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

Brian L. Fisher[1]

Abstract

Leaf litter ant faunas were inventoried in Madagascar at 430, 800, and 1250 m in parcel 1 of the Réserve Naturelle Intégrale (RNI) d'Andohahela. Within each elevational zone, survey methods involved a combination of pitfall and leaf litter sampling along a 250 m transect. From pitfall and leaf litter samples, I collected and identified 12,285 ants belonging to 25 genera and 111 species; general collecting yielded an additional 28 species.

For each elevation, two species richness estimators—incidence-based coverage estimator (ICE) and first-order jackknife—gave comparable results. Species accumulation curves showed decreased rates of species detection and demonstrated the efficacy of these inventory techniques. Species collected and their relative abundances are presented. Species richness peaked at mid-elevation. Species turnover, complementarity, and faunal similarity measures demonstrated a division in ant communities between lowland forest at ≤800 m and montane forest at 1250 m. A mid-elevation peak in species richness is probably the result of the mixing of two distinct, lower and montane forest, ant assemblages.

In addition, I compare complementarity and species turnover values, the number of species restricted to a locality, and the number of species shared between the RNI d'Andohahela, the RNI d'Andringitra, the Réserve Spéciale d'Anjanaharibe-Sud, and the western Masoala Peninsula.

Résumé

Les fourmis de litières ont été inventoriés sur les élévations de 430, 480 et 1250 m dans parcelle 1 de la Réserve Naturelle Intégrale (RNI) d'Andohahela à Madagascar. Pour chaque zone d'élévation, les méthodes d'inventaires utilisées combinent les trous pièges et les échantillonnages de litières le long d'un transect de 250 m.

Avec les trous pièges et les échantillonnages de litières, j'ai pu collecter et identifier 12.285 fourmis appartenant à 111 espèces et 25 genres. Les collections générales ont acquis 28 espèces en plus. Pour chaque élévation, les deux estimateurs de richesse d'espèces telles que l'ICE (Incidence-based coverage estimator) et le premier ordre jacknife ont donnés des résultats comparables. Les courbes d'accumulation d'espèces ont approchées une asymptote et ont montrées l'efficacité de la technique d'inventaires utilisées. Les espèces collectées et leur abondance relatives sont présentées. La richesse d'espèce est au pic à la mid-elevation. Les mesures de la succession continue d'espèces "species turnover," de la complémentarité et de la similarité ont démontrées une division sur la communauté des fourmis entre forets basse de ≤800 m et les

[1] Life Sciences Division, South African Museum, P.O. Box 61, 8000 Cape Town, South Africa.

forets de montagnes de 1250 m. Le pic en richesse d'espèces, à la mi-elevation est probablement le résultat de la mixture des fourmis des deux milieux distinctes: fourmis de la foret basse et ceux de la foret de montagne.

En plus, j'ai fait une comparaison entre la RNI d'Andohahela, la RNI d'Andringitra, la Réserve Spéciale d'Anjanaharibe-Sud, et l'Ouest du péninsule de Masoala. La comparaison est basée sur les valeurs de la complémentarité et la succession continue d'espèces "species turnover," le nombre d'espèces unique d'un localité, et le nombre d'espèces communs pour les sites.

Introduction

Geographical patterns of species richness and areas of endemism are two criteria for conservation assessment that require baseline information on species distributions (McNeely et al., 1990). For most invertebrates, we lack this necessary information and even the practical approaches and methods to obtain it. To assign priority to areas with high species richness and endemism in Madagascar, we need methods to inventory the most diverse taxa.

Sampling and estimation procedures for a diverse and ecologically important group of terrestrial insects, ants, were used to assess diversity along elevational gradients in the Réserve Naturelle Intégrale (RNI) d'Andohahela. Similar methods were used to inventory ants in the RNI d'Andringitra (Fisher, 1996a), and in the Réserve Spéciale (RS) d'Anjanaharibe-Sud and on the western Masoala Peninsula (Fisher, 1998). I evaluate the efficacy of the inventory methods and the effect of elevation on species richness in the RNI d'Andohahela. I compare measures of faunal similarity and complementarity for ant species across elevations sampled from 430 to 1250 m. In addition, I compare the ant fauna in the RNI d'Andohahela with those of three other localities and discuss the nature and causes of geographical variation in ant diversity in eastern Madagascar. A complementary aspect of this study is the substantial increase in taxonomic and ecological knowledge of the ant fauna in one of the most threatened regions of the world.

Methods

Study Sites

Surveys were conducted between 12 November and 10 December 1992 near the northern boundary of the RNI d'Andohahela, parcel 1. RNI d'Andohahela comprises 63,100 ha of humid forest within the elevational range of 350–1972 m (Nicoll & Langrand, 1989). Collection sites differed from those during the 1995 inventory discussed elsewhere in this volume. The ant inventory transects were located at: (1) 10 km NW of Enakara, 24°34′S, 46°49′E, transect at 430 m and general collecting from 400 to 450 m; (2) 11 km NW of Enakara, 24°34′S, 46°49′E, transect at 800 m and general collecting from 750 to 850 and 900 to 1000 m; and (3) 13 km NW of Enakara, 24°33′S, 46°48′E, transect at 1,250 m and general collecting from 1180 to 1300 m. Estimated canopy height was 20–30 m at 430 m, 15 m at 800 m, and 6–8 m at 1250 m.

There was no evidence of recent exploitation of the forest at the three transect sites. The transect at 430 m, however, was approximately 200 m from the trail along the northern boundary of the park. The trail was frequently used by local inhabitants for transporting agricultural products and cattle and subsequently showed signs of disturbance.

Survey Methods

In the RNI d'Andohahela, intensive ant surveys were conducted at three sites located at 430, 800, and 1250 m. At each elevation I used 50 pitfall traps and 50 leaf litter samples (mini-Winkler) in parallel lines 10 m apart along a 250 m transect. The site for each transect was chosen with the intent of sampling representative microhabitats found at each elevation (Palmer, 1995). Pitfall traps were placed and leaf litter samples gathered every 5 m along the transect. Pitfall traps consisted of test tubes with an 18 mm internal diameter and 150 mm long, partly filled to a depth of about 50 mm with soapy water and a 5% ethylene glycol solution, inserted into PVC sleeves and buried with the rim flush with the soil surface.

To prevent rainfall from filling the traps, an opaque, ridged piece of plastic was suspended approximately 5 cm above the trap by means of a metal wire support. Traps were left in place for 4 days.

I extracted invertebrates from samples of leaf litter (leaf mold, rotten wood) using a modified form of the Winkler extractor (see Fisher, 1996a, Fig. 8-1, and Fisher, 1998, Fig. 4-1). The leaf litter samples involved establishing 50 1 m^2 plots separated by 5 m along the transect line. The leaf litter inside each plot was collected and sifted through a wire 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 was taken from each 1 m^2 plot. At the low elevations (<800 m) litter was occasionally sparse, and sometimes less than 2 liters was taken. If the subsample plot contained a large rotten log or thick litter, 2 liters of litter was the maximum amount taken at each subsample site. This 2 liter limit was imposed because of the size of the Winkler extractor. In those sites where 1 m^2 provided an excess of leaf litter, the plot was subsampled until 2 liters of litter was obtained. Ants and other invertebrates were extracted from the sifted litter during a 48 hr period in mini-Winkler sacks (for a detailed discussion of the mini-Winkler method, see Fisher, 1996a, 1998).

I also surveyed ants through general collecting, defined as any collection that was separate from the mini-Winkler 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. At each transect site, general collections were conducted for an approximately 2-day period. General collections were made within 500 m ground distance and within 75 m in elevation of each transect site. In addition, general collecting was conducted between 900 and 1000 m. General collections included samples of the arboreal ants found on low vegetation that were not sampled by pitfalls or leaf litter. Ants sampled with 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 complementarity.

Sample Processing

For every 50-station transect, which took from 5 to 7 field days to conduct, an average of 1 month was spent in the laboratory sorting, identifying, and curating specimens. After I returned from the field, ant specimens from the pitfall and leaf litter samples were sorted. The saturated salt water extraction procedure described below was very effective in removing organic matter from inorganic matter in the leaf litter samples. Each sample was emptied into a 40 mm diameter, 250 ml graduated cylinder. A near boiling saturated salt water solution was then added until the cylinder was half filled. After 2 minutes the solution was stirred. After settling for about 2 minutes the organic matter was decanted off the top into a strainer and rinsed with water, then with 95% ethanol. This process was repeated two to three times for each sample. The residue at the bottom of the cylinder was checked for large arthropods that were too heavy to float to the top of the cylinder.

Next, each sample was sorted by genus. Trained student assistants (parataxonomists *sensu* Wheeler, 1995) sorted and identified all material down to the genus level. All ant specimens from a single genus were then sorted to species by me, by examining specimens sequentially from each elevational site. This method allowed the greatest number of specimens within an elevational site to be identified while in alcohol and thus limited the cost in time of mounting specimens. Data for specimens were managed using Biota (Colwell, 1996).

Identification

Specimens were identified to morphospecies by me, based on characters previously established to be important at the species level for each genus. When possible, species names were attached to these morphospecies by using taxonomic descriptions (see Fisher, 1997, for a list of references) and by comparing specimens with those previously collected by P. S. Ward and me in Madagascar that had been compared to type material. Species codes used in this paper correspond to species codes used in Fisher (1996a, 1998). A representative set of specimens will be deposited at the Museum of Comparative Zoology at Harvard University and in Madagascar.

Data Analysis

Evaluation of Sampling Method—To assess survey completeness for the elevations sampled,

TABLE 9-1. Ant species list for the RNI d'Andohahela, including elevation and collection method.

Genus	Species	430 m	800 m	900–1000 m	1250 m
CERAPACHYINAE					
Cerapachys	2		W		
	3		W, G	G	
	4				G
	5		W		W
	6		P		
	7				W
	8		W		W, G
Simopone	2	G			
FORMICINAE					
CAMPONOTINI					
Camponotus	2				G
	5	G			P
	6		W, P, G		
	7				G
	8				G
	9				G
	10		G		G
	12				W, G
	15		W, G		
	23				G
	24				P
	28				W
	hildebrandti	G			
LASIINI					
Paratrechina	1	W, P, G	W, P, G		W, P, G
	4				W
	5	W, P, G	W, P, G	G	W, G
	6	W	W		W
PLAGIOLEPIDINI					
Plagiolepis	2				G
	3	W	W		W
MYRMICINAE					
CREMATOGASTRINI					
Crematogaster	3	W	W		
	4				G
	11	W	W		W, G
	schenki				W, P, G
DACETONINI					
Kyidris	1	W	W		
Smithistruma	2				W, G
	3		G		
Strumigenys	1		W, P		W
	2				W
	3	G			
	13	W	P		
	14	W	W		
	16	W	W		W
	18	W, G	W		W, G
	20	W	W		
	21				W
	51		W		
	grandidieri				W, G

TABLE 9-1. *Continued*

Genus	Species	430 m	800 m	900–1000 m	1250 m
PHALACROMYRMECINI					
Pilotrochus	*besmerus*				W, G
PHEIDOLINI					
Aphaenogaster	1				G
Pheidole	6		W, P		W, G
	7	W, P, G	W		
	8				W, P, G
	10	W, P	W, P		W, P
	11	P			W, G
	13		W		
	14	W, P	W, P, G		
	17			G	
	23	P, G	W, P		W
	24				W
	25	W, P	P		
	26		W		
	27	W	W, P		
	28	W, P, G	P		
	29	W, P			
	31			G	W, P
	32	W			
	33	W			
	34				G
	35	W			W
	38	W			
	longispinosa	W, P, G	W, P, G		W
	nemoralis	W, P	W, P		
	veteratrix	W, P, G	W, P, G	G	W, P
PHEIDOLOGETONINI					
Oligomyrmex	3	W			
	6	W	W		
SOLENOPSIDINI					
Monomorium	5	W, G	W		W
	7	W	W		
	14	W			
	17				P
	18	W	W		
	19				W
	20				W, P
	21		W		
	22				W
	25		W		W, P, G
	43	G			
TETRAMORIINI					
Tetramorium	6	G	W, P	G	W, P, G
	13		P		P
	14				W, P
	15				P
	16	W, P			
	18	W	W, P		W, P, G
	19	G			
	20		W, G		
	22	W	W, P		
	23	W, P	P		
	27	W, G	W		
	30	G			
	31		W, G		W
	32				G
	33		W, P		W, G
	dysalum		W, P		
	electrum	W, P	W, P		

Genus	Species	430 m	800 m	900–1000 m	1250 m
INCERTAE SEDIS					
Undescribed genus	1		W	G	
PONERINAE					
AMBLYOPONINI					
Amblyopone	1		W		
	2				W, G
	3				W
Mystrium	1	W	W		
	2	G		G	
Prionopelta	2	W			
	4		W		
ECTATOMMINI					
Discothyrea	1				W, G
Proceratium	1		W		
PLATYTHYREINI					
Platythyrea	*bicuspis*		P		
PONERINI					
Anochetus	*grandidieri*	W	W, P, G		
Hypoponera	1		W		W, P, G
	4	G			W
	5		W		
	6	W	W		
	7		W		W, G
	8				W, G
	9		W		W
	11		W		W, G
	12		W		
	13		W		
	14	G			
	16	W			
	18		W		
	sakalava	G		G	W, G
Leptogenys	1			G	P, G
	2	P	P		W, P, G
	4				W
Pachycondyla	*cambouei*	W, P, G	W, P, G	G	W, P, G
	sikorae	G		G	
PSEUDOMYRMECINAE					
Tetraponera	*grandidieri*	W, G	W, P		
	hysterica	G			
	psw-70		G		
	psw-81	W	W, P		
	psw-92	G			
Total species: G		27	15	12	39
Total species: P		18	30		20
Total species: W		46	63		53
Total species: W and P		**49**	**71**		**59**
Total species: all methods		**64**	**74**		**71**
Number (%) of unique species: all methods		18 (28%)	20 (27%)	1 (8%)	35 (49%)
Number (%) of unique species: W and P		9 (18%)	20 (28%)		29 (49%)
Total number of G collections		40	12	12	23
Number of workers: G		814	172	98	348
Number of workers: P		852	1,038		430
Number of workers: W		4,032	3,679		2,254
Total number of workers		5,698	4.889		3,032
Abundance: total number stations collected		519	641		528

Notes: Only collections of workers are presented (G = from general collections; P = from pitfall transect samples; W = from mini-Winkler, leaf litter transect samples). A total of 137 ant species and 13,717 workers were collected. In addition, *Cardiocondyla emeryi* and *Eutetramorium* sp. 1 from 1250 m were recorded from queens only. Abundance refers to the total number of stations where each species was collected.

I plotted species accumulation curves for each elevation. Species accumulation was plotted as a function of the number of leaf litter and pitfall trap 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, as well as incidence-based coverage estimator (ICE) and first-order jackknife estimates of the total number of species in the local community from which the samples were taken, were plotted for each succeeding station sample. ICE and the first-order jackknife methods are nonparametric approaches to improving the estimate of species richness. ICE is based on species found in 10 or fewer sampling units (Lee & Chao, 1994; Chazdon et al., 1998). Standard deviations of ICE are based on bootstrap estimates (Colwell, 1997). The first-order jackknife is based on the observed frequency of unique species at a 50-station transect. The jackknife estimator and its standard deviation are defined in Heltshe and Forrester (1983). For species accumulation curves, sample order was randomized 100 times, and the means and standard deviations of ICE and the jackknife estimates were computed for each succeeding station using the program EstimateS (Colwell, 1997; see also Colwell & Coddington, 1994; Chazdon et al., 1998).

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 bias the relative abundance of the species. Because ants are colonial, abundance measures were not based on the total number of individual workers collected at each transect site, but rather on species frequency defined as the proportion of stations, out of 50, in which each species was collected at a site.

For each elevation, I compared ICE and first-order jackknife estimates of total species richness and their 95% confidence limits. Overlap and complementarily (distinctness or dissimilarity *sensu* Colwell & Coddington, 1994) of the ant assemblages at different elevations were assessed using distance, faunal similarity, and beta-diversity indices. The proportion of all species in two sites that occurred in only one or the other was calculated using the Marczewski-Steinhaus (M-S) distance index based on presence/absence data: $C_{MS} = (a + b - 2j)/(a + b - j)$, where j = number of species found at both elevations, a = number of species at elevation A, and b = number of species at elevation B (Pielou, 1984; Colwell & Coddington, 1994). Similarity of the ant fauna was assessed using the simplified Morisita Index, which incorporates abundance data:

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

where

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

aN = total number of station/species occurrences in elevation A, bN = total number of station/species occurrences in elevation B, an_i = the number of stations occupied by the ith species in elevation A, and bn_i = the number of stations occupied by the ith species in elevation B (Horn, 1966; Wolda, 1981). Indices based on presence/absence data have been shown to be strongly influenced by species richness and sample size (Wolda, 1981). The Morisita Index is nearly independent of species richness and sample size (Wolda, 1981) and may therefore be more appropriate for comparisons of ant assemblages between sites along an elevational gradient that differ greatly in species richness.

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} = the maximum value of alpha-diversity (i.e., number of species) among the elevations compared. The number of species unique to an elevation and the number of species shared between elevations were also compared.

In addition, I also calculated complementarily, species turnover, number of unique species, and number of species shared among the RNI d'Andohahela and three other localities surveyed using the same methods: the RNI d'Andringitra,

TABLE 9-2. Abundance measured as frequency of occurrence (proportion of stations out of 50 paired pitfall and leaf litter samples at which each species was recorded) for each elevation in the RNI d'Andohahela.

Genus	Species	430 m	800 m	1250 m
CERAPACHYINAE				
Cerapachys	2		0.04 (5)	
	3		0.06 (10)	
	5		0.02 (1)	0.06 (9)
	6		0.02 (1)	
	7			0.08 (4)
	8		0.04 (5)	0.08 (5)
FORMICINAE				
CAMPONOTINI				
Camponotus	5			0.02 (1)
	6		0.04 (2)	
	12			0.06 (126)
	15		0.02 (1)	
	24			0.02 (1)
	28			0.08 (4)
LASIINI				
Paratrechina	1	1.00 (2,090)	0.32 (103)	0.36 (112)
	4			0.10 (42)
	5	0.48 (254)	0.44 (754)	0.04 (29)
	6	0.02 (2)	0.06 (6)	0.02 (1)
PLAGIOLEPIDINI				
Plagiolepis	3	0.02 (1)	0.08 (8)	0.42 (112)
MYRMICINAE				
CREMATOGASTRINI				
Crematogaster	3	0.02 (1)	0.02 (1)	
	11	0.08 (6)	0.04 (4)	0.28 (17)
	schenki			0.72 (166)
DACETONINI				
Kyidris	1	0.04 (6)	0.02 (1)	
Smithistruma	2			0.06 (4)
Strumigenys	1		0.90 (989)	0.02 (1)
	2			0.04 (13)
	13	0.04 (4)	0.02 (1)	
	14	0.14 (8)	0.32 (38)	
	16	0.04 (4)	0.02 (1)	0.04 (6)
	18	0.42 (39)	0.20 (41)	0.62 (113)
	20	0.04 (3)	0.10 (8)	
	21			0.08 (6)
	51		0.02 (1)	
	grandidieri			0.02 (2)
PHALACROMYRMECINI				
Pilotrochus	*besmerus*			0.08 (4)
PHEIDOLINI				
Pheidole	6		0.24 (75)	0.02 (3)
	7	0.38 (133)	0.28 (82)	
	8			0.74 (332)
	10	0.04 (2)	0.12 (28)	0.48 (76)
	11	0.04 (12)		0.04 (2)
	13		0.02 (1)	
	14	0.14 (16)	0.44 (178)	
	23	0.12 (95)	0.12 (26)	0.02 (1)
	24			0.02 (1)
	25	0.54 (110)	0.16 (48)	

TABLE 9-2. *Continued*

Genus	Species	430 m	800 m	1250 m
	26		0.36 (110)	
	27	0.36 (72)	0.32 (120)	
	28	0.90 (224)	0.02 (1)	
	29	0.12 (72)		
	31			0.06 (11)
	32	0.02 (1)		
	33	0.02 (1)		
	35	0.02 (1)		0.04 (8)
	38	0.02 (3)		
	longispinosa	0.98 (1,010)	0.68 (510)	0.04 (2)
	nemoralis	0.28 (78)	0.32 (76)	
	veteratrix	0.24 (80)	0.52 (218)	0.38 (107)
PHEIDOLOGETONINI				
Oligomyrmex	3	0.02 (1)		
	6	0.10 (6)	0.14 (37)	
SOLENOPSIDINI				
Monomorium	5	0.50 (67)	0.40 (57)	0.34 (142)
	7	0.02 (3)	0.10 (69)	
	14	0.16 (28)		
	17			0.02 (1)
	18	0.30 (108)	0.48 (81)	
	19			0.02 (2)
	20			0.18 (48)
	21		0.02 (3)	
	22			0.10 (98)
	25		0.10 (7)	0.04 (3)
TETRAMORIINI				
Tetramorium	6		0.18 (21)	0.10 (8)
	13		0.02 (1)	0.02 (5)
	14			0.20 (39)
	15			0.02 (1)
	16	0.24 (37)		
	18	0.02 (1)	0.80 (253)	0.52 (109)
	20		0.18 (18)	
	22	0.02 (4)	0.12 (17)	
	23	0.14 (19)	0.02 (1)	
	27	0.02 (1)	0.02 (1)	
	31		0.06 (3)	0.06 (5)
	33		0.14 (9)	0.30 (43)
	dysalum		0.30 (151)	
	electrum	0.26 (76)	0.18 (28)	
INCERTAE SEDIS				
Undescribed genus	1		0.02 (1)	
PONERINAE				
AMBLYOPONINI				
Amblyopone	1		0.06 (8)	
	2			0.12 (10)
	3			0.08 (5)
Mystrium	1	0.10 (5)	0.02 (1)	
Prionopelta	2	0.14 (9)		
	4		0.16 (18)	
ECTATOMMINI				
Discothyrea	1			0.10 (6)
Proceratium	1		0.02 (1)	

Genus	Species	430 m	800 m	1250 m
PLATYTHYREINI				
Platythyrea	*bicuspis*		0.02 (1)	
PONERINI				
Anochetus	*grandidieri*	0.40 (35)	0.20 (27)	
Hypoponera	1		0.06 (14)	0.82 (389)
	4			0.02 (8)
	5		0.02 (1)	
	6	0.50 (71)	0.24 (86)	
	7		0.18 (11)	0.38 (42)
	8			0.16 (18)
	9		0.10 (6)	0.08 (14)
	11		0.46 (56)	0.66 (232)
	12		0.02 (1)	
	13		0.36 (33)	
	16	0.02 (2)		
	18		0.06 (5)	
	sakalava			0.34 (42)
Leptogenys	1			0.02 (2)
	2	0.08 (4)	0.16 (10)	0.34 (33)
	4			0.02 (1)
Pachycondyla	*cambouei*	0.68 (72)	0.90 (221)	0.36 (56)
PSEUDOMYRMECINAE				
Tetraponera	*grandidieri*	0.04 (4)	0.04 (2)	
	psw-81	0.06 (3)	0.06 (3)	

The number of individual workers collected is given in parentheses.

the RS d'Anjanaharibe-Sud, and the western Masoala Peninsula.

Results

In the RNI d'Andohahela I collected and identified 13,717 ants comprising 29 genera and 139 species from general collections, leaf litter, and pitfall methods. These included 155 queens and 86 males. Leaf litter and pitfall methods yielded 12,285 worker ants belonging to 25 genera and 111 species. A list of ant species from this study in the RNI d'Andohahela based on all collecting methods and separated by elevation and technique is presented (Table 9-1). General collections from 900 to 1000 m are also presented. Absent from Table 9-1 are records of species known from queens only: *Cardiocondyla emeryi* and *Eutetramorium* sp. 1, both from 1250 m.

Within the RNI d'Andohahela, the 800 m zone had the greatest total number of species recorded (74 species total from all methods; 71 species total from litter and pitfall samples; Table 9-1). The same relative ranking in observed species richness between sites was reached and maintained after three station samples (Table 9-5). The numbers of species and individuals collected from pitfall traps were low compared to those collected by mini-Winkler methods. Only six species that were collected by pitfall traps were not also collected by the mini-Winkler method. In a study using comparable methods in dry forest in southwestern Madagascar, however, pitfall traps collected a greater proportion of individuals and species (Fisher & Razafimandimby, 1997).

The abundance of ant species is presented in Table 9-2. Both the proportion of stations at which each species was collected and the number of individuals collected are given. General collections are not included. Only 15 species out of 111 (14%) were found at all three elevations. The relative frequencies of occurrence of these species, however, often differed considerably from one site to the next. For example, *Paratrechina* sp. 5 had relative frequencies of 0.48 at 430 m, 0.44 at 800 m, and 0.04 at 1250 m (Table 9-2). Thirty-eight species (34%) were collected at two of the three elevational sites.

The number of ant species and their abundance, measured as the total number of stations where

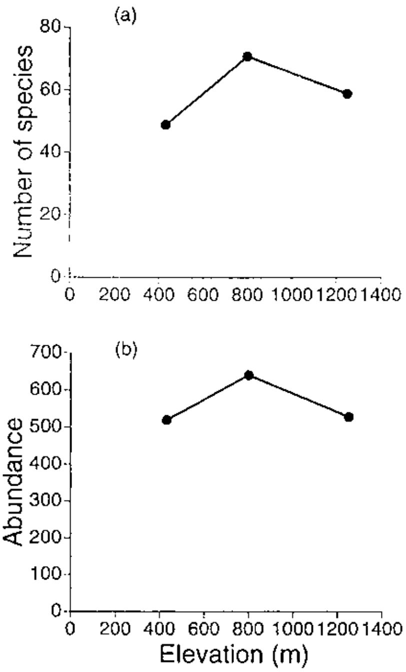

FIG. 9-1. The number of ant species (a), and the total abundance (b) as a function of elevation. Abundance is measured as the total number of stations where each species was collected (see text for details). Data are from pitfall and mini-Winkler samples.

each species was collected, peaked at 800 m (Fig. 9-1). The relative prevalence of each subfamily for the combined pitfall and leaf litter samples for each elevation and for all elevations is shown in Table 9-3. The fauna was dominated by Myrmicinae in both numbers of species and individuals, followed by Ponerinae. The ratio of Ponerinae to Myrmicinae was similar at 800 and 1250 m (0.41 and 0.42, respectively), but was lower at 430 m (0.19).

Observed number of species, ICE, and first-order jackknife estimates of species richness, their standard deviation, and 95% confidence intervals are presented for the RNI d'Andohahela (Table 9-4). Observed species richness for each elevation surveyed in the RNI d'Andohahela, evaluated at different sample sizes, is presented in Table 9-5. Species accumulation curves for observed, ICE, and jackknife estimates showed a decrease in the rate of species accumulation, but were still increasing slowly (Fig. 9-2). In a combined analysis of the three elevations in the RNI d'Andohahela, the pitfall and mini-Winkler methods collected 86% of the total number of leaf litter ant species estimated by ICE that could be collected using these methods in the transect areas (Fig. 9-2d).

The greatest dissimilarity (M-S Index) and lowest similarity (simplified Morisita Index) values between adjacent elevations occurred between 800 and 1250 m (Table 9-6). Similarly, the greatest species turnover (beta-diversity) occurred between 800 and 1250 m (Table 9-7). The overall beta-1 and beta-2 values of species turnover between all elevations were 0.860 and 0.563, respectively.

The 1250 m site had the greatest number and the highest percentage of species restricted to one specific elevation (Table 9-1). The 800 m site had the highest number of species shared with other sites (Table 9-6). The 800 m site shared more species with the 1250 m site than with the 430 m site (Table 9-6).

The ant fauna at the RNI d'Andohahela was compared to the fauna at three other localities where similar inventories have been conducted. The elevations surveyed at all four localities are presented in Table 9-8, and their distances apart (km) are presented in Table 9-9. The matrix of complementarity values shows a high level of distinctness between localities (Table 9-10). The ant faunas of the RNI d'Andohahela and the RNI d'Andringitra (65% distinct; 275 km apart), and between the RS d'Anjanaharibe-Sud and the western Masoala Peninsula (72% distinct; 110 km apart) show the lowest level of distinctness. The RNI d'Andringitra and the RS d'Anjanaharibe-Sud (87% distinct; 900 km apart) and the RNI

TABLE 9-3. Total number and percentage (%) of species of each subfamily for pitfall and leaf litter collections on the RNI d'Andohahela (general collections are excluded). P/M refers to the taxonomic ratio of species in the Ponerinae and Myrmicinae. Subfamily names are abbreviated (see Table 9-1).

Elevation (m)	Cerap	Form	Pon	Myrm	Pseudo	P/M
430	0	4 (8%)	7 (14%)	36 (74%)	2 (4%)	0.19
800	5 (7%)	6 (8%)	17 (24%)	41 (58%)	2 (3%)	0.41
1250	3 (5%)	9 (15%)	14 (24%)	33 (56%)	0	0.42
All elevations	**6 (5%)**	**11 (10%)**	**27 (24%)**	**65 (59%)**	**2 (2%)**	**0.41**

TABLE 9-4. The number of species collected, incidence-based coverage estimator (ICE), and first-order jackknife estimates of total species richness (with 95% confidence intervals, CI), based on pitfall and leaf litter transects in the RNI d'Andohahela. Statistics are given for each altitude and for all elevations combined.

Elevation (m)	Observed	ICE	95% CI	Jackknife	95% CI
430	49	61.7	0.32	61.7	0.61
800	71	90.3	0.28	90.6	0.79
1250	59	72.0	0.31	73.7	0.70
All elevations	**111**	**129.4**	**0.11**	**135.8**	**0.20**

d'Andohahela and the western Masoala Peninsula (87% distinct; 845 km apart) had the greatest complementarity. Species turnover values show the same pattern (Table 9-10). In a comparison of all 800 m zone sites (Table 9-11) and all 1200 m

TABLE 9-5. Observed species richness for each elevation surveyed in the RNI d'Andohahela, evaluated at different sample sizes. Richness values are the means of 100 randomizations of sample accumulation order. Standard deviations are given in parentheses.

Stations sampled	430 m	800 m	1250 m
1	10.7 (2.90)	12.7 (4.01)	10.8 (2.53)
3	18.8 (3.19)	25.5 (4.09)	20.8 (2.69)
5	23.5 (3.01)	33.6 (3.81)	26.7 (2.72)
10	30.6 (2.49)	44.4 (3.09)	35.3 (2.91)
15	34.7 (1.95)	50.6 (3.06)	41.2 (2.94)
20	37.7 (1.96)	55.2 (2.70)	45.5 (2.84)
25	40.4 (1.84)	68.7 (2.52)	48.8 (2.73)
30	42.5 (1.77)	61.7 (2.35)	51.3 (2.30)
35	44.4 (1.51)	64.4 (2.25)	53.8 (2.07)
40	46.2 (1.28)	66.8 (1.78)	55.8 (1.57)
45	47.7 (0.98)	69.0 (1.18)	57.5 (1.19)
50	49	71	59

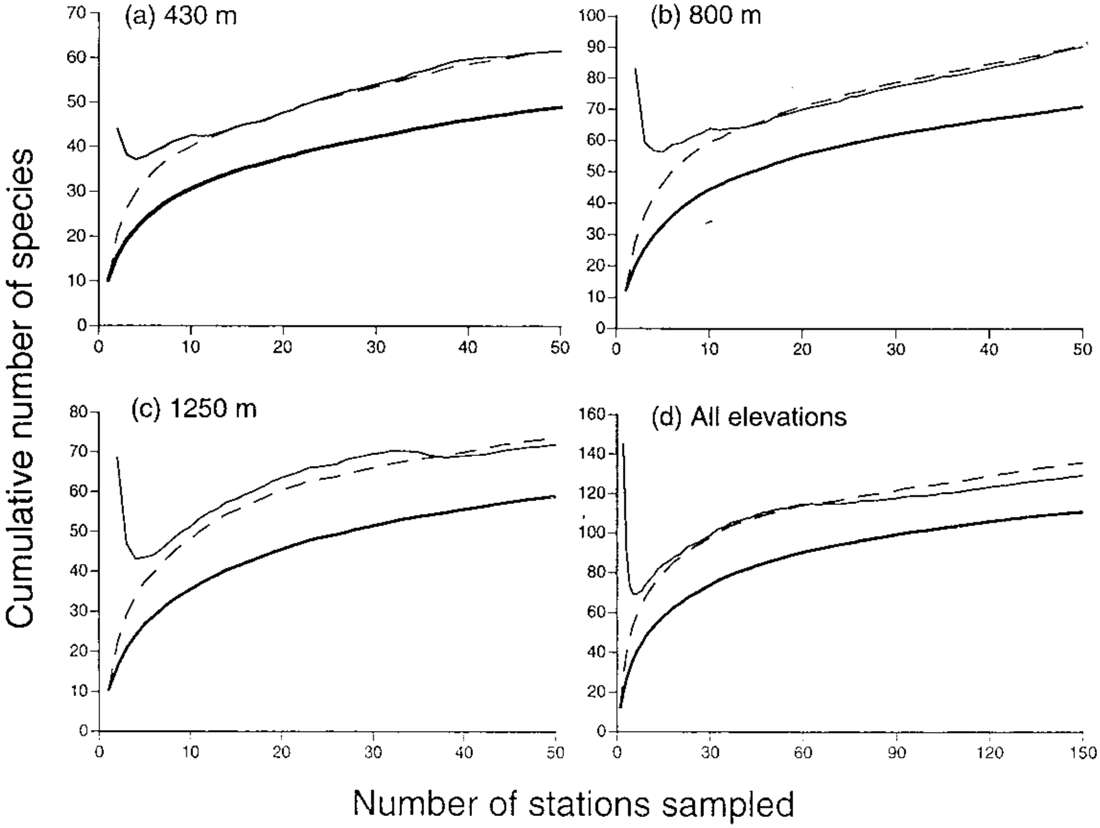

FIG. 9-2. Assessment of leaf litter ant sampling technique for each elevation (**a–c**) and for all elevations combined (**d**) in the RNI d'Andohahela. The lower species accumulation curve (*thick line*) in each chart plots the observed number of species as a function of the number of stations sampled. The upper curves display the nonparametric first-order jackknife (*dashed line*) and incidence-based coverage estimator (ICE) (*solid line*) estimated total species richness based on successively larger numbers of samples from the data set (Heltshe & Forrester, 1983; Lee & Chao, 1994). Curves are plotted from the means of 100 randomizations of sample accumulation order.

TABLE 9-6. Complementarity and faunal similarity between the three elevational zones sampled in the RNI d'Andohahela. Above the diagonal is the Marczewski-Steinhaus (M-S) distance index (presence/absence data; Pielou, 1984) and below the diagonal, simplified Morisita index of similarity (abundance data: Horn, 1966). Higher values represent greater distinctness (M-S) or similarity (Morisita). Bold values represent comparisons of altitudinally adjacent transects. The number of species shared between elevations is presented in parentheses above the diagonal.

Elevation	430 m	800 m	1250 m
430 m	—	**0.537 (38)**	0.813 (17)
800 m	**0.584**	—	**0.725 (28)**
1250 m	0.257	**0.411**	—

zone sites (Table 9-12), the same pattern of complementarity and species turnover values were found. In Table 9-11, data from the 785 and 825 m sites in the RNI d'Andringitra (see Table 9-8) were combined. The same pattern was obtained when the 785 or 825 m sites were analyzed separately with the balance of the 800 m zone sites from the other localities.

Discussion

The RNI d'Andohahela Ant Fauna

We are far from the saturation point in our efforts to discover undescribed ant species in Madagascar. In terms of numbers of new species collected per site inventoried, we are still on the steep part of the curve. There may be 1,000 species on the island, with two-thirds of the species undescribed (Fisher, 1996b, 1997). No previous records exist for ants collected in the RNI d'Andohahela. Subsequent collections of ants in other parts of the RNI d'Andohahela region have been made by P. S. Ward, G. D. Alpert, and K. C. Emberton, and they reveal additional species diversity within the region not recorded during this 1992 survey.

For the island of Madagascar, 90% of the valid specific and subspecific ant taxa are endemic (Fisher, 1996b, 1997). In the RNI d'Andohahela, nearly 100% of the ants collected are thought to be endemic to Madagascar, except for *Cardiocondyla emeryi*, which is a pantropical tramp species and is known throughout the Malagasy region (Bolton, 1982; Fisher, 1997).

TABLE 9-7. Beta-1 (above the diagonal) and beta-2 (below the diagonal) diversity values of each pair of altitude sites in the RNI d'Andohahela. Higher values represent greater species turnover. Bold values represent comparisons of altitudinally adjacent transects. Overall beta-1 diversity was 0.860 and that of beta-2 was 0.563.

Elevation	430 m	800 m	1250 m
430 m	—	**0.366**	0.685
800 m	**0.155**	—	**0.569**
1250 m	0.542	**0.437**	—

Many interesting and rare taxa were collected at the 1250 m site. For example, a single worker of *Aphaenogaster* sp. 1 was collected in a general collection from the leaf litter. This is the first record from the southern half of the island of a montane forest *Aphaenogaster*. At the 1250 m site, seven workers and two queens of *Pilotrochus besmerus* were collected; this is the second record of this endemic Malagasy monotypic genus. *Pilotrochus* was previously known only from a single worker collected in a Berlese sample along the road to Anosibé An'Ala, 33 km south of Moramanga, in east central Madagascar in 1975 (Brown, 1978). The generic name is derived from the Greek *pilos* (hair) + *trochos* (wheel), in reference to its amazing mesopleural "hair-organ."

In addition, other rare species and genera collected at the 1250 m site include two species of *Amblyopone*, one species each of *Smithistruma, Discothyrea, Eutetramorium,* and an undescribed myrmicine genus. Previously, *Eutetramorium* was thought to be endemic to the dry and eastern humid forests of the northern half of Madagascar. At the 1250 m site, a queen of *Eutetramorium* sp. 1 was collected in a leaf litter sample. In 1993, P. S. Ward collected a single worker-queen intermediate in a Winkler sample in humid forest at 1050 m in the RNI d'Andohahela, 3 km east of Mahamavo. This suggests that although queens and worker-queen intermediates may be found in the leaf litter, the nest is located elsewhere, in the canopy or in fallen hard wood that is not sampled by the leaf litter technique. Fallen trees with hard wood are a microhabitat that is often overlooked by ant collectors.

The undescribed myrmicine genus was thought to be endemic to the humid forest of northeastern Madagascar (Fisher, 1998). In the RNI d'Andohahela, a different species of the undescribed genus of myrmicine was collected in a large rotten log at 950 m and in a leaf litter sample

Table 9-8. Elevations surveyed within each elevational zone in the RNI d'Andohahela, the RNI d'Andringitra, the RS d'Anjanaharibe-Sud, and on the western Masoala Peninsula.

Location	0 m	400 m	800 m	1200 m	1600 m	2000 m
Andohahela		430	800	1250		
Andringitra			785, 825	1275	1680	
Anjanaharibe-Sud			875	1200	1565	1985
Masoala	25	425	825			

at 800 m. These records of *Pilotrochus*, *Eutetramorium* and the undescribed genus suggest that the geographical ranges of these genera may extend patchily across the entire length of the eastern humid forest.

Elevational Gradient and Complementarity

Faunal similarity, distinctness, and species turnover measures (Tables 9-5 and 9-7) support a division of the ant fauna into two assemblages, one occurring in lowland forests ≤800 m and the other in montane forests at 1250 m. Between adjacent sites, species turnover was greater between 800 and 1250 m than between 430 and 800 m. In previous studies in the RNI d'Andringitra (Fisher, 1996a), and in the RS d'Anjanaharibe-Sud and on the western Masoala Peninsula (Fisher, 1998), mid-elevation sites (ca. 800 m) had the highest rate of species turnover.

Species richness did not decrease monotonically as a function of elevation (Fig. 9-1). A mid-elevation peak has been documented for ants in Madagascar (Fisher, 1996a, 1998), in Panama (Olson, 1994), and for other taxa (Rahbek, 1995). The mid-elevation peak observed in ant species richness in Madagascar may be the result of a mixing of two distinct ant assemblages along an ecotone.

As suggested in Fisher (1998) for the ant fauna in the RS d'Anjanaharibe-Sud and on the western Masoala Peninsula, species richness may increase from low elevation (430 m) to mid-elevation (800 m) because the 800 m site is adjacent to the source-pool of the distinct montane ant fauna as well as those from lower elevations. The proximity of elevational zones encourages the establishment of marginal populations from adjacent elevations (Pulliam, 1988; Stevens, 1989, 1992; Rahbek, 1997). A mixing of the lowland and montane ant assemblages results in the peak in species richness. In the RNI d'Andohahela, the mid-elevation site (800 m) has the highest number of species shared with other sites: 38 species with 430 m and 28 species with 1250 m (Table 9-6). The number of species shared by the lowest elevation site decreases with increasing change in elevation.

An alternative hypothesis to that of the mixing of lowland and montane ant assemblages is that mid-elevations provide the most "suitable" environment for ants (Rosenzweig & Abramsky, 1993). This assumes that the suitable environment favors an increase in species richness rather than an increase in the population numbers of species. There is currently no accepted explanation of why the most suitable habitats would occur at mid-elevations or how these habitats would increase species richness (Rosenzweig & Abramsky, 1993; Rahbek, 1997).

Table 9-9. Distance (km) between the RNI d'Andohahela, the RNI d'Andringitra, the RS d'Anjanaharibe-Sud, and the western Masoala Peninsula.

	Andohahela	Andringitra	Anjanaharibe-Sud
Andringitra	275	900	110
Anjanaharibe-Sud	1,170	845	
Masoala	1,200		

Efficacy of Inventory Methods

The efficacy of the inventory methods can be evaluated by using species accumulation curves (Colwell & Coddington, 1994). The criterion I use to evaluate efficacy is the number of species collected per unit effort. For every 50-station transect, which takes an average of 7 field days to conduct, 1 month must be spent in the laboratory sorting, identifying, and curating specimens. If increased sampling efforts always collect additional species, how many subsamples should be taken?

An accumulation curve is specific to the area

TABLE 9-10. Complementarity (M-S, above the diagonal) and beta-1 (below the diagonal) diversity values between the RNI d'Andohahela, the RNI d'Andringitra, the RS d'Anjanaharibe-Sud, and the western Masoala Peninsula. The number (percentage) of species specific to the locality are presented along the diagonal. Total number of species for all localities is 381.

	Andohahela	Andringitra	Anjanaharibe-Sud	Masoala
Andohahela	**37 (33)**	0.647	0.850	0.846
Andringitra	0.478	**45 (39)**	0.874	0.872
Anjanaharibe-Sud	0.739	0.776	**79 (44)**	0.720
Masoala	0.734	0.773	0.562	**78 (47)**

of the survey, the season or year, and the collecting techniques employed. Additional collecting methods, or a survey in a different area or season at the same elevation, would most likely collect additional species. If an observed or estimated species accumulation curve demonstrates a sufficient decrease in the rate of species accumulation, then the number of subsamples is arguably adequate for collecting the species in the area surveyed for the particular methods employed. Conversely, if the curves are rising rapidly, more intensive sampling may be necessary to accurately compare diversities between elevations. For hyperdiverse groups with large numbers of rare species, more intensive sampling (i.e., larger numbers of subsamples) typically never generate curves that completely flatten out and reach an asymptote. For these taxa, rates of species accumulation are expected to slowly decrease with more sampling. The entire area may need to be exhaustively surveyed before one can be sure that every species has been collected, but in most cases complete sampling is not possible and is often not the objective.

Sufficient sampling for a high level of completeness is therefore the point at which the accumulation curves show an adequate decrease in species detection. The problem is the lack of existence of an asymptote for diverse taxa and the difficulty in quantifying "an adequate decrease in species detection." One possibility is to sample until a certain percentage—say, 80%—of the estimated species are sampled. In this study, between 78% and 82% of the species had been sampled from 50 stations based on ICE and jackknife estimates of species richness (Table 9-4). For all elevations combined, 86% of the ICE and 82% of the jackknife-estimated species richnesses were sampled. The problem with this approach is that the ICE and jackknife-estimated values are sensitive to sample size (Fig. 9-2). For example, after 10 stations, comparable percentages of ICE and jackknife estimates were obtained, but species accumulation was still rising rapidly. Therefore, the percentage sampled of the ICE and jackknife-estimated species richness was not a reliable indicator of completeness. For example, at 1250 m (Fig. 9-2a), the ICE, jackknife, and observed curves between 10 and 50 stations are parallel. ICE and jackknife estimates predict comparable levels of completeness within this range of samples (10–50) even though species accumulation was still rising rapidly after 10 stations (Fig. 9-2a). Sensitivity to sample size prevents using this method for assessing the level of completeness of these inventories.

An alternative approach is to sample until additional sampling efforts achieve a defined percentage increase in the number of species sampled. Species accumulation curves can be extrap-

TABLE 9-11. Complementarity (M-S, above the diagonal) and beta-1 (below the diagonal) diversity values for the 800 m zone sites between the RNI d'Andohahela, the RNI d'Andringitra, the RS d'Anjanaharibe-Sud, and the western Masoala Peninsula. Data from the 785 and 825 m transects from the RNI d'Andringitra were combined. The numbers (percentage) of species specific to the locality within the 800 m zone are presented along the diagonal. Total number of species for all 800 m sites is 242.

	Andohahela	Andringitra	Anjanaharibe-Sud	Masoala
Andohahela	**25 (35)**	0.664	0.880	0.861
Andringitra	0.487	**37 (42)**	0.886	0.848
Anjanaharibe-Sud	0.786	0.795	**45 (46)**	0.714
Masoala	0.756	0.763	0.563	**50 (46)**

TABLE 9-12. Complementarity (M-S, above the diagonal) and beta-1 (below the diagonal) diversity values for the 1200 m zone sites between the RNI d'Andohahela, the RNI d'Andringitra, and the RS d'Anjanaharibe-Sud. The numbers (percentage) of species specific to the locality within the 1200 m zone are presented along the diagonal. Total number of species for all 1200 m sites is 151.

	Ando-hahela	Andrin-gitra	Anjana-haribe-Sud
Andohahela	**32 (54)**	0.795	0.867
Andringitra	0.660	**23 (56)**	0.933
Anjanaharibe-Sud	0.766	0.874	**68 (79)**

olated to project the increase in species richness expected for a increase in sampling effort (Soberón & Llorente, 1993; Colwell & Coddington, 1994). In Figure 9-3, I fitted the observed species accumulation curves using the Soberón and Llorente (1993) logarithmic model: $S(t) = \ln(1 + zat)/z$, where t is the measure of sampling effort (samples or individuals), and z and a are curve-fitting parameters. Log models do not have an asymptote and are considered appropriate for species-rich taxa (Soberón & Llorente, 1993). That is, I use a nonasymptotic model because I assume the curves will never completely flatten, even with complete sampling. Using a nonasymptotic model may therefore result in a conservative estimate of the number of species predicted with increasing effort. I fitted the log model using the nonlinear least squares method of regression in JMP (SAS Institute, 1994). Based on the extrapolation of these curves, a doubling of sampling effort (an additional 50 stations) would achieve only a 13% gain in species richness at the 430 m site, 14% at 800 m, and 15% at 1250 m (Fig. 9-3). If all samples are combined, only 17 more species (13%) are predicted from a doubling of sampling effort (an additional 150 stations).

The relative between-site pattern of species richness would change very little if collection had been made at an additional 50 stations at each elevation. The relative ranking of between-site pattern of species richness stabilized after a few stations (Table 9-5) and is not predicted to change with the addition of 50 more stations at each transect.

Additional species from 100 station transects, however, could affect the relative between-site pattern of complementarity. If increased sampling collects rare species that are restricted to a particular elevation, then complementarity can be underestimated with the 50-station transect. Complementarity is initially overestimated, on the other hand, if additional sampling collects rare species that are also widespread and found at one or more other sites, or collects rare species at a site that are commonly found at one or more other sites. The problem is that we do not know the identity of the unsampled species or the direction of the bias.

The stability of the complementarity values between sites at 50 samples can be evaluated by examining smoothed complementarity accumula-

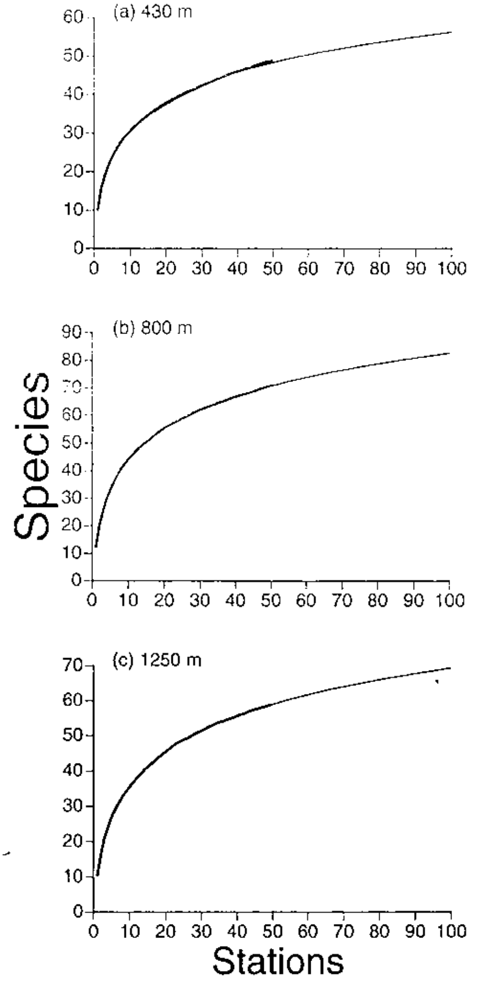

FIG. 9-3. Projection of species accumulation curves for each elevation (a–c) in the RNI d'Andohahela. The *thick line* corresponds to the observed species for the 50 stations sampled. The *thin line* is the logarithmic function fitted to the observed species curve by standard least squares method. The logarithmic curves predict the number of species expected from a doubling of sampling effort (100 stations).

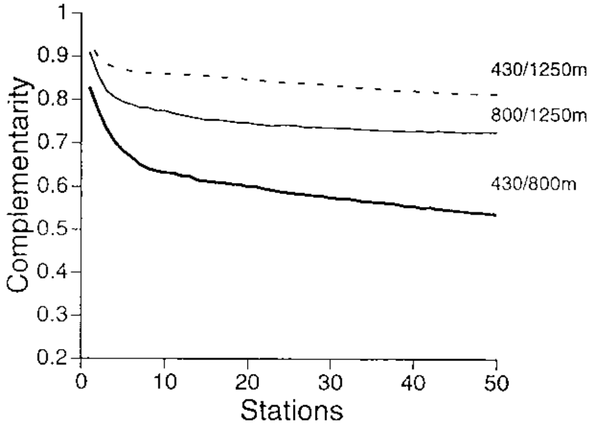

FIG. 9-4. Complementarity (M-S) accumulation curves for each between-site comparison in the RNI d'Andohahela. Each curve is plotted from the mean complementarity value of 100 randomizations of sample accumulation order.

tion curves, which were produced by calculating mean complementarity values for each value of n between 1 and 50 chosen from each site, with 100 random reorderings of sample order (J. A. Umbanhowar, unpubl. program). For example, for $n = 5$, five samples were chosen from each site and the complementary value calculated. This was repeated 99 times, and each time sample order was randomized. These 100 complementary values were used to compute the mean for $n = 5$.

For RNI d'Andohahela, the relative ranking of between-site complementarity values stabilized after a few stations were sampled (Fig. 9-4). The relative magnitude of between-site complementarity generally stabilized after about 25 samples. With increased sampling, however, the 430 and 800 m comparison showed an almost linear decrease in complementarity. The analysis of complementarity accumulation curves suggests that the rate of accumulation of rare and shared species is relatively constant and will change little with additional collecting.

For the goals of this study, a doubling of the number of stations sampled—and the subsequent increase in the time spent sorting, identifying, and curating the additional specimens—is not worth the minimal gain in information (estimated 13% gain in number of species). It appears that relative patterns of species richness and complementarity would change little with additional collecting. What is lost, however, is the identity of the additional species that could be collected. Different criteria would apply for evaluating inventories addressing questions about faunal composition (identity), as opposed to species diversity and complementarity.

For all elevations sampled, therefore, species accumulation curves indicate that with increased sampling effort using the same methods (i.e., adding more pitfall and litter stations) in the same area, only marginal increases in species richness would be attained. The ICE and jackknife estimates of the actual species richnesses were almost identical for each elevation when all stations were pooled (Fig. 9-2) and were between 4% and 9% greater than the species richness predicted from 100 station samples. The precision of the ICE and jackknife estimators is difficult to determine because a site would need to be exhaustively surveyed to produce a complete species list. Nevertheless, these results show that the inventory techniques used in this study provide sufficient sampling for comparisons of species richness, faunal similarity, and species turnover among sites.

Comparisons with Other Faunas

The degree of complementarity (M-S index) at the local scale of between elevations (54–81%) was similar to the level of distinctness between localities (65–87%). The distance between localities and the elevations surveyed within each locality affect complementarity (compare the RNI d'Andohahela and the RNI d'Andringitra, with the RS d'Anjanaharibe-Sud and the western Masoala Peninsula; Table 9-10). For the 800 m zone comparison (Table 9-11) there was a positive relationship between the distance separating localities and complementarity values measured as the M-S index ($r^2 = 0.83$).

The relative prevalence of species from the subfamily Ponerinae and Myrmicinae was similar for the 800 and 1250 m sites (0.41 and 0.42, respectively, Table 9-3). The Ponerinae/Myrmicinae (P/M) ratio for 430 m (0.19) was smaller because of a fewer number of ponerine species present. At the 425 m site on the western Masoala Peninsula, however, 24 species with a relative prevalence of 24% were found (Fisher, 1998, Table 4-6). The 1985 m site in the RS d'Anjanaharibe-Sud is the only elevation surveyed with a similar low P/M ratio (P/M = 0.17 with nine species total; Fisher, 1998). The region- and elevation-specific P/M ratios in Madagascar preclude the use of the P/M ratio to estimate whole ant faunas (Fisher, 1998).

Conclusion

An evaluation of the efficacy of the transect methods suggests that even though increased sampling would collect new species, the results for relative species richness and complementarity values between sites in the RNI d'Andohahela would change little. To better understand the effect of scale on these results, additional surveys are needed. Replicate transects at various distances apart at the same elevation in the RNI d'Andohahela would provide information on the scale of species turnover at a specific elevation in the reserve and would indicate which patterns of species richness and composition at one transect are characteristic of that elevation.

Inventories provide baseline information for understanding geographic variation in biotic assemblages. They are the first step to defining areas of endemism and patterns of species richness. In addition, these inventory methods provide a new tool for evaluating environmental change.

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