

# LEAF-CUTTER ANTS (*ATTA CEPHALOTES*) ARE SIMILARLY ABUNDANT IN PRIMARY AND SECONDARY FOREST

STEPHEN J. TAERUM

Faculty editor: Matthew P. Ayres

*Abstract:* Forest disturbances strongly influence herbivore-forest interactions. I examined how forest disturbances affect the abundance of leaf-cutter ants, *Atta cephalotes*, at La Selva Biological Reserve in Costa Rica. In addition, I tested for evidence of different plant palatabilities between primary and secondary forests, and tested for differences in interspecific interactions involving *At. cephalotes* in both forest types. Contrary to previous studies, leaf-cutter ant abundance tended to be higher in primary forests than secondary forests. There was no difference in feeding preferences of *At. cephalotes* on leaf pieces collected from the two forest types. In addition, there were more minimas hitchhiking on leaves carried by foragers in primary forest, suggesting that parasitic phorid flies may be more abundant in primary than secondary forest. Future studies should elucidate the causes of these patterns.

*Key words:* disturbance, herbivory, interspecific interactions, tropical forests, leaf-cutter ants

## INTRODUCTION

Forest disturbance can affect herbivore populations by changing plant species compositions, and by altering community interactions between herbivores and their natural enemies, competitors, and mutualists. In turn, herbivores influence forest structure and function by speeding or slowing successional processes, increasing or decreasing plant diversity, and altering trophic interactions. The effects of forest disturbance on herbivores, and the reciprocal impacts of herbivores on disturbed forests, are of great interest in tropical forests, where human activities are converting large amounts of primary forest to secondary forest.

Depending on the circumstances, forest disturbance could harm herbivore populations (for example, by removing obligate food sources) or benefit them (for example, by lowering the abundance of natural enemies). Leaf-cutter ants, *Atta cephalotes* (Formicidae: Attini), often have higher densities in secondary forests than in primary forests suggesting that *At. cephalotes* benefit from certain disturbances (Farji-Brener 2001). *At. cephalotes* feed on a mutualist fungal cultivar that the ants provision with leaves, fruits, and flowers from a diversity of plants. This symbiosis makes *At. cephalotes* a generalist herbivore that may more readily adjust to changes in plant community than specialist herbivores. In addition, the fungal

cultivar is negatively affected by plant secondary compounds, which are more prevalent in climax tree species (which dominate primary forests) than pioneer species (which dominate secondary forests). Therefore, higher palatability of plants may result in higher *At. cephalotes* densities in secondary forests than primary forests.

*At. cephalotes* may also benefit from low abundances of natural enemies or competitors in secondary forests. Enemies of *At. cephalotes* include phorid flies that attack foraging ant workers, and the specialist fungal parasite, *Escovopsis*, which attacks leaf-cutter ant fungal cultivars. Populations of *At. cephalotes* could be favored by forest disturbance if secondary forests are unfavorable for these or other enemies. In addition, *At. cephalotes* competes for resources with other herbivores, such as other leaf-cutter ant species. Low competitor abundances in secondary forests would tend to increase *At. cephalotes* abundance.

Alternatively, *At. cephalotes* abundance may depend on soil properties that are correlated with forest disturbance more than they are influenced by primary vs. secondary forest directly. For example, human development (and therefore forest disturbance) tends to be concentrated on areas with good soils and plants growing on high nutrient soils tend to produce less

anti-herbivore defenses such as tannins. So *At. cephalotes* could be more abundant in areas of high nutrient soils, which tend to be the areas where forest disturbance by humans is most likely. Soil type could also influence *At. cephalotes* if some soils are more suitable for nest excavation.

The purpose of this study was to determine which of the above theoretical models explain the abundance patterns of *At. cephalotes*. I estimated ant abundances in both primary and secondary tropical forests to determine if *At. cephalotes* has a higher abundance in secondary forests, and I sampled primary and secondary forests on both alluvial (i.e., nutrient-rich) and residual (i.e., nutrient-poor) soils to separate the contributions of soil type *At. cephalotes* abundance (Nichols-Orians 1991). I collected data at 3 separate times of day to test if the foraging habits of *At. cephalotes* remain constant throughout the day, or if foraging increases during daytime, as previously shown with *At. colombica* (Liebert and Ruel 1994).

I conducted assays to test if *At. cephalotes* preferentially select leaves from secondary forest over leaves from primary forests, as predicted if leaf palatability is higher in secondary forests. I tested indirectly for habitat differences in parasitic phorid flies (Diptera: Phoridae) by comparing the proportion of foraging workers (medias and

maximas) that carried minima workers on their leaf fragments (minor workers are hypothesized to protect foraging workers from phorids). Finally, I examined the abundance of *At. colombica* near the *At. cephalotes* nests to test if competitors are more or less abundant in different forest types.

## METHODS

During 18 – 20 February 2008, I studied the abundance of *At. cephalotes* in the La Selva Biological Reserve in Costa Rica. La Selva was ideal for this study as it has large areas of primary and secondary forest on both alluvial and residual soils.

I conducted field observations on the evening of the 18<sup>th</sup> (starting at 21:00), the afternoon of the 19<sup>th</sup> (starting at 13:00), and the morning of the 20<sup>th</sup> (starting at 08:00). I established four 20 × 200 m transects along concrete or dirt trails within 2 km of the La Selva Biological Station such that one transect was on each of the following forest type-soil combinations: primary forest on alluvial soil (Camino Experimental Sur trail), primary forest on residual soil (Sendero Surá trail), secondary forest on alluvial soil (Sendero Tres Rios trail), and secondary forest on residual soil (Lindero Occidental trail). I started the transects at random distances from the starts of each trail.

During my initial observation period, I walked the length of each transect and counted the trails of *At. cephalotes* and *At. colombica* (which compete with *At. cephalotes* for resources) within each transect. I followed each leaf-cutter ant trail carefully to prevent counting a leaf-cutter ant trail more than once. For all observation periods at each *At. cephalotes* trail, I counted the number of ants that crossed an imaginary line within 2 minutes. To calculate *At. cephalotes* abundances, I obtained the mean values of the ants counted in 2 minutes for each transect, and multiplied these means by the number of trails observed in each transect. If ants carried leaves during the observation period, I sampled 20 leaf-carrying workers and counted the number of those leaf fragments that had minor workers.

On 18 February, I collected 40 leaf pieces each from *At. cephalotes* workers foraging in the primary and secondary forests (no more than 15 pieces from any one trail). On the afternoon of 19 February, I placed a line of 20 leaves on one active *At. cephalotes* trail on each transect, alternating leaves collected in the primary and secondary forests. I counted the leaf pieces that remained from the primary and secondary forests the following morning to test for preference between leaves from both forest types.

## RESULTS

I observed a total of nine *At. cephalotes* trails on my transects: six in the primary forest (three on alluvial soil, three on residual soil) and three in the secondary forest (one on alluvial soil, two on residual soil). No *At. colombica* trails were observed on any transects. I counted a total of 1181 *At. cephalotes* workers across all observation periods. Although some ants foraged throughout the day, diurnal foraging seemed to be minor. I only observed 12 ants during the afternoon and 5 ants at morning, as opposed to 1164 ants at night. Consequently, I excluded the afternoon and morning data from analyses.

*At. cephalotes* were not more abundant in secondary forests. Actually, they tended to be more abundant in primary than in secondary forests (Figure 1a), although the difference was not significant ( $t = 2.52$ , d.f. = 2,  $P = 0.13$ ). There was no apparent difference in *At. cephalotes* abundance between forests on alluvial vs. residual soils (Figure 1b;  $t = 0.01$ , d.f. = 2,  $P = 0.99$ ). Minor workers on leaves were more common on *At. cephalotes* trails in primary than in secondary forests ( $t = 2.32$ , d.f. = 7,  $P = 0.053$ ; Figure 2). *At. cephalotes* workers showed no preference for leaf pieces collected in primary or secondary forest ( $t = 1.46$ , d.f. = 3,  $P = 0.12$ ; Figure 3).

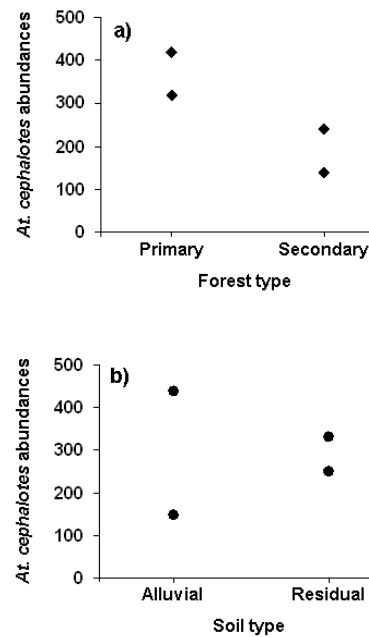


Figure 1. *At. cephalotes* abundances a) in primary vs. secondary forests and b) on alluvial vs. residual soils.

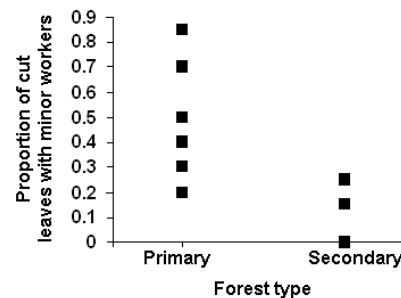


Figure 2. Proportions of *At. cephalotes* workers that carried minor workers on their leaves in primary and secondary forests.

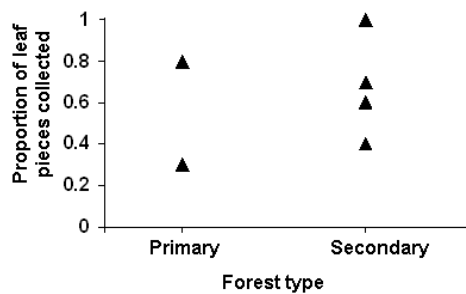


Figure 3. Proportions of leaf pieces originating from the primary and secondary forest that were collected by *At. cephalotes* workers in the preference assays.

## DISCUSSION

My studies failed to support previous findings that *At. cephalotes* is more prevalent in secondary forest than in primary forest. Perhaps different mechanisms influence patterns of leaf-cutter ant abundance at La Selva than at other locations. Higher *At. cephalotes* abundances in primary forests than in secondary forests may suggest that *At. cephalotes* are adapted to the plants in primary forests, that secondary forests are less suitable for nest or trail construction than primary forests (e.g., because of high tree density), or that secondary forests favor an enemy of *At. cephalotes* or its mutualist fungus. Of course it is also possible that more intensive sampling would reveal a different pattern. Low sample sizes in my study would have increased the likelihood of spurious patterns (e.g., from chance location of transects relative to nests of *At. cephalotes*).

Future studies could conduct more thorough tests of spatial patterns in ant abundance.

There seemed to be a striking difference in forest types in that there was a higher frequency of minor workers travelling with foraging workers in primary than secondary forest. This suggests that more phorid parasitism may be more intense in the primary forest. This was the opposite of my theoretical prediction, as *At. cephalotes* abundances were higher in the primary forest than the secondary forest. However, these patterns might be explained if phorid prevalence depends on *At. cephalotes* abundances, or if phorids are more able to find or track leaf-cutter ants in primary forests. Additional studies that quantify phorid prevalence as well as studies examining the interactions between minor workers and phorids are required. In addition, future studies could evaluate the prevalence of other parasites on *At. cephalotes*, such as mites or *Escovopsis*, in primary and secondary tropical forests.

*At. cephalotes* showed no preference for leaf pieces from primary or secondary forest, suggesting that leaves from both forest types were equally palatable. This argues against the importance of the resource availability hypothesis of genotypic patterns in plant defenses for explaining patterns in *At. cephalotes* abundance.

However, the sample sizes were again quite small, and results may have been biased because ants in the primary forest likely preferentially foraged on the most palatable plant species in the primary forest. Therefore, the leaf pieces collected in both forest types may have been equally palatable, even if primary forests have fewer palatable plant species. Alternatively, the trails in the primary forests may have led to more palatable trees in secondary forests.

Although the soil properties I examined did not affect *At. cephalotes* numbers, other soil properties, such as grain size and moisture retention, may influence *At. cephalotes* abundance. Future studies could address how these additional soil properties influence leaf-cutter ant abundance.

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