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Leaf litter ant diversity in Guyana

JOHN S. LAPOLLA[1,*], TED SUMAN[1], JEFFREY SOSA-CALVO[1,2] and TED R. SCHULTZ[1]
*[1]Department of Entomology, National Museum of Natural History, Smithsonian Institution, POB 37012, NHB, CE518, MRC 188 Washington, D.C. 20013-7012, USA; [2]Department of Entomology, University of Maryland, 4112 Plant Sciences Building, College Park, MD 20742, USA; *Author for correspondence (e-mail: lapollaj@si.edu; phone: +1-202-633-1002; fax: +1-202-786-2894)*

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Abstract. Leaf litter ants are an important group of organisms for informing conservation planning. This study presents the beginning of a leaf litter ant dataset for Guyana. Following the ants of the leaf litter protocol, ants were extracted from sifted leaf litter sampled along eight transects from across Guyana. A total of 230 species were collected from 44 genera. Of those 230 species, 122 species (ca. 53%) were found at only one site. Out of the 122 species found at only one site, 43 species (ca. 19%) were singletons, being known from only one specimen. Using a cluster analysis, faunistic composition was compared among sites. While the lowland sites accounted for the highest species richness, Mt. Ayanganna possessed an especially distinctive ant fauna and may represent a center of endemism. Three leaf litter ant communities were identified: lowland and two Mt. Ayanganna communities, mid-elevation and upper elevation. Recent mining operations on Mt. Ayanganna threaten its pristine nature and this study confirms the need for further biological study of the area. With upwards of 70% of its area still forested Guyana has the opportunity to preserve its biological heritage before widespread deforestation occurs. If expanded, this leaf litter ant dataset will be increasingly useful for country-wide conservation planning.

Introduction

Due to the combined efforts of a global community of ant systematists and ecologists, codified in Agosti et al. (2000), leaf litter-dwelling ants are currently used as bioindicators in dozens of biodiversity studies conducted at localities across the globe (Brühl et al. 1998; Fisher 1999, 2002; Delabie et al. 2000; Longino et al. 2002; Leponce et al. 2004). The so called A.L.L. protocol (Ant of the Leaf Litter) provides a quantitative methodology for sampling leaf litter ants in a manner that allows for across site species richness comparisons. This is important because there are few standardized methods for sampling invertebrates, despite the growing call for the use of invertebrates in conservation biology New 1995; Samways 2005). Ants have numerous attributes that make them valuable for conservation planning. Among those are: (1) they are ecological dominant in most terrestrial ecosystems (especially in the tropics); (2) they are easily sampled, with statistically representative samples possible within a week or less (Agosti et al. 2000); (3) they are sensitive to environmental change (Kaspari and Majer 2000); and (4) ant species diversity is manageable (they are not hyperdiverse) compared to many other insect groups. We present here an A.L.L. style study of the leaf litter ant fauna of Guyana. As we discuss below, Guyana, with its pristine forests, is an ideal place to collect baseline data that can contribute biological information to conservation efforts.

The ant diversity of Guyana is largely unknown. Wheeler (1916, 1918) produced the only publications specifically addressing this fauna. Weber (1946) examined the fungus-growing tribe Attini from Guyana. Kempf (1972) recorded a total of 330 described ant species from Guyana based primarily on literature reports, but this figure undoubtedly vastly underestimates the true number of species present in the country. The Neotropics possess one of the richest ant faunas in the world, with around 3100 known species (Fernández and Sendoya 2004). For example, one locality in Costa Rica alone, La Selva, an approximately 1500 ha biological preserve, possesses at least 437 ant species (Longino et al. 2002). By comparison, Guyana remains largely unexplored and only recently have many areas become accessible to biologists.

Geographically, Guyana is centrally located within a large geological area known as the Guiana Shield, encompassing roughly 1,000,000 km^2. This formation stretches between the Orinoco and Amazon River Basins, with its western edge reaching as far as the foot of the Andes Mountains in southern Colombia (Gibbs and Barron 1993). The Shield is an ancient rock massif dating back to the Proterozoic (ca. 2.5 billion years ago) that was once attached to modern-day West Africa (Gibbs and Barron 1993). In geological terms, a shield is a formation that has been stable, i.e., that has not been affected by orogenic (mountain-building) activity for at least 1 billion years (Gibbs and Barron 1993). During the Cretaceous, the igneous-metamorphic basement of the Shield was covered in layers of sand that were compressed and fused into what today is known as the Roraima Formation (Gibbs and Barron 1993). Since its creation, erosion has worn away large areas of the Roraima Formation, creating the flat-top mountains, or tepuis, that have fascinated biologists as well as the lay public for over a century. Mount Roraima, on the border of Guyana and Venezuela, is perhaps the most famous tepui, being the inspiration for Arthur Conan Doyle's *The Lost World* (Doyle 1912).

Unlike most tropical countries, the majority of Guyana remains covered by primary rainforest. Approximately 70% of Guyana's land remains intact or only marginally damaged by human populations (Funk and Richardson 2002). The country is centrally located in what has been called the largest undisturbed block of tropical forest in the world. With such a large amount of original forest remaining, Guyana retains a real opportunity to preserve most of its biological diversity. Although Guyana is currently undergoing an internal assessment of areas to place under formal protection (Funk and Richardson 2002), increasing pressure from mining and other resource extraction industries threatens its pristine nature. The flora of Guyana has been extensively surveyed (see Clarke and Funk 2005 for review), and this information has to some extent already been incorporated into conservation planning (Steege 1993; Funk and Richardson 2002). We present a preliminary survey of the patterns of leaf litter ant diversity within Guyana, with the hope that this information will serve as a baseline dataset to help inform critical conservation decisions to be made in the near future.

Materials and methods

Study sites

Eight study sites sampled across Guyana (map of sites, (Figure 1)).

Code	Site name	GPS coordinates	Elevation (m)
CWC	Calm Water Creek	6°28.06′ N, 58°37.16′ W	20
IFR	Iwokrama Forest Reserve; Whitewater Camp	4°43.89′ N, 58°50.99′ W	60
KMM	Kanuku Mountains; near Moca-Moca Village	3°17.29′ N, 59°38.37′ W	224
MAB	Base Camp; Mt. Ayanganna	5°20.06′ N, 59°55.48′ W	732
MAD	*Dicymbe* Camp; Mt. Ayanganna	5°17.76′ N, 59°54.63′ W	717
MAF	Falls Camp; Mt. Ayanganna	5°22.33′ N, 59°57.56′ W	1134
MAU	Upper Forest; Mt. Ayanganna	5°22.48′ N, 59°57.96′ W	1300
MHC	Mabura Hill	5°09.31′ N, 58°41.98′ W	64

We have categorized each study site according to the vegetation map of Guyana by Huber et al. (1995). Both IWR and MHC are classified as lowland rainforest: evergreen, non-flooded forest in which *Chlorocardium* trees are often dominant. CWC consists of evergreen sclerophyllous forest, also called ‘‘Wallaba’’ forest due to the presence of the tree *Eperua falcata*. KMM is evergreen, lower montane forest, found along the slopes of the Kanuku Mountains. MAB and MAD are classified as lower montane sclerophyllous forest, with MAD particularly dominated by *Dicymbe* trees. MAF and MAU are the highest elevation localities, but still below the designation of true cloud forests. Instead they are classified as evergreen montane forest. MAU forest is unique in that the trees are not only short (typically between 5 and 10 m high), but spaced widely, creating an open canopy. This area is heavily dominated by mosses that cover most surfaces.

Field methods

The sampling method described here is a slightly modified version (done without pitfall traps) of the ‘‘A.L.L. protocol,’’ as described in Agosti et al. (2000). A 200-m linear transect was marked off at each locality, with the exception of CWC, where only a 100-m transect was completed. At 10-m intervals along these transects,1-m^2 samples of leaf litter were collected. Leaf litter was sifted through a wire sieve of 1-cm mesh size, by shaking the sifter vigorously at least 15 times. The sifted leaf litter was then placed in a mini-Winkler extractor for 48 h (see Agosti et al. 2000 for a detailed discussion of this method). If the sifted leaf litter volume exceeded the capacity of a single mini-Winkler extractor, a second extractor was used. Only worker ants were counted in the samples and recorded as incidence data for analysis. Subsequently, in the laboratory, ants were sorted to morphospecies, vouchers of each morphospecies were mounted, and morphospecies were identified to named species whenever permitted by current taxonomy. Voucher specimens are deposited in the National Museum of Natural History, Washington D.C., and in the Centre for the Study of Biological Diversity, University of Guyana, Georgetown, Guyana.

Data analysis

The program EstimateS (version 7.5) (Colwell 2005) was used to construct species accumulation curves. The form of a species accumulation curve can depend on the ordering of samples (Colwell and Coddington 1994); therefore, sample order was randomized 100 times. Species were plotted against the total number of individuals of all species collected, the procedure recommended by Gotelli and Colwell (2001) when you have variable species density but want to compare whole community richness. EstimateS was used to calculate the ICE (incidence-based coverage estimator) species estimator. Hierarchical cluster analysis was performed using Systat program (Systat Software 2002). The analysis was performed using average linkage on a similarity matrix constructed using a modified Jaccard index (incidence based) (Chao et al. 2005) calculated using EstimateS.

Results

From 150 1-m^2 leaf litter samples, a total of 25,927 worker specimens were collected representing 44 genera and 230 species (Table 1). Of those 230 species, 122 (ca. 53%) were found at only one site. Forty three (ca. 19%) were global singletons, known from only one specimen in the entire study. Subfamilies and genera were unequally represented with respect to number of species (Figures 2 and 3), and genera varies with respect to number of individuals (Figure 4). The subfamily Myrmicinae was represented by the largest number of species (143), accounting for 62.2% of the total species. The next two most speciose subfamilies, Formicinae and Ponerinae, each contributed 28 species (12.2% each). The most speciose genus was *Pheidole* with 74 species (32.2% of total). The next most speciose genus was *Pyramica* with 15 species (6.5% of total). With regard to number of individuals collected, however, the ranking of genera changes,

Table 1. Species collected at each locality.

Species	CWC	IFR	KMM	MAB	MAU	MAD	MAF	MHC
Acanthognathus brevicornis				3				
Acropyga ayanganna					23		122	
Acropyga donisthorpei	20							
Acropyga fuhrmanni				111				
Acropyga panamensis		2						
Acropyga romeo				49				
Acropyga stenotes						20		
Amblyopone lurilabes			1					
Amblyopone mystriops		2						
Anochetus sp. 001				1	1	6	5	
Anochetus sp. 002		6						
Anochetus mayri		25	6			2		
Azteca sp. 01		1						
Basiceros nr. *militaris*						3		
Basiceros militaris		3	1					2
Brachymyrmex sp. 001	1	5	1	7				3
Brachymyrmex sp. 002						21		
Brachymyrmex sp. 003				3				
Brachymyrmex sp. 004				14				
Brachymyrmex sp. 005				1				
Brachymyrmex sp. 006	1							
Brachymyrmex sp. 007			24					
Camponotus sp. 01		2						
Camponotus sp. 02					3			
Camponotus sp. 03		1						
Carebara brevipilosa		71	1					
Carebara nr. *inca*			1	2				
Carebara sp. 01		2						
Cheliomyrmex sp. 001						6		
Crematogaster sp. 001		3	19	5	160			
Crematogaster sp. 002			13					
Crematogaster sp. 003	79		43					
Crematogaster sp. 004	32	328		188				11
Crematogaster sp. 005	86			653				1576
Crematogaster sp. 006	102	2						213
Crematogaster sp. 007	95							
Crematogaster sp. 008						634		
Cyphomyrmex laevigatus								23
Discothyrea cf. *denticulata*						2		
Discothyrea denticulata	4							
Dolichoderus attelaboides		4						
Dolichoderus imitator	1	24						
Dolichoderus sp. 001		1						
Ectatomma edentatum	2	3	2	6				
Ectatomma lugens	6	1						
Gigantiops destructor			1					
Gnamptogenys hartmani		1						
Gnamptogenys regularis				2				
Gnamptogenys sp. 001					25		42	

Table 1. Continued.

Species	CWC	IFR	KMM	MAB	MAU	MAD	MAF	MHC
Gnamptogenys sp. 002				2				
Gnamptogenys sp. 003				5				
Gnamptogenys sp. 004				7				3
Gnamptogenys sp. 005								5
Gnamptogenys sp. 006		203	21	11				33
Gnamptogenys sp. 007				192	3	16	49	
Gnamptogenys sp. 008					1			
Gnamptogenys sp. 009				42			27	
Gnamptogenys sp. 010		13						
Gnamptogenys sp. 011	85			7				
Gnamptogenys sp. 012		1						
Hylomyrma nr. *immanis*	6	31						
Hylomyrma nr. *reginae*	5			1	2		8	21
Hypoponera sp. 001		73	6	19		44	1	10
Hypoponera sp. 002					5			
Hypoponera sp. 003			48					
Hypoponera sp. 004			5					
Hypoponera sp. 005							9	1
Hypoponera sp. 006						39		
Hypoponera sp. 007						2		
Hypoponera sp. 008	11	7	56	56	25		60	3
Hypoponera sp. 009	53	36	3	5				12
Hypoponera sp. 010							30	
Hypoponera sp. 011	20	225	65	113			1	
Lachnomyrmex sp. 001					1			
Leptogenys cf. *donisthorpei*								1
Leptogenys sp. 001							9	
Linepithema sp. 001					3		1	
Megalomyrmex sp. 001					1		13	
Megalomyrmex sp. 002		1						
Mycocepurus sp. 001				4				
Myrmelachista sp. 001				23				
Myrmicocrypta sp. 001		22						
Myrmicocrypta sp. 002		1						
Myrmicocrypta sp. 003		10						
Myrmicocrypta sp. 004			1					
Nesomyrmex pleuriticus								1
Ochetomyrmex subpolitus	6	31	290					1
Octostruma balzani	15	33		49				2
Octostruma iheringi		1						
Octostruma sp. 001					21	5	26	
Octostruma sp. 002					4			
Odontomachus bauri		3				5		6
Odontomachus sp. 001								1
Odontomachus sp.002				1				
Odontomachus sp. 003			2		2			
Pachycondyla constricta	2	1	1					
Pachycondyla sp. 001	1		2					
Pachycondyla sp. 002				1				

Table 1. Continued.

Species	CWC	IFR	KMM	MAB	MAU	MAD	MAF	MHC
Pachycondyla sp. 003							1	
Pachycondyla sp. 004		1						
Pachycondyla sp. 005	9	5	1	8				
Pachycondyla sp. 006						3		
Paratrechina sp. 001						14		
Paratrechina sp. 002	27	82						563
Paratrechina sp. 003				343		55		
Paratrechina sp. 004		51						
Paratrechina sp. 005					14		11	
Paratrechina sp. 006					13		2	
Paratrechina sp. 007					9		25	
Paratrechina sp. 008					4			
Paratrechina sp. 009				1		15		
Paratrechina sp. 010								1
Pheidole allarmata	52	129						172
Pheidole aripoensis	206	222		370	2	180		99
Pheidole biconstricta	62	11	40	135		144	2	
Pheidole cramptoni		5						
Pheidole sp. *distorta group*			16					
Pheidole fimbriata				5			12	
Pheidole flavens		5				184	1	
Pheidole gibbata	2	65	41					
Pheidole mamore		9						
Pheidole meinertopsis		127						14
Pheidole minutula					9		65	
Pheidole nr. *ademonia*		3						
Pheidole nr. *nitella*		2						
Pheidole nr. *sospes*		2						
Pheidole nr. *nigricula*		2			37		11	
Pheidole pedana	4	87			1	135		84
Pheidole perpusilla				1				
Pheidole prostrata	5							3
Pheidole rugiceps							4	
Pheidole ruida	109	2	3	694	125	408	1306	60
Pheidole scolioceps			36					
Pheidole sp. 001			3	2				
Pheidole sp. 002	1							
Pheidole sp. 003		10						22
Pheidole sp. 004					13			
Pheidole sp. 005	1		4					
Pheidole sp. 006			1					2
Pheidole sp. 007		44						
Pheidole sp. 008							1	
Pheidole sp. 009	89	1						45
Pheidole sp. 010					1		66	
Pheidole sp. 011		1						
Pheidole sp. 012				1				
Pheidole sp. 013		4		9				
Pheidole sp. 014	1			116		38		

Table 1. Continued.

Species	CWC	IFR	KMM	MAB	MAU	MAD	MAF	MHC
Pheidole sp. 015				1	1			
Pheidole sp. 016		2					82	
Pheidole sp. 017	2							
Pheidole sp. 018			3					
Pheidole sp. 019		3						
Pheidole sp. 020		3						
Pheidole sp. 021								1
Pheidole sp. 022								21
Pheidole sp. 023	59							4
Pheidole sp. 024	4							98
Pheidole sp. 025							1	
Pheidole sp. 026								1
Pheidole sp. 027	15							
Pheidole sp. 028								2
Pheidole sp. 029								1
Pheidole sp. 030			52					
Pheidole sp. 031								2
Pheidole sp. 032	21							3
Pheidole sp. 033			20					
Pheidole sp. 034					5			
Pheidole sp. 035					14			
Pheidole sp. 036				19				
Pheidole sp. 037			1					
Pheidole sp. 038							1	
Pheidole sp. 039	9							1
Pheidole sp. 040			2					
Pheidole sp. 041		1	24	23		50		
Pheidole sp. 042		1				4		1
Pheidole sp. 043			1					
Pheidole sp. 044			2					
Pheidole sp. 045								
Pheidole n. sp. A							5	
Pheidole n. sp. B	8	1						
Pheidole n. sp. C					5			
Pheidole n. sp. D				40		4		
Pheidole n. sp. E							5	
Pheidole n. sp. F						16		
Pheidole n. sp. G		11		1		8		
Pheidole n. sp. H						1		
Prionopelta marthae	10			87		503		
Prionopelta modesta	8			14	22		16	
Probolomyrmex petiolatus		3	1					
Pyramica auctidens			1					
Pyramica beebei		1		9				
Pyramica cincinnata				2				
Pyramica denticulata	75	315	186	521		162		226
Pyramica glenognatha		8	2				1	
Pyramica orchibia					1			
Pyramica stenotes								6

Table 1. Continued.

Species	CWC	IFR	KMM	MAB	MAU	MAD	MAF	MHC
Pyramica subedentata		3	9	1			23	4
Pyramica valliersi		15	1					2
Pyramica zeteki					23		8	
Pyramica sp. 001				2				
Pyramica sp. 002								1
Pyramica sp. 003					4			
Pyramica sp. 004	1							
Pyramica sp. 005					29		39	
Rhopalothrix weberi		1						1
Rogeria innotabilis		2		1				
Rogeria micromma								1
Rogeria sp. 001		5						1
Rogeria sp. 002								7
Solenopsis sp. 001	689	680	368	2127	185	442	80	636
Solenopsis sp. 002			7		8			
Solenopsis sp. 003			20					
Solenopsis sp. 004		4	12	3				18
Solenopsis sp. 005						1665		
Strumigenys cf. *carinithorax*						8		
Strumigenys dolichognatha							1	2
Strumigenys dyseides	4							
Strumgenys elongata	2	1	18	14	1	45		7
Strumigenys perparva	6	14	5	11		74		9
Strumigenys precava							17	1
Strumigenys smithii					1			
Strumigenys trinidadensis								1
Strumigenys sp. 001				3				
Strumigenys sp. 002								1
Strumigenys sp. 003								1
Tapinoma melanocephalum		1						2
Thaumatomyrmex atrox		8						
Typhlomyrmex pusillus				1				1
Wasmannia auropunctata	1	664	6	15		104	47	145
Wasmannia scrobifera		16						
Total	2117	3822	1501	6163	807	5067	2114	4214

Abbreviations of localities as follows: Calm Water Creek (CWC); Iwokrama Forest Reserve (IFR); Kanuku Mountains (KMM); Base Camp, Mt. Ayanganna (MAB); Upper Forest, Mt. Ayanganna (MAU); *Dicymbe* Camp, Mt. Ayanganna (MAD); Falls Camp, Mt. Ayanganna (MAF); Mabura Hill Camp (MHC).

with *Solenopsis* having the highest rank (6944 individuals, 26.8% of total) followed by *Pheidole* (6662 individuals, 25.7% of total).

Species richness

Table 2 summarizes the relative species richness of all eight localities, along with species estimates and other values. Iwokrama Forest Reserve (IFR), with

84 species, possesses the richest ant fauna in this survey. The other lowland rainforest localities, Calm Water Creek (CWC) and Mabura Hill (MHC), also possess high species richness: CWC with 53 spp. and MHC with 66 spp. The Kanuku Mountains (KMM) locality has 55 species. The Mt. Ayanganna localities have a range of species richnesses. At Base Camp (MAB), 63 species were collected. In contrast, only 38 species, the lowest number collected at any locality, were found at *Dicymbe* Camp (MAD). Both sites are at similar elevations: MA13 at 732 m and MAD at 717 m. The highest elevation localities in this study are from Mt. Ayanganna, Upper Forest (MAU) at 1300 m and Falls Camp at 1137 m. The total species richness at each transect is similar: MAU with 40 species and MAF with 43 species.

For none of the localities does the mean, randomized observed species accumulation curve reach an asymptote (Figures 5–12). Only MAD and CWC show a slight drop in the number of uniques, but at all other localities the measure is either rising or slightly flattening out. At two localities, CWC and MAD, the species estimator, ICE, approaches or meets the species accumulation curves (Figures 5 and 10), but for all other sites species estimator consistently estimates species numbers above those observed.

Comparisons between localities

The hierarchical cluster analysis found three distinct clusters of sites (Figure 13): a lowland cluster (consisting of CWC, MHC, IFR, and KMM), mid-elevation Mt. Ayanganna cluster (consisting of MAB and MAD), and upper elevation Mt. Ayanganna cluster (MAF and MAU).

Discussion

Perhaps not surprisingly, our preliminary inventory of the leaf litter ant fauna clearly demonstrates that much remains to be learned about Guyanan ant diversity. Kempf (1972) listed 330 ant species known from Guyana. Our result of 230 ant species recorded from seven 200-m and one 100-m leaf litter transects from around the country suggests a much higher ant diversity for the country than is currently known (see species estimators for each locality, Figures 5–12). Leponce et al. (2004) estimated that single leaf litter A.L.L. style transects capture on average $<45\%$ of the actual leaf litter ant community. Fortunately, despite the fauna not being completely sampled, the degree of representativeness of A.L.L. style transects does allow for between site comparisons (Leponce et al. 2004).

Although it is difficult to quantify precisely due to the high number of unnamed morphospecies in our dataset, at least half (and probably more) of the species we collected are not recorded in Kempf. Large numbers of ant species are expected in the wet tropics: Longino et al. (2002) report 437 species at the 1500-ha La Selva Biological Station, while Brühl et al. (1998) report 524 species for the 400-ha Kinabaloo National Park in Borneo. Fisher reports and estimated 1000 species for Madagascar (418 with names) and nearby islands (Fisher 2003), largely as a result of dozens of leaf litter ant surveys from around the country (Fisher 1999, 2002, 2003). The foregoing examples are the results of extensive field sampling, with dozens of leaf litter transects and other methods being conducted over periods of many years. As our data indicate, our survey was by no means exhaustive, and further collections will undoubtedly increase the number of Guyana ant species by many hundreds.

There are two species common to all eight sites, *Pheidole ruida* and *Solenopsis* sp. 001. The widespread occurrence of *Pheidole ruida* is interesting because prior to this study it was known only from Costa Rica and Panama. It should be noted, however, there was some difficulty distinguishing the morphological

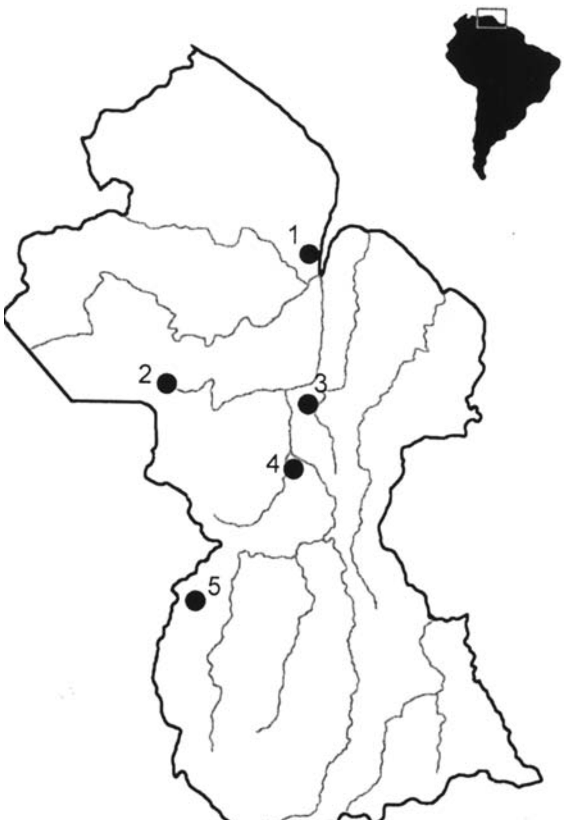
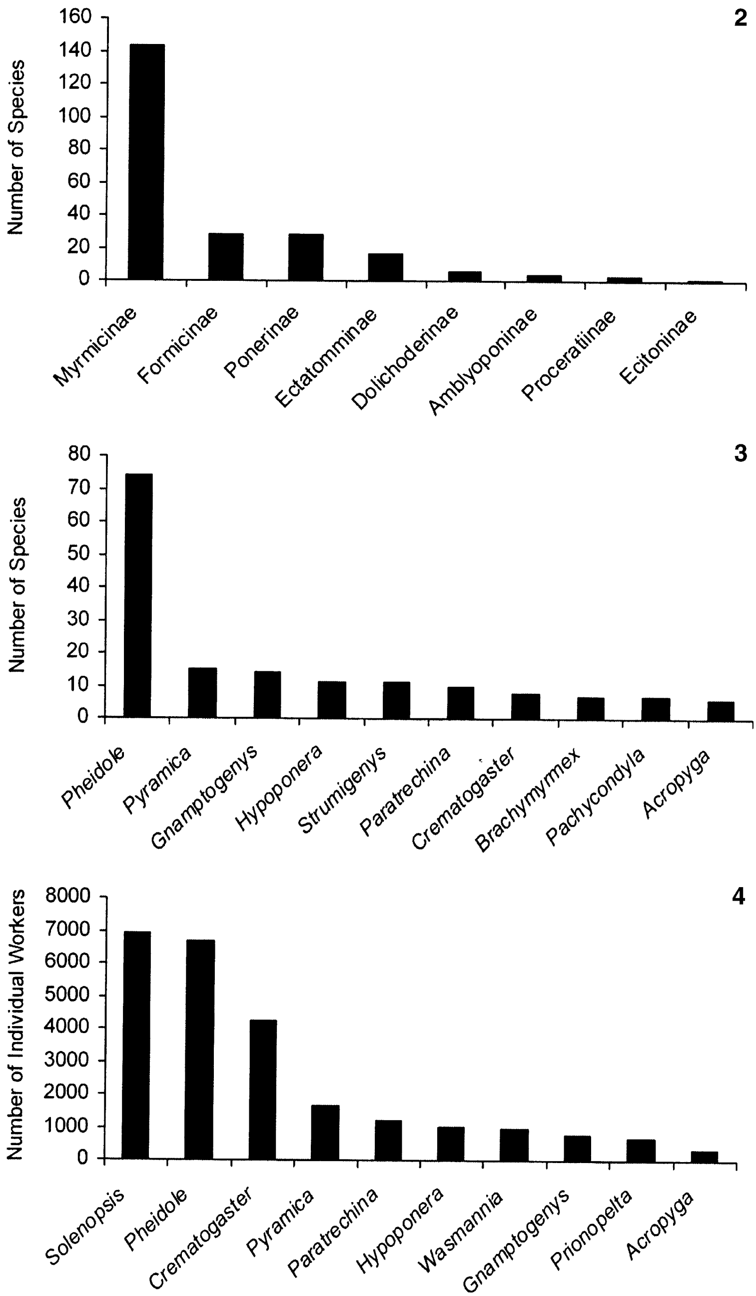


Figure 1. Map of Guyana with locations of collecting sites. Legend: (1) Calm Water Creek; (2) Mt. Ayanganna sites; (3) Mabura Hill Camp; (4) Iwokrama Forest Reserve; (5) Kanuku Mountains.



Figures 2–4. Taxonomic composition of the survey. (2) Total number of ant species in the different subfamilies collected at the eight localities. (3) The ten most speciose ant genera collected at the eight localities and (4) The ten most individual rich (adult workers only) genera collected at the eight localities.

limits of this species and more study is needed to determine if all of the individuals recorded as *P. ruida* really are this species, or if in fact there is a complex of morphologically similar species. Two more species were common to all but one site. *Hypoponera* sp. 008 was found at all sites except, *Dicymbe* Camp, and *Strumigenys elongata* was found at all sites except Falls Camp. A few species that appear to be uncommon are edge effects. For instance, *Gigantiops destructor* was collected only at the Kanuku Mountains site, but this species was common at all lowland sites. The combination of being a highly visual species, coupled with quick speed made its capture in leaf litter quadrats unlikely. There are also several groups of ants that are largely arboreal and therefore occur sporadically in our dataset. For example, this is true for the genera *Azteca* and *Camponotus*.

The hyperdiverse genus *Pheidole* (Wilson 2003) proved to be the most speciose genus in our survey. With 74 species, *Pheidole* represents nearly 33% of ant species collected (Figure 3). By comparison, the next most speciose genus, *Pyramica*, is represented by only 15 species. This taxonomic dominance of *Pheidole* is typical for the Neotropics (Ward, 2000). *Pheidole* drops to second place when number of individuals is ranked, however, with nearly 7000 *Solenopsis* workers collected (Figure 4). Combined, the two genera represent over 50% of all individuals collected. Breaking down the number of species by subfamily is consistent with other studies, in which the Myrmicinae represent the largest number of the total species present in leaf litter surveys (Figure 2) (Ward 2000).

The total number of *Solenopsis* species recovered in this survey warrants mention. We found only five species among the eight localities, a low number compared to Ward (2000), who found an average of 3.14 species per Winkler sample. We have almost certainly underestimated the true number of *Solenopsis* species because the genus is without a modern taxonomic revision and thus most *Solenopsis* species remain poorly defined and difficult to diagnose. As an example, *Solenopsis* sp. 001, is present at every locality and is present in nearly every quadrat sampled. This species exhibits considerable morphological variation, and future work will most likely reveal that what we have here called one species is in fact a composite of several morphologically similar, cryptic species. Another genus in which species number is probably similarly underestimated due to lack of taxonomic synthesis is *Hypoponera*. These problems only emphasize the need for taxonomic revisionary research in those two genera.

Although the species accumulation curves slowly continue to rise for both the *Dicymbe* Camp and CWC sites, the decline in the number of uniques may indicate an approach to inventory completion (Longino et al. 2002). The species estimators also begin to converge upon the species accumulation curves for both sites. This is especially surprising for CWC because only 10 quadrats were collected. Since we did not replicate transects at each site, it is difficult to know what these two results indicate, and further sampling is needed.

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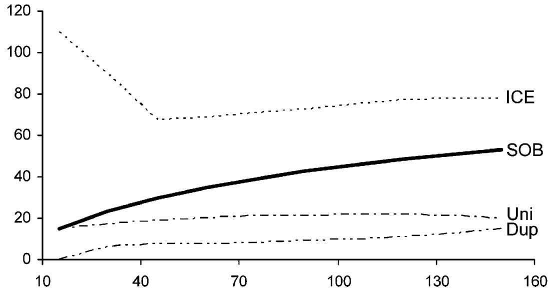

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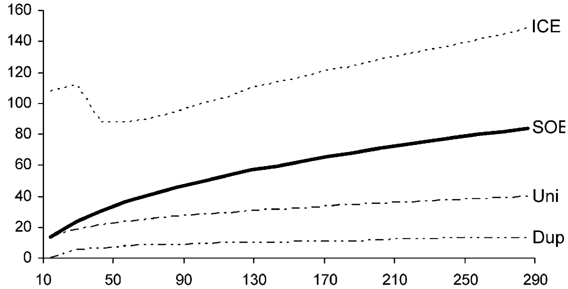

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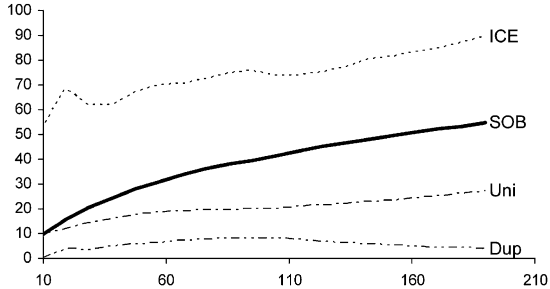

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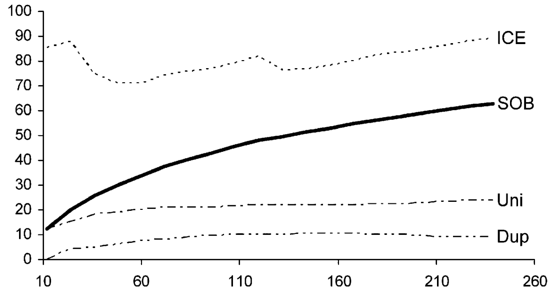
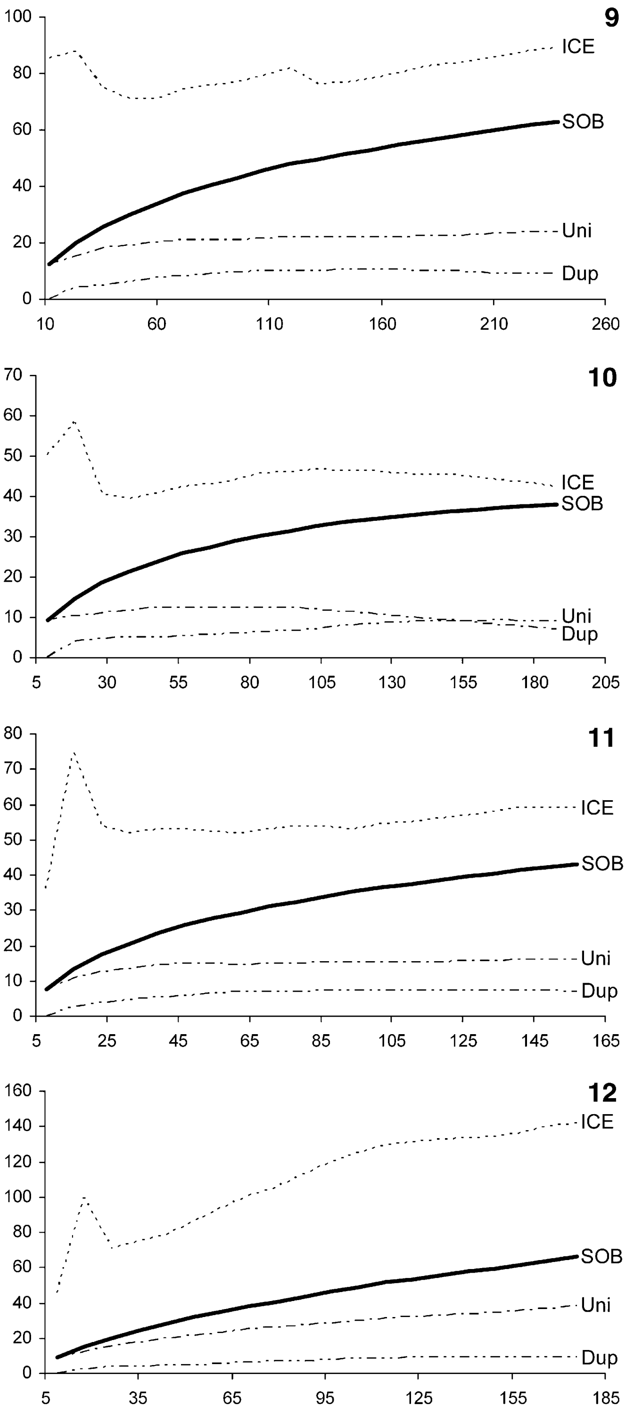


Figures 5–12. Sample-based rarefaction curves and corresponding estimators for: (5) Calm Water Creek, (6) Iwokrama Forest, (7) Kanuku Mountains, (8) Mt. Ayanganna, Base Camp, (9) Mt. Ayanganna, Upper Forest, (10) Mt. Ayanganna, *Dicymbe* Camp, (11) Mt. Ayanganna, Falls Camp, (12) Mabura Hill Camp. The *Y*-axis represents number of species, the *X*-axis represents number of species occurences. Abbreviations are as follows (see text for further information): Species richness estimator; ICE = incidence-based coverage estimator. Other measures: SOB = species observed, Dou = doubletons, Dup = duplicates, Sin = singletons, Uni = uniques.



Figures 5–12. Continued.

Overall, lowland forest sites proved to be the most species rich. Iwokrama, with 84 species, is the single richest locality. Iwokrama also yielded some very interesting ant species, the most spectacular perhaps being the rarely collected *Thaumatomyrmex atrox*. The richest locality on Mt. Ayanganna is Base Camp (63 species), while the lowest species richness is recorded for *Dicymbe* Camp (38 species). Both of these localities are at about equivalent elevations, 732 m for the former, 717 m for the latter, so the large difference in species richness between the two sites is not due to elevation. Though dominant at both sites, *Dicymbe* trees appear to be more dominant at *Dicymbe* Camp than at Base Camp, but further research is needed to explain whether this or some other factor is responsible for the difference between those localities. They are, however, the most similar to each other among the Ayanganna sites (Figure 13). It is interesting to note that *Dicymbe* Camp and Base Camp both produced the largest collections of individual ant specimens, i.e., they accounted for the highest abundances of all the sampled Guyana localities (Table 2).

A high endemic ant fauna for Mt. Ayanganna is indicated. High ant endemicity at Mt. Ayaganna has also been qualitatively suggested by ongoing taxonomic studies. LaPolla (2004) found three new species of *Acropyga* from Mt. Ayanganna; all were taken in leaf litter samples. Several additional new ant species taken in our Mt. Ayanganna survey await description (unpublished data; including *Pyramica* and *Pheidole* spp.). New non-insect species from Mt. Ayanganna have been reported by MacCulloch and Lathrop (2002), who described three new species of the frog genus *Stefania*, and by Matheny et al. (2003), who reported 4 new species of *Inocybe* fungi from on and around Mt. Ayanganna. Like nearby Mt. Roraima (Rull 2004), it appears that Mt. Ayanganna also hosts a high number of endemic species. Until recently, Mt. Ayanganna has remained largely out of reach to biologists, but an airstrip, recently constructed by miners, has made the mountain more accessible. Results from our survey suggest the need for more research at Mt. Ayanganna in order to fully understand its biological uniqueness. Unfortunately, pressure from miners, primarily entering the country from Brazil, already threatens the pristine nature of this probable biodiversity "hot spot" (JSL and TRS, pers. obser.).

Our survey in the Kanuku Mountains took us only to the base of the mountains (elev. 224 m), For a variety of other organisms, the Kanukus are a center of high endemicity (Parker et al. 1993). Our results indicate a similarity to the lowland localities surveyed (Figure 13), but because we did not sample upper or mid elevations within the Kanukus this result is not surprising. The region certainly warrants more myrmecological research, especially at high elevations, along both the eastern and western portions of the mountains. As plants have shown marked changes in diversity from lower to higher elevations in the Kanukus (Parker et. al 1993), leaf litter ant studies would profit by similarly sampling along an elevational gradient.

Conservation implications

Leaf litter ants are a demonstrably important group of organisms for informing conservation planning (Agosti et al. 2000), and their value for Guyana biodiversity conservation could be great. With upwards of 70% of its forests intact (Funk and Richardson 2002), the time for Guyana to act is now, before widespread deforestation occurs. While the exploitation of some natural resources is inevitable for the country's economic health, with proper planning the rich biodiversity of the country can be preserved as well. The information presented here provides only the beginning of a leaf litter ant dataset that will need to be significantly expanded in order to be maximally useful for country-wide conservation planning. Nonetheless, a few patterns of leaf litter ant diversity emerge from the current data.

The isolated mountaintops and dense forests of the Pakaraima Mountains of western Guyana are biologically unique. Our data from Mt. Ayanganna indicate that the leaf litter ant fauna there is quite different from other localities, and expanded sampling in the region will further evaluate this conclusion. We recommend that the government of Guyana monitor, and in many cases, stop the expanding and largely illegal mining operations in the area.

The similarity of lowland forest leaf litter ant faunas (CWC, Mabura Hill, and Iwokrama) does not suggest that these areas have little to contribute to the biodiversity of the country. Not only are these lowland forest sites among the richest of the sampled localities, they are also areas of high endemism: about 32% of the 230 species were only recorded from these sites. It is these lowland forests that are most immediately threatened by large-scale resource extraction industries. For instance, the presence of international logging interests near Mabura Hill challenges conservation efforts in that area (Funk and Richardson 2002). Finally, the far southern stretches of Guyana have yet to be surveyed in

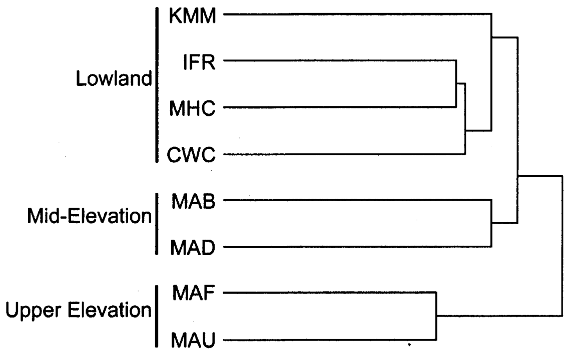


Figure 13. Cluster diagram showing degree of similarity between ants from leaf litter samples. Abbreviations of localities as follows: Calm Water Creek (CWC); Iwokrama Forest Reserve (IFR); Kanuku Mountains (KMM); Base Camp, Mt. Ayanganna (MAB); Upper Forest, Mt. Ayanganna (MAU); *Dicymbe* Camp, Mt. Ayanganna (MAD); Falls Camp, Mt. Ayanganna (MAF); Mabura Hill Camp (MHC).

Table 2. Richness estimates and other summary values for each locality.

	CWC	IFR	KMM	MAB	MAU	MAD	MAF	MHC
Observed richness	53	84	55	63	40	38	43	66
No. of samples	10	20	20	20	20	20	20	20
No. of adult workers	2117	3822	1501	6163	807	5067	2114	4214
No. of singletons	11	19	15	13	10	1	10	21
No. of doubletons	5	11	7	6	3	3	2	8
No. of uniques	20	40	27	24	17	7	16	38
No. of duplicates	15	13	4	9	7	9	7	9
ICE	77.52	148.43	89.55	89.28	63.3	42.33	59.06	141.56
Chao 1	62.32	98.32	68.24	74.28	51.56	38.03	58.56	89.46
Chao 2	64.91	139.82	125.74	90.72	57.13	40.14	58.13	136.49
Jackknife 1	71	122	80.65	85.8	56.15	44.65	58.2	102.1
MM Mean	72.46	108.18	70.56	79.02	50.7	44.89	54.8	97.71

Each richness estimate represents the mean for 100 randomizations of sample order.

any way for ants or, indeed, for most organisms. With continuing pressure to pave the road from Georgetown to Lethem in order to link the capital with Brazil, biological surveys in these currently remote localities are urgently needed. The remote regions of southern Guyana may not remain remote for long and the time remaining for gathering baseline biodiversity data is rapidly running out.

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