

Mechanisms for the Structure of Sonoran Desert Ant-Plant Mutualistic Communities

Background: Fundamental to ecology is understanding the structure of communities (1). Much theoretical and empirical attention has been given to the structure of predator-prey food webs. Although there is still much to learn about food webs, we know far less about the structure of mutualistic communities. New insights into mutualistic communities (and food webs) are being made through the application of network theory, which in ecology depict species (nodes) with interactions (links) among them. Through the application of network theory, mutualistic communities of plant-pollinator and plant-seed disperser interactions are now recognized to form 2-mode, bipartite networks, with structural properties of nestedness (2), degree distribution (3), and asymmetric interaction strength (4). Nestedness entails a central core of highly connected nodes, with species with few species interactions attaching to the central core (2,5). In contrast to nested mutualistic communities, predator-prey food webs tend to be compartmentalized, such that subsets (compartments) of species have more interactions within than among subsets (2). Degree is the number of links (interactions) a node (species) has. Degree distribution describes the probability distribution of degree for all nodes in a network. Degree distribution of mutualistic networks and food webs has been described as a truncated power law, $P(k) \sim k^{-\gamma} e^{-k/k_x}$ where $P(k)$ is degree distribution, k is degree, γ is the degree exponent constant, and k_x is the truncation value, such that degree distribution decays faster than a scale-free power law (3). Mutualistic networks tend to have small exponent values (γ) with many highly connected species (3). Using relative frequency of interaction as a surrogate for interaction strength, mutualistic communities are characterized by a pattern of many weak and often asymmetric interaction strengths (4).

Despite recent progress in understanding the structure of mutualistic communities, only two studies have examined the underlying biological mechanisms for mutualistic community structure. The first study on an evolutionary scale suggested that morphological trait-matching among species contributes to community structure (6). The second study on an ecological scale suggested that the relative abundance of species predicts community structure (7). Although these studies are key to our

current understanding of mutualistic communities, to my knowledge no study has experimentally tested hypotheses of biological mechanisms giving rise to structures of mutualistic communities.

Network theory is advancing our understanding of multiple types of mutualistic communities (e.g., plant-pollinator, plant-seed disperser) across a variety of ecosystems (e.g., tropical, arctic, marine), but little attention has been given to ant-plant mutualistic communities. Common throughout the Sonoran Desert are interactions among ants and extra-floral nectar (EFN; nectar not associated with pollination) bearing plant species. Using Sonoran Desert ant-plant communities I propose to experimentally test one biological mechanism that may underlie now well-established structural properties of nestedness, degree distribution, and asymmetric interaction strength, namely interspecific competition among ant species for EFN resources of plant species.

Objectives: I hypothesize that interspecific competition among ants for limiting resources (EFN) produced by plants may explain structural properties of Sonoran Desert ant-plant networks.

Competition hierarchies are well known to occur among ants (8,9). Specifically, there is often a dominance-discovery tradeoff among ant species: dominant species discover resources slowly, while subordinate species discover resources quickly but are displaced by dominants (9). Dominant ant species can be selective of EFN resources, such that subordinates are less selective of EFN resources, even though subordinates can be equally selective of their use of EFN resources when experimentally isolated from other species (10). Thus, interspecific competition is predicted to be a strong determinant of ant interactions among plant species that vary in their EFN resources. Such competition hierarchies among ants may manifest themselves most conspicuously in environments where EFN constituents of water and sugar resources are most limiting, such as the Sonoran Desert. Given the scarcity of water and sugar resources in deserts, competition among ant species for limiting EFN resources may play an important role in shaping the structure ant-plant communities.

Study System: Many parts of the Sonoran Desert have substantial vegetative cover of EFN-bearing plants, making them an important resource for ants, and their interactions an important component of desert communities. A diversity of ant species are conspicuous consumers of EFN resources of Sonoran Desert plants (e.g., Cactaceae, Fabaceae). I have recently collected preliminary data on ant-

plant networks across eight sites throughout the Sonoran Desert in Mexico and Arizona. The proposed work will include some of these sites, in particular those near Bahia de Kino (BK), Sonora and Organ Pipe Cactus National Monument (ORPI), Arizona. Preliminary data show ant-plant communities to be comprised of between 5-14 ant and 6-10 plant species. Cacti secrete copious amounts of EFN relative to other plants (e.g., legumes). Preliminary data indicate that both the abundance and diversity of ant species consuming EFN differ among cacti and legumes.

Methods: I will examine community structure of ant-plant interactions using quantitative census methods, and then examine the role of competition in explaining those structural properties through experimental manipulation of EFN resources mediating ant-plant interactions. Below, I first describe my census methods for quantifying network structural properties. I then present methods to assess competition hierarchies among ants, followed by experimental manipulations of ant-plant interactions through a resource supplementation/reduction experiment.

Network census methods: To determine the structure of ant-plant networks I will use five 3.6 ha plots (120 m x 300 m) randomly positioned within relatively homogenous habitat near BK. These five plots will serve as control and manipulated plots as described below. Within each plot I will identify all EFN-bearing plants, quantify their relative abundances, and quantify for each plant the number of individual ants of each ant species interacting with them (interaction frequency). For the same individual plants, I will conduct diurnal (ca 1600-1830 hrs) and nocturnal censuses (ca 2000-2200 hrs) of ant species and their abundance on all EFN bearing plant species. I will census the same number of individuals (ca 25) of each plant species to avoid well-established biases in sampling accumulation curves. In censusing each plant for ants, I will also avoid sampling biases associated with more numerically dominant species by censusing each individual plant for the abundance of ants for a standardized amount of time (one minute each by day and night). These methods have been feasibly employed in collecting the preliminary ant-plant interaction data sets. Importantly, these methods overcome drawbacks of previous studies of mutualistic networks in controlling for sampling biases due to relative abundance of interacting plant and ant species. Network structural properties will be calculated from these data following established computational protocols (2-6). These census

methods will be used to quantify response variable of network structures of mutualistic communities for the observational and experimental studies of competition described below.

Resource competition hierarchies: Ant competition for artificial resources: Here, I propose to test how the competitive hierarchy among ant species is structured, and how network structural properties vary with the competitive hierarchy. Specifically, ant species will be ranked according to relative competitive ability within the community; this rank score will serve as an explanatory variable against which network structural properties are analyzed. I will quantify the ability of ants to compete relative to one another using established protocols of food baits (8,9), sugar water on petri dishes. An array of 40 equally spaced food baits will be set up within one plot, and the identity and abundance of ants at individual food baits will be quantified every 15 minutes for 3 hours by both day and night. From observations at baits competitive behavioral dominance hierarchies will be determined following established protocols (8,9), where wins and losses at baits are recorded for each interspecific interaction, and summed for each ant species. Additionally, ecological dominance hierarchies, the ratio of a species foraging success to its abundance in the environment, will be determined by dividing behavioral dominance by ant relative abundance in pitfall traps. I will quantify degree (number of plant species with which an ant species interacts) and interaction frequency (mean abundance of ants across plant species) for the ant-plant network. I will examine how degree and interaction frequency (surrogate for interaction strength; 4) vary with behavioral and ecological dominance hierarchies using correlation analyses.

Experimental test of EFN resources, competition, and ant-plant network structure: Here, I experimentally test how network structural properties of ant-plant communities vary due to manipulated EFN resource supply. Like Inouye and Tilman's (11,12) manipulation of supply of nutrient levels to infer competition among plant species, I will manipulate the supply of EFN resources to examine competition among ant species, which will allow me to infer how competition among ant species influences network structural properties. I will determine how network structural properties of nestedness, degree distribution, and interaction frequency vary with five experimentally established EFN resource supply rates: control plots, plots increased by 40% and 80%, and plots

decreased by 40% and 80%. EFN will be increased by use of artificial nectaries attached to plants, while EFN will be decreased by a combination of knocking off EFN-secreting structures or gluing nectaries. Each treatment will be applied to one 3.6 ha plot. Using above described census methods, I will quantify nestedness, degree distribution, and interaction frequency before and after establishing each treatment. For each plot, I will calculate regression (linear or nonlinear) parameters (and their variance) for each treatment for each of nestedness, degree distribution, and interaction frequency. As each regression parameter has a measure of central tendency and variance, I can test the hypothesis that EFN resource supply, and hence competition (11,12) influences structural properties by statistically testing for differences among regression parameters of the five treatments (13,14).

Importance: The proposed work experimentally tests a key biological mechanism (interspecific competition) for the structure of mutualistic communities. If resources are important for the structure of ant-plant communities, then results of this study may have important implications for changes in community structure associated with altered rainfall and temperature due to global climate change in arid regions (15). For example, anticipated changes in rainfall in the Sonoran Desert may alter EFN production, potentially altering the structure of ant-plant interactions.

Literature Cited: 1. Elton, C.S. 1927. *Animal Ecology*. London, Sidgwick and Jacksons. 2. Lewinsohn, T.M., *et al.* 2006. *Oikos*, 113, 174. 3. Jordano, P., *et al.* 2003. *Ecol. Lett.*, 6, 69. 4. Bascompte, J., *et al.* 2006. *Science*, 312, 431. 5. Bascompte, J., *et al.* 2003. *PNAS*, 100, 9383. 6. Santamaría, L. & M.A. Rodríguez-Gironés. 2007. *PLOS Biology* 5: e31. 7. Vázquez, D.P., *et al.* 2007. *Oikos*, doi:10.1111/j.2007.0030-1299.15828.x. 8. Andersen, A.N. 1992. *Am. Nat.*, 140, 401. 9. Holway, D.A. 1999. *Ecology*, 80, 238. 10. Blüthgen, N. & K. Fiedler. 2004. *Ecology*, 85, 1479. 11. Inouye, R.S. & D. Tilman. 1988. *Ecology*, 69, 995. 12. Inouye, R.S. & D. Tilman. 1995. *Ecology*, 76, 1872. 13. Zar, J.H. 1999. *Biostatistical Analysis*, 3rd ed. Prentice Hall. 14. Hilborn, R. & M. Mangel. 1997. *The Ecological Detective*. Princeton University Press. 15. Weiss, J.L. & J.T. Overpeck. 2005. *Global Change Biol.*, 11, 2065.

Budget:

Housing -- 3 months @ \$300 / month	\$900
Food -- 90 days @ \$6 / day	\$540
Transportation -- \$0.485 per mile for 850 miles	\$412
Materials -- Ant collecting equipment, flagging, stakes, misc. supplies	\$148
Total	\$2000

The majority of costs are housing, food, and transportation. I request only a small amount of money for field equipment. Price estimates are based on Forestry Suppliers catalog.