Ant diversity patterns along an elevational gradient in the Réserve Spéciale de Manongarivo, Madagascar

Chapter 8. Ant diversity patterns along an elevational gradient in the Réserve Spéciale de Manongarivo, Madagascar

BRIAN L. FISHER

ABSTRACT

FISHER, B. L. (2002). Ant diversity patterns along an elevational gradient in the Réserve Spéciale de Manongarivo, Madagascar. *Boissiera* 59: 311-328.

Leaf litter ant faunas were inventoried in the Réserve Spéciale (RS) de Manongarivo, Madagascar at 400, 780, 1240, 1580, and 1860 m. Within each elevational zone, survey methods involved a combination of leaf litter and beating samples along a 250 m transect. From leaf litter and beating samples, 33 genera and 182 species were recorded; general collecting yielded an additional 29 species. Species accumulation curves of observed species showed decreased rates of species detection and were used to evaluate the efficacy of two inventory techniques. Leaf litter sifting collected more species than beating methods. A transect of 50 leaf litter samples taken 10 m apart captured the same or slightly greater number of species than samples taken 5 m apart. Species richness was greatest at 400 and 780 m depending on method of collection. The number of species collected by elevation was greatest at 780 m (112 spp.) and lowest at 1860 m (41 spp.). Species turnover measures demonstrated a division in ant communities between lowland forest $\leq$ 780 m and montane forest $\geq$ 1240 m. Zoogeographic analysis supports the classification of the Sambirano region based on botanical data, including the lowland forest of RS de Manongarivo, as distinct from lowland forest in the east.

VERSION ABRÉGÉE EN FRANÇAIS

FISHER, B. L. (2002). Variation de la diversité des fourmis le long d'un gradient altitudinal dans la Réserve Spéciale de Manongarivo, Madagascar. *Boissiera* 59: 311-328.

Un obstacle important à l'établissement de priorités en matière de conservation à Madagascar est la difficulté rencontrée à définir clairement des schémas expliquant la diversité et l'endémisme des espèces dans l'île, ainsi que la manière dont l'assemblage spécifique change d'un milieu à un autre. Bien que les arthropodes représentent la plus grande majorité des espèces animales à Madagascar, leur faune reste mal connue et insuffisamment représentée dans les collections muséologiques. Dans le but d'arriver à terme à dresser une carte de la biodiversité à Madagascar, ce travail utilise des méthodes de récolte standardisées pour un groupe d'insectes terrestres diversifiés et de grande importance biologique, les fourmis, afin d'évaluer leur diversité le long d'un gradient altitudinal dans la Réserve Spéciale (RS) de Manongarivo, au nord-ouest de Madagascar.

La faune myrmécologique de la litière y a été inventoriée à 400, 780, 1240, 1580 et 1860 m d'altitude. Dans chaque zone altitudinale, deux méthodes d'inventaire ont été utilisées le long d'un transect de 250 m: l'échantillonnage de la myrmécofaune de la litière et l'échantillonnage par battage. A partir de ces méthodes, 33 genres et 182 espèces de fourmis ont été recensées. Des récoltes générales ont permis d'inventorier 29 espèces supplémentaires.

Les courbes d'accumulation des espèces démontrent des taux décroissants de détection d'espèces supplémentaires avec l'augmentation de l'effort de récolte. Ils ont pu être utilisés pour évaluer l'efficacité de capture des deux méthodes d'inventaire. Les prélèvements de litière ont permis de recenser plus d'espèces que l'échantillonnage par battage. Un transect

CODEN: BOISB2
ISSN: 0373-2975
59 311 (2002)

de 50 échantillons de litière prélevés tous les 10 m a permis la capture d'un nombre d'espèces égal ou légèrement supérieur à celui obtenu lorsque les échantillons étaient prélevés tous les 5 m. La plus grande richesse spécifique a été trouvée à 400 m ou à 780 m, selon la méthode de récolte. Le nombre d'espèces inventoriées en fonction de l'altitude se situe entre un maximum de 112 espèces à 780 m et un minimum de 41 espèces à 1860 m. La mesure du changement dans l'assemblage des espèces en fonction de l'altitude démontre une nette séparation entre la forêt de basse altitude (≤ 780 m) et la forêt de montagne (≥ 1240 m). L'analyse zoogéographique confirme la distinction basée sur les données botaniques entre les forêts denses de basse altitude du Domaine du Sambirano, représenté ici par les stations inférieures du Manongarivo, et celles du Domaine de l'Est.

Ces résultats démontrent par ailleurs qu'il existe des méthodes efficaces pour récolter et traiter des données sur la diversité des fourmis sur l'île. Néanmoins, un obstacle de taille demeure le manque de taxinomistes expérimentés pour décrire et identifier les nouveaux taxons. Une cartographie de la diversité des arthropodes de l'île et son application au niveau de la conservation nécessite le développement d'une collection entomologique nationale ainsi que la formation de scientifiques malgaches en taxonomie, en détermination et en gestion muséologique. Il nous faut stimuler l'avènement d'une nouvelle génération de scientifiques autochtones, à même de poursuivre et de prendre en main la carte de la biodiversité des fourmis de Madagascar.

KEY-WORDS: Ants – Collection methods – Conservation – Diversity – Elevational gradient – Inventory design.

Introduction

A major obstacle to establishing priorities for conservation in Madagascar has been the inability to clearly define patterns of species richness, turnover, and endemism on the island. The current data available for conservation planning in Madagascar is often restricted to select vertebrate and plant groups (GANZHORN & al., 1997; LOURENÇO & GOODMAN, 2000). Although arthropods make up the vast majority of animal species in Madagascar, the arthropod fauna remains poorly understood and inadequately represented in museums (LOURENÇO, 1996; FISHER, 1997; LOURENÇO & GOODMAN, 2000). Efforts to document and analyze the biogeographic patterns of arthropod diversity across the island are needed for effective conservation practices. In basic sciences, these inventories are needed to understand the complex historical factors that have shaped the origin and evolution of the remarkable fauna and flora of Madagascar.

As a step toward achieving a map of biodiversity in Madagascar, this project used standardized sampling procedures for a diverse and ecologically important group of terrestrial insects – ants – to assess diversity along an elevational gradient in the Réserve Spéciale (RS) de Manongarivo. The efficacy of the inventory methods and the effect of elevation on species richness in the RS de Manongarivo are evaluated, measures of faunal similarity are compared, and complementarity established for ant species across elevations sampled from 400 to 1860 m. Finally, the biogeographic affinities of the ant assemblage in the reserve are discussed.

Methods

Study Sites

Ants were intensively surveyed in the RS de Manongarivo between 10 October and 14 November 1998. The Reserve is located in northwestern Madagascar in the Province of Antsiranana. The inventories were conducted at the following sites and habitats within the reserve.

1) 400 m, 10.8 km 229°SW Antanambao, 13°57.7'S, 48°26.0'E, lowland rainforest
2) 780 m, 12.8 km 228°SW Antanambao, 13°58.6'S, 48°25.4'E, lowland rainforest

3) 1240 m, 14.5 km 220°SW Antanambao, 13°59.9'S 48°25.7'E, montane rainforest

4) 1580 m, 17.3 km 218°SW Antanambao, 14°01.3'S, 48°25.1'E, montane rainforest

5) 1860 m, 20.4 km 219°SW Antanambao, 14°02.8'S, 48°24.1'E, montane rainforest

Survey Methods

Two quantitative methods (leaf litter sampling and beating) and general collecting were used to sample ants in each elevational zone. Each quantitative method consisted of taking samples at intervals along a 250 m transect at each study site.

(1) Leaf litter sifting (= L): Invertebrates were extracted from samples of leaf litter (leaf mold, rotten wood) using a modified form of the Winkler extractor (see Figure 2 in FISHER, 1998). The leaf litter samples involved establishing fifty 1 m^2 plots, separated by 5 m intervals, along the 250 m transect line. The leaf litter inside each plot was collected and sifted through a wire sieve with square holes of 1 cm × 1 cm. Before sifting, the material was chopped with a machete to disturb ant nests in small twigs and decayed logs. Ants and other invertebrates were extracted from the sifted litter during a 48-hour period in mini-Winkler sacks (for a detailed discussion of the mini-Winkler method, see FISHER, 1998).

Additional sampling was conducted to ascertain the effects of two aspects of sampling design: number of samples, and distance between samples. In addition to this standardized 50-sample method described above, 25 additional leaf litter samples were taken at the three lowest elevations (400, 780, 1240 m). At these three sites, these additional samples were taken 10 m apart and were placed along a continuation of the same transect line as the initial 50. Each leaf litter transect was therefore 500 m long, with the first 50 samples taken 5 m apart in the first 250 m and the last 25 samples taken 10 m apart in the second 250 m.

(2) Beating low vegetation (= B): Along the 50-sample leaf litter transect, 25 beating stations were established 10 m apart. Ants on low vegetation and arboreal ants were sampled by holding a stretched 1 m × 1 m white nylon platform below the undergrowth and beating the trunk of a tree three times with a stick. The dislodged ants were aspirated and placed in ethanol. This process was repeated 6 times for each of the 25 beating samples. Therefore each beating sample consisted of 6 different plant subsamples, each beaten three times with a stick. The 6 beating subsamples were taken within a 5 m radius of the beating station along the transect.

(3) General collecting (= G): Ants were also surveyed through general collecting, defined as any collection method that was separate from the two quantitative transect methods described above. It included searching in rotten logs and stumps, in dead and live branches, in bamboo, on low vegetation, under canopy moss and epiphytes, and under stones.

Data Analysis

Only records of ant workers were used in data analysis since the presence of queens or males in samples does not necessarily signify the establishment of a colony of that species within the transect habitat type. Voucher specimens for this study have been deposited at the California Academy of Sciences, San Francisco, USA and representative specimens will be returned to the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar.

To assess survey completeness for each of the two quantitative methods, species accumulation curves were plotted for each method singly and for methods combined. Species accumulation was plotted as a function of both the number of samples taken and as a function of number of species occurrences. Species accumulation curves plotted as a function of the number of samples measures species density, the number of species per unit of sample effort, and may not reflect species richness (GOTELLI & COLWELL, 2001). If habitats differ in density of individuals, or if two habitats differ in structure in a way that influences the effectiveness of a

particular sampling method, then species accumulation curves plotted as a function of sample effort may not reflect the actual species richness of the community. GOTELLI & COLWELL (2001) argue that to compare species richness, species accumulation curves should be plotted as a function of individuals. Ants, like other social insects, pose a problem since they are colonial. Since it is impossible to count colonies in beating and leaf litter-sampling methods, a compromise is to use frequency of occurrence. Species occurrence is the total number of times a species was captured independently in the samples and ignores the number of individuals of a species in any one sample. To evaluate these two approaches, species accumulation were plotted both as a function of samples and a function of species occurrence.

Since the shape of a species accumulation curve can depend on the ordering of samples (PALMER, 1990; COLWELL & CODDINGTON, 1994), curves were smoothed through the process of randomization. Sample order was randomized 100 times and means were computed for each succeeding station using the program EstimateS version 6.0 (COLWELL, 1997).

The redundancy of leaf litter (L) and beating (B) methods to capture the same portion of the fauna was evaluated using two methods. First, I compared combined leaf litter and beating accumulation curves to curves of each method singly (combined curve method outlined in LONGINO & COLWELL, 1997). If each method singly collects a distinct portion of the fauna, then the combined curve will be steeper than the single method curves. Such a result indicates that the methods are not redundant. If the combined curve is similar to one of the single method curves, then the methods capture a similar assemblage of species.

In addition to combined curves, I calculated the redundancy index (R) of beating and leaf litter sifting methods: $R = 1 - u/a$, where u = the number of species found only by method *min*, where *min* is the method that collected the fewest number of species, and a = the total number of species collected by the method that captured the fewest species. Higher values represent greater redundancy: a value of 1 represents complete redundancy where all species collected by the method that captured the fewest species are also collected by the other method, and a value of 0 represents no overlap between species captured by each method.

Overlap and complementarity (distinctness or dissimilarity, *sensu* COLWELL & CODDINGTON, 1994) of the ant assemblages at different elevations were assessed using distinctness and beta-diversity indices. Complementarity of ant assemblages at different elevations was assessed using the proportion of all species in two sites that occurred at only one site. Complementarity was calculated using the Marczewski-Steinhaus (M-S) distance index: $C_{MS} = (a + b - 2j)/(a + b - j)$ 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). M-S was chosen because of its simple and statistically valid approach to comparing two biotas (PIELOU, 1984; COLWELL & CODDINGTON, 1994).

Beta-diversity (species turnover between elevations) was calculated using the measure of beta-diversity developed by HARRISON & al. (1992) because it distinguishes between species turnover and the loss of species along a gradient without adding new species. $\text{Beta} = (S/a_{max}) - 1$, where S = the total number of species in the two elevations combined, and a_{max} = the maximum value of alpha-diversity (i. e., number of species) between the elevations compared. The number of species unique to an elevation and the number of species shared between elevations were also compared.

Results

Ant Richness

A total of 33 genera and 204 species were obtained from general collections, leaf litter and beating methods from the five elevation zones sampled. These include the second record of the ant genus *Anopolepis* in Madagascar and the first record of *Probolomyrmex* for the Malagasy

Table 8-1. – Ant species list for the RS de Manongarivo, according to elevation and collection method. Only collections of workers are presented (G = from general collections; B = from beating transect samples; L = leaf litter transect samples). A total of 33 genera and 204 ant species were collected.
— Liste des espèces de fourmis de la RS de Manongario en fonction de l'altitude et de la méthode de récolte. Seules les récoltes d'ouvrières sont présentées (G = récoltes générales; B = récoltes issues de l'échantillonnage par battage; L = récoltes issues de l'échantillonnage de la litière). Au total, 33 genres et 204 espèces ont été récoltés.

Genus	Species	400 m	780 m	1240 m	1580 m	1860 m
CERAPACHYINAE						
Cerapachys	sp. 01				L	L
Cerapachys	sp. 02			L	L	
Cerapachys	sp. 03					L
Cerapachys	sp. 04			L	L	
Cerapachys	sp. 05	L	L			
Cerapachys	sp. 06	L		L		
Cerapachys	sp. 07		L	L		
Cerapachys	sp. 08				L	
Cerapachys	sp. 09	L	G	L, G	L, G	
Cerapachys	sp. 10		L			
Cerapachys	sp. 11		L	L		
Simopone	sp. 1		G			
DOLICHODERINAE						
Tapinoma	sp. 1	L, B	B, G			
Technomyrmex	sp. 1		L, B, G	L		
Technomyrmex	sp. 2	L, B	B			
Technomyrmex	sp. 3		G			
FORMICINAE						
Anoplolepis	sp. 1				B	
Camponotus	sp. 01		L, B	G		
Camponotus	sp. 02		B, G	G		
Camponotus	sp. 03		L, B, G			
Camponotus	sp. 04	G			G	
Camponotus	sp. 05				B, G	
Camponotus	sp. 06			G		
Camponotus	sp. 07	L, B	B, G		B	
Camponotus	sp. 08	B		L		
Camponotus	sp. 10	L				
Camponotus	sp. 11	L				
Camponotus	sp. 12				G	B
Camponotus	sp. 13	B	L, B, G	B, G		
Camponotus	sp. 14	L	L, B, G	B		
Camponotus	sp. 15		L		L, G	G
Camponotus	sp. 16	L, G	L, G	L, G		
Camponotus	sp. 17				B	B
Camponotus	sp. 18	G	L, G	G	L, B	B
Camponotus	sp. 19	G	G	L, G		
Camponotus	sp. 20		L, B, G			
Camponotus	sp. 21	G				
Camponotus	sp. 22			L		
Camponotus	sp. 23	L, G				
Camponotus	sp. 24	L, B	G			
Camponotus	sp. 25	B, G	G			
Camponotus	sp. 26		G			
Camponotus	sp. 27	G	L, G			
Camponotus	sp. 28		G			
Camponotus	sp. 29	L, B				
Camponotus	sp. 30			G		
Camponotus	sp. 31	G	G			
Paratrechina	sp. 1	L, G	L	L	L	L

Table 8-1. – Ctd.

Genus	Species	400 m	780 m	1240 m	1580 m	1860 m
Paratrechina	sp. 2	L	L, B	L	L, G	L, B
Paratrechina	sp. 3	L	L	L		
Paratrechina	sp. 4	L	L	L		L
Plagiolepis	sp. 1	L, B	L	L, B	B	
Plagiolepis	sp. 2			L	L, B, G	L, B
MYRMICINAE						
Aphaenogaster	sp. 1	L	L	L, B		
Cataulacus	sp. 1	B		G		
Cataulacus	sp. 2	L, B	B, G			
Cataulacus	sp. 3	G				
Crematogaster	sp. 1	L, B, G	L, B, G	L, B	L, B, G	L, B
Crematogaster	sp. 2				B	
Crematogaster	sp. 3	L, B, G	L, B			
Crematogaster	sp. 4	L, B	L, B	L, B		
Crematogaster	sp. 5	B				
Leptothorax	sp. 1				B	B
Leptothorax	sp. 2	B	B			
Leptothorax	sp. 3	B	L, B			
Leptothorax	sp. 4				B	B
Leptothorax	sp. 5	B				
Monomorium	sp. 01				L	L
Monomorium	sp. 02	L	L, G	L, B	L, B	L
Monomorium	sp. 03	L	L	L, B		
Monomorium	sp. 04	L	L	L		
Monomorium	sp. 05	L, B		B		
Monomorium	sp. 06		G			
Monomorium	sp. 07			L, B		
Monomorium	sp. 08	G				
Monomorium	sp. 09	L				
Monomorium	sp. 10		G		L, B	L
Monomorium	sp. 11			G		
Monomorium	sp. 12	L	L			
Monomorium	sp. 13	L			B	L, B
Monomorium	sp. 14	L	L			
Monomorium	sp. 15	L	L	L	L	L
Monomorium	sp. 16		L	L	B	
Monomorium	sp. 17			L		
Oligomyrmex	sp. 1		L	L		
Oligomyrmex	sp. 2	L	L, G	L		
Pheidole	sp. 01			L, G		
Pheidole	sp. 02			L		
Pheidole	sp. 03			L		
Pheidole	sp. 04			L		
Pheidole	sp. 05	L	L	L, G		
Pheidole	sp. 06					L, B
Pheidole	sp. 07		L	G		
Pheidole	sp. 08	L, G	L, G			
Pheidole	sp. 09		L			
Pheidole	sp. 10	L				
Pheidole	sp. 11	L, G				
Pheidole	sp. 12	L, G	L, G			
Pheidole	sp. 13	L	L	L		
Pheidole	sp. 14					L
Pheidole	sp. 15			L	L	
Pheidole	sp. 16		L	L, G	L, B, G	
Pheidole	sp. 17	L, G	L, B, G	L, B, G		
Pheidole	sp. 18	L	L	L	L	
Pyramica	*erynnes*	L	L	L		
Pyramica	*khakaura*				L	

Table 8-1. – Ctd.

Genus	Species	400 m	780 m	1240 m	1580 m	1860 m
Pyramica	*ludovici*		L, G			
Pyramica	*olsoni*	L				
Pyramica	*seti*				L	L
Strumigenys	*apios*				L	L
Strumigenys	*bibiolona*	L	L	L		L
Strumigenys	*carolinae*	L	L	L	L	
Strumigenys	*chroa*		L	L		
Strumigenys	*covina*			L		
Strumigenys	*dicomas*	L	L	L		
Strumigenys	*finator*					L
Strumigenys	*glycon*			L	L	L
Strumigenys	*inatos*		L	L	L	L
Strumigenys	*labaris*			L	L	
Strumigenys	*lucomo*	L				
Strumigenys	*nambao*	L	L			
Strumigenys	*origo*		L			
Strumigenys	*rabesoni*			L		
Strumigenys	*schuetzi*	L	L	L		
Strumigenys	*scotti*			L		
Strumigenys	*sphera*	L		L	L	L
Strumigenys	*sylvaini*				L	L
Terataner	*alluaudi*			G		
Terataner	cf. *bellicosus*	L				
Tetramorium	cf. *andrei*	L	L	L, G	L	L
Tetramorium	cf. *kelleri*	L	G			
Tetramorium	sp. 02	L, G	L, G			
Tetramorium	sp. 03		G	L, G	B	
Tetramorium	sp. 04		L	L, G		L, B
Tetramorium	sp. 05				B	L
Tetramorium	sp. 06			L		
Tetramorium	sp. 08		L	L		
Tetramorium	sp. 09	L		L		
Tetramorium	sp. 10	G	G	G		
Tetramorium	sp. 11	L	L	L		
Tetramorium	sp. 12			L		
Tetramorium	sp. 13			L	L	L
Tetramorium	sp. 14	L	L			
Tetramorium	sp. 15	B				
Tetramorium	sp. 16	L	L	L		
Tetramorium	sp. 17			B		
Tetramorium	sp. 18	L	L, G			
Tetramorium	sp. 19			B		
Tetramorium	sp. 20	L	L	L		
Tetramorium	sp. 21	L	L	L		
Tetramorium	sp. 22		L			
Unnamed genus #1	sp. 1				B, G	B
Unnamed genus #1	sp. 2				L, G	
Unnamed genus #1	sp. 3	L				
PONERINAE						
Amblyopone	sp. 1	L		L		
Anochetus	*grandidieri*	L	L	G		
Anochetus	*madagascariensis*	L, G	L, G			
Discothyrea	sp. 1			L	L	L
Discothyrea	sp. 2	L				
Hyopoponera	*sakalava*		L, G	L, G		
Hyopoponera	sp. 01	L	L	L	L	L
Hyopoponera	sp. 02		L		L	L
Hyopoponera	sp. 03	L	L			
Hyopoponera	sp. 04			L	L	

Table 8-1. – Ctd.

Genus	Species	400 m	780 m	1240 m	1580 m	1860 m
Hyopoponera	sp. 05			L		
Hyopoponera	sp. 06	L, G	L			
Hyopoponera	sp. 07			L	L	
Hyopoponera	sp. 08		L	L	L	L
Hyopoponera	sp. 09		L	L		
Hyopoponera	sp. 10	L		L		
Hyopoponera	sp. 11					L
Hyopoponera	sp. 12			L	L	L
Hyopoponera	sp. 13	L				
Hyopoponera	sp. 14		G			
Hyopoponera	sp. 15	L		L		
Hyopoponera	sp. 16	L				
Leptogenys	sp. 1	L	L, G	L	B	
Leptogenys	sp. 2		G			
Leptogenys	sp. 3		G			
Leptogenys	sp. 4			G		
Leptogenys	sp. 5			L		
Mystrium	sp. 1	L		L		
Mystrium	sp. 2	L		G		
Odontomachus	*coquereli*			L, G		
Pachycondyla	*ambigua*	L	L			
Pachycondyla	*cambouei*	L, G	L, G	L, G		
Pachycondyla	*comorensis*	L, G	L, G			
Pachycondyla	*perroti*	L, G	L			
Pachycondyla	*sikorae*		G			
Platythyrea	sp. 1	L	G			
Prionopelta	sp. 1		L	L		L
Prionopelta	sp. 2	L	L	L	L	
Prionopelta	sp. 3	L	L			
Probolomyrmex	sp. 1		L			
Proceratium	sp. 1			L	L	L
Proceratium	sp. 2	L				
PSEUDOMYRMECINAE						
Tetraponera	*grandidieri*	G	L, G	L, B, G		
Tetraponera	*mandibularis*	G		G		
Tetraponera	nr. *longula*			G		
Tetraponera	psw-081	L	L, B			
Tetraponera	psw-086	B	B			
Tetraponera	psw-092	L, G	G			
Tetraponera	psw-110	L, G	L, G			
Tetraponera	psw-111		B	G		
Total G C	84	29	48	31	11	1
Total Beating	57	21	21	14	20	12
Total leaf litter	163	79 (87)	69 (84)	71 (85)	39	34
Total L + B	182	97	92	90	53	40
Total all methods	**204**	**108**	**112**	**106**	**55**	**41**
Redundancy of L and B		0.52	0.62	0.64	0.30	0.50
Number (%) unique species: L + B		26 (27%)	13 (14%)	18 (20%)	6 (12%)	5 (13%)
Number (%) unique species: all methods		21 (19%)	17 (15%)	23 (22%)	6 (11%)	5 (12%)

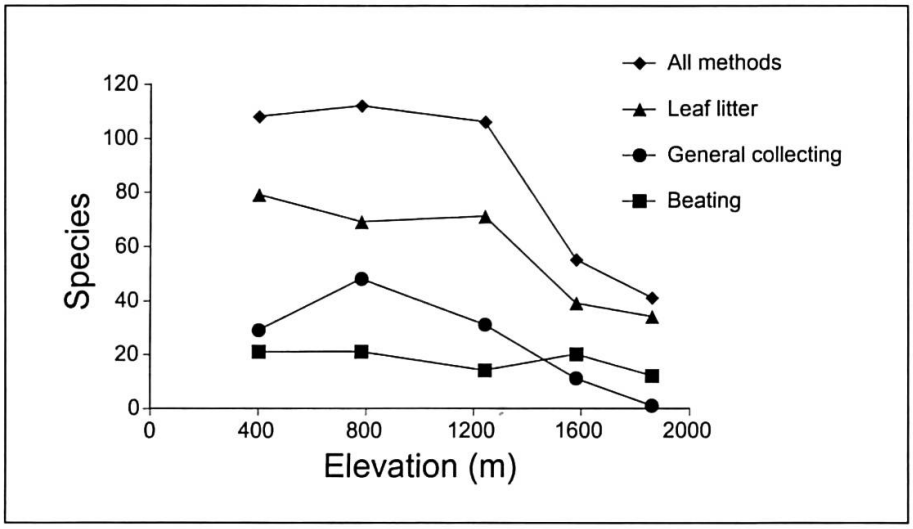

Fig. 8-1. – Number of ant species as a function of elevation. Data are from leaf litter, beating, general collecting and all methods combined. Leaf litter samples include 75 samples at 400, 780, and 1240 m and 50 samples at 1580 and 1860 m. — *Nombre d'espèces de fourmis en fonction de l'altitude. Les données proviennent de l'échantillonnage de la litière, de l'échantillonnage par battage, des récoltes générales, et de l'ensemble des 3 techniques. L'échantillonnage de la litière se base sur 75 échantillons à 400, 780 et 1240 m et sur 50 échantillons à 1580 et 1860 m.*

Table 8-2. – Observed species richness for leaf litter collections at each elevation surveyed in the RS de Manongarivo evaluated at different sample sizes. Richness values are the means of 100 randomizations of sample accumulation order. — *Richesse spécifique observée à partir de l'échantillonnage de la litière aux différentes altitudes, en fonction de la taille de l'échantillon. La valeur de la richesse spécifique est la moyenne de 100 tirages aléatoires de l'ordre des échantillons.*

Number of samples	400 m	780 m	1240 m	1580 m	1860 m
1	13.3	13.5	12.6	8.5	7.1
3	27.3	27.6	27.5	15.3	13.8
5	35.3	35.3	35.5	18.7	17.5
10	47.3	47.1	46.3	24.1	22.1
15	54.7	53.7	52.9	27.2	25.1
20	59.9	58.6	58.0	29.9	27.3
25	64.2	62.7	62.3	32.3	29.1
30	67.7	66.3	66.0	34.0	30.4
35	70.8	69.3	69.2	35.6	31.5
40	73.5	71.8	71.8	36.9	32.4
45	75.6	74.1	74.2	38.1	33.3
50	77.8	76.2	76.5	39.0	34.0
55	79.9	78.1	78.7		
60	81.9	79.8	80.1		
65	83.5	81.3	82.1		
70	85.2	82.6	83.6		
75	87.0	84.0	85.0		

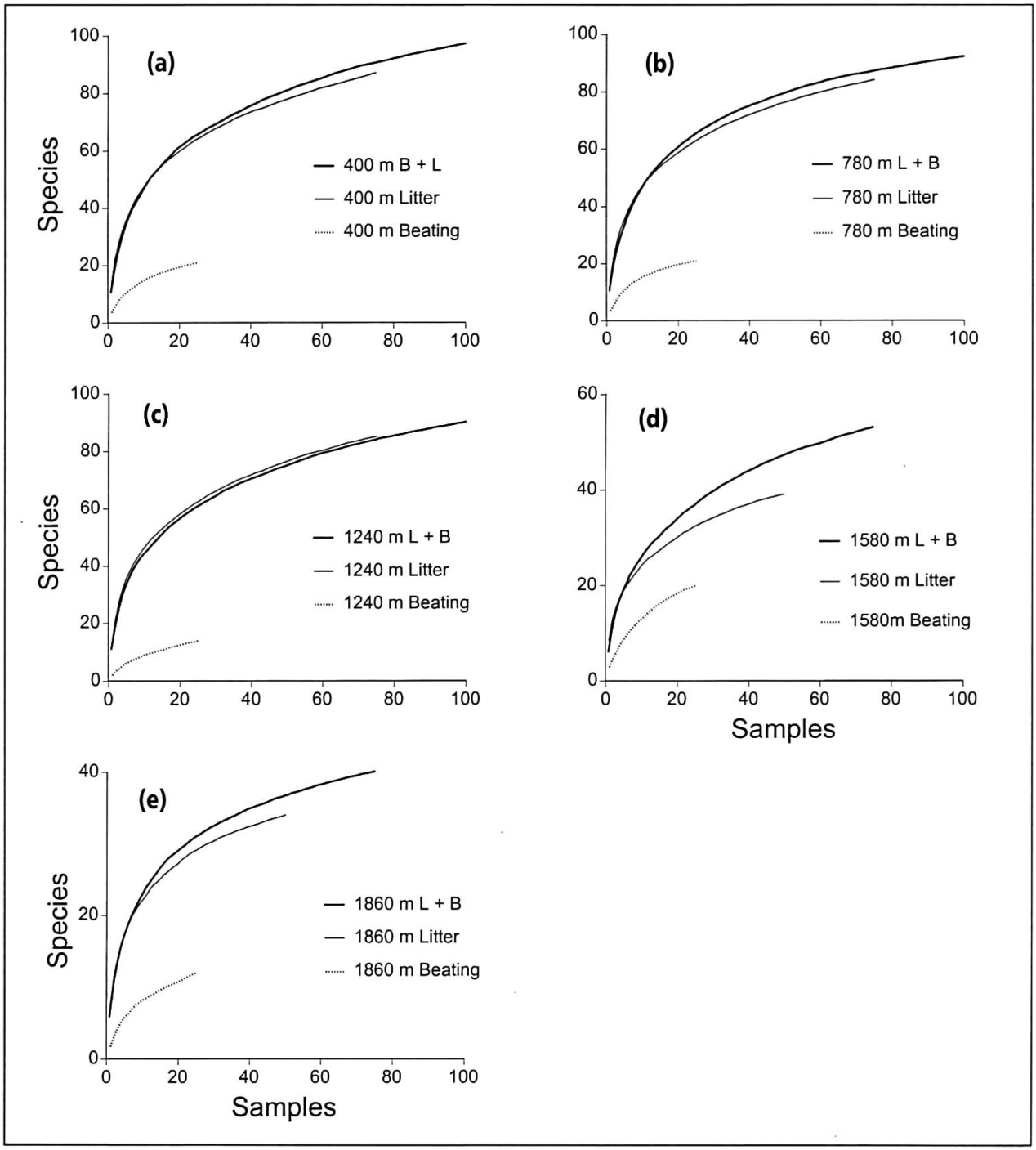

Fig. 8-2. – Assessment of leaf litter (L: 50 or 75 samples), beating (B: 25 samples), and combined methods (B + L: 75 or 100 samples) of ant sampling at **(a)** 400 m, **(b)** 780 m, **(c)** 1240 m **(d)** 1580 m, and **(e)** 1860 m. The species accumulation curve in each chart plots the observed number of species as a function of the number of stations sampled. Curves are plotted from the means of 100 randomizations of sample accumulation order. — *Evaluation des méthodes de récolte des fourmis par l'échantillonnage de la litière (L: 50 ou 75 échantillons), l'échantillonnage par battage (B: 25 échantillons) et par la combinaison des deux méthodes (B + L: 75 ou 100 échantillons) à* ***(a)*** *400 m,* ***(b)*** *780 m,* ***(c)*** *1240 m* ***(d)*** *1580 m et* ***(e)*** *1860 m. La courbe d'accumulation des espèces de chaque graphique représente le nombre d'espèces observées en fonction du nombre d'échantillons relevés. Les courbes ont été tracées à partir de la moyenne de 100 tirages aléatoires de l'ordre des échantillons.*

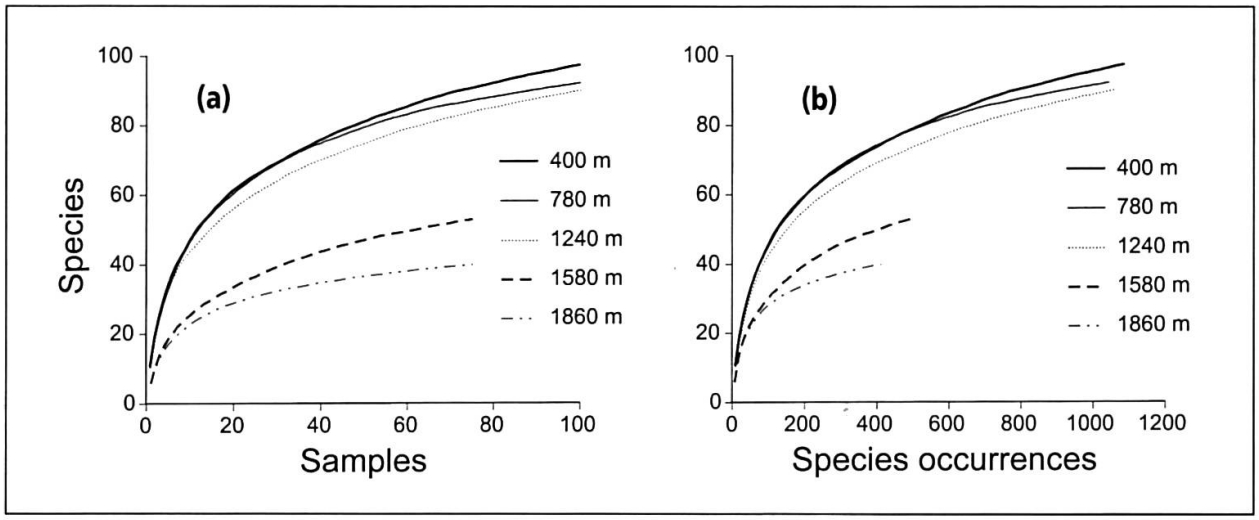

Fig. 8-3. – Assessment of species richness using species accumulation curves for combined leaf litter and beating methods at each elevation. The species accumulation curves plot the observed number of species as a function of **(a)** the number of stations sampled; and **(b)** the number of species occurrences. All curves are plotted from the means of 100 randomizations of accumulation order. — *Evaluation de la richesse spécifique en utilisant les courbes d'accumulations des espèces pour l'échantillonnage de la litière et l'échantillonnage par battage combinés, à chaque altitude. La courbe d'accumulation représente le nombre d'espèces observées en fonction* ***(a)*** *du nombre d'échantillons et* ***(b)*** *du nombre d'occurrence des espèces. Les courbes ont été tracées à partir de la moyenne de 100 tirages aléatoires de l'ordre des échantillons.*

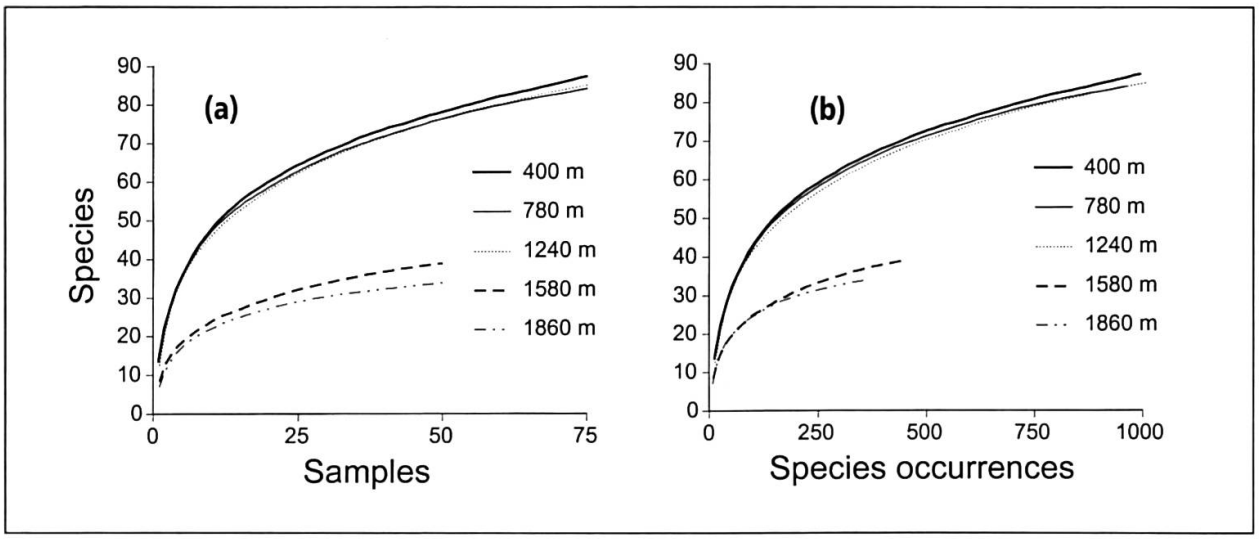

Fig. 8-4. – Comparison of species accumulation curves plotting the observed number of species as a function of the number of: **(a)** stations sampled; and **(b)** species occurrences. Curves are based on litter samples (50 or 75 samples) at each elevation. All curves are plotted from the means of 100 randomizations of accumulation order. — *Comparaison des courbes d'accumulation des espèces en fonction* ***(a)*** *du nombre d'échantillons et* ***(b)*** *du nombre d'occurrence des espèces. Les courbes sont basées sur l'échantillonnage de la litière (50 ou 75 échantillons) à chaque altitude. Les courbes ont été tracées à partir de la moyenne de 100 tirages aléatoires de l'ordre des échantillons.*

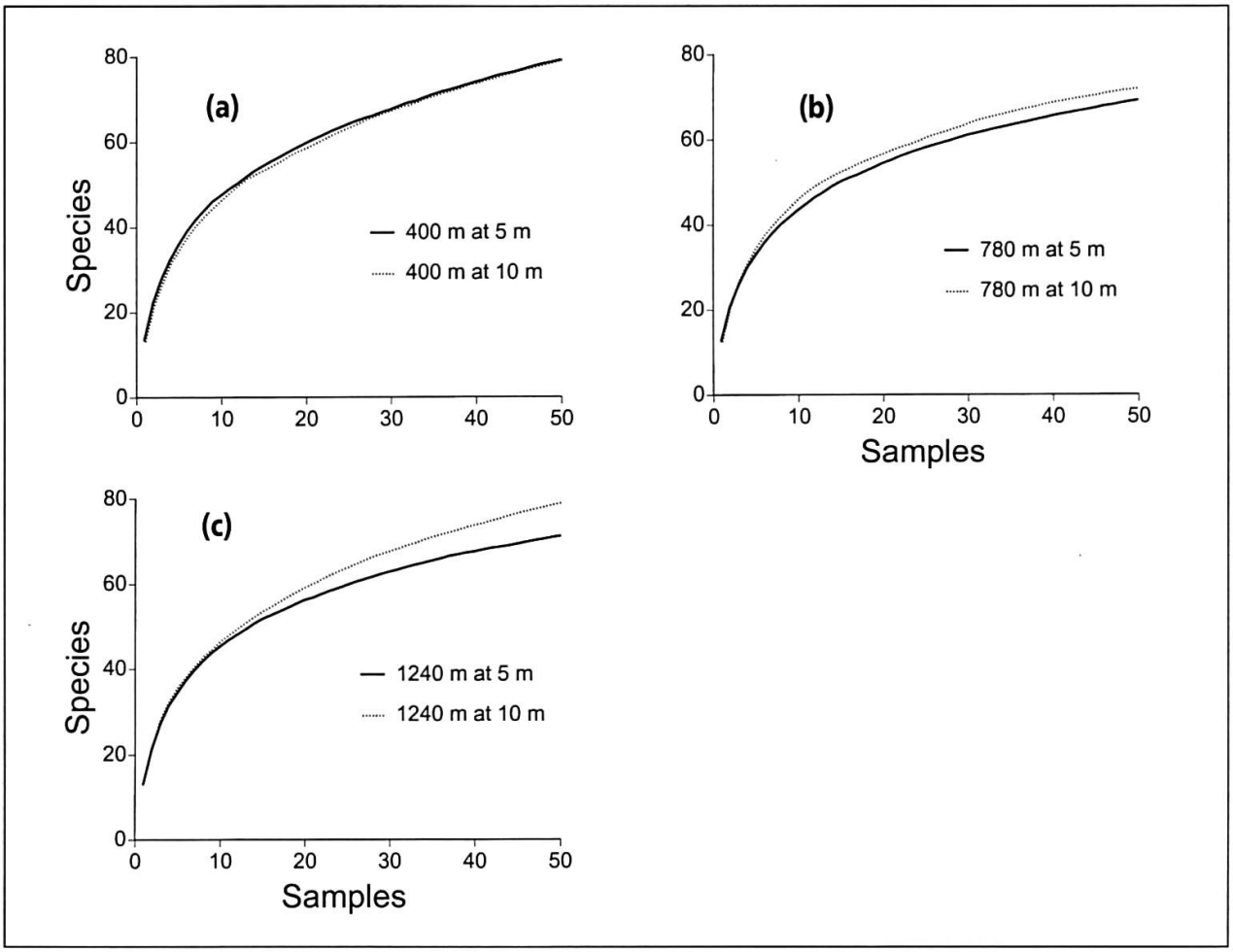

Fig. 8-5. – Assessment of the efficiency of taking 50 leaf litter samples 5 m or 10 m apart at **(a)** 400 m, **(b)** 780 m, and **(c)** 1240 m. The species accumulation curve in each chart plots the observed number of species as a function of the number of stations sampled. Curves are plotted from the means of 100 randomizations of sample accumulation order. — *Evaluation de de l'efficacité de récolte par échantillonnage de la litière pour 50 échantillons distants de 5 ou 10 m, à* ***(a)*** *400 m,* ***(b)*** *780 m et* ***(c)*** *1240 m. La courbe d'accumulation des espèces de chacun des graphiques représente le nombre d'espèces en fonction du nombre d'échantillons. Les courbes ont été tracées à partir de la moyenne de 100 tirages aléatoires de l'ordre des échantillons.*

region. Of the 204 species collected, only one species (*Pyramica ludovici*) is known to be exotic. It was collected at the 780 m site. A list of ant species from this study based on all collecting methods and separated by elevation is presented (Table 8-1).

Species richness patterns along the elevation gradient for each method and for all methods combined are presented in Figure 8-1. The number of species collected by elevation was greatest at 780 m (112 spp.) and the least at 1860 m (41 spp.). When general collections are excluded, the greatest number of species was collected at the 400 m site (Table 8-1).

Efficacy of inventory methods

Species accumulation curves of observed species plotted as a function of number of leaf litter and beating samples taken singly by elevation (Fig. 8-2, Table 8-2) and for both methods combined (Fig. 8-3a) showed decreased species accrual with increased sampling, but did not reach

an asymptote at the end of each transect. Visual inspection of species accumulation curves showed that litter samples had a higher rate of species accumulation than the beating methods (Fig. 8-2).

Species accumulation curves plotted as a function of species occurrence produced similar results as curves plotted as a function of number of samples. For example, Figure 8-3 compares sample (Fig. 8-3a) and species occurrence (Fig. 8-3b) curves for combined beating and litter methods. Figure 8-4 compares sample (Fig. 8-4a) and species occurrence (Fig. 8-4b) of litter methods singly for each elevation. In all comparisons, species occurrence curves were similar to sample curves.

Leaf litter sifting captured the greatest number of species at each elevation when compared to beating and general collecting (Table 8-1). Overall, leaf litter methods collected 163 species. Beating trapped an additional 19 species not obtained by leaf litter sifting and general collecting captured 29 species not collected by leaf litter sifting. Of these 29 species, beating also collected seven species.

Combined beating and leaf litter accumulation curves had a greater rate of species accrual than individual methods alone at all elevations except 1240 m (Fig. 8-2). Redundancy index values for the leaf litter and beating methods ranged from 0.30 to 0.64, with the lowest levels of redundancy occurring at the highest elevations. Beating was most redundant at 1240 m (Table 8-1, Fig. 8-2c). The rate of species accumulation and the number of species collected for 50 leaf litter samples taken 5 m apart was similar to samples taken 10 m apart (Fig. 8-5). Sampling separation of 5 m and 10 m collected: 79 and 79 spp. at 400 m; 69 and 71 spp. at 780 m, and 71 and 79 spp. at 1240 m, respectively.

Species turnover patterns

The highest species turnover (Beta-diversity) values between adjacent elevations occurred between 780 and 1240 m (Table 8-3). Species turnover was also high between the 400 and 780 m site. The greatest dissimilarity (Marczewski-Steinhaus Index) values between adjacent elevations occurred between 1240 and 1580 m. The second greatest dissimilarity value occurred between 780 and 1240 m (Table 8-3)

Table 8-3. – Complementarity and species turnover between the five elevational zones, based on leaf litter and beating samples in the RS de Manongarivo. The Marczewski-Steinhaus (M-S) complementarity measure is above the diagonal and Harrison index of Beta-diversity is below. Higher values represent greater distinctness (M-S) or turnover (Beta). Bold values represent comparisons of elevationally adjacent transects. The number of species shared between elevations is presented in parentheses. — *Complémentarité et "turnover" des espèces entre les cinq zones altitudinales, basés sur l'échantillonnage de la litière et l'échantillonnage par battage dans la RS de Manongarivo. La mesure de complémentarité de Marczewski-Steinhaus (M-S) est présentée en-dessus de la diagonale du tableau et l'indice de Beta-diversité de Harrison en-dessous. Les valeurs élevées représentent une plus grande complémentarité (M-S) ou "turnover" (Beta). Les valeurs en caractères gras mettent en évidence les comparaisons effectuées entre transects adjacents dans la séquence altitudinale. Les valeurs entre parenthèses représentent le nombre d'espèces communes entre deux altitudes.*

Elevation	400 m	780 m	1240 m	1580 m	1860 m
400 m	—	**0.523 (61)**	0.692 (44)	0.881 (16)	0.913 (11)
780 m	**0.320**	—	**0.632 (49)**	0.840 (20)	0.872 (15)
1240 m	0.474	**0.446**	—	**0.723 (31)**	0.818 (20)
1580 m	0.381	0.359	**0.244**	—	**0.524 (30)**
1860 m	0.299	0.272	0.222	**0.189**	—

The 400 m site had the greatest number and the highest percentage of species restricted to one specific elevation (Table 8-1). The 780 m site had the highest number of species shared with other sites and also shared more species with the 400 m site than with the 1240 m site (Table 8-3).

Discussion

Efficiency of methods and sampling completeness

Arthropods constitute more than 75% of the earth's terrestrial biodiversity and deserve increased attention in regions of the world, such as Madagascar, where species-rich habitats are under threat of destruction. Inventories of arthropods are essential to provide data on patterns of species richness, turnover, and endemism and for developing conservation priorities that can potentially preserve the greatest diversity. Because of a lack of appropriate collection methods, invertebrates are often excluded from terrestrial inventory projects despite their importance in ecosystem functioning and ability to elucidate fine-scale patterns of diversity (FISHER, 1999a; 1999b).

A critical issue associated with invertebrate inventories is determining which method and sampling design is the most efficient. This study compares two sampling methods, leaf litter sifting and beating and two sampling designs for leaf litter sifting (5 m and 10 m distances between sampling points).

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 example, the leaf litter transect takes on average 5 days in the field to conduct and 30 days in the laboratory to sort, identify, and curate the specimens. If increased sampling efforts always collect additional species, how many subsamples should be taken? Species accumulation curves help evaluate this question.

An accumulation curve is specific to the area 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 species 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 (see FISHER, 1999b). For these taxa, rates of species accumulation are expected to slowly decrease with more sampling.

In this study, the rate of species accrual was greatest for leaf litter sampling at all elevations (Fig. 8-2). Beating, however, captured new species (low redundancy; Table 8-1) at all elevations. When combined with the leaf litter samples, the resulting species accumulation curve had a greater rate of species accrual at all elevations except 1240 m (site of greatest redundancy).

Accumulation curves plotted as a function of species occurrences differed little from curves plotted as function of number of samples (Fig. 8-3; 8-4). This suggested that the habitats do not differ in species density or that the habitat structure at each elevation did not differ in ways to influence the effectiveness of the litter and beating methods method. Species occurrence may be more important when comparing inventories across different habitats like grassland to forest, or comparing dry season sampling to wet season sampling.

Another factor to consider besides rate of species capture is cost of processing. Though not measured systematically in this study, the beating transect samples on average were processed in

two days of laboratory work, while each 50 sample leaf litter transect took 30 days of laboratory work. Beating transects are process efficient because of the small number of specimens per species. Overall, the beating method, which captured fewer species at a slower rate than leaf litter methods, is recommended as part of the standard ant inventory protocol because of the low cost in processing and because beating captures species not collected by leaf litter methods (19 species in this study; Table 8-1).

The relative ranking of species richness values based on leaf litter sampling did not change with the additional 25 samples at the three lower sites, which also had the highest species richness (Fig. 8-4, Table 8-2). The relative ranking of between-elevation pattern of species richness stabilized after a few stations (Fig. 8-4, Table 8-2). Plotting species accumulation as function of samples (Fig. 8-4a) or species occurrences (Fig. 8-4b) had little effect on the relative ranking of species richness at each elevation. Based on this analysis, the standard ant protocol used at numerous sites on Madagascar of 50 samples (FISHER, 1999b) is sufficient to compare relative ranking of species richness and there is little to be gained by adding 25 more samples, which involve an additional 15 days of lab processing. In this study, these 15 additional days of work per 25 samples (total of 45 days) produced 8 species at 400 m, 15 species at 780 m, and 14 species at 1240 m. Overall, additional sampling beyond the standard 50 samples is only recommended in cases where there is a greater need for completeness at a site.

With the current goal to map an overview of ant diversity in Madagascar to undergird conservation and evolution research, effort would be better spent sampling additional localities with the standard 50 sample leaf litter and 25 sample beating protocols rather than spending additional time collecting at a single site. This strategy will best address our current lack of knowledge of ants for most areas of Madagascar, and thus provide baseline data for conservation work in Madagascar and provide needed specimens for understanding ant evolution.

Elevational gradient

This study is important because it offers the rare chance in Madagascar to look at the change in biotic assemblages along a continuous gradient of forest from 400 to 1860 m. Previous studies on ants have often lacked inventories below 750 m (FISHER, 1999b). Despite this difficulty in finding lowland forest a consistent picture of ant species richness patterns along elevational gradients had emerged. Species richness increased until mid-elevation (ca 800 m) and then rapidly declined (FISHER, 1999b). In this study, however, 400, 780, and 1240 m were very similar in total species richness when measured by beating and leaf litter methods (Fig. 8-3, 8-4). These results differ by having a reduced 780 m species richness, while a similar 400 and 1240 m richness value is consistent with previous work.

General collecting, however, produced the greatest number of species at the 780 m site, many of which are normally caught by the litter technique. One hypothesis for the reduced number of species captured by the leaf litter and beating methods is that differences in habitat or weather (e.g., dryer conditions brought on by a lack of rain) resulted in fewer individuals captured and thus fewer species. A comparison of species occurrence accumulation curves suggest otherwise (Fig. 8-3, 8-4). Based on a similar number of species occurrences, the 400 m site still had a greater number of species than the 780 and 1240 m site. Another hypothesis is that the 780 m transect site was by chance lacking an important microhabitat such as rotten logs. Ants specific to this habitat were therefore missed by the leaf litter and beating methods but captured elsewhere at that elevation in general collecting. This explanation is supported by the observation that many of the species that beating and leaf litter techniques failed to collect were eventually collected in rotten logs and sticks by general collecting methods.

Faunal distinctness and species turnover measures (Table 8-3) support a division of the ant fauna into two assemblages, one occurring in lowland forests $\leq$ 780 m and the other in montane forests greater than 1240 m. Between adjacent sites, species turnover was greater between

780 and 1240 m than between 400 and 780 m. In previous studies in the Parc National (PN) d'Andringitra, in the RS d'Anjanaharibe-Sud, on the western Masoala Peninsula, and PN d'Andohahela, mid-elevation sites (ca. 800 m) had the highest rate of species turnover (FISHER, 1996; 1998; 1999a). Despite a lack of mid-elevation peak in species richness, species turnover was greatest at middle elevations. This is consistent with other studies on ants in Madagascar that show a distinct lowland and montane ant assemblage (FISHER, 1996; 1998; 1999a). On the Manongarivo Massif distinctness measures, however, show a slightly different pattern, where 1240 and 1580 m had a slightly greater value of distinction than the 780 and 1240 m sites. This may have occurred because of the dramatic drop in species richness from the 1240 m site to the 1580 m site or may reflect a disjunct high montane assemblage that occurs in northern Madagascar. Further studies at the adjacent Tsaratanana Massif, which is the highest in Madagascar, are needed to further evaluate this possibility.

Biogeographic affinities

The recent completion of the revision of dacetine ants (*Strumigenys:* FISHER, 2000) and *Pyramica:* BOLTON, 2000) permitted an analysis of the biogeographic relationships of the ant assemblage from RS de Manongarivo with other sites throughout Madagascar (FISHER & GIRMAN, 2000). Specifically, this study provided a means to assess aspects of the zoogeographic affinities of the Sambirano region.

Biogeographic divisions in Madagascar based on plant data have often included a distinct Sambirano region in the northwest (reviewed in LOWRY & al., 1997). The Sambirano Domain is defined as low elevation (< 800 m) forest in a narrow portion of the northwestern coast where the moist climatic conditions typical of the east extend to the west coast. FISHER & GIRMAN (2000) used Parsimony Analysis of Endemism to analyze patterns of endemism of dacetine across numerous sites on Madagascar, principally in the east and on the Manongarivo Massif. Their results show that the montane forest sites of Manongarivo (1240 – 1860 m) are faunistically close with the montane sites of the eastern slopes of Anjanaharibe-Sud (1180-1995 m), forming a northern highland group. The Manongarivo lowland forest sites (400-780 m), however, did not group with the other eastern lowland site. The lowland forests of Manongarivo formed an isolated clade but shared unique taxa with two southern sites of Vohibasia and Isalo and the northern site of Montagne d'Ambre. This suggests that they are more closely related to western than to central and eastern forests. Thus, these data are supportive of HUMBERT's (1965) assessment of the montane zones of the Manongarivo Massif having strong biogeographic relationships to the Central Domain. For ants, however, further evaluation of the lowland areas of the Sambirano region and other areas in the west will be necessary before the affinities of these animals across this zone, as well as patterns of local endemicity, are sufficiently clear to be able to test the separation for the Sambirano Domain (*sensu* HUMBERT, 1965).

The northern montane sites hold a disjunct group of endemic species. The montane forests of RS de Manongarivo and RS d'Anjanaharibe-Sud grouped in a separate clade from the adjacent lowland sites from these same mountains. FISHER & GIRMAN (2000) offer two hypotheses to explain these disjunct distributions: (1) long distance dispersal or (2) vicariance. Though dispersal cannot be ruled out as an explanation, the dynamic environmental history of the island during the Pleistocene may explain the current distributions. During cooler periods, montane forests belts may have spread to lower altitudes, forming a contiguous zone of montane forests between these mountains (BURNEY, 1997 and references therein). Montane vicariance occurred when the climate warmed and montane ant populations became isolated on mountain tops. RAXWORTHY & NUSSBAUM (1996) to explain disjunct montane distributions of reptiles also suggested this model of climate-induced vicariance.

Conclusion

The inventory of RS de Manongarivo addresses the urgent need to map biodiversity in Madagascar. Given the current levels of habitat loss and continued high rates of deforestation, this map is vital for effective conservation practices on the island. Now is the time to document and analyze biodiversity within the island before the chance to develop effective conservation strategies is forever lost. The ant study demonstrates that the tools are in place to efficiently collect and process diversity data on ants across the island. However, the final stages of this effort are seriously impeded by a lack of trained taxonomists to describe and identify the newly discovered taxa. To effectively map arthropod diversity across the island and to rapidly apply this data to conservation efforts requires the development of a national entomological collection in Madagascar and the training of Malagasy scientists in curation, identification, and taxonomy. We must foster a new generation of host-country scientists capable of conducting and continuing the map of biodiversity.

ACKNOWLEDGMENTS

Fieldwork could not have been completed without the gracious field support from the people of Antanambao. Special thanks to Aisha Fredericks, Leticia Njozela, Helian Ratsirarson, and Jean Claude Rakotonirina for assistance in processing and sorting the specimens. Steven M. Goodman and an anonymous reviewer provided valuable comments on the manuscript, greatly improving the clarity of presentation. The work was partially supported by a grant from the National Science Foundation (INT 9600364) to B. Fisher and the National Geographic Society to S. M. Goodman (6338-98).

REFERENCES

BOLTON, B. (2000). The ant tribe Dacetini. *Mem. Amer. Entomol. Instit.* 65: 1-1028.

BURNEY, D. A. (1997). Theories and facts regarding Holocene environmental change before and after human colonization. *In*: GOODMAN, S. M. & B. D. PATTERSON (eds.), *Natural change and human impact in Madagascar:* 75-89. Smithsonian Institution Press, Washington, D. C.

COLWELL, R. K. (1997). *EstimateS: Statistical estimation of species richness and shared species from samples. Version 5.* User's Guide and application published at: http://viceroy.eeb.uconn.edu/estimates.

COLWELL, R. K. & J. A. CODDINGTON (1994). Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. Royal Soc. London*, ser. B, 345: 101–118.

FISHER, B. L. (1996). Ant diversity patterns along an elevational gradient in the Réserve Naturelle Intégrale d'Andringitra, Madagascar. *In:* GOODMAN, S. M. (ed.), A floral and faunal inventory of the eastern slopes of the Réserve Naturelle Intégrale d'Andringitra, Madagascar: With reference to elevational variation. *Fieldiana: Zoology*, new series, 85: 93-108.

FISHER, B. L. (1997). Biogeography and ecology of the ant fauna of Madagascar. *J. Nat. Hist.* 31: 269–302.

FISHER, B. L. (1998). Ant diversity patterns along an elevational gradient in the Réserve Spéciale d'Anjanaharibe-Sud and on the western Masoala Peninsula, Madagascar. *In*: GOODMAN, S. M. (ed.), A floral and faunal inventory of the Réserve Spéciale d'Anjanaharibe-Sud, Madagascar: With reference to elevational variation. *Fieldiana: Zoology,* new series, 90: 39-67.

FISHER, B. L. (1999a). Ant diversity patterns along an elevational gradient in the Réserve Naturelle Intégrale d'Andohahela, Madagascar. *In*: GOODMAN, S. M. (ed.), A floral and faunal inventory of the Réserve Naturelle Intégrale d'Andohahela, Madagascar: With reference to elevational variation. *Fieldiana: Zoology,* new series, 94: 129-147.

FISHER, B. L. (1999b). Improving inventory efficiency: A case study of leaf litter ant diversity in Madagascar. *Ecological Applications* 9: 714-731.

FISHER, B. L. (2000). The Malagasy fauna of Strumigenys: 612-696. *In*: BOLTON, B, The ant tribe Dacetini. *Mem. Amer. Entomol. Inst.* 65: 1-1028.

FISHER, B. L. & D. GIRMAN (2000). Biogeography of ants in eastern Madagascar. *In*: LOURENÇO, W. R. & S. M. GOODMAN (eds.), *Diversité et endémiseme à Madagascar:* 331-344. Mémoires de la Société de Biogéographie, Paris.

GOTELLI, N. J. & R. K. COLWELL (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and estimation of species richness. *Ecol. Letters:* 4: 379-391.

GANZHORN, J. U., B. RAKOTOSAMIMANANA, L. HANNAH, J. HOUGH, L. LYER, S. OLIVIERI, S. RAJAOBELINA, C. RODSTROM & G. TILKIN (1997). Priorities for biodiversity conservation in Madagascar. *Primate Rep.* 48: 1-81.

HUMBERT, H. (1965). Description des types de végétation. *In* HUMBERT, H. & G. COURS DARNE (eds.), *Notice de la carte. Madagascar*. Travaux de la Section Scientifique et Technique de l'Insitut Français de Pondichéry, Hors série n° 6: 46-78

HARRISON, S., S. J. ROSS & J. H. LAWTON (1992). Beta diversity on geographic gradients in Britain. *J. Anim. Ecol.* 61: 151–158.

LONGIONO, J. T. & R. K. COLWELL (1997). Biodiversity assessment using structured inventory: Capturing the ant fauna of a tropical rain forest. *Ecological Applications* 7: 1263-1277.

LOURENÇO, W. R. & S. M. GOODMAN (2000) (eds.). *Diversité et endémisme à Madagascar*. Mémoires de la Société de Biogéographie, Paris.

LOURENÇO, W. R. (1996) (ed.). *Biogéographie de Madagascar*. Editions ORSTOM, Paris.

LOWRY, P. P. II., G. E. SCHATZ, and P. B. PHILLIPSON (1997). The classification of natural and anthropogenic vegetation in Madagascar. *In:* S. M GOODMAN & B. D. PATTERSON (eds.), *Natural change and human impact in Madagascar:* 93-123. Smithsonian Institution Press, Washington, D. C.

PALMER, M. W. (1990). The estimation of species richness by extrapolation. *Ecology* 71: 1195–1198.

PIELOU, E. C. (1984). *The interpretation of ecological data*. Wiley, New York.

RAXWORTHY, C. J. & R. A. NUSSBAUM (1996). Montane amphibian and reptile communities in Madagascar. *Conserv. Biol.* 10: 750-756.

Address of the author: Department of Entomology, California Academy of Sciences, Golden Gate Park, San Francisco, CA 94118-4599. E-mail: bfisher@calacademy.org