

Biotic interactions in the genus *Macaranga* (Euphorbiaceae) in SE Asia

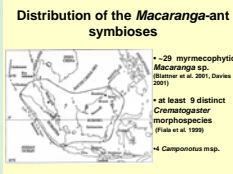
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Introduction. Biotic interactions between organisms can be a crucial factor driving diversification and speciation. *Macaranga* trees are the biotic environment for a number of other organisms which are fully or partly specialized on this genus. Most conspicuous is the association with ants. Due to the anthropogenic destruction of the tropical forests, *Macaranga* pioneers have become one of the most abundant tree genera along roadsides and in cleared areas in SE Asia. In a broad approach our team has been studying biology and ecology of plants, ants and coccids (review e.g., Fiala et al. 1999, Moog, et al 2002). The various types of interaction in this complex and its considerable degree of radiation concerning all partners offer an **exceptional model system for studying the processes of speciation and radiation in mutualistic systems** in general.

Diverse (partly highly specialized) biotic interactions:

Symbiotic associations with obligate ant-partners (mainly *Crematogaster*), also involving more than 25 specific coccid species



Stem interior with ant brood and coccids



Colonising *Crematogaster* queen in *M. winkleri* sapling

Pollination by thrips



Flowers and fruits of *M. indistincta*



Thrips with tiny pollen grains attached. Photo Ute Moog



Flowering *M. winkleri*



Fruits of *M. lamellata*

The approach: Our aim is to investigate possible **mechanisms of speciation** within the diverse ant-plant system *Macaranga*. Our work comprises phylogeny, phylogeographic patterns, and population structure of the host plants, partner ants and associated coccids (in cooperation with our colleagues Kurt Weising, Ute Moog, Frank Blattner, and Penny Gullan). A long-term goal is to estimate gene flow in *Macaranga* species via seed and pollen dispersal, where thrips pollination could pronounce isolation between remote populations. One goal is to analyse the proximate factors that can lead to divergent or disruptive selection in our system (ecological, genetical or behavioural mechanisms). We will test whether competition, changes in colony structure or the evolution of specific interactions between species can lead to a genetic substructuring.

Structuring mechanisms of the *Crematogaster*-*Macaranga* association

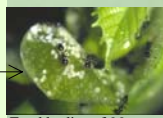
Despite the sympatric occurrence of host-plant species non-random patterns of ant-association with different degrees of specificity are observed (see Fiala et al. 1999).

Possible structuring factors of these patterns:

- **Habitat preferences**
- **Morphological plant traits** (wax, trichomes, domatia structure)
- **Resource availability:** nesting space and food as limiting factors for colony growth
- **Inter- and intraspecific competition**
- **Colony structure, life history traits** (size, onset of reproduction)
- **Specific adaptations**
- **Coevolution??**



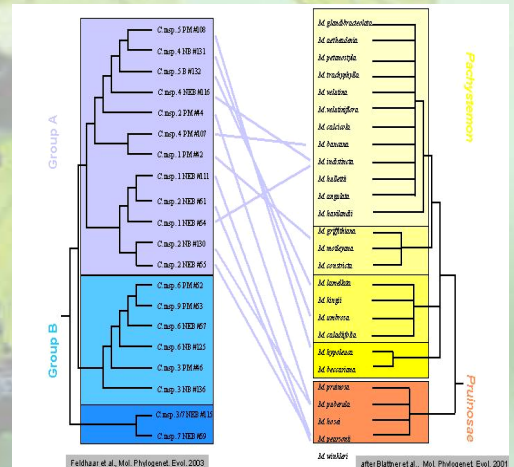
Wax cover in *M. griffithiana*



Food bodies of *M. hoseri*

Onset of production of reproductives

- **late:** from > 5000 workers
Colonies get big
Crematogaster from group A: msp. 1, 2, 4;
- **early:** from ca. 500 to 700 workers
Colonies stay small
Crematogaster from group B: msp. 3, 6, 7, 9



Comparison of the phylogeny of symbiont *Crematogaster* ants (mtDNA, left side) with the phylogeny of their *Macaranga* host plants (schematic, based on ITS sequences). Lines between the two phylogenies exemplarily connect the ant specimens of group A with their host plants. (Group characteristics: A: queens are small, small-eyed, nearly black, queens only search for host plant saplings near the ground. B: queens are bigger, with larger eyes, light brown, queens found colonies in saplings as well as in the crown region.)

First conclusions: Such obligate ant-plant associations have long been viewed as classical examples of strict coevolution. However, comparison of the phylogenies of the *Crematogaster* -morphospecies with that of their *Macaranga*-host plants does not suggest strict cocladogenesis between the two species groups. Ants of the two groups are not restricted to one specific clade of host plants. Host plants are often colonized by multiple ant species. Rather, the observed colonization pattern can be better explained by ecological characteristics or morphological traits of the host plants. For example the wax cover of the tree stems in several *Macaranga* species might prevent 'non-wax-runners' (e.g., msp. 3 and msp. 4) which inhabit the majority of non-waxy species in the section *Pachystemon* from colonizing host plants with waxy stems (e.g. all members of Section *Pruniosae*). Our results rather support the view that host-shifting and/or host-expansion is common in this ant-plant system. We consider **ecological speciation** a likely mechanism of speciation for the *Macaranga*-associated ants. Differences in *Macaranga* host-plants would then result in functional and phenotypic differentiation in the ants due to divergent selection. First results from field studies show that different but closely related *Decacrema* species colonizing the same *Macaranga* species show differences in traits associated with host usage, possibly resulting in fitness effects for ants and plants.

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