

Spatial Ecology of Leafcutter Ants,
Isla del Cielo Reserve, Barú, Costa Rica

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I. Introduction

There are 38 different species of Leaf-cutting ants restricted to two genera *Acromyrmex* (24 species) and *Atta* (14 species). These two genera belong to the tribe of fungus-growing ants called, Attini. Attini are confined to the New World between the latitudes of ~33oN and ~44oS. Though considered a pest, these species of leaf-cutting ants cause damage only in the areas that they are indigenous to (except for a few exceptions) (Lofgren & Meer, 1986). Townsend (1923) reported that in the absence of their control, leaf-cutting ants are capable of affecting 1000 million U.S dollars of damage a year. The damage covers a wide array of industries, damaging pastureland and stock, agricultural and horticultural crops, plantation forests, dried foodstuffs, roads, and the foundations of buildings (Lofgren & Meer, 1986).

Leaf-cutting ants express a striking degree of polyphagy. Even in species-rich tropical rain forests, 50% to 77% of the plant species are harvested by leaf-cutting ants (Lofgren & Meer, 1986). Leaf-cutting ants are the dominant herbivore in the neotropics, harvesting an estimated 12-17% of all leaf production in a forest (Perfecto & Vandermeer, 1993). These harvested leaf fragments are brought underground to the ants' colony where they are used as a medium for fungus. This fungus is the main food source for the whole colony. The spent leaf fragments are then either brought to the surface and deposited onto large nutrient-rich refuse piles, or transported to another chamber underground where they are mixed with excavated earth. This rotation of nutrients leads to the creation of a dynamic mosaic of soil microhabitats. For all these reasons, leaf-cutting ants are considered very important for soil genesis and structure, nutrient cycling, and plant community dynamics and structure. Some have even argued that these polyphagous herbivores are a keystone species (Perfecto & Vandermeer, 1993).

The placement of leaf-cutting ant colonies also affects the plant community dynamics, but in a manner akin to gap phase dynamics. Leaf-cutting ant colonies form a small vegetation-free gap in the forest floor. Upon the colony's mortality, seedlings are then allowed to grow in the light gap, as is the case in light gaps created by fallen trees (Perfecto & Vandermeer, 1993). Jaffe & Vilela (1989) propose that it is infact the initial presence of these light gaps, or clearings that dictate the presence of *Atta* colonies, and the subsequent density of leaf-cutting ants. It is repeatedly found that the population density of leaf-cutting ants (especially *Atta*) is significantly higher in disturbed forests. Increased tree falls and trail forming is associated with a human preference, and it is in the proximity to these that the highest densities of colonies are found. Another possible hypothesis that explains this observation is that undisturbed forests though containing a larger biomass, also contain plants with higher developed defense mechanisms and a wide dispersion of palatable plants. *Atta* colonies might be less equipped to recognize the toxins of such a diverse flora that poisoning the fungus and the colony is more probable (Jaffe & Vilela, 1989).

Agriculture in tropical regions has been associated with the rapid population increase of leaf-cutting ants in clearings since an initial report in 1587. Numerous studies document higher population densities in "man-simplified habitats than in natural ones" (Lofgren & Meer, 1986b). Besides this human impact, little else is known about colony distribution. It has been observed that at sites where there are multiple colonies, these colonies are usually in close proximity together forming aggregations of colonies

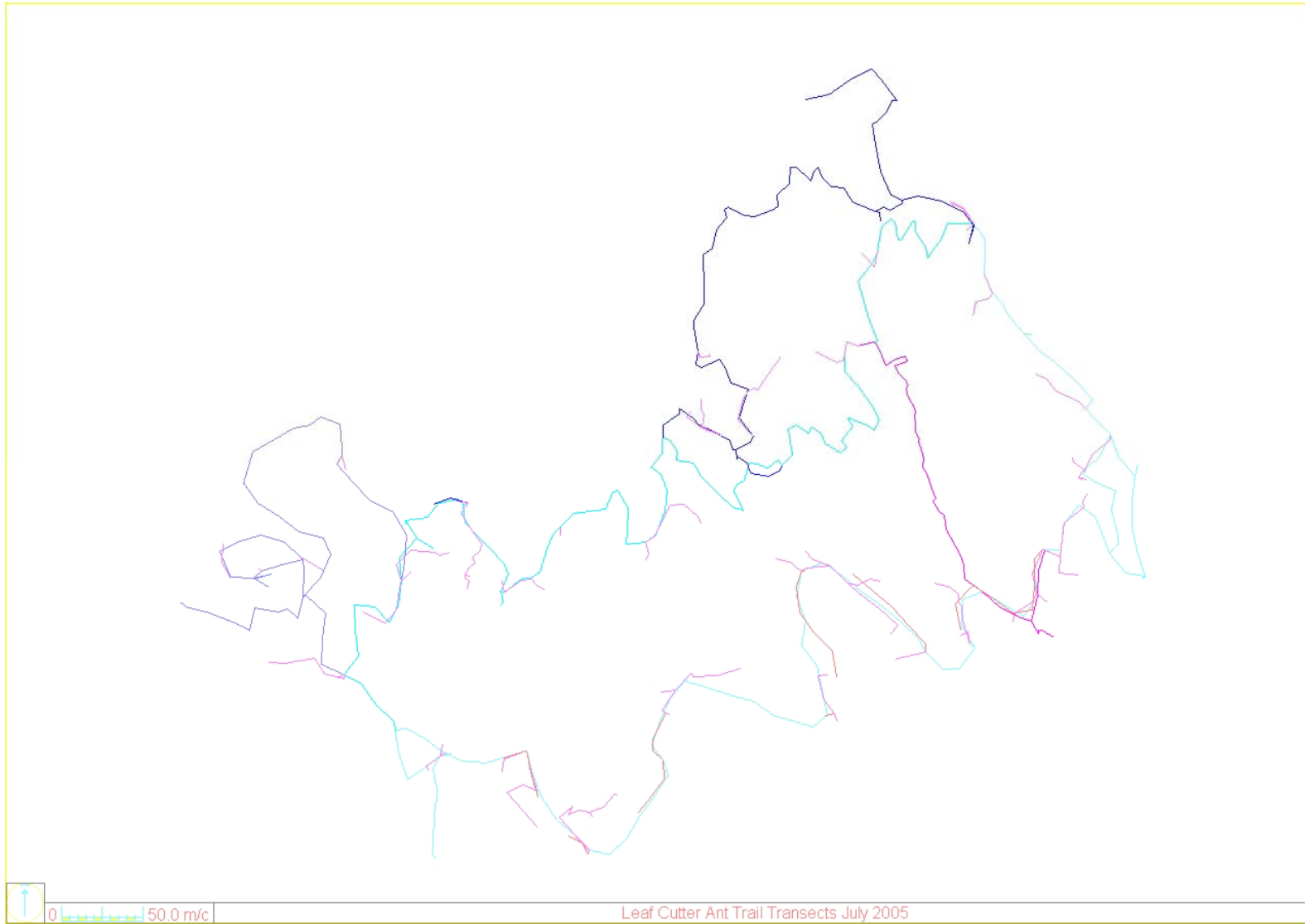
dispersed over a wide range (Jaffe & Vilela, 1989). Also that some species may exhibit preferences to different habitats. As seen with *A. sexdus* that prefers to inhabit grasslands and grassland-forests, while *A. cophalotes* and *A. colombica* prefer to inhabit purely forested habitats (Weber, 1968). Predation is also a limiting factor in leaf-cutting ant population densities. A comparison study between sites with numerous predators and sites relatively free of predators, found that predation was possibly the essential factor underlying the observed variation in *Atta* density patterns (Madhu, 2000).

The newly acquired Firestone Ecology Center, Pitzer College in Costa Rica (formerly a farm known as: Finca Isla del Cielo) incorporates tree stands at various degrees of regeneration (secondary growth and abandoned or regenerated forest, a bamboo plantation, pasture, and mature riparian). This study examines leafcutter ant colony densities in these different habitats.

II. Materials and Methods

Population Density

Leaf-cutting ant colonies were located by following foraging trails that crossed or ran along all roads and paths within the study site. The location of each colony was surveyed and inserted into mapping software (COMPASS: Fountain Software) to determine the exact location. The roads and trails surveyed were treated as random line transects, and divided into consecutive 100m segments in each of the five habitats of abandoned reforestation, pasture, bamboo plantation, secondary growth, and riparian forest. The number of colonies encountered in each transect segment were counted and colony density was tabulated in three different manners. Similar approaches have been used before to determine colony density. Madhu (2000) treated the paths as transects and broke them up into 100m long segments counting colonies within 5m of either side. Jaffe & Viela (1989), counted colonies within 10m of either side of paths, and Perfecto & Vandermeer (1993), simply counted colonies visible from the path. Many of the colonies within this study were within 10m of the path, however some colonies were as far as 50m from the trail. In one analysis these distant colonies were still used because their foraging trails were in a direct relationship with the walking trail. Though the transect in this analysis may be viewed as extremely wide, it still represents an accurate portrayal of the number of ant colonies that traverse and harvest along the transect. The other analysis only includes nests within 10m of either side of the walking trail (technically nests within 20m of either side because a nest has an average of diameter of 25m). Restricting the transect in this way, allows density to be computed per hectare.



Colony Productivity

Finding the flow rate of laden foragers into a colony's entrances approximated the colony size or productivity. It was assumed that larger, more productive colonies would have a higher rate of influx. Many colonies had multiple entrance holes, thus great care was taken in finding every active hole and finding the flow rate of each to tabulate together to determine the flow rate of the whole colony. For similar methods refer to Perfecto & Vandermeer (1993). Flow rate data was taken in the afternoons (9:30am-3:00pm) no less than 9 hours after the last rainstorm. Colony sites were carefully investigated, and all active entrance holes were found and data was taken from each in the same manner.



A 30cm segment of foraging trail at 30cm to 1m from the entrance hole was located and marked. The segments were marked either by placing a ruler beside the trail, or if on unstable ground by way of loose sticks, engraved lines, or paper markers. Some foraging trails were heavily obscured by sticks, leaves, and/or soil. In cases where a clear segment could not be found, the obscured trail was carefully cleared and 30 minutes were allowed to elapse before data was recorded.

Flow rate was determined in two parts. First, 10 repeat samples were taken by way of macro-photography or on-site counts (depending on the density of the foraging paths), of the number of laden foragers within the segment. Counts and photos were taken when an uncounted laden forager reached the end of the 30cm segment. Thus the next photo or count was taken when all laden foragers from the previous sample had passed through the segment, and only new uncounted laden foragers were in the new segment; with the exact moment of recording being when one of these uncounted foragers approached the very end of the 30cm segment. Secondly, 5 repeat samples were taken timing the number of seconds it took for a laden forager to walk the same 30cm segment. Foragers were timed with a digital stopwatch; time was recorded to the hundredth of a second. Data was then tabulated to determine the flow rate, or ants per second.

III. Results, Analysis, and Observations

57 *Atta* colonies were located within the study site. Of the 57 a few have not yet been properly surveyed and entered into the mapping software. These colonies are labeled accordingly on the compass software files, and should be surveyed in the near future. Care should be taken when relocating nests. Foraging paths should not be trampled nor should the nest mounds. Most colonies have one refuse pile that is located within a 45° span, downhill from the colony. Trails vary daily, thus transects should be frequently revisited to insure that every colony has been identified.

Population Density

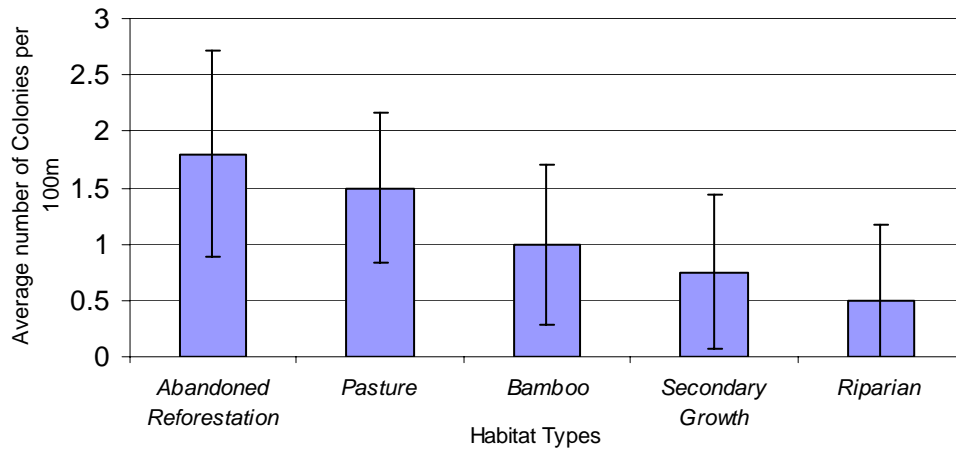


Fig 1. The number of ant colonies past in 100m sections of trails and roads within five different habitat types. [1st analysis method]

Table 1: The number of ant colonies past in 100m sections of trails and roads within five different habitat types. [1st analysis method]

Reforested Land	Pasture	Bamboo	Secondary Forest	Riparian
1	1	1	1	0
1	1	1	2	1
3	2	2	2	1
3	1	0	0	1
1	2	1	1	2
2	3		1	0
2	1		0	0
1	2		0	0
1	1		0	0
3	1		0	0
	2		1	0
	1		1	1
			1	
			0	
			1	
			1	
Total transect length (m)				
1,000	1,200	500	1,600	1,200
Averages +/- SD				
1.80 ± 0.92	1.50 ± 0.67	1.00 ± 0.71	0.75 ± 0.68	0.50 ± 0.67

Table 2. ANOVA and Tukey tests of data on ant colonies (table 1). [1 st analysis method]			
ANOVA	Significant Tukey HSD Tests between each habitat type		
P value = .0004 <i>significant</i>	Reforested Land vs Secondary Forest	Reforested Land vs. Riparian	Pasture vs. Riparian

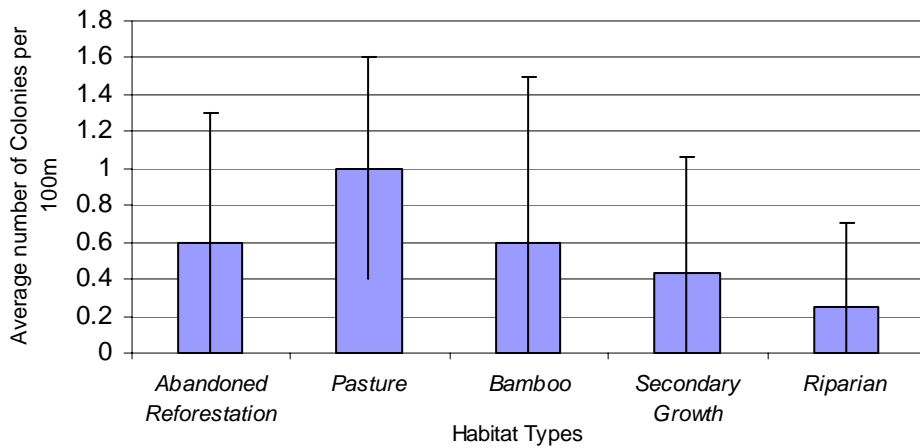


Fig 2. The number of ant colonies past within 10m on either side of 100m sections of trails and roads within five different habitat types. [2nd analysis method]

Table 3: The number of ant colonies past within 10m on either side of 100m sections of trails and roads within five different habitat types. [2nd analysis method]

Reforested Land	Pasture	Bamboo	Secondary Forest	Riparian
0	1	0	1	1
0	0	0	1	1
1	2	2	2	0
2	0	1	0	0
0	1	0	1	0
1	1		0	0
1	1		0	0
1	1		0	1
0	1		0	0
0	1		0	0
	2		1	0
	1		1	0
			0	
			0	
			0	
			0	
<i>Total transect length (m)</i>				
1,000	1,200	500	1,600	1,200
<i>Averages +/- SD</i>				
0.60 ± 0.70	1.00 ± 0.60	0.60 ± 0.90	0.44 ± 0.63	0.25 ± 0.45

Table 4. ANOVA and Tukey tests of data on ant colonies (table 3). [2 nd analysis method]	
ANOVA	Significant Tukey HSD Tests between each habitat type
P value = .065 <i>not significant</i>	None

The second analysis method included only the nests within 10m of either side of the transect. This method gives an observable area of 2 ha per km of transect.

Table 5. Nests and nest density in five different habitats. 2 ha per km of transect [2 nd analysis method]			
HABITAT	Transect length (km)	No. of nests	Nest density (nest/ha)
Reforested land	1.0	6	3
Pasture	1.2	12	5
Bamboo	0.5	3	3
Secondary forest	1.6	7	2.19
Riparian	1.2	3	1.25
<i>Total</i>	<i>5.5</i>	<i>31</i>	<i>2.82</i>

Colony Productivity

Of the 57 nests located, 45 were analyzed for flow rate. Taking the measurements necessary to determine flow-rate is a time consuming process that is riddled with many variables that can cause error. The season, temperature, humidity, sunlight, and time of day all play a huge role in the productivity of *Atta* colonies. Rainstorms and the resulting moisture have a huge affect on foraging trails. Heavy rain forces foraging ants to drop their loads and return to the nest. The rain also often floods the little foraging trails the ants carve through the forests. Observations also seem to show a daily fluctuation in flow rate that may be caused by some unforeseen variable. Future measurements of flow rate at colonies should occur during similar weather a repeat samples should be taken of the same colony on different days.

Table 6. Flow rate of ant colonies in five habitat types					
	Abandoned Reforestation	Pasture	Bamboo	Secondary Growth	Riparian
Flow	4.58	0.16	2.72	5.22	4.45
Rate	3.07	2.74	0.34	9.41	1.37
Ants/sec	0.54	2.70		2.92	1.98
	0.66	1.45		4.34	2.72
	0.60	2.56		0.52	1.07
	0.84	1.88		2.3	
	1.75	2.41		4.43	
	7.55	2.72			
	0.65	5.73			
	0.3	0.65			
	0.08	4.55			
		5.81			
		2.45			
Avg ±		0.90			
SD	1.93 ± 2.29	2.62 ± 1.72	1.53 ± 1.68	4.16 ± 2.80	2.32 ± 1.35

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