variation in the structure of mutualistic networks (Olesen and Jordano 2002). A few studies have recently begun to evaluate spatiotemporal variation in ecological networks (Alarcón et al. 2008; Olesen et al. 2008; Dupont et al. 2009; Díaz-Castelazo et al. 2010).

The conservation of network structure is one of many goals in conservation ecology. However, certain attributes of web structure that are predicted to confer stability or increased function to a system are in need of empirical evaluation, and there is also a need to analyze whether stability is really desirable in all contexts. To incorporate web attributes requires that these attributes can be recorded with relative ease (Tylianakis et al. 2010). One such attribute is nestedness. A network is considered nested if a central core of species (generalists) has many interactions among themselves, peripheral species with few interactions (specialists) interact with proper subsets of the central core of generalists, and few interactions occur among the specialists (Guimarães et al. 2006; Bascompte 2009). Even though the use of nestedness has been discussed and questioned in many ways (e.g., Lázaro et al. 2005; Almeida-Neto et al. 2007, 2008; Krishna et al. 2008; Bascompte 2009; Tylianakis et al. 2010), we used this bipartite metric because we consider it a way to compare community organization within our study and with others. We do recognize that other network descriptors could be analyzed (e.g., community size, Guimarães et al. 2006, 2007); however, for the purposes of this comparison, nestedness was considered sufficient.

Among some of the most variable but routinely mutualistic interactions in nature are those involving plants that produce extrafloral nectar resources to attract and reward ants for their biotic defense against natural enemies (Bronstein 1998; Heil and McKey 2003; Rico-Gray and Oliveira 2007; Chamberlain and Holland 2009b). Ant-plant communities, which are gaining greater attention in the study of mutualistic networks (Guimarães et al. 2006, 2007; Blüthgen et al. 2007; Chamberlain and Holland 2009a; Díaz-Castelazo et al. 2010; Chamberlain et al. 2010), exhibit a number of structural properties, including

nestedness. Previous research in the study area suggested that vegetation diversity determined to a certain extent the nature of the ant community, and that plant diversity is driven by the abiotic environment (Rico-Gray 1993; Rico-Gray et al. 1998). Thus, using mutualistic ant-plant networks of lowland tropical seasonal vegetation on the coast of Veracruz, Mexico (Rico-Gray 1993; Díaz-Castelazo et al. 2010), we tested the hypothesis that abiotic variables of temperature and precipitation may contribute to variation in nestedness of mutualistic networks, and also, in order to support the view that networks are dynamic and that between-month species shifts affect the number of interactions and in turn network nestedness, and we tested for the presence of shifts of species between the central core group of generalists and the peripheral group of specialists in the network.

## Materials and methods

For our analyses, we used an ant-plant network describing interactions mediated by the presence of extrafloral nectaries on plants in lowland tropical seasonal vegetation at La Mancha field station on the central coast of Veracruz, Mexico (Rico-Gray 1993). Climatic data (mean monthly temperature and precipitation) for this time period were obtained from the meteorological station at the field site (CICOLMA).

### Field observations and data collection

Ant-plant interactions were sampled biweekly between May 1989 and April 1991. Field observations were conducted along six arbitrarily selected but representative 1-km trails that sampled different vegetation associations within the field station (Rico-Gray 1993; Díaz-Castelazo et al. 2004): 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. We recorded all occurrences of ants collecting liquids from plants. On each visit, we noted ant species, plant species, and the food source or structure mediating the ant-plant interaction. Once an individual plant was marked as visited by ants, it was subsequently rechecked throughout the study. The food resource used by ants was extrafloral nectar, either produced by the surface of reproductive structures such as the spike, pedicel, bud, calyx, or fruit or secreted by special structures on vegetative parts such as leaves, shoots, petioles, bracts, or stems. Ants were considered to be feeding on nectar when they were immobile, with mouthparts in

contact with nectar-secreting tissues, for periods of up to several minutes. Nectar-feeding ants often showed obviously distended gasters (Rico-Gray 1993).

#### Data analyses and statistics

Network nestedness was described by NODF using Aninhado (Guimarães and Guimarães 2006; Almeida-Neto et al. 2008). A network was considered nested if the observed NODF value was higher than that predicted by a null model, where the probability of drawing an interaction between a plant and an animal is the arithmetic mean of the generalization levels (i.e., fraction of interactions) of the plant and the animal and keeps the heterogeneity of interactions across species (null model 2, Bascompte et al. 2003, Guimarães et al. 2006; Díaz-Castelazo et al. 2010; 1000 randomizations for each network). Furthermore, we estimated *z*-score values or standard normal deviates of each network in order to control for differences in species richness among months; these *z*-scores were obtained from the value of nestedness for the actual matrix minus the average nestedness of the random replicates (1,000) divided by the standard deviation of the replicates (Bascompte et al. 2003; Almeida-Neto et al. 2008). We controlled for the effect of connectance on nestedness using *z*-scores. The categorical core versus periphery analysis was used to describe species as core (generalist species, those with the most interactions) or peripheral (specialist species, those with fewer interactions) components of the network ( $n = 20$  runs/network, analysis performed in UCINET, Borgatti et al. 1999). Further details on the methodology can be found in Guimarães et al. (2006, 2007) and Díaz-Castelazo et al. (2010).

We investigated the relationship between nestedness, connectance, and two abiotic variables (mean monthly temperature and mean monthly precipitation). We included precipitation as a variable because of the seasonal nature of the tropical system studied, which entails a long dry period (up to 7–8 months) with direct consequences for plant phenology and the availability of food resources for ants (Rico-Gray 1993). We included temperature because it correlates strongly with ant metabolism, ant activity, and colony growth (Rico-Gray and Thien 1989). We used simple linear regression analyses to examine the relationships between the abiotic variables and nestedness (NODF, Almeida-Neto et al. 2008). We first attempted a multiple regression analysis, but since the two climatic variables were highly correlated, we then performed single regression analysis. We are aware that this single variable regression does not remove the inherent collinearity of the predictors, since the two do not represent independent predictions. Data were checked for normality and homoscedasticity. Temperature data were not transformed, whereas

precipitation data were square-root-transformed. Analyses were performed using BioEstat (Ayres et al. 2005). Since NODF is strongly dependent on connectance in random networks, we tested whether nestedness increased via an indirect effect of increasing connectance by controlling for connectance effects on nestedness. Finally, because both temperature and precipitation are highly correlated abiotic factors, we used principle components analysis (PCA) to create a single variable that described changes in the abiotic factors (see Sazima et al. 2010).

## Results

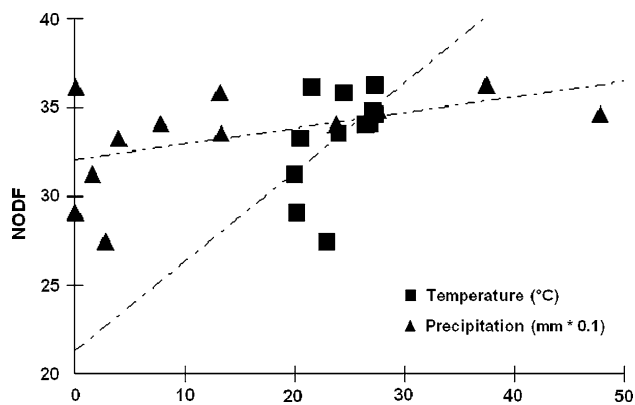
### Abiotic variables and contribution to variation in nestedness

Over the course of a year, all 12 networks (1 per month) exhibited a significantly nested topology ( $P < 0.01$ ). NODF values and their associated *z*-scores from January to December are shown in Table 1. Nestedness was not static but varied significantly among months, ranging from 27.4 to 36.3 ( $P < 0.0001$ ), as well as their standard normal deviate (Table 1). Nestedness increased with both precipitation and temperature (Fig. 1), but the regression between precipitation and nestedness exhibited only marginal significance, so we performed a bootstrap procedure with 1000 simulations which confirmed the significant relationship. Moreover, because both temperature and precipitation are highly correlated abiotic factors (Pearson  $r = 0.82$ ,  $df = 10$ ,  $n = 2$ ,  $P = 0.001$ ), we used principle components analysis (PCA) to create a single variable describing changes in the abiotic factors. The first principal component (PC1) described by temperature and

**Table 1** Nestedness (NODF) and *z*-score values per month (see text)

Month	NODF	<i>z</i> -score
January	31.24	4.16
February	33.23	5.05
March	36.12	6.8
April	35.82	5.59
May	34.08	5.72
June	36.28	5.14
July	34.82	5.41
August	34.62	5.08
September	34.04	5.44
October	33.54	5.51
November	27.43	3.89
December	29.12	3.87

Annual NODF value = 40.89



**Fig. 1** Regressions of nestedness against precipitation ( $\text{NODF} = 25.7(\text{precipitation}) - 744.64$ ,  $R^2 = 0.29$ ,  $F = 5.53$ ,  $df = 11$ ,  $P = 0.04$ ) and temperature ( $\text{NODF} = 0.72 (\text{temperature}) - 3.04$ ,  $R^2 = 0.57$ ,  $F = 15.42$ ,  $df = 11$ ,  $P = 0.0031$ ) (also see “Materials and methods”)

precipitation retained 90.9% of the variance in the analysis, and we used it to describe abiotic factors. The higher the value of PC1, the higher is precipitation and temperature, confirming results of the simple linear regression analyses. The pattern of nestedness increasing with temperature and precipitation is not an indirect effect of connectance, as nestedness was not affected by connectance (Pearson  $r = -0.007$ ,  $P > 0.98$ ). Nestedness, as measured by NODF, was significantly associated with PC1 ( $\text{NODF} = 1.58 (\text{PC1}) + 33.4$ ,  $R^2 = 0.51$ ,  $F = 12.45$ ,  $df = 11$ ,  $P = 0.005$ ).

#### Shifts of species along the core-periphery gradient of the network

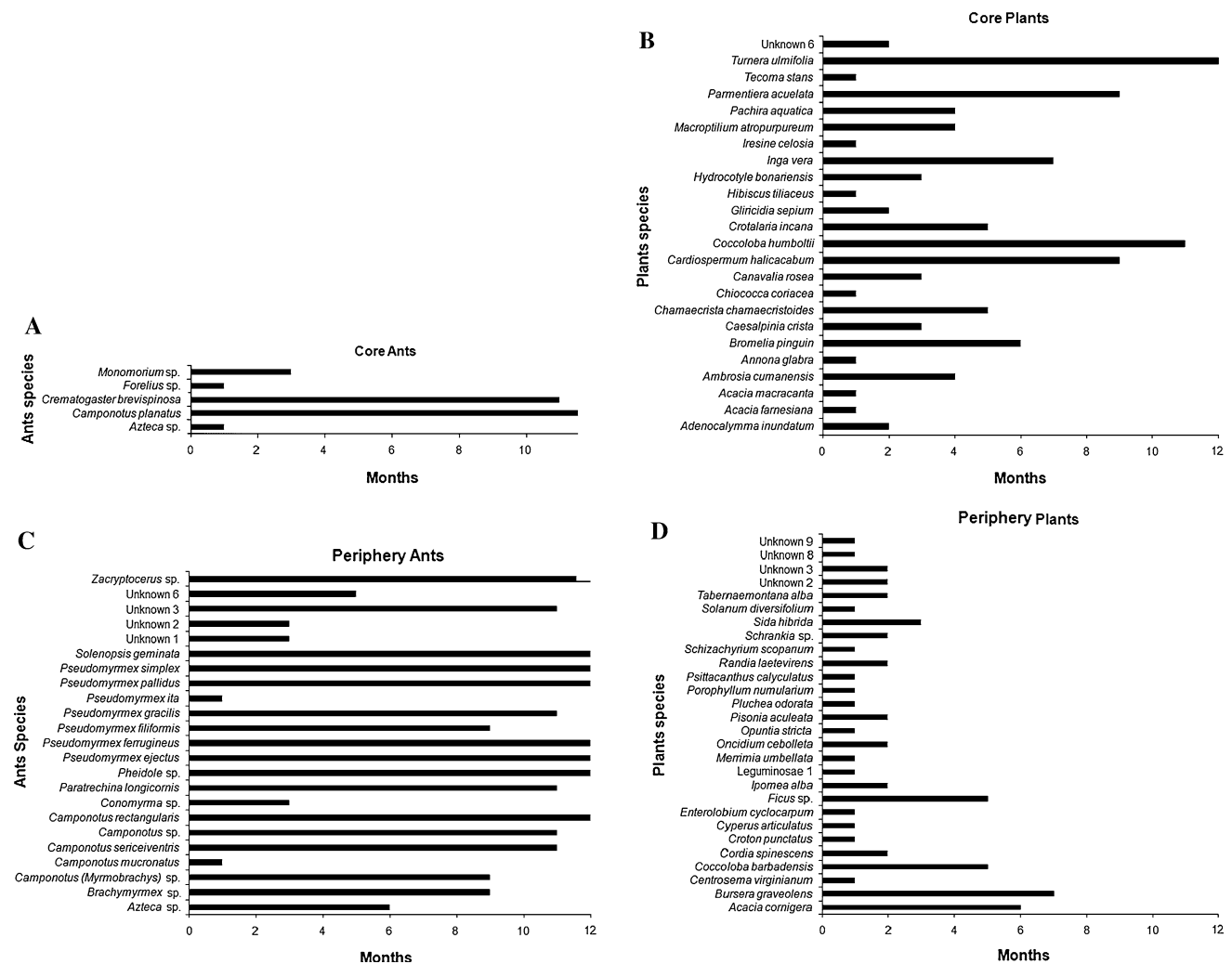
The proportion of species constituting the core and the periphery in each network did not change with time. However, the identities of individual species constituting the core and the periphery changed throughout the year (Fig. 2). For example, *Azteca* species were part of the core and periphery for months one and six, respectively (100% of runs,  $P < 0.0001$ ), whereas other ant species, e.g., *Camponotus planatus* and *Crematogaster brevispinosa* (= *C. rochai*), remained a part of the core for 12/12 and 11/12 months, respectively ( $P < 0.001$ ). Also, there was 1 year-round species-specific ant–plant interaction, that of *Acacia cornigera* and its symbiotic ant *Pseudomyrmex ferrugineus* (Fig. 2). Other ant or plant species switch from having two or three links to having one link in a given month. In general, ants shift plant species based on availability of food resources, offering a dynamic view of a network. In other words, we could think of network dynamics as an ongoing series of switches (i.e., plant food

sources) turning off and on along the year and ants responding to these with a link. The above are only examples, and the analysis could be done for each ant species within the network.

#### Discussion

Our results show that abiotic factors, like biotic variables, can contribute to variation in structural properties of mutualistic networks (e.g., nestedness). While mutualistic networks maintained their nested structure, an invariant property of mutualistic networks (Bascompte 2009), temporal variation in nestedness did occur influenced by abiotic variables. Notably, the underlying effects of abiotic conditions on nestedness likely arise from their influence on the richness and phenology of plants with nectaries, as plant and ant species shift between the peripheral and core groups within the network.

Previous work in the study area has shown the presence of considerable variation among habitats in the number, diversity, and seasonal distribution of ant–plant interactions, suggesting that inter-habitat variation in ant–plant interactions is the effect of variation in environmental parameters, the richness of plants with nectaries in the vegetation, and the richness in habitat heterogeneity (Rico-Gray 1993; Rico-Gray et al. 1998). In other words, there are seasonal patterns in the presence of food resources, (1) extrafloral nectaries, which are associated with leaves, are present during the flush of new leaves after the onset of the annual rainy season; (2) both ant–extrafloral nectar and ant–Hemiptera associations show a significant increase after the start of the rainy season, decreasing abruptly once the dry season begins; and (3) in contrast, associations between ants and both floral nectar and nectar produced on other reproductive structures reach their peak during the dry season (Rico-Gray 1993). Thus, the diversity of the vegetation determines the nature of the ant community to a certain extent, while plant diversity is driven by the abiotic environment (Rico-Gray 1993; Rico-Gray et al. 1998; but see Stang et al. 2006). We could then summarize that abiotic factors affect plant species in the vegetation (e.g., phenology), which can be translated to presence/absence of food sources, to an increase/decrease of associations with ants, and finally, these variations to fluctuations in nestedness. Also, higher ant activity is associated with higher precipitation and temperature, which may lead to an increase in the number of interactions (Rico-Gray 1993). This increase might reinforce the nested patterns of interaction, since nestedness is intimately associated with the connectivity of the network (Almeida-Neto et al. 2008). Therefore, we should expect that the higher the



**Fig. 2** **a** Ant and **b** plant species that appeared in the core of the networks in 100% of the runs. **c** Ant and **d** plant species that appeared in the periphery of the networks in 100% of the runs (see “Materials

and methods”). Also shown is the number of months that a species appeared either in core or in periphery of the networks

temperature and precipitation, the higher the connectance and the higher the degree of nestedness. In addition to biotic factors that mediate ant–plant interactions, such as nectar resource availability, abiotic factors can also influence the physiological tolerances of ants, such that during cooler temperatures ants are less active (Rico-Gray and Thien 1989; Oliveira et al. 1999), thereby showing how the physiology of individual ants scales up to community-level organization of networks.

A pattern emerging from the core-periphery analysis is that throughout the year, ants switch from one food resource to another depending on availability (i.e., active extrafloral nectaries), which then influences the actual nestedness value. Temporal variation in nestedness may be explained by (1) the influence of abiotic factors on plant phenology (Rico-Gray 1993; Rico-Gray et al. 1998), (2) plant communities of the study site being subject to a

recurrent successional process (Rico-Gray and Castro 1996), and (3) ants have more links than plants (Díaz-Castelazo et al. 2010). In the scenario of natural plant succession and transformation of plant communities caused by human activities and natural processes at La Mancha (Moreno-Casasola 2006), generalist ant species use nectar from alternative plant species, which leads to stronger stratification of ant assemblages and reduces microenvironmental influences at the study site (Gove et al. 2009).

In summary, abiotic factors affect the network through their influence on particular plant and ant species, and these factors then translate to emergent properties of the network (e.g., Thompson 2009). We explain the mechanistic links causing changes in nestedness, i.e., from the abiotic factors through biotic factors (plant phenology-food resources) on to the structure of the network (nestedness). These changes



in functionality imply changes in community structure “guided” by abiotic parameters, which in turn affect the nested structure of the network. In other words, we dwell in a relatively novel aspect to consider in network analysis, which rarely dwells beyond patterns. Finally, we should not forget that there may be direct abiotic effects which can affect the foraging behavior of animals at both individual and population levels. It is important that we begin to recognize that abiotic effects scale up to community organization of mutualistic interactions observed as network topology.

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