



Near-complete biomass decomposition in fungus-farming termites: Integrated symbiont management in space and time

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Fungus-farming termites are a paramount example of symbiotic association between an insect host, a basidiomycete fungus (genus *Termitomyces*) maintained as a crop in external gardens, and co-diversified gut microbial communities. Efficient biomass decomposition involves intricate steps across space (different locations within colonies) and time (different stages of biomass break down), including complementary enzyme contributions from all partners in the symbiosis. This includes a first gut passage, where plant biomass is mixed with fungal spores, followed by external digestion within fungus gardens and a second gut passage, after which essentially all organic matter is utilized. Here we investigate what enzymes are expressed and what plant components are decomposed through time and space. Our findings indicate that different enzymes are active from the start to the end of the decomposition process, with a concomitant decrease in plant polymers. Comparative metagenome analyses of carbohydrate-active enzymes targeting plant and fungus cell wall components across two fungus-growing and seven other higher termites, revealed that enzymes targeting plant-cell walls are enriched

in other termites, but relatively low in abundance in fungus feeders. In contrast, fungus-cell-wall-targeting enzymes are enriched in fungus farmers. This indicates functional adaptations in the gut microbiota to the diets displayed by different termites, and our analyses further show that the most abundant bacterial taxa in a given termite species provide the majority of genes encoding relevant enzymes. Symbiont management for biomass break down in time and space reflects the synergistic efforts from partners in the association, and this integrative division of symbiont labor in enzyme provisioning could explain the success of this symbiosis.

