E. Pringle. **The *Cordia alliodora* mutualism:**

- Three-way mutualism: plant (1 species – *Cordia alliodora*), ants (1 species in Chamela, Mexico – *Azteca pittieri*; up to 5 species in Santa Rosa, Costa Rica, including *Azteca pittieri* and another *C. alliodora* specialist, *Cephalotes cetulifer*), **coccoids** (*e.g.* insects in the families Coccidae (scale insects) and Pseudococcidae (mealybugs), several species)
- *Azteca* ants protect plants from damage caused to leaves by some types of herbivores (many species, both caterpillars and beetles), thus frequently thought of as "biotic defense" against herbivores for the plant. Other ants, including *Cephalotes setulifer*, do not appear to be very aggressive or good defenders of the plant against herbivores. These ants may be parasites of the mutualism. It is interesting that these "parasitic" ants are only found in high densities in some geographic locations and not others. In addition, *Azteca* ant defensive behavior appears to vary geographically.
- New plants form domatia (hollow cavities that house the ant colony) automatically (ant-plants, also known as myrmecophytes, are usually defined as those plants that are genetically programmed to have these cavities). Plants may be colonized initially by one or several ant queens.
- Queen ants arrive by flying in search of new host plant. Upon arrival, the queen must chew a hole in a new domatium in order to move in.
- Newly arrived queens produce ant workers. A founding colony (i.e. queen plus initially small number of workers) will usually NOT come out to defend the plant. When the colony grows large enough, worker ants begin to respond to disturbance and therefore begin to defend the plant effectively against herbivores.
- If the plant was colonized initally by several queens, the colony that grows the larger worker force more quickly will outcompete the other founding colonies and take over the plant, *i.e.* usually only one mature ant colony per plant.
- Different colonies of unrelated ants will fight each other.
- **Coccoids** are insects of the order Hemiptera that suck plant phloem. They represent a direct cost to the plant. They produce carbohydrate-rich honeydew as a waste product.
- **All *Cordia* ants tend coccoids inside plant domatia**, and benefit from the sugar resources provided by the honeydew. In doing this, they also protect scales from parasites and pathogens. *Cordia* plants themselves produce no food rewards for ants.
- *Azteca* ants appear to be more active and defend plants better against herbivores in the presence of higher densities of coccoids. (So, coccoids may incur indirect benefits for the plant separate from their direct costs).
- Although we are not sure how coccoids arrive at the plant, ants have some control over coccoid populations once they are in the plant. *Azteca* ants frequently carry juvenile coccoids around between domatia, just as they carry their own larvae.
- The ant *Azteca pittieri* is always found with coccoids, usually with 2 or more species in the same domatium. The other specialist *Cordia* ant that is found in Costa Rica, *Cephalotes setulifer*, usually tends a single species of coccoids at lower overall densities than coccoid populations in *Azteca* colonies. Thus, although *Cephalotes* may not defend the tree as well against herbivores as *Azteca* (see above), it is also imposing less of a direct cost to the plant in terms of densities of coccoids.
- *Cordia alliodora* loses its leaves in the dry season in seasonal tropical forest. During this time, the ants are not "useful" to the tree in terms of defense against herbivores (there are no leaves and no herbivores either). The plant supports the ants and the coccoids throughout the entire year. Thus, for the mutualism to provide the plant with a net benefit, the ants must provide sufficient benefits to plant fitness during the wet season (and especially during the ~ 1 month window when the tree puts out new leaves because new leaves are more valuable than old leaves to the plant) for the tree to support the ants and coccoids all year round.