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Ant Diversity Patterns Along an Elevational Gradient in the Réserve Naturelle Intégrale d'Andringitra, Madagascar

Brian L. Fisher

Abstract

Inventory methods designed to permit rapid, replicable, and quantitative sampling of the leaf litter ant fauna were tested in wet tropical forest in eastern Madagascar in the Réserve Naturelle Intégrale d'Andringitra. Methods involved a combination of pitfall and leaf litter sampling along a 250 m transect. Surveys were conducted at four sites, located at 785, 825, 1275, and 1680 m. From pitfall and leaf litter samples, I collected and identified 27,866 ants belonging to 114 species and 28 genera; general collecting yielded an additional 34 species. The first-order jackknife produced an estimate of a total of 132 species for the four sites collectively. Species accumulation curves demonstrate the efficacy of these techniques in sampling the majority of the ants in the leaf litter. The species collected and their relative abundance are presented. The composition of the fauna is compared with that of other tropical forest sites. Species diversity decreased with elevation. Species turnover and faunal similarity measures showed a division in ant communities between the lowest elevation sites (785 and 825 m) and the highest elevation sites (1275 and 1680 m) that corresponded to the cloud forest transition.

Résumé

Dans la forêt tropicale humide de la Réserve Naturelle Intégrale d'Andringitra à l'est de Madagascar, des techniques d'inventaire, conçues pour permettre un échantillonnage quantitatif rapide et répétitif des fourmis vivant dans la litière de feruilles mortes ont été testées. Les techniques combinent l'utilisation de pièges "pitfall" et l'échantillonnage de la litière de feruilles mortes le long d'un transect de 250 m. Des inventaires ont été effectués dans quatre sites, localisés respectivement à 785, 825, 1275 et 1680 m d'altitude. A partir des pièges "pitfall" et des échantillonnages effectués à partir de la litière de feuilles mortes, 27866 fourmis appartenant à 114 espèces et 28 genres ont été recueillis et identifiés; une collecte aléatoire a permis de récolter 34 espèces supplémentaires. Le "first-order jackknife" a produit un total d'environ 132 espèces pour quatre sites. Les courbes d'accumulation des espèces ont démontré l'efficacité de ces techniques qui permettent de répertorier la majorité des fourmis dans la litière de feuilles mortes. Les espèces collectées et leur abondance relative sont présentées. La composition de la faune de fourmis est comparée à celle d'autres sites forestiers tropicaux. La diversité des espèces diminue à mesure que l'on monte en altitude. Le remplacement des espèces et la similarité de la composition de la faune de fourmis montrent une division des communautés de fourmis entre les deux altitudes les moins élevées (785 et 825 m) et entre les deux altitudes les plus élevées (1275 et 1680 m). Ces derniers correspondent à la transition vers la forêt d'altitude caractérisée par la présence de nébulosité fréquente.

Introduction

Insects constitute 85% of the world's animal biodiversity (Groombridge, 1992) and deserve increased attention in regions of the world, such as Madagascar, where species-rich habitats are under threat. Conservation methods that prioritize areas based on diversity patterns (species richness and local endemism) of birds and mammals and do not include insect diversity overlook most organisms and thus do not guarantee preservation of the greatest diversity. Few studies have investigated the correlation between invertebrate and vertebrate diversity. Pearson and Cassola (1992) showed that for gridded squares, 275 km on a side, across North America, the Indian subcontinent, and Australia, species richness levels of tiger beetles, birds, and butterflies were positively correlated. On a finer geographical scale, however, there is evidence that vertebrate diversity is not an accurate indicator of invertebrate diversity. Prendergast et al. (1993) showed low overlap between highly diverse sites of butterflies, dragonflies, liverworts, aquatic plants, and breeding birds in Britain. At 32 sites in southeastern Australia, Yen (1987) found no correlation between the number of species of vertebrates and beetles. Scharff (1992) concluded that sites in tropical rain forests of eastern Africa where linyphiid spiders showed the highest diversity were not necessarily the same as those documented for birds, mammals, amphibians, and reptiles. Thus, arthropod patterns of diversity cannot be assumed to be correlated with those of vertebrates, and methods are needed to quantify species richness and endemism in insect taxa.

In this chapter, I propose and evaluate inventory methodologies to survey leaf litter ant diversity along an elevational gradient. The elevational transect specifically addresses the following question: To what degree does elevation influence diversity and abundance of ants? I address this question by comparing species richness estimates, measures of faunal similarity, and species turnover (beta diversity) for ant species across four sampled elevations in the Réserve Naturelle Intégrale (RNI) d'Andringitra. Future work will compare these patterns with those exhibited by a sympatric assembly of vertebrates.

Study Organism and Methods

Importance of Ants

Madagascar's ant fauna is remarkable for its diversity, endemism, ancient affinities, and ecological dominance. Because of its long isolation from other land masses, the level of endemism of ant species on Madagascar is high. In the only regional study of ants conducted on the island, D. M. Olson and P. S. Ward (pers. comm.) found 92% of the ants at a dry forest site in western Madagascar to be endemic to the island. Moreover, the ant fauna of Madagascar is one of the least understood. For example, two of the better known ant genera in the world still have over 50% of their species undescribed in Madagascar (*Tetraponera*: 24 undescribed out of 36 known, P. S. Ward, pers. comm.; *Tetramorium*: 33 undescribed out of 62 known, B. Bolton, pers. comm.). There are no valid species described from the region of RNI d'Andringitra. There is one form, *Camponotus hova becki* var. *altior* Santschi, recorded from near the RNI d'Andringitra (Santschi, 1923; Perrier de la Bâthie, 1927), but this name is unavailable taxonomically. The taxonomy of *Camponotus* is in chaos, and the identity of this specimen cannot be understood until the complex of forms related to *Camponotus hova* have been thoroughly revised taxonomically.

Assessment of Ant Diversity

A primary objective of this project was to develop standardized methods for assessing terrestrial ant diversity that can be used in other tropical wet forests. The proposed method does not sample the entire ant community (arboreal, subterranean, and terrestrial), but only those ant species that nest or forage in the forest leaf litter layer. Subterranean and arboreal ant faunas pose specific technical problems in developing standardized survey methods. Leaf litter lends itself to replicable sampling with pitfall traps and leaf litter sifting. These two techniques are effective for collecting many ant species from a wide variety of habitats, and they provide data on abundance and diversity suitable for rigorous statistical analysis (Olson, 1991). Because we do not yet understand the relationship between leaf litter ant diversity patterns and the total ant fauna in any wet tropical forest, results from the following survey technique may not be representative or indicative of

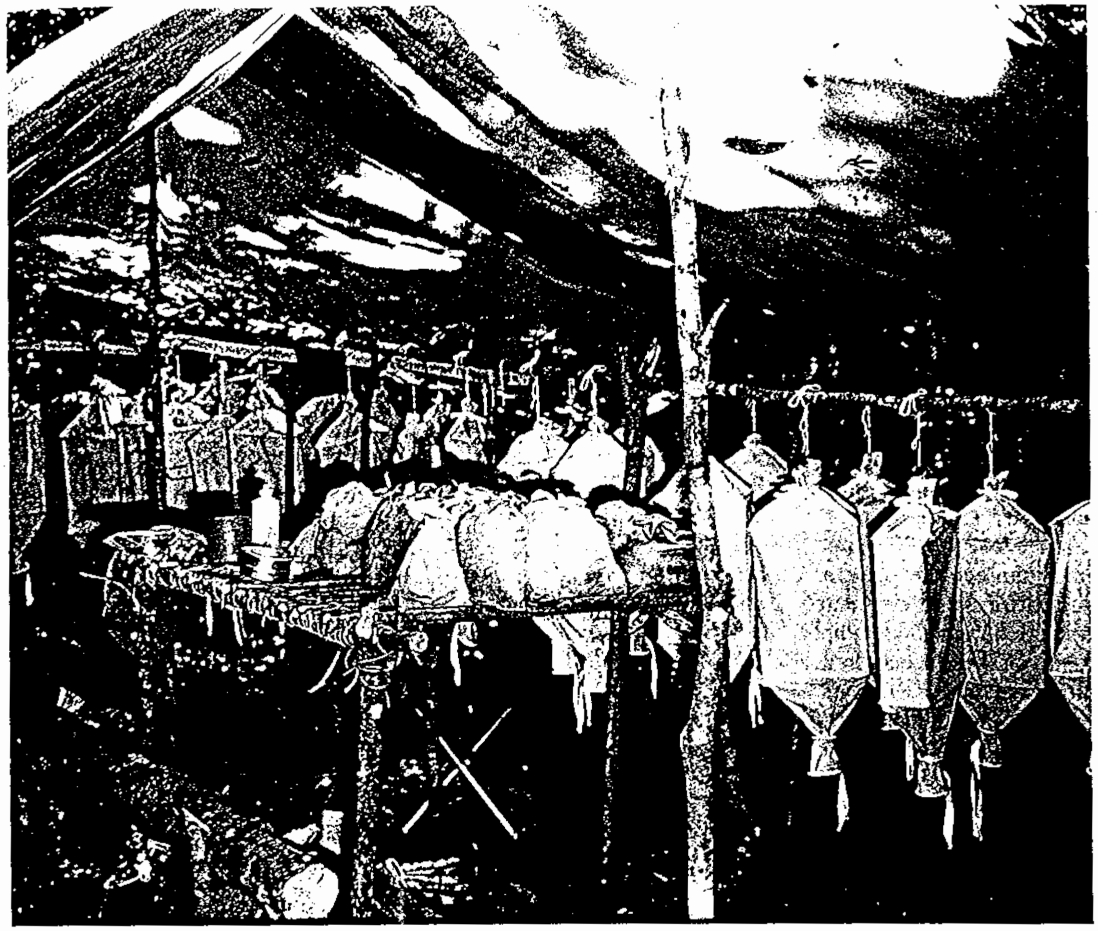

FIG. 8-1. Mini-Winkler sacks used for extracting leaf litter ants. At each elevation there were 26 mini-Winkler sacks, which were suspended under a tarp. See text for explanation of sampling methods.

patterns of rarity, endemism, or species richness of arboreal or subterranean ant communities.

In the RNI d'Andringitra, intensive ant surveys were conducted at four sites located at 785, 825, 1275, and 1680 m. These fell within 75 m in elevation of the project transects centered at 720, 810, 1210, and 1625 m. At each elevation the survey method employed 50 pitfalls and 50 leaf litter samples in parallel lines 10 m apart along a 250 m transect. The site for the transect was chosen with the intent of sampling representative microhabitats at each elevation. Pitfall traps were placed and the leaf litter samples gathered every 5 m. Pitfall traps consisted of test tubes, 18 mm internal diameter by 150 mm long, that were partly filled with soapy water and a 5% ethylene glycol solution, inserted into polyvinyl chloride (PVC) sleeves, and buried with the rim flush with the soil surface. Traps were left in place for 4 days.

I extracted arthropods from samples of leaf litter using a modified form of the Winkler extractor (Besuchet et al., 1987; Ward, 1987; Olson, 1991). The leaf litter samples involved establishing two 1-m² plots on each side of the transect line, separated by 1 m. The leaf litter inside each 1-m² plot was collected and sifted through a sieve of 1 cm grid size. Before sifting, the leaf litter material was minced using a machete to disturb ant nests in small twigs and decayed logs. Approximately 2 liters of sifted litter were taken from the two 1-m² plots. Ants were extracted from the sifted litter during a 48-hour period in modified Winkler sacks ("mini-Winkler"; Fig. 8-1). The standard Winkler sacks can hold up to four 2-liter samples of sifted litter; mini-Winkler sacks are designed to hold only one 2-liter sample. Each sifted litter sample was held in a mesh sack that was suspended in a larger cotton enclosure. The ants dropped out of the mesh sack and were collected in plastic bags ("Whirl Packs") containing 70% ethanol at the bottom of the mini-Winkler sack. At each elevational zone, a tarp was used to protect the 25 mini-Winkler sacks from rain. Because insects are less effectively extracted from wet leaf litter, sifting was done at least 24 hours after significant rainfall.

I also surveyed ants through general collecting, defined as any collection that is separate from the mini-Winkler sack or pitfall transects, including searching in rotten logs and stumps, in dead and live branches, in bamboo, on low vegetation, under canopy moss and epiphytes, under stones, and leaf litter sifting (four leaf litter samples were taken between 1800 and 2000 m elevation). At each transect site, general collections were conducted for an approximately 2-day period. These collections included samples of the arboreal ants found on low vegetation that were not sampled by pitfalls or leaf litter. Ants sampled using general collection methods, therefore, were not used in the analysis of the efficacy of the survey of the leaf litter ants, of faunal similarity, or beta diversity.

Identification

Specimens were identified to morphospecies based on characters previously established to be important at the species level for each genus. When possible, names were attached to these morphospecies by using taxonomic descriptions (Bolton, 1979) and by comparing specimens to material previously collected by Ward, Olson, and Fisher in Madagascar that was compared to type material. Specimens will be deposited at the Museum of Comparative Zoology, Harvard University, and a representative set will be returned to Madagascar.

Data Analysis

Evaluation of Sampling Method—Analyses of ant diversity patterns require an understanding of the extent to which the inventory technique samples the leaf litter ant community in each transect zone. To assess the completeness of the survey for the elevation sampled, I plotted cumulative species per sample curves for each elevation. Species accumulation is plotted as a function of the number of leaf litter and pitfall traps samples taken. For the analysis, each leaf litter sample was paired with the adjacent pitfall sample, collectively termed a station sample. Species accumulation curves for the 50 stations per transect and first-order jackknife estimates of total number of species in the local community from which the samples were taken are plotted for each succeeding station. The first-order jackknife method is a nonparametric approach to improving the estimate of species richness and is based on the observed frequency of unique species (the jackknife estimator and standard deviation are defined in Heltshe & Forrester, 1983). For both species accumulation curves, sample order was randomized 100 times, and the means and standard deviation of the jackknife estimates were computed for each succeeding station using the program EstimateS (R. K. Colwell, unpubl.; see also Colwell & Coddington, 1994). If the species accumulation or jackknife estimate curves appear to level off before 50 stations, then the transect is arguably sufficient. Conversely, if the curves do not flatten out, a longer sampling transect may be necessary to accurately compare diversity between elevations.

Ant Diversity—Data on both species richness and abundance were used to assess the change in species composition along the elevational gradient. Only records of ant workers were used in these calculations. Because alates may travel considerable distances during dispersal, their presence does not necessarily signify the establishment of a colony of that species within the transect zone. In addition, collections of queens and males dispersing from nearby nests at the time of the survey may not reflect relative abundance of the species. Because ants are colonial, abundance measures were based not on the total number of individual workers collected at each transect site but on species frequency (proportion of stations, out of 50, in which each species was collected at a site).

For each elevation, I compared first-order jackknife estimates of total species richness and 95% confidence limits. Similarity of the ant fauna of the different elevations was assessed using two different measures: (1) the Jaccard Index, based on presence/absence data only: $C_j = j/(a + b - j)$, where j = number of species found at both elevations, a = number of species at elevation A, and b = number of species at elevation B (Magurran, 1988); and (2) the simplified Morisita Index, which incorporates abundance data:

$$C_{MH} = \frac{2\,\Sigma\,(an_i \times bn_i)}{(da + db)aN \times bN}$$

where

$$da = \frac{\Sigma\,an_i^2}{aN^2} \text{ and } db = \frac{\Sigma\,bn_i^2}{bN^2}$$

where aN = total number of station/species occurrences at elevation A, bN = total number of station/species occurrences at elevation B, an_i = the number of stations occupied by the ith species at elevation A, and bn_i = the number of stations occupied by the ith species at elevation B (Horn, 1966; Wolda, 1981).

Beta diversity (species turnover between elevations) was calculated in two ways. First, the beta diversity measure of Whittaker (1960) was used: beta-1 = $(S/a) - 1$, where S = the total number of species in the two elevations combined, and a = the mean number of species in each elevation. Because this measure does not distinguish between species turnover and the loss of species along a gradient without adding new species, the measure of beta diversity developed by Harrison et al. (1992) was also calculated: beta-2 = $(S/a_{max}) - 1$, where S is the same as beta-1 above and a_{max} is the maximum value of alpha diversity among the elevations compared. Finally, the proportions of species unique to an elevation were also compared.

Results

I collected and identified 30,708 ants, comprising 148 species and 28 genera, from general collections, leaf litter, and pitfall methods. These include 705 queens and 441 males that were not used in any of the following analyses. Leaf litter and pitfall methods produced 27,866 worker ants belonging to 114 species. A list of ant species in the RNI d'Andringitra, based on all collecting techniques, and separated by elevation and technique, is presented in Table 8-1. General collections within each ±75 m transect zone are presented. The 785 and 825 m general collections were separated by 3 km and did not overlap spatially.

The total number of species was greatest in the lowest elevations sampled (89 at 785 m and 81 at 825 m). These two zones also contained the greatest number of unique species, but the highest percentage of species unique to an elevation was found at 1800–2000 m (50%). If the data for 785 and 825 m are combined, 70% of the species (74 of 105 spp.) are unique to the lowest elevations. The number of species and number of individuals collected from pitfall traps was low compared to mini-Winkler sack and general collection methods. For example, at 785 m, 8,582 workers in 76 species were collected from leaf litter samples, whereas only 218 workers in 19 species were collected from pitfall traps. Based on the number of ants extracted from the leaf litter samples over a 48-hour period using mini-Winklers sacks the average density of worker ants in the leaf litter layer was 67 per m^2.

The relative prevalence of the different subfamilies in the combined pitfall and leaf litter samples is shown in Figure 8-2. The fauna is dominated by Myrmicinae in both number of species and number of individuals, followed by Ponerinae.

The abundance of ant species is presented in Table 8-2. Both the proportion of stations at which each species was collected and the number of individuals collected are presented. Four out of 114 species were present at every elevation, but the abundance of individual species often differed considerably from one site to the next. For example, *Hypoponera* sp. 1 had a low abundance at 785 and 825 m (0.08 in bqth), while at 1275 and 1680 m its abundance was much higher (0.88 and 0.46, respectively).

Species-accumulation curves and first-order jackknife estimates of species richness with their standard deviations are presented for each transect zone (Fig. 8-3a–d, Table 8-3). Jackknife and observed species accumulation curves leveled off, indicating that within the area of the survey, the techniques employed collected the majority of the ants foraging or living in the leaf litter. In a combined analysis of all elevations, the pitfall and mini-Winkler sack methods collected 86% of the total number of leaf litter ant species estimated by first-order jackknife technique to occur in the region (Fig. 8-3e).

Faunal similarity values (Table 8-4) based on presence/absence data (Jaccard's Index) and abundance (simplified Morisita Index) were lowest between 1680 m and the two lowest elevations (785 and 825 m). The highest value of similarity was between the 785 and 825 m sites. The 1275 m transects had a greater faunal similarity with the

TABLE 8-1. Ant species list for the RNI d'Andringitra, including altitude and collection method.

Genus	Species	785 m	825 m	1275 m	1680 m	1800–2000 m
CERAPACHYINAE						
Cerapachys	1	W, G	G			
	2		W	G		
	3	W, G	W, G			
	5	W, G	W	W		
	8	W, G	W, G		W, G	
	9		G			
Simopone	1	G				
DOLICHODERINAE						
Technomyrmex	*mayri*	W				
FORMICINAE						
CAMPONOTINI						
Camponotus	1					G
	2			G	G	
	3				G	
	4					G
	5	G		W		
	10		G			
	11		P, G			
	13			W, G		
	14					G
	15			W, G		
	16	G				
	17			P	P, W	
	hildebrandti	G	G	G		
LASIINI						
Paratrechina	1	W, P, G	W, G	W, P, G		
	2	G				
	3	G				
	4	W, G	W, G	W, G	W	
	5	W, P, G	W, P, G			
	6	W				
PLAGIOLEPIDINI						
Plagiolepis	1				G	
	3	W, G	W, P, G			
MYRMICINAE						
CREMATOGASTRINI						
Crematogaster	1					G
	2					G
	3		W			
	lobata				G	
	schenki	W, G	P	P, W, G		G
DACETONINI						
Glamyromyrmex	1	W, G	W			
Kyidris	1	W, G	W			
Smithistruma	2		G	G		
	3	W, G				
	5			G		
Strumigenys	1	W, G				
	2			W	W, G	
	3	W, G				
	4				W, G	
	5				W	
	6				W	
	7		G	W, G		
	8	W, P, G	W	W, G		
	9	W	W	W, G		
	10			W, G		
	11			W		
	12	W	W			
	13	W	W			
	14	W, P, G	W, G			

TABLE 8-1. *Continued.*

Genus	Species	785 m	825 m	1275 m	1680 m	1800–2000 m
	15	W				
	16	W				
	17			W		
	18	W, G	W, G			
FORMICOXENINI						
Leptothorax	1	G	G			
PHEIDOLOGETONINI						
Oligomyrmex	1	W, G	W, G			
	2	W, P	W, G			
PHEIDOLINI						
Pheidole	1					G
	2				W, P, G	
	3					G
	6			W, G	W, P, G	
	7	W	W		W	
	8			W, P, G		
	9			W, P, G	W,P, G	
	10			W, P		
	11	W, P	W, P, G			
	12	W	W, P			
	13	W		G		
	14	W	W, P, G			
	15	W	W			
	16	W	W			
	17	W, P	W, P, G			
	18				G	G
	19					G
	20	W				
	22	W				
	nemoralis	W, P, G	W, P, G			
	veteratrix	W, P, G	W, P, G	P		
	longispinosa	W, P, G	W, P, G			
SOLENOPSIDINI						
Monomorium	1			W, P, G	W, P, G	G
	2	W	W			
	3			W, P, G	W, G	G
	4				G	G
	5	W	W, G			
	6	W	W, G			
	7	W, G	W			
	8			W	W, G	
	9			W	W	
	10		W	W, P, G		
	12			P		
	13					G
	14	W, G				
TETRAMORIINI						
Tetramorium	1		W		W, P, G	G
	2			G		
	3	W	W, G			
	4			P	W	
	5	G		G	W, P, G	
	7	W, G	W	W, G		
	9	W				
	10	W, P	W, P, G	W, P, G	W, P, G	
	11	W, P	W, P			
	13		P			
	14	W, P	G	W, P, G		
	15		W			
	16	W	W			
	17			G		

TABLE 8-1. *Continued.*

Genus	Species	785 m	825 m	1275 m	1680 m	1800–2000 m
	andrei	W, P	W			
	cognatum	W	W, G	W, G		
	dysalum	W, P, G	W, P, G			
	electrum	W, P	W, P			
	marginatum	W, P	W, P			
PONERINAE						
AMBLYOPONINI						
Amblyopone	2			W		
	3		W			
Mystrium	1	W	W, G			
	2	G	G			
Prionopelta	1	W, G	W, G			
	3	W, G	W			
ECTATOMMINI						
Discothyrea	1	W	W, P	G		
Proceratium	1	W				
PLATYTHYREINI						
Platythyrea	*bicuspis*		G			
PONERINI						
Anochetus	*grandidieri*	W, G	W, G			
Hypoponera	1	W	W	W, G	W, G	G
	2	W, G	W	W		
	3				G	G
	6	W	W			
	7	W	W	W, G	G	
	8			W		
	9	W		W, G	W, G	G
	10			W, G	W, G	G
	11	W, G	W	W, G	W, G	
	12	W	W			
	13	W	W			
	14	W, G	G			
	15	W				
	17					G
	sakalava	W, G	W, G	G		
Leptogenys	1		W			
	3	P				
Odontomachus	*coquereli*	W, G	W, G			
Pachycondyla	*cambouei*	W, P, G	W, P			
	sikorae	G	G			
PSEUDOMYRMECINAE						
Tetraponera	*exasciata*	G				
	grandidieri	G		G		
	psw-*81*		W, G			
	psw-*92*	W, G	G			
	Total species: G	47	42	36	24	20
	Total species: P	19	19	14	8	
	Total species: W	76	64	35	23	
	Total species: All methods	**89**	**81**	**51**	**31**	**20**
	Number (%) of unique species	21 (24%)	11 (14%)	9 (18%)	3 (10%)	10 (50%)
	Total number of G collections	55	41	24	36	16
	Number of workers: G	479	306	382	256	273
	Number of workers: P	218	255	238	127	
	Number of workers: W	8,582	6,479	5,467	6,500	
	Total number of workers	**9,279**	**7,040**	**6,087**	**6,883**	**273**

Only collections of worker ants are presented. Only general collections were conducted at 1800–2000 m; these included four leaf litter samples. P, from pitfall transect samples; W, from mini-Winkler sack and leaf litter transect samples; G, from general collection. A total of 148 ant species and 29,562 workers were collected.

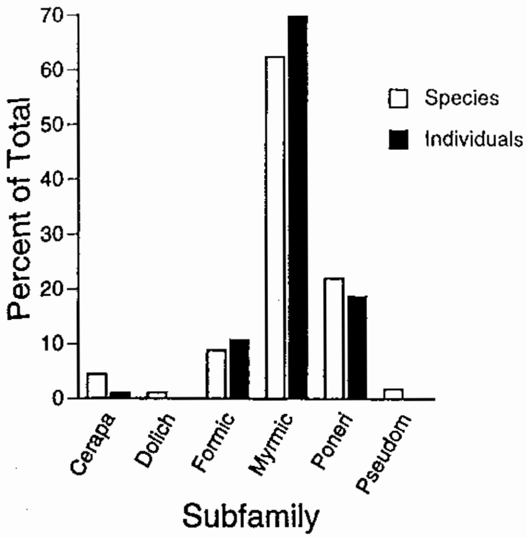

FIG. 8-2. Relative importance of the different subfamilies in number of species and individuals for pitfall and leaf litter collections for all four elevations combined (general collections are excluded). Subfamily names are abbreviated (see Table 8-1).

1680 m transect than with the two lowest elevations.

Beta-1 and beta-2 values showed similar trends in levels of species turnover between elevations (Table 8-5). The lowest levels of species turnover were between 785 and 825 m and between 1275 and 1680 m. Beta-1 and beta-2 values differed from each other when comparing elevations with the greatest species turnover. Beta-1 values indicated that the highest species turnover was between the lowest elevations (785 and 825 m) and 1680 m, whereas beta-2 values indicated that this occurred between the lowest elevations and 1275 m. Considering only altitudinally adjacent sites, however, the two measures were concordant.

Discussion

Efficacy of the Survey Technique

The leveling off of the jackknife and observed species accumulation curves (Fig. 8-3) indicated that the mini-Winkler sack and pitfall methods used in this survey were effective and produced rapid, replicable, and quantitative results. This study showed that insects can be successfully included in rapid biological inventory programs. Insects are not too numerous to survey and provide valuable information about patterns of species richness and abundance. Future surveys will be directed toward testing the efficacy of the ant survey methods in other tropical habitats.

Elevational Gradient

The number of ant species decreased as a function of elevation (Fig. 8-4). Olson (1994) documented a similar rate of decrease of ant species richness in Panama (Fig. 8-4). Brown (1973) suggested that the reduction in ant diversity at higher elevations is the result of lower levels of radiant heat. For ants in montane forests, the most important factor regulating colony survival may be clouds and high humidity, which prevent bright sunlight from raising the ground temperature toward the optimal level for larval development and for worker foraging activities. The biology of humid forest ants is poorly known; therefore, it is unclear what traits allow certain species to persist in the cloud zone while others disappear.

At higher elevations above the tree line (>2000 m) in the RNI d'Andringitra, the leaf litter layer in open grassland/heath environment may receive more radiant heat during fog-free periods and thus support a greater ant diversity than at 1680 m. Although only 20 species were found in one afternoon of general collection at 1800–2000 m, compared with 31 species found using all methods at 1680 m, I predict that a thorough study of the grassland/heath ant community at 2000 m will show a greater diversity of ant species than at 1680 m. This would be consistent with Brown's (1973) hypothesis about the role of radiant energy in determining ant diversity.

Faunal Similarities and Species Turnover

Faunal similarity and beta diversity measures (Tables 8-3 and 8-4) suggest a division of the RNI d'Andringitra ant fauna into two communities, one occurring in lowland forest (785 and 825 m) and the other in montane cloud forest (1275 and 1680 m). Species turnover is greatest and faunal similarity is lowest between 1275 m and the two low-elevation sites. Although there is no detailed study of the temperature gradient along these elevations, the montane cloud forest community zone corresponds to the area in which clouds habitually develop on a daily basis (see also Chapter

TABLE 8-2. Proportion of stations (out of 50 paired pitfall and leaf litter samples at each altitude) each species was recorded. The number of individual workers collected is given in parentheses.

Genus	Species	785 m	825 m	1275 m	1680 m
CERAPACHYINAE					
Cerapachys	1	0.04 (90)			
	2		0.02 (3)		
	3	0.10 (49)	0.06 (23)		
	5	0.02 (14)	0.02 (1)	0.04 (30)	
	8	0.10 (9)	0.12 (46)		0.12 (21)
DOLICHODERINAE					
Technomyrmex	*mayri*	0.04 (2)			
FORMICINAE					
CAMPONOTINI					
Camponotus	5			0.02 (1)	
	11		0.02 (3)		
	13			0.04 (2)	
	15			0.02 (1)	
	17			0.02 (1)	0.04 (2)
LASIINI					
Paratrechina	1	0.82 (869)	0.58 (546)	0.38 (232)	
	4	0.16 (32)	0.62 (349)	0.04 (4)	0.02 (4)
	5	0.22 (132)	0.80 (560)		
	6	0.02 (1)			
PLAGIOLEPIDINI					
Plagiolepis	3	0.80 (146)	0.54 (66)		
MYRMICINAE					
CREMATOGASTRINI					
Crematogaster	3		0.32 (53)		
	schenki	0.02 (1)	0.02 (2)	0.26 (18)	
DACETONINI					
Glamyromyrmex	1	0.06 (5)	0.02 (1)		
Kyidris	1	0.16 (151)	0.14 (130)		
Smithistruma	3	0.20 (31)			
Strumigenys	1	0.02 (2)			
	2			0.08 (5)	0.06 (3)
	3	0.06 (6)			
	4				0.18 (14)
	5				0.02 (1)
	6				0.02 (2)
	7			0.72 (154)	
	8	0.36 (56)	0.08 (4)	0.46 (78)	
	9	0.06 (4)	0.02 (1)	0.24 (25)	
	10			0.32 (32)	
	11			0.06 (5)	
	12	0.06 (3)	0.22 (21)		
	13	0.02 (1)	0.02 (1)		
	14	0.24 (41)	0.16 (11)		
	15	0.02 (1)			
	16	0.02 (1)			
	17			0.02 (1)	
	18	0.98 (417)	0.74 (183)		
PHEIDOLOGETONINI					
Oligomyrmex	1	0.64 (228)	0.50 (114)		
	2	0.08 (69)	0.16 (42)		
PHEIDOLINI					
Pheidole	2				0.60 (768)
	6			0.08 (30)	1.00 (3,772)
	7	0.02 (1)	0.02 (1)		0.02 (7)
	8			0.76 (547)	
	9			0.76 (892)	0.38 (531)
	10			0.44 (102)	
	11	0.66 (188)	0.74 (348)		
	12	0.08 (40)	0.14 (60)		
	13	0.30 (83)			

TABLE 8-2. *Continued.*

Genus	Species	785 m	825 m	1275 m	1680 m
	14	0.26 (325)	0.52 (472)		
	15	0.02 (3)	0.10 (13)		
	16	0.10 (20)	0.16 (24)		
	17	0.42 (165)	0.46 (332)		
	20	0.16 (24)			
	22	0.02 (1)			
	nemoralis	0.80 (828)	0.56 (349)		
	veteratrix	0.60 (147)	0.54 (186)	0.02 (4)	
	longispinosa	0.30 (171)	0.66 (482)		
SOLENOPSIDINI					
Monomorium	1			0.14 (29)	0.44 (246)
	2	0.08 (10)	0.28 (95)		
	3			0.28 (165)	0.04 (31)
	5	0.32 (146)	0.14 (11)		
	6	0.88 (1,862)	0.82 (953)		
	7	0.58 (228)	0.36 (186)		
	8			0.42 (191)	0.44 (158)
	9			0.16 (169)	0.04 (10)
	10		0.12 (14)	0.42 (239)	
	12			0.02 (1)	
	14	0.32 (63)			
TETRAMORIINI					
Tetramorium	1		0.02 (2)		0.86 (247)
	3	0.02 (1)	0.80 (256)		
	4			0.02 (1)	0.04 (2)
	5				0.16 (13)
	7	0.10 (11)	0.04 (4)	0.08 (6)	
	9	0.12 (37)			
	10	0.58 (100)	0.34 (46)	0.62 (157)	0.50 (179)
	11	0.20 (20)	0.06 (4)		
	13		0.02 (1)		
	14	0.18 (216)		0.26 (24)	
	15		0.02 (1)		
	16	0.08 (5)	0.02 (1)		
	andrei	0.12 (44)	0.08 (5)		
	cognatum	0.58 (99)	0.22 (15)	0.22 (31)	
	dysalum	0.34 (110)	0.30 (45)		
	electrum	0.16 (12)	0.06 (6)		
	marginatum	0.10 (7)	0.20 (16)		
PONERINAE					
AMBLYOPONINI					
Amblyopone	2			0.06 (3)	
	3		0.02 (1)		
Mystrium	1	0.02 (1)	0.02 (1)		
Prionopelta	1	0.56 (122)	0.18 (12)		
	3	0.22 (12)	0.10 (5)		
ECTATOMMINI					
Discothyrea	1	0.02 (1)	0.04 (3)		
Proceratium	1	0.02 (1)			
PONERINI					
Anochetus	*grandidieri*	0.38 (96)	0.30 (113)		
Hypoponera	1	0.08 (45)	0.08 (57)	0.88 (896)	0.46 (339)
	2	0.44 (154)	0.04 (3)	0.02 (26)	
	6	0.44 (236)	0.02 (23)		
	7	0.20 (16)	0.24 (24)	0.90 (875)	
	8			0.04 (10)	
	9	0.02 (4)		0.46 (92)	0.60 (119)
	10			0.68 (275)	0.02 (3)
	11	0.72 (345)	0.36 (48)	0.76 (351)	0.46 (155)
	12	0.18 (21)	0.06 (3)		
	13	0.76 (227)	0.88 (326)		
	14	0.04 (10)			
	15	0.18 (25)			

TABLE 8-2. *Continued.*

Genus	Species	785 m	825 m	1275 m	1680 m
	sakalava	0.20 (20)	0.12 (12)		
Leptogenys	1		0.02 (1)		
	3	0.08 (4)			
Odontomachus	*coquereli*	0.06 (4)	0.02 (1)		
Pachycondyla	*cambouei*	0.50 (66)	0.06 (4)		
PSEUDOMYRMECINAE					
Tetraponera	psw-*81*		0.08 (9)		
	psw-*92*	0.04 (2)			

3). Further investigations of the high mountain grassland/heath ant community in Madagascar may also show a distinct ant community. Initial collection revealed 50% of the species unique to 1800–2000 m in the RNI d'Andringitra.

Additional ant surveys in eastern Madagascar will help to evaluate whether there exists a distinct, homogeneous, and disjunct montane cloud forest plus grassland/heath ant community in Madagascar. Currently we lack distribution records on those elevation-specific species to determine whether they are part of a cloud forest or grassland/montane community on other mountain ranges in eastern Madagascar. Because the heath community is limited to the highest mountains of Madagascar, this disjunct habitat may have species or clades that are more closely related to taxa in other heath communities than in adjacent cloud forest ants.

Beta-1 and beta-2 values differed from each other in comparisons of sites with high species turnover (Table 8-5). Beta-1 and beta-2 indices differ in their propensity to emphasize either species replacement or species loss, the two means of obtaining species turnover. Species replacement is most prevalent at the lower elevations. For example, the measured species turnover between 785 and 825 m is the result of a difference in species, not just the loss of species at 825 m. At higher elevations, however, there is species loss along the gradient without replacement. A nested dropout of species dominates the differences between the 1275 and 1680 m ant communities. Under these circumstances, beta-2, which emphasizes species replacement over species loss, is the preferred measure of beta diversity (Harrison et al. 1992).

TABLE 8-3. The number of species collected and first-order jackknife estimates of total species richness, based on pitfall and leaf litter transects. Statistics are given for each altitude and for all elevations combined.

Altitude (m)	Observed	Species richness estimate	95% C.I.
785	77	91.7	0.363
825	67	83.7	0.395
1,275	39	46.8	0.247
1,680	23	27.9	0.242
All elevations	114	131.9	0.193

95% C.I. indicates 95% confidence intervals.

Ant Fauna of RNI d'Andringitra

In 1891, Forel provided keys and descriptions to 86 ant species known from Madagascar (Forel, 1891). This was the last comprehensive treatment of the ant fauna of Madagascar. In 1922, Wheeler recorded 207 species from Madagascar (Wheeler, 1922). Considering the number of undescribed taxa, the actual number of ant species in Madagascar may be on the order of 800.

The chaotic state of the taxonomy of Malagasy ants makes it impossible to estimate the number of undescribed species listed in Table 8-1 without comparison to type material. There are a few genera, however, where recent revisions and type comparison make accurate estimates possible. Of the 19 species of *Tetramorium* collected in RNI d'Andringitra, only five are apparently described species. At least 17 of the 18 *Strumigenys* are undescribed because there is only one available name for the entire Malagasy fauna (assuming that none of these specimens are tramp species). Two of the four *Tetraponera* are undescribed (P. S. Ward, pers. comm.). In addition, because there are no described species of *Glamyromyrmex, Kyidris, Smithistruma, Leptothorax, Amblyopone,* and *Discothyrea* from Madagascar, all species in these genera in Table 8-1 (eight total) are presumed to be undescribed.

All 148 ant species in Table 8-1 are believed to

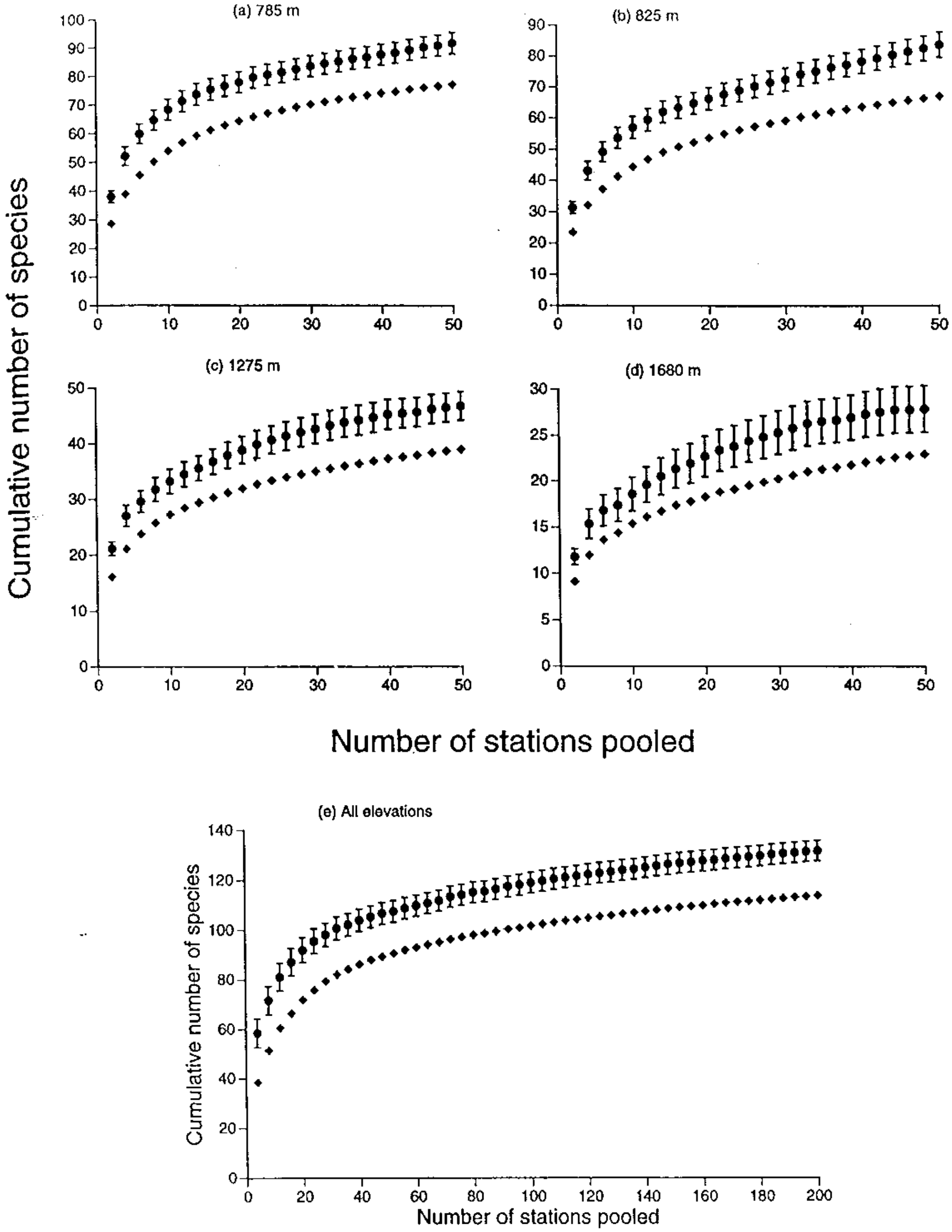

FIG. 8-3. Assessment of leaf litter ant sampling technique for each elevation (a–d) and for all elevations combined (e). The lower species accumulation curve in each chart plots the observed number of species as a function of the number of pooled stations sampled (stations = paired leaf litter and pitfall collections). The upper curve displays the non-parametric first-order jackknife estimated total species richness (error bars are standard deviation) based on successively larger number of samples from the data set (Heltshe & Forrester, 1983). Only every other point is shown in (a–d) and every fourth point is shown in (e). For all curves, each point is the mean of 100 estimates based on 100 randomizations of sample accumulation order, calculated using the program EstimateS (R. K. Colwell, unpublished).

TABLE 8-4. Two measurements of faunal similarity between the four elevational zones sampled.

Elevation	785 m	825 m	1275 m	1680 m
785 m	—	**0.655**	0.160	0.075
825 m	**0.805**	—	**0.165**	0.084
1275 m	0.229	**0.164**	—	**0.319**
1680 m	0.096	0.068	**0.394**	—

Above the diagonal is the Jaccard Index of similarity (presence/absence data) and below the diagonal, the simplified Morisita Index of similarity (abundance data; Horn, 1966). Higher values represent greater similarity. Values in boldface represent comparisons of altitudinally adjacent transects.

be endemic to Madagascar. This is greater than the estimated 92% endemism in ant species in the dry forest of Kirindy, western Madagascar (P. S. Ward, pers. comm.). The lower level of disturbance and the lack of open habitats may have prevented the invasion of introduced species into the RNI d'Andringitra.

Comparison with Other Faunas

There is currently no other site in eastern Madagascar whose leaf litter ant fauna has been sampled with comparable intensity and identified to species. One comparison, however, can be made at the generic level. Most of the ant genera collected in RNI d'Andringitra (Table 8-1) were also collected in the RNI d'Andohahela in the Anosy Mountains, southeastern Madagascar, in a parallel survey conducted in 1992 (Fisher, unpubl.) The only exceptions are the genera *Pilotrochus*, *Eutetramorium*, and *Aphaenogaster*, which were encountered only in RNI d'Andohahela, and *Technomyrmex*, *Leptothorax*, and *Odontomachus*, which were collected only in RNI d'Andringitra.

The relative prevalence of species from different subfamilies in the RNI d'Andringitra ant fauna (62% Myrmicinae and 22% Ponerinae; Fig. 8-1) shows striking similarities to other tropical forest leaf litter ant communities (Table 8-6). All of the following studies found the Myrmicinae to be the most common subfamily, followed by the Ponerinae, with an average Ponerinae/Myrmicinae species ratio of 0.336 ± 0.037 (SD) (Table 8-6): Belshaw and Bolton (1994), in moist tropical forest in Ghana; Levings (1983), in moist forest on Barro Colorado Island, Panama; Olson (pers. comm.), in tropical wet forest in western Panama; Longino (1986), in tropical wet forest in Costa Rica; Andersen and Majer (1991), in seasonally dry forest in Kimberley, northwestern Australia; and D. M. Olson and P. S. Ward (pers. comm.), in the dry Kirindy forest. The 1:3 ratio of Ponerinae to Myrmicinae in these studies suggests that the species richness of the Myrmicinae can be interpolated from the richness of the Ponerinae. In addition, if future studies in Madagascar confirm an approximate prevalence of 22% Ponerinae or 62% Myrmicinae, investigations directed at determining the species richness of leaf litter ants in an area may be able to use the number of Ponerinae or Myrmicinae species as an indicator for the entire family Formicidae. This extrapolation applies only for estimating the ground-dwelling, leaf litter ant fauna.

TABLE 8-5. Beta-1 (above the diagonal) and beta-2 (below the diagonal) diversity values of each pair of altitude sites.

Elevation	785 m	825 m	1275 m	1680 m
785 m	—	**0.208**	0.724	0.860
825 m	**0.130**	—	**0.717**	0.844
1275 m	0.300	**0.358**	—	**0.516**
1680 m	0.210	0.239	**0.205**	—

Higher values represent greater species turnover. Values in boldface represent comparisons of altitudinally adjacent transects. Overall beta-1 diversity was 1.214 and beta-2 diversity was 0.481.

Potential Effects of Human Disturbance

The 785 and 825 m transects differed slightly in ant composition, with low values of beta-1 and

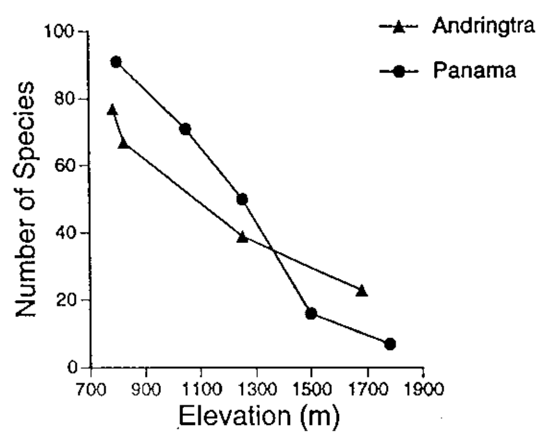

FIG. 8-4. The number of ant species as a function of elevation. RNI d'Andringitra data are from pitfall and mini-Winkler sack samples. Panama data are from leaf litter samples (Olson, 1994).

TABLE 8-6. The percentages of ant species collected in the Ponerinae and Myrmicinae subfamilies in six tropical forests. Only leaf litter and ground nesting ants, not arboreal were considered in the analysis.

Location	Ponerinae (%)	Myrmicinae (%)	P/M	Total spp.	Source
RNI d'Andringitra	22	62	0.35	114	This study
Ghana	22	63	0.35	176	Belshaw & Bolton, 1994
BCI, Panama	23	65	0.36	108	Levings, 1983
western Panama	23	67	0.34	196	D. M. Olson, pers. comm.
Costa Rica	20	70	0.29	134	Longino, 1986
Kimberley, Australia	14	37	0.38	115	Anderson & Majer, 1991
Kirindy, Madagascar	15	53	0.28	60	P. S. Ward & D. M. Olson, pers. comm.

Total species refers to the number of terrestrial ants at the location. The taxonomic ratio of species in the two subfamilies (P/M) is on average 0.336, with a standard deviation of 0.037.

beta-2 (0.208 and 0.130, respectively). In addition, the 825 m transect had fewer species and fewer individuals than at 785 m. These differences could be the result of the distance or habitat differences between the two transect sites. The ability of species to disperse between the two transect sites could be affected by distance (3 km), with potential barriers being the two rivers separating the transects, the Iantara and Sahanivoraky. The differences in diversity could also be the result of microhabitat differences in the forest. The 785 and 825 m transects were conducted in forest with similar structure, slope, and aspect, however, and the level of recent human disturbance appeared to be comparable and low. One potentially important habitat difference is that the 785 m transect began 75 m from a recently disturbed and cleared forest (*tavy*); this could affect abiotic conditions (relative humidity, soil temperature, and moisture content of soil and litter) that affect ant distributions within the forests (Adis, 1988). None of the transects, nor an afternoon of collecting in the adjacent *tavy*, however, revealed any exotic or introduced ants.

Summary

This is the first intensive study of the leaf litter ant community in eastern Madagascar. When compared with data on other biotic groups, it will provide a unique basis for studying how species composition and diversity change with elevation and latitude. These comparative data are important for understanding intertaxon differences in diversity patterns that should be factors critical for developing a conservation strategy based on diversity. In addition, results of this study will provide baseline data for monitoring future biological changes in this region of Madagascar.

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