The diverse kinds of associations of vascular plants with ants are themes of both evolutionary and ecological interest in the tropics (e.g. Davidson 1988, Davidson et al. 1988, Huxley & Cuttler 1991, Beattie & Hughes 2002, Heil & McKee 2003, Rico-Gray & Oliveira 2003) and it has been mostly considered that these ant-plant interactions are beneficial to one or both of the participants through defense against predators and the provision of nesting space and/or food rewards.

Morphological adaptations to myrmecophyly in ferns include the development of hollow structures or domatia (e.g. Gómez, 1974, Benzing 1991) and nectaries (e.g. Koptur et al. 1982, Jan. 1988) Several gametophytes and young sporophytes were found growing on the external surface of the mat of roots before the establishment of the fern (Fig. 2). The Cordia nodosa tree was surrounded in a 2m radius by a tree and two lianas, each with a distinct epiphyte community (Table 1). The ants apparently kept all surfaces directly in contact with the Cordia free of other plant species except for the fern and a Philodendron epiphyte (P. cf. heterophyllum Engl.) (Araceae)

The dorsiventral rhizome and the dense mat of roots of P. cajenense (Fig. 1) provided the bases for the development of a pseudo-domatia or “external” domatia and its host were inhabited by the same ants of the genus Azteca (collected specimen identified to genus by E. O. Wilson, pers. comm., 6 Jan. 1988) Several gametophytes and young sporophytes were also found growing on the external surface of the mat of roots of the largest sporophyte individual (Fig. 1). The Cordia nodosa tree was surrounded in a 2m radius by a tree and two lianas, each with a distinct epiphyte community (Table 1). The ants apparently kept all surfaces directly in contact with the Cordia free of other plant species except for the fern and a Philodendron epiphyte (P. cf. heterophyllum Engl.) (Araceae)

While recording fern species diversity in 1987, in a forest on sandy-loam soils near the settlement of Quebrada Castillo in the Amuesha community of Siete de Junio, in the Palcazu valley of central Peru at 350 m elevation (Young & Leon 1989), we found two adult sporophyte individuals of Polytaenium cajenense (Desv.) Benedict (León & Young 1085 USM-148929) on a 2m tall tree of Cordia nodosa Lamarck (León & Young 1067 USM-110731). Both the largest P. cajenense individual and its host were inhabited by the same ants of the genus Azteca (collected specimen identified to genus by E. O. Wilson, pers. comm., 6 Jan. 1988) Several gametophytes and young sporophytes were also found growing on the external surface of the mat of roots of the largest sporophyte individual (Fig. 1). The Cordia nodosa tree was surrounded in a 2m radius by a tree and two lianas, each with a distinct epiphyte community (Table 1). The ants apparently kept all surfaces directly in contact with the Cordia free of other plant species except for the fern and a Philodendron epiphyte (P. cf. heterophyllum Engl.) (Araceae)

The dorsiventral rhizome and the dense mat of roots of P. cajenense (Fig. 1) provided the bases for the development of a pseudo-domatia or “external” domatia (sensu Hauffler et al. 2003) for the Azteca ants. Internally the mat of roots included debris and some roots of the Philodendron plant, and it appears that this plant might have grown simultaneously or perhaps before the establishment of the fern (Fig. 2).

In the fern family Pteridaceae, all genera in the vittarioids are epiphytes, all considered non-myrmecophyloous. The Neotropical fern genus Polytaenium (Crane 1997) includes taxa without domatia and none have leaf nectaries. Wall spores found in Polytaenium have micro-ornamentations varying from scattered granules to clustered rod-like structures, none of which appear to resemble the spore walls of the polypods identified by Tryon (1985) as associated with myrmecochory.

There are a number of implications arising from these observations. Ecologically, it is striking how important spatial and temporal contingencies were to the development of the patterns reported here. As we interpret the scene, the Polytaenium spores landed on a Cordia tree probably before it was occupied by Azteca ants (see Yu et al. 2001 for colonization in Cordia nodosa). The Polytaenium might have grown to a size such that its rhizomes permitted an additional colonization space, through the development of a domatia-like space for the ants. Polytaenium is found...
only as an epiphyte and its rhizomes and roots grow in such a fashion that it can adhere to irregular shapes and on rough surfaces. The outside of the rhizome mass of the *Polytaenium* supported gametophytes and young sporophytes of additional plants of *Polytaenium*, showing that the site was favorable for its growth and establishment. The other epiphytic species in the assemblage observed, a *Philodendron* species, was also not removed/pruned by the *Azteca* ants. In fact, the aroid was partially rooted into the domatia of the *Polytaenium*. Thus, the series of events involved likely included colonization of a myrmecophyte tree species, starting with the two unrelated epiphytic plant species, followed by the *Azteca* ants, which later pruned other plant species that neighbored on or dispersed to the *Cordia* tree, and accompanied by the ant use of the domatia-like shelters of the *Polytaenium*. These events would have collectively created this palimpsest of a multi-species assemblage.

Evolutionarily, these observations point to a prevalence of diffuse selection acting upon the outcomes of stochastic dispersal events and as shaped by pre-existing species mutualisms (*Azteca-Cordia*, in this case) and by pre-existing morphological adaptations and growth responses of the two epiphytic plant species permitted by the ants to remain on the *Cordia*.

Bronstein et al. (2006, p. 419) pointed out that often “... outcomes of ant-plant associations are strongly context-dependent.” For *Azteca-Cecropia* relations, Longino (1989) stressed the prevalence of spatial variation, effects of the order of colonization of host trees, and other stochastic events that lead to non-equilibrium conditions. Our observations show that several unlinked events can set up a fairly complicated multi-species assemblage. Those same authors, and as earlier also noted by Fonseca & Ganade (1996), note that frequently ant-plant associations are asymmetrical, with many costs and benefits (sensu Bronstein 1998) assumed by the ants. In this case, the ants provide pruning that presumably benefited and even encouraged successful colonization by the two epiphytic species. Benefits to the ants are not obvious, although the rhizome mass of the *Polytaenium* and the intertwined roots of the *Philodendron* at least appeared to provide a habitat space to the ants. They were not using that space for the raising of their young, an activity taking place in the axillary bud (domatia) of the *Cordia* tree.

There is also likely to be an important additional dimension associated with nutrients and nutrient limitations. Walkins et al. (2008) recently showed through the use of stable isotopes that ants benefit epiphytic nonspecialized (ie. non-myrmecophilous) ferns by bringing in substances (or producing wastes) that provided extra nitrogen to the fern roots. This was demonstrated in *Antrophyum lanceolatum* (= *Polytaenium lanceolatum* (L.) Benedict) in Costa Rica, with *Phediole flavens* ants, making their study directly relevant to our observations in Peru. The unspecialized domatia of the Costa Rican fern, nevertheless provided
considerable benefits in terms of nitrogen when fortuitously the fern had ant residents (62% of 93 sampled ferns had ants). Epiphytism in general has been proposed as an evolutionary strategy for plants found in nutrient-limited tropical environments (Benzing 1991, Dubuisson et al. 2009). The rhizome mats of the Polytaeium of our study can form microenvironments attractive to ants. Presumably this fern species evolved its morphology to facilitate epiphytism, but secondarily may also benefit from increased nitrogen availability when ants utilize the “accidental” domatia. Speculatively, it also seems possible that the Philodendron would fortuitously have benefited from more nitrogen availability in what is a very low-nutrient environment (Young & León 1989).

In conclusion, we use observations of a particular example of a complex ant-plant species assemblage where the respective spatio-temporal arrangements appear to provide some insights into the complexity of ecological relationships that potentially give rise to mutualistic relationships, some of which are facultative, some of which are dependencies, and some of which are only expressed fortuitously.

Acknowledgments

We thank the community of Siete de Junio for their hospitality, E. O. Wilson for kindly identifying the ants, and CONCY-TEC for financial assistance.

Literature cited


