Yeast assemblages in the fungal gardens of leaf-cutting ants

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Resumo

Uma análise dos dados publicados de leveduras associadas com o fungo simbiótico de Atta sexdens rubropilosa e Atta laevigata não revelou um conjunto estruturado. As comunidades de leveduras não correspondem às regras de assembléia de ecologia de comunidades. As combinações de espécies coexistentes dificilmente podem ser separadas ecologicamente, e por isso, provavelmente não são reguladas pelo fungo ou pelas formigas.

Unitermos: fungos, mutualismo, leveduras, Atta.

Summary

A reanalysis of published data on yeasts associated with the symbiotic fungal gardens of Atta sexdens rubropilosa and Atta laevigata did not indicate that these were a structured assortment. Although two yeasts were specific to A. laevigata, six were for A. sexdens rubropilosa. Yeast assemblages could not be fit to assembly rules of community ecology, and combinations of coexisting species are therefore difficult to attribute to any known ecological function, and thus are unlikely to be regulated by the fungus or the ants.

Key words: fungi, mutualism, yeasts, Atta.
Introduction

The nutritional ecology of fungus-growing ants (Formicidae: Attini) is practically unknown (Fowler et al., 1991). Fungus-growing ants have a symbiotic relationship with their food fungus, which is apparently grown as a pure culture (Kermarrec et al., 1986). There is considerable evidence that the fungal strain grown by each species (or colony?) is cloned from highly productive stocks (Stradling and Powell, 1986). The fungus is thought to be a monoculture, and recent evidence suggests that its evolution parallels that of ants (Hinkle et al., 1994). There is still no common accepted name for this fungus (Kermarrec et al., 1986). Most of researchers agree with the name Leucocprinus gongylophoros (Moeller) Heim (Bononi et al., 1981; Kermarrec et al., 1986; Fowler, et al., 1991), but some prefer the name Attamyces bronomatificus (Kermarrec et al., 1986), or even Aspergillus sp. (Lehmann, 1974).

However, a number of other microorganisms are associated with the fungus. The interaction of fungus with microorganisms is still not well understood, as many of these have not been identified. Given that antibiotic properties have been described for both ants and fungi (Papa and Papa, 1982a, 1982b; Kermarrec et al., 1986; Fowler, et al., 1991), many could be contaminants. It is possible, however, that other microorganisms form an additional symbiotic loop, ants-fungus-microorganisms, without whose presence the symbiosis of ants with fungus would fail (Fowler et al., 1991). If such is the case, then patterns of occurrences should be fairly stable and fixed. Of the microbiota with recorded presence in the leaf-cutting ant fungus gardens are the yeasts (Craven et al., 1970; Angelis et al., 1983). Compared with bacteria, yeasts have limited physiological capabilities. Most yeasts colonize carbon rich substrates and are poorly adapted physiologically to extreme chemical and physical conditions. Yeasts generally do not have, however, specialized nutritional requirements. Yeasts are thus like most plants and animals, given their small range of physiological capabilities. This physiological uniformity suggests mechanisms of coexistence not found in bacterial communities. Here, we examine assemblage structure of fungal garden yeasts of Atta, based upon a reanalysis of published data (Angelis et al., 1983) in a attempt to look for consistent patterns.
Thirteen yeasts species from four genera were isolated from 40 fungal gardens of *Atta sexdens rubropilosa* (Forel), and 10 fungal gardens of *Atta laevigata* (Fr. Smith) (Fig. 1). The yeast species encountered were *Candida krusei*, *Candida jadinica*, *Candida membranaefaciens*, *Candida stellatoidea*, *Candida utilis*, *Candida variopina*, *Kloeckera apiculata*, *Rhodotorula glutinis*, *Torulopsis candida*, *Torulopsis datti*, *Torulopsis etchellsii*, *Torulopsis magnoliae* and *Torulopsis parapsilosis* (Angelis, et al., 1983). No fungal garden was free of yeasts species. Furthermore, *R. glutinis* was found in all *A. laevigata* fungal gardens, but was not present in the fungus gardens of *A. sexdens rubropilosa* ($z = 7.141; p < 0.0001$), suggesting that this species is specific to the former. However, because only presence-absence sampling was used, there was a significant probability that species was present but not sampled. A Bayesian estimate of the Beta distribution (Nicholson and Barry, 1995) was used to infer the probability that a species was not sampled. In this case, the probability for yeasts in *A. sexdens* nests was 0.016, while for *A. laevigata* nests was 0.019, and for the combined nests was 0.020.

![Figure 1: Number of yeast species per fungus garden in species of Atta.](image-url)
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The number of yeast species per fungus garden (Fig. 2) deviated significantly from a Poisson distribution ($X^2 = 28.21, p < 0.01$) (Zar, 1974). Five yeasts species were found to always occur in combination with other yeasts. Additionally, 7 yeast species were found to occur with at most one other yeast species. Species of yeasts never found occurring solitarily were T. magnoliæ, C. vartiovaarai, C. utilis, T. dattila, and C. javenica. Yeast species found associated with a maximum of one other yeast species were C. humicola, T. candida, C. membareaefaciens, C. stellatoidea, C. javenica, T. dattila, and C. vartiovaarai. Estimated alpha yeast species diversity from the log-series distribution was 4.42, with large sample variance of 1.505 (Zar, 1974). However, two null models of species cooccurrences (17-18) were not falsified. Probabilities for models were: (Connor and Simberloff, 1979) = 0.328 (Fox and Brown, 1993) = 0.063, based upon 200 randomizations. This suggests that yeast species present random combinations of potential yeast colonizers (Drake, 1990; Wilson, 1995). Without detailed nutritional studies (Lachance and Starmer, 1986) yeast assemblage structure of Atta fungus gardens thus remains unknown, although these may supply vitamins needed by the fungi or the ants (Fowler et al. 1991). If these fungi are indeed mutualistic partners of the ant-fungus symbiosis, collections of fungus gardens are unable to detect assemblage structure (Lachance and Starmer, 1986), due perhaps to sampling problems (Zar, 1974). Because of similar dietary demands, it is possible that any combination of yeast species may be possible, and it seems unlikely that the fungus or the ants regulate species occurrences.
Figure 2: Species specific occurrences of yeast species per Atta nest.

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