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Trade-offs between complementarity and redundancy in the use of different sampling techniques for ground-dwelling ant assemblages

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ABSTRACT

Sampling ground-dwelling ants in the field is relatively fast, but sorting and identifying in the laboratory is costly and time-consuming. Using sub-samples collected in 25 km^2 grids, we surveyed ant assemblages using sardine baits, pitfall traps and Winkler extraction in three Amazonian vegetation types. Combining all three techniques detects the greatest number of species, but may be inefficient. Therefore, we compared the pooled results from the three techniques to results using one or two techniques combined. We evaluated whether the extra information acquired by adding a sampling technique compensates for the time and money associated with the extra processing. We also evaluated the consequences of the reduced effort on the retention of ecological information captured by the three techniques, using soil clay content, terrain slope and altitude as predictor variables in an ecological analysis. Pitfall traps captured the largest number of species and had the highest congruence with ant assemblages recorded by other techniques. Redundancy analysis indicated that pitfall-trapping is the most efficient technique, allowing reduction of 48% in cost and 43% in time. The loss of information about species richness when using only pitfall traps is apparently compensated by the saving of cost and time in the field and laboratory, because use of this technique alone was sufficient to detect all the responses of the ant assemblage to environmental variables that were detected by other techniques. These results indicate that considerable gains in efficiency can be obtained in most Amazonian-forest monitoring programs for ants by using only pitfall traps.

1. Introduction

One of the main goals of biodiversity surveys is to reveal the spatial distribution of species to give support to environmental-management decisions (Evans and Viengkham, 2001). However, the designs of most surveys are not spatially explicit and a complete list of species is hard to obtain (Gotelli et al., 2011). Many biodiversity surveys aim to evaluate ecological processes and patterns, in which a complete list of species is not needed and a small set of indicator species is used to save time and money. Independent of study aims, researchers often face a tradeoff between area sampled and sampling intensity in initial or sequential biological surveys, where sampling should result in more than species lists, and the costs should not exceed the potential economic benefits resulting from the investigations (Evans and Viengkham, 2001).

Invertebrates can be valuable indicators of changes in the integrity and biological functioning of ecosystems (Vohland and Schroth, 1999; Barros et al., 2001; Lavelle et al., 2006). Invertebrate sampling is relatively fast, but requires a lot of laboratory work to sort and identify specimens (Santos et al., 2008; Gardner et al., 2008; Souza et al., 2009). The time required for laboratory work increases dramatically as the body size of the organisms decreases (Lawton et al., 1998), and it is often extremely time consuming to effectively survey hyper-diverse groups over extensive areas (Jiménez-Valverde and Lobo, 2006). Associated with the problems of spatial scale of the study and the taxonomic challenges, the abundance of some invertebrate groups, such as ants, can reach several hundred individuals per square meter (Fittkau and Klinge, 1973; Adis and Schubart, 1984; Ellwood and Foster, 2004). Therefore, invertebrate experts in hyperdiverse groups often cannot meet deadlines and the invertebrate data set often cannot be included in the initial ecological analyses or management actions (e.g. Santos et al., 2008).

Several strategies have been used to reduce labor time and costs associated with sorting and identification of ants to provide

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a comprehensive and analyzable dataset. These include (1) use of taxa whose diversity is correlated with others (surrogates) coupled with use of sampling methods that produce diversity estimates representative of more intensive sampling, (2) use of morphospecies surveys undertaken by parataxonomists, (3) use of genera or morphospecies as a surrogates for species, (4) selection of larger species, (5) use of presence or absence of species, and (6) estimation of the lowest number of subsamples needed to detect the effects of environmental variables (e.g. Oliver and Beattie, 1993; Longino and Colwell, 1997; Andersen, 1995; Oliver and Beattie, 1996; Andersen et al., 2002; Souza et al., 2009). In addition, relationships between animal assemblages and environmental variables detected using larger sampling effort can be compared to studies at smaller scales or with fewer sampling methods. For example, the ecological responses of an oribatid-mite assemblage in an Amazonian savanna could be evaluated even after sampling reduction in the field and sorting only a small proportion of samples in the laboratory, retaining most of the ecological information (Santos et al., 2008).

Ants are relatively easy to collect and have been used as model organisms in conservation assessments, monitoring, reforestation programs, and ecosystem management (Folgarait, 1998; Andersen and Majer, 2004; Andersen et al., 2004). They can be sampled with different techniques and the advantages of using one or a combination of sampling techniques depends on the nature of the study (Bestelmeyer et al., 2000). The most common sampling techniques are Winkler extraction, pitfall traps and sardine or tuna baits (Alonso and Agosti, 2000; Bestelmeyer et al., 2000; Delabie et al., 2000). These techniques are complementary for estimating species richness (e.g. Olson, 1991; Delabie et al., 2000), although the use of more than one technique results in some redundancy, principally in non-forest habitats (Parr and Chown, 2001; Lopes and Vasconcelos, 2008).

A reduction in the number of sampling techniques would decrease monetary costs and time of sampling and sorting ants. Therefore, the amount saved could be used to increase the number of sites surveyed. The most efficient sampling protocol to be chosen should satisfy taxonomic, ecological and financial aspects of the investigations. We investigated the mesoscale patterns of ground-dwelling ant assemblages in three Amazonian forests using sardine baits, pitfall traps, and Winkler extraction. The monetary cost and time required for each sampling technique, and combinations of techniques, was evaluated to identify the most cost-effective protocols. We also evaluated whether the assemblage composition obtained using one or two techniques responded similarly to topographical environmental gradients (e.g. soil clay content, slope and altitude), as when using information from the three techniques combined.

2. Materials and methods

2.1. Study site

The study was conducted in three Amazonian forests. Two of them (Maracá Ecological Station, 3°22′N, 61°27′W and Viruá National Park, 1°27′N, 61°01′W) are situated in forest reserves in Roraima State (extreme north of Brazil). The third (Ducke Reserve, 2°57′S, 59°56′W) is situated 25 km north of Manaus, Central Amazonia. The Maracá Ecological Station is located on an island in the Uraricoera River in Roraima State, which is at the confluence of savannas and the Amazon rainforest (Thompson et al., 1992). The terrain is flat with small intermittent streams. Viruá National Park is located on low-lying plains subject to flooding, with some residual hills that reach moderate altitudes. The soil is predominantly sandy, poorly drained and the flood regime is similar to that of the Branco River (RADAMBRASIL, 1978). Ducke Reserve is covered by relatively undisturbed evergreen rainforest on moderately rugged terrain, with small perennial streams in the valleys. The sites cover a latitudinal gradient in Amazonian forests and encompass wide environmental heterogeneity, including areas of open and dense forests, and areas subject to different degrees of seasonal flooding which are dominated by grasses or shrubs. The vegetation types, soil characteristics, elevation and rainfall of the study areas are summarized in Table 1.

Table 1

Vegetation, soil characteristics, rainfall, stream seasonality and elevation range in the study sites (Viruá National Park, Maracá Ecological Station and Ducke Reserve), in the Brazilian Amazon.

	Ducke	Maracá	Viruá
Vegetation types (number of plots)	Evergreen forest (30)	Semi-deciduous *terra-firme* forest (30)	Open savannas (6), closed savannas (5) and open forest (19)
Coordinates	−3.01 S, −59.59 W	3.38 S, −61.48 W	1.44 S, −61.04 W
Soil characteristics (%)			
Clay	42.6 (36.3)	8.6 (3.3)	19.8 (16.8)
Silt	3.1 (1.8)	11.4 (5.3)	17.5 (5.9)
Sand	54.4 (36.8)	80.0 (7.4)	62.7 (18.7)
Elevation range (m a.s.l.)	50–120	55–83	48–130
Mean annual rainfall (mm)	2507[a]	1718[b]	1682[c]
Number of dry months (<100 mm)	0	6	7
Number of wet months (>300 mm)	2	2	0
Seasonal flooded area (%)	0	~5	~60

[a] Based on time series of: 1979–2008.

[b] Based on time series of: 1979–2005.

[c] Based on time series of: 1984–2004.

2.2. Sampling design

We used the RAPELD sampling design (Magnusson et al., 2005; Costa and Magnusson, 2010) to survey ground-dwelling ant assemblages in a sampling grid covering an area of 25 km^2 in each reserve. Each sampling grid was composed of six regularly spaced 5 km-long north–south and six 5 km-long east–west trails. Each east–west trail has five 250 m-long permanent plots that follow terrain contours, giving 30 plots per site that are uniformly distributed across the landscape. As the plot follows the contours lines, variation in altitude within the plot is negligible, minimizing the effects of topographical variation on ant assemblage structure. The minimum distance between plots was 1 km.

2.3. Ant sampling

Ground-dwelling ants were collected in 30 plots per site using pitfall traps, sardine baits and litter samples extracted by the Winkler method. The ants were sampled from the 1 m^2 sifted litter in Winkler sacks in sampling stations located at 25 m intervals along the center line of each plot. Pitfall traps and sardine baits were placed at the same stations after litter collection, giving 10 subsamples for each method per plot (10 subsamples × 30 plots × 3 techniques resulted in 900 subsamples per site). The ants were extracted from the 1 m^2 of sifted litter in a Winkler extractor through a 1 cm^2 mesh sieve. The sieved litter was placed in a mesh bag suspended inside a cotton bag for 48 h. Before the bag was suspended, the litter material was mixed to improve chances of the ants falling into the collecting pot. The ants and other invertebrates migrate from the suspended litter sample as a behavioral response to drying and fall into the pot partially filled with alcohol at the bottom of the bag (Bestelmeyer et al., 2000). The pitfall traps (95 mm diameter; 8 cm depth; 500 ml volume) were partially filled with water and detergent, buried with the rim at ground level, and left for 48 h. After removing the pitfall traps, approximately 5 g of canned sardine was placed on a plastic card (10 cm by 7 cm) on the litter surface and after 45 min all ants on the plastic card were collected and preserved in 90% alcohol. The baiting and litter-sampling procedures were undertaken between 8:00 am and 17:00 pm. All sites have seasonal rainfall, with more rain falling from October to March at Ducke, and from July to September in Maracá and Viruá (Marques-Filho et al., 1981). Ducke was sampled in September 2006 and Viruá and Maracá were both sampled in February 2007, at the beginning of their respective rainy seasons. We lost Winkler extraction samples from five plots in Ducke Reserve due to logistical error. Therefore, all analyses for Ducke Reserve were based on the results of 25 plots, rather than the 30 original samples.

Ants from the Winkler extraction, pitfall traps and bait samples were identified to species or morphospecies, using specialized papers and reference material in the Entomological Collection of the Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Brazil. Nomenclature follows Bolton et al. (2005). Vouchers for this material are deposited in the INPA Entomological Collection. Raw data are available from the PPBio web site (http://ppbio.inpa.gov.br).

2.4. Data analysis

2.4.1. Species accumulation curves

The effectiveness of any sampling technique depends on sampling intensity, and results of comparative analyses can be biased by variation in sampling intensity between techniques. To assess how many samples are needed to record a comparable number of species we used average species accumulation curves from 999 random permutations of samples.

2.4.2. Redundancy in sampling techniques

As sampling techniques may have different responses in different areas, we used non-parametric MANOVA (Anderson, 2001) to test for differences in ant assemblages among areas and techniques. We compared the congruence between ant assemblages sampled by each technique and by all possible pairs of techniques to the full data set (all techniques combined). We reduced the dimensionality of data from each technique or combination of techniques using Nonmetric Multidimensional Scaling (NMDS, Minchin, 1987) based on the Sørensen dissimilarity index. Occurrence data (presence/absence) were used to avoid over estimation of species with larger nests (Hölldobler and Wilson, 1990) and to minimize differences in individual abundances between sampling techniques. The congruence between the NMDS ordinations was quantified by Procrustean superimposition with 999 Monte Carlo permutations to test for statistical significance (Peres-Neto and Jackson, 2001).

2.4.3. Relationships with environmental gradients

We investigated whether relationships between ant assemblages and some environmental variables (altitude, slope and soil granulometry) were retained using only one, or a combination of two sampling methods. Data on percentage soil clay content, terrain slope and altitude were used as predictor variables in analyses. The datasets are available in the PPBio web site (http://ppbio.inpa.gov.br/) where the sampling protocols (metadata) for each variable are described in detail. Altitude, slope and soil granulometry were selected because previous studies have shown them to be associated with variation in ant assemblage composition (Vasconcelos et al., 2003; Oliveira et al., 2009). Altitude per se probably does not directly affect organisms, as variation within most of lowland Amazonia is less than 150 m, but it is related to many other characteristics such as drainage, soil granulometry, light and litter deposition which may directly affect ant species distribution, and it is easily retrieved from maps or satellite images (Costa and Magnusson, 2010). Therefore, factors such as topography (altitude and slope) and clay content can generate microhabitat variability which may affect spatial patterns of ground-dwelling ant assemblages (Vasconcelos et al., 2003; Oliveira et al., 2009).

We used redundancy analysis (RDA) to estimate how much of the variance in the response variable (species composition matrix) can be explained by the environmental variables and to determine if the ecological patterns recovered using all techniques combined were also recovered when using one or two techniques combined. RDA is a direct extension of multiple regression analysis to model multivariate response data (Borcard et al., 2011). The statistical significance of RDA models was tested by 1000 permutations per test.

2.4.4. Project costs

The time and monetary costs for the three techniques combined were considered in relation to the maximum effort, and the fractions of these costs were calculated for each combination of sampling techniques. The costs were based on the acquisition of material, maintenance, field sampling and laboratory activities (mainly salary and scholarships). The laboratory costs were those associated with species sorting, mounting, identifying and chemicals for conservation of voucher species. As recommended by Gardner et al. (2008), capital costs that vary greatly among projects, such as non-perishable laboratory equipment (e.g. microscopes) and accommodation buildings for field staff, were not included. The time to carry out the work was the sum of the time spent to collect samples in the field plus the time spent sorting and identifying ants in the laboratory.

3. Results

A total of 343 species/morphospecies distributed in 11 subfamilies and 57 genera was collected using pitfall traps, Winkler extraction and sardine baits combined (Table 2). The genera with more species/morphospecies were *Pheidole* (83), *Crematogaster* (21), *Camponotus* (17), *Strumigenys* (15), *Pachycondila* and *Trachymyrmex* (14), *Dolichoderus* and *Solenopsis* (13), and *Gnamptogenys* and *Hypoponera* (9). The most frequent species recorded in all sites using all sampling techniques were *Azteca* sp. 01, *Crematogaster tenuicula*, *Nylanderia* sp. 01, *Solenopsis* sp. 3, and *Wasmannia auropunctata*. Also frequent and represented in at least 88% of the sampling events shown in Table 2, *C. brasiliensis*, *C. limata*, *Ectatomma edentatum*, *Nylanderia* sp. 02, *Pheidole* sp. 06, and *Solenopsis* sp. 6 were captured with pitfall traps in all three reserves, but the other sampling methods failed to capture one or another in Maracá and/or Viruá. About 35% of the species were represented by singletons or doubletons and 72 species (20%) were shared among the three sites.

The greatest number of species sampled by the three techniques combined (Table 2) was detected in Ducke (236), followed by Maracá (207) and Viruá (153). The three techniques combined were far more effective, with a much steeper species accumulation curve than any single technique (Fig. 1). However, the species accumulation for pitfall traps increase more rapidly than other techniques in all three sites. Pitfall trapping was the most effective sampling technique and had the highest number of exclusive species in all sites. Pitfall traps captured 89%, 94% and 86% of the total number of species recorded in Ducke, Maracá and Viruá, respectively (Table 3).

Table 2
Ground-dwelling-ant species sampled by Pitfall trapping, Sardine baits and Winkler extraction in sampling grids in the Viruá National Park, Maracá Ecological Station and Ducke Reserve, in the Brazilian Amazon.

Subfamily/taxon	Ducke			Maracá			Viruá		
	Bait	Pitfall	Winkler	Bait	Pitfall	Winkler	Bait	Pitfall	Winkler
Amblyoponinae									
Prionopelta punctulata		1	1						
Cerapachyinae									
Acanthostichus sp. 01		1							
Dolichoderinae									
Azteca sp. 01	1	1	1	1	1	1	1	1	1
Dolichoderus bispinosus		1		1	1			1	
Dolichoderus cf. *atelaboides*					1		1		
Dolichoderus sp. 01		1							
Dolichoderus sp. 02		1							
Dolichoderus sp. 03		1			1				1
Dolichoderus sp. 05		1			1			1	
Dolichoderus sp. 07				1					
Dolichoderus sp. 08					1				
Dolichoderus sp. 09					1				
Dolichoderus sp. 10					1				
Dolichoderus sp. 11					1	1			
Dolichoderus sp. 12					1				
Dolichoderus sp. 13					1				
Dorymyrmex sp. 01								1	
Linepithema sp. 01				1					
Tapinoma sp. 01		1							
Ecitoninae									
Eciton burchellii					1			1	
Eciton dulcius		1							
Eciton rapax		1							
Labidus coecus		1			1			1	
Labidus mars		1							
Labidus praedator		1						1	
Labidus spininodis		1			1				
Neivamyrmex gibbatus		1						1	
Neivamyrmex sp. 01		1						1	
Neivamyrmex sp. 02		1							
Neivamyrmex sp. 03		1							
Neivamyrmex sp. 04		1							
Neivamyrmex sp. 05					1				
Neivamyrmex sp. 06					1				
Nomamyrmex esenbeckii		1							
Nomamyrmex hartigi		1							
Ectatomminae									
Ectatomma brunneum							1	1	
Ectatomma edentatum	1	1	1	1	1		1	1	1
Ectatomma lugens	1	1		1	1		1	1	1
Ectatomma tuberculatum	1			1	1		1	1	
Gnamptogenys acuminata		1							
Gnamptogenys horni	1	1	1					1	1
Gnamptogenys lineolata					1				
Gnamptogenys moelleri		1						1	
Gnamptogenys regularis					1				
Gnamptogenys relicta			1						
Gnamptogenys sulcata		1			1				
Gnamptogenys tortuolosa		1			1				
Gnamptogenys sp. 06					1				
Formicinae									
Acropyga sp. 01		1	1		1			1	
Acropyga sp. 02		1			1				
Brachymyrmex heeri	1	1		1	1	1	1	1	
Camponotus atriceps		1			1			1	
Camponotus crassus		1			1		1	1	
Camponotus femoratus							1		
Camponotus latangulus							1		
Camponotus leydigi								1	
Camponotus novogranadensis	1	1	1	1	1		1	1	
Camponotus rapax	1	1	1				1	1	
Camponotus retangularis					1				
Camponotus sericeventris							1	1	
Camponotus sp. 02		1			1			1	
Camponotus sp. 04	1	1						1	
Camponotus sp. 05	1	1			1				
Camponotus sp. 06		1			1	1		1	
Camponotus sp. 08		1							
Camponotus sp. 10		1							
Camponotus sp. 11			1					1	

Table 2 (*Continued*)

Subfamily/taxon	Ducke			Maracá			Viruá		
	Bait	Pitfall	Winkler	Bait	Pitfall	Winkler	Bait	Pitfall	Winkler
Camponotus sp. 14					1			1	
Gigantiops destructor	1	1		1	1			1	
Nylanderia sp. 01	1	1	1	1	1	1	1	1	1
Nylanderia sp. 02	1	1	1	1	1	1		1	1
Nylanderia sp. 03	1	1		1	1			1	1
Nylanderia sp. 04					1		1		
Myrmicinae									
Acanthognathus ocellatus								1	
Acromyrmex sp. 01		1							
Acromyrmex sp. 02				1	1				
Allomerus octoarticulatus		1						1	
Allomerus vogeli								1	
Apterostigma sp. 01		1			1			1	
Apterostigma sp. 02		1			1			1	
Apterostigma sp. 03		1	1						
Apterostigma sp. 04		1	1		1				
Atta sp. 01	1	1			1		1	1	
Atta sp. 02		1			1			1	
Basiceros balzani		1	1						
Basiceros iheringi			1						
Basiceros pilulifera			1						
Basiceros sp. 01		1							
Blepharidatta brasiliensis	1	1	1						
Carebara urichi		1	1						
Carebara sp. 01		1	1	1	1			1	
Carebara sp. 03			1						
Carebara sp. 04			1		1	1		1	
Carebara sp. 05								1	
Cephalotes opacus								1	
Cephalotes pellans								1	
Cephalotes pusilus					1		1	1	
Cephalotes sp. 03		1			1			1	
Cephalotes sp. 04		1							
Cephalotes sp. 05		1							
Cephalotes sp. 06					1			1	
Cephalotes sp. 07					1			1	
Cephalotes umbraculatus								1	
Crematogaster brasiliensis	1	1	1	1	1	1	1	1	
Crematogaster curvispinosa	1								
Crematogaster erecta	1	1	1	1	1				
Crematogaster evallans								1	
Crematogaster flavomicrops		1							
Crematogaster flavosensitiva	1	1	1	1	1		1	1	
Crematogaster jardineiro							1		
Crematogaster levior			1						
Crematogaster limata	1	1	1	1	1	1	1	1	
Crematogaster longispina					1				
Crematogaster nigropilosa						1		1	
Crematogaster sotobosque	1	1	1		1				
Crematogaster sp. 01	1	1							
Crematogaster sp. 02		1							
Crematogaster sp. 03		1							
Crematogaster sp. 04		1							
Crematogaster sp. 05		1							
Crematogaster sp. 06					1	1			
Crematogaster stollii		1							
Crematogaster tenuicula	1	1	1	1	1	1	1	1	1
Crematogaster torosa					1				
Cyphomyrmex cf. *lectus*			1						
Cyphomyrmex cf. *peltatus*		1	1		1			1	
Cyphomyrmex laevigatus		1	1		1				
Cyphomyrmex rimosus								1	
Cyphomyrmex sp. 01		1							
Daceton armigerum					1			1	
Hylomyrma immanis			1						
Lachnomyrmex amazonicus			1						
Megalomyrmex balzani	1	1		1					
Megalomyrmex leoninus					1		1	1	
Megalomyrmex sp. 02		1	1				1	1	
Megalomyrmex sp. 04		1	1						
Megalomyrmex sp. 05			1		1				
Megalomyrmex sp. 06					1				
Monomorium floricola				1		1	1		1
Monomorium panamanus					1				
Monomorium pharaonis	1	1		1	1				

Table 2 (*Continued*)

Subfamily/taxon	Ducke			Maracá			Viruá		
	Bait	Pitfall	Winkler	Bait	Pitfall	Winkler	Bait	Pitfall	Winkler
Monomorium stollii			1						
Mycocepurus smithii		1			1				
Mycocepurus sp. 01		1			1	1			
Myrmicocrypta sp. 01		1	1		1	1			
Myrmicocrypta sp. 02			1					1	1
Nesomyrmex cf. *asper*					1				
Nesomyrmex echinatinodis					1				
Nesomyrmex pleuriticus					1				
Nesomyrmex sp. 01					1				
Ochetomyrmex semipolitus		1	1	1	1	1	1	1	
Oxyepoecus sp. 01					1				
Pheidole cephalica	1	1	1	1	1			1	
Pheidole exigua				1					
Pheidole fracticeps	1	1	1	1	1				
Pheidole meinerti	1	1	1	1	1			1	
Pheidole sp. 101							1		
Pheidole sp. 103							1		
Pheidole sp. 104							1		
Pheidole sp. 107							1		
Pheidole sp. 108							1		
Pheidole sp. 110							1		
Pheidole sp. 111							1		
Pheidole sp. 112							1		
Pheidole sp. 113							1		
Pheidole sp. 01	1	1	1	1				1	
Pheidole sp. 02	1	1	1	1					
Pheidole sp. 04		1		1					
Pheidole sp. 05		1		1	1				
Pheidole sp. 06	1	1	1	1	1	1		1	1
Pheidole sp. 07		1		1					
Pheidole sp. 08	1	1	1	1	1				
Pheidole sp. 09	1	1	1					1	
Pheidole sp. 11	1	1	1	1	1				
Pheidole sp. 12		1			1				
Pheidole sp. 13	1	1		1	1		1	1	
Pheidole sp. 14	1	1			1			1	
Pheidole sp. 15	1	1	1		1				
Pheidole sp. 16		1						1	
Pheidole sp. 17		1	1						
Pheidole sp. 18	1								
Pheidole sp. 19	1	1	1		1				
Pheidole sp. 21	1	1			1			1	
Pheidole sp. 22		1	1		1			1	1
Pheidole sp. 23	1	1						1	
Pheidole sp. 24	1	1		1	1	1	1	1	
Pheidole sp. 25	1	1	1	1	1				
Pheidole sp. 26	1	1			1			1	
Pheidole sp. 27	1	1			1			1	
Pheidole sp. 28		1	1		1				
Pheidole sp. 29	1	1	1		1				
Pheidole sp. 30		1							
Pheidole sp. 31	1	1	1		1				
Pheidole sp. 32	1	1	1					1	
Pheidole sp. 33		1			1				
Pheidole sp. 34	1	1	1		1			1	
Pheidole sp. 35		1	1		1				
Pheidole sp. 36	1	1			1				
Pheidole sp. 37	1	1	1		1				
Pheidole sp. 38	1	1	1					1	
Pheidole sp. 39	1	1	1		1			1	
Pheidole sp. 40	1								
Pheidole sp. 41		1							
Pheidole sp. 42		1			1	1		1	
Pheidole sp. 43		1						1	
Pheidole sp. 44		1			1				
Pheidole sp. 45		1							
Pheidole sp. 46		1							
Pheidole sp. 47		1	1		1				
Pheidole sp. 48		1			1				
Pheidole sp. 49		1	1		1				
Pheidole sp. 50		1							
Pheidole sp. 51		1							
Pheidole sp. 52		1			1				
Pheidole sp. 53		1							
Pheidole sp. 54		1	1						

Table 2 (*Continued*)

Subfamily/taxon	Ducke			Maracá			Viruá		
	Bait	Pitfall	Winkler	Bait	Pitfall	Winkler	Bait	Pitfall	Winkler
Pheidole sp. 55		1	1		1				
Pheidole sp. 56			1						
Pheidole sp. 57					1		1	1	1
Pheidole sp. 58			1						
Pheidole sp. 59					1				
Pheidole sp. 60					1		1	1	
Pheidole sp. 61					1			1	
Pheidole sp. 62					1				
Pheidole sp. 63					1				1
Pheidole sp. 64					1				
Pheidole sp. 70					1		1	1	
Pheidole sp. 71					1		1		
Pheidole sp. 73							1		
Pheidole sp. 75					1	1		1	
Pheidole sp. 76					1			1	
Pheidole sp. 77							1		
Pheidole sp. 78				1	1			1	
Pheidole sp. 79					1				
Pheidole sp. 85					1			1	
Procryptocerus attenuatus					1				
Procryptocerus marginatus		1							
Rogeria alzatei		1	1						
Rogeria foreli					1				
Rogeria leptonana					1				
Sericomyrmex sp. 01		1			1			1	
Sericomyrmex sp. 02		1							
Sericomyrmex sp. 03					1			1	
Sericomyrmex sp. 04					1			1	
Solenopsis geminata		1	1	1	1	1	1	1	
Solenopsis sp. 01		1	1	1	1	1		1	1
Solenopsis sp. 02	1	1	1	1	1	1		1	
Solenopsis sp. 03	1	1	1	1	1	1	1	1	1
Solenopsis sp. 04		1	1	1	1	1		1	
Solenopsis sp. 05		1	1	1	1		1	1	1
Solenopsis sp. 06	1	1	1	1	1	1		1	1
Solenopsis sp. 07		1	1		1		1	1	
Solenopsis sp. 08	1								
Solenopsis sp. 09	1	1	1		1				
Solenopsis sp. 10			1		1				
Solenopsis sp. 11				1	1			1	
Solenopsis sp. 12					1		1		
Solenopsis sp. 13					1	1			
Strumigenys carinithorax		1							
Strumigenys elongata			1		1				1
Strumigenys perparva		1	1						
Strumigenys precava		1							
Strumigenys smithii			1						
Strumigenys trinidadensis		1			1				
Strumigenys trudifera			1						
Strumigenys sp. 01		1	1		1	1		1	1
Strumigenys sp. 02		1	1		1				
Strumigenys sp. 03		1	1		1				
Strumigenys sp. 04		1	1						
Strumigenys sp. 05			1		1				
Strumigenys sp. 06					1				
Strumigenys sp. 07			1						
Strumigenys sp. 08					1				
Strumigenys sp. 09						1			
Trachymyrmex bugnioni		1						1	
Trachymyrmex opulentus		1			1				
Trachymyrmex sp. 01		1							
Trachymyrmex sp. 02		1	1						
Trachymyrmex sp. 03		1			1				
Trachymyrmex sp. 04		1			1				
Trachymyrmex sp. 05	1	1	1		1		1	1	
Trachymyrmex sp. 06		1			1			1	
Trachymyrmex sp. 07		1			1			1	
Trachymyrmex sp. 08		1			1				
Trachymyrmex sp. 09		1			1				
Trachymyrmex sp. 10		1			1			1	
Trachymyrmex sp. 11		1							
Trachymyrmex sp. 12					1			1	
Wasmannia auropunctata	1	1	1	1	1	1	1	1	1
Wasmannia iheringi		1							
Wasmannia rochai					1	1			

Table 2 (*Continued*)

Subfamily/taxon	Ducke			Maracá			Viruá		
	Bait	Pitfall	Winkler	Bait	Pitfall	Winkler	Bait	Pitfall	Winkler
Wasmannia scrobifera		1							
Paraponerinae									
Paraponera clavata		1			1				
Ponerinae									
Anochetus diegensis		1	1		1			1	
Anochetus emarginatus		1							
Anochetus horridus		1	1						
Centromyrmex alfaroi					1				
Centromyrmex brachycola		1			1				
Centromyrmex gigas					1				
Hypoponera sp. 01		1	1		1				
Hypoponera sp. 02		1	1						
Hypoponera sp. 03		1	1		1				
Hypoponera sp. 04		1	1		1			1	
Hypoponera sp. 05		1	1		1				
Hypoponera sp. 06		1	1		1				
Hypoponera sp. 07		1	1		1	1			
Hypoponera sp. 08		1	1						
Hypoponera sp. 09					1				
Leptogenys *wheeleri*		1							
Leptogenys sp. 01		1							
Leptogenys sp. 02		1						1	
Odontomachus bauri				1	1	1	1	1	
Odontomachus brunneus		1							
Odontomachus caelatus	1	1	1					1	
Odontomachus haematodus	1	1			1		1	1	
Odontomachus laticeps		1							
Odontomachus meinerti		1		1	1	1		1	
Odontomachus opaciventris		1	1						
Odontomachus scalptus		1	1						
Pachycondyla apicalis		1		1	1		1	1	
Pachycondyla arhuaca		1			1				
Pachycondyla commutata		1			1			1	
Pachycondyla constricta	1	1	1	1	1		1	1	
Pachycondyla crassinoda	1	1		1	1			1	
Pachycondyla crenata					1				
Pachycondyla harpax		1	1	1	1		1	1	
Pachycondyla impressa								1	
Pachycondyla inversa				1					
Pachycondyla laevigata								1	
Pachycondyla obscuricornis				1	1		1	1	
Pachycondyla unidentata								1	
Pachycondyla sp. 01	1								
Pachycondyla sp. 03								1	
Proceratiinae									
Discothyrea sp. 01			1						
Discothyrea sp. 02					1				
Pseudomyrmicinae									
Pseudomyrmex sp. 01		1			1				
Pseudomyrmex sp. 02		1							
Pseudomyrmex sp. 03		1			1			1	
Pseudomyrmex sp. 04					1				
Pseudomyrmex sp. 05							1	1	
Pseudomyrmex sp. 06					1			1	
Pseudomyrmex sp. 07					1	1		1	
Pseudomyrmex sp. 08					1				

Table 3
Number and proportion of ant species sampled by Pitfall trapping, Sardine baits, Winkler extraction, and all possible combinations in the Viruá National Park, Maracá Ecological Station and Ducke Reserve, in the Brazilian Amazon.

Techniques	Areas					
	Ducke		Maracá		Viruá	
	N	%	*N*	%	*N*	%
Bait	67	28	57	28	57	37
Winkler	110	47	35	17	22	14
Pitfall	210	89	195	94	131	86
Bait and winkler	135	57	72	35	69	45
Bait and pitfall	214	91	205	99	150	98
Pitfall and winkler	230	97	198	96	135	88
Bait, pitfall and winkler	236	100	207	100	153	100

Baits caught about 39% and 61% more species than Winkler extraction at Maracá and Viruá, respectively. In Ducke, Winkler extraction captured 61% more species than baits.

The species composition of ground-dwelling ants sampled by the three techniques combined (Fig. 2) differed among the study sites (non-parametric MANOVA: $F_{8,\,239} = 83.46$; $r^2 = 0.736$; $P < 0.001$). The highest level of congruence (Table 4) was between the data of all sampling techniques and bait plus pitfall data for Viruá samples ($r = 0.99$; P 0.001), and the lowest congruence was between all sampling techniques and Winkler extractions in Maracá ($r = 0.35$; $P = 0.62$). Considering the sampling techniques individually, the highest level of congruence in all sites was with pitfall traps. In Maracá and Viruá, the congruence between pitfall traps and combined techniques were above 90%. In general,

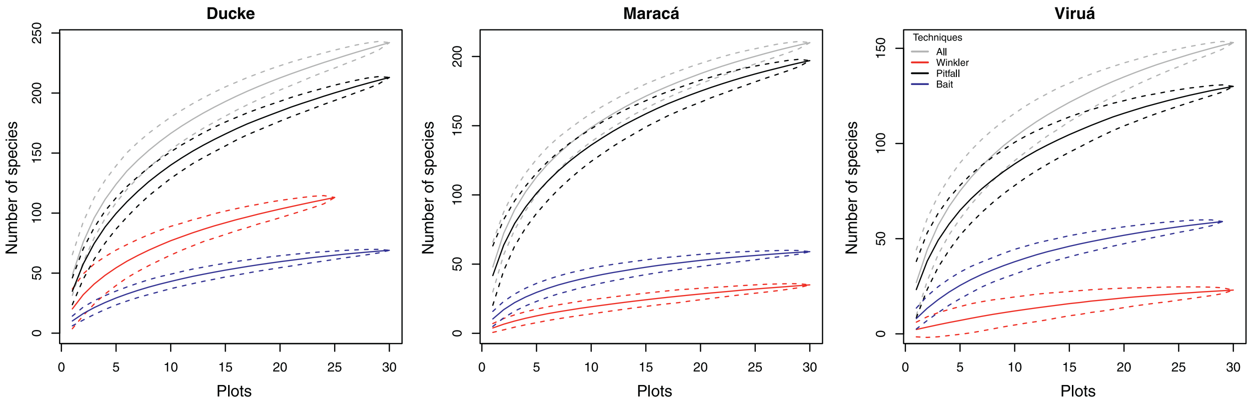

Fig. 1. Ground-dwelling-ant species accumulation curves for Pitfall trapping, Sardine baits and Winkler extraction, and combination of all techniques in three study sites (Viruá National Park, Maracá Ecological Station and Ducke Reserve), in the Brazilian Amazon. Dotted lines mark the 95% confidence intervals.

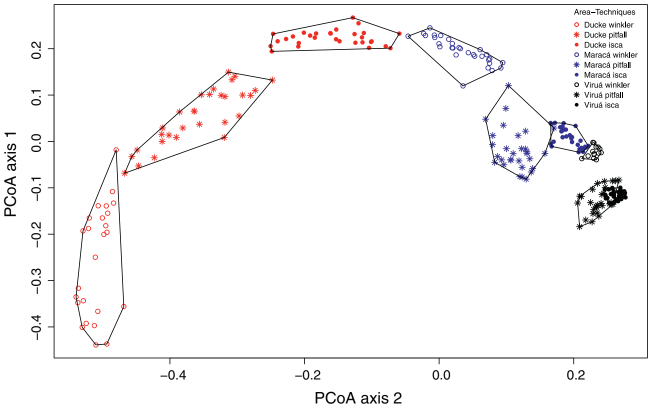

Fig. 2. An NMDS ordination plot indicating the congruence in ground-dwelling ant species associations among sites and among sampling techniques (Pitfall trapping, Sardine baits and Winkler extraction) in three study sites (Viruá National Park, Maracá Ecological Station and Ducke Reserve), in the Brazilian Amazon.

the assemblage data collected with pitfall traps was similar to the assemblage data collected with the three techniques combined, indicating redundancy of some techniques.

RDA analysis showed that the ant assemblage composition was significantly correlated with soil clay content, altitude and terrain slope (Table 5). These relationships were not detected with bait data at Ducke (RDA = 0.1234) or Maracá (RDA = 0.1244), or with Winkler data at Maracá (RDA = 0.1132).

Table 5
Proportion of variance in the ant-assemblage composition explained by the environmental variables in redundancy analysis (RDA) models within each site (Viruá National Park, Maracá Ecological Station and Ducke Reserve) sampled in the Brazilian Amazon. Predictor variables used in the RDA analyses were the percentage of soil clay content, altitude and terrain slope.

Techniques	Ducke RDA	Maracá RDA	Viruá RDA
Bait	0.123	0.124	0.144*
Pitfall	0.157**	0.140**	0.162**
Winkler	0.158**	0.113	0.368**
Bait + pitfall	0.149**	0.135**	0.163**
Bait + winkler	0.165**	0.132**	0.151**
Pitfall + winkler	0.158**	0.139**	0.162**
Bait + pitfall + winkler	0.157**	0.136**	0.165**

* Significance level $P < 0.05$.
** Significance level $P < 0.01$.

The sampling techniques differed in their relative monetary and time costs (Table 6). Winkler extraction was the most expensive technique, accounting for 48% of the total monetary cost when using the three techniques combined. Pitfall traps and baits accounted for 41% and 11% of the total cost, respectively. The same general pattern was detected for time costs. Winkler extraction and pitfall traps were the two most time-consuming techniques, each accounting for 43% of the total time. Much less time, 14% of the total effort, was required for sampling and sorting species collected at baits. Pitfall traps plus Winkler extraction was the most effort demanding combination, amounting to 89% of the cost and 86% of the time. The combinations of bait with pitfall traps or Winkler extraction were the least expensive (52% to 59% of the monetary cost) and the less time demanding (57% of the time) of the techniques combinations.

Table 4
Congruence between ant-assemblage datasets sampled by one or by combinations of two sampling techniques compared to the ant-assemblage composition sampled with the three sampling techniques. Congruence was evaluated by symmetric Procrustean rotations using the Sørensen dissimilarity index calculated for ant presence/absence data. *P* values were estimated by 999 Monte Carlo permutations.

Techniques	Ducke		Maracá		Viruá	
	r	*P*	*r*	*P*	*r*	*P*
Bait	0.405	0.039	0.360	0.035	0.539	0.001
Winkler	0.597	0.001	0.347	0.062	0.587	0.015
Pitfall	0.655	0.001	0.941	0.001	0.940	0.001
Bait + winkler	0.720	0.001	0.437	0.006	0.589	0.001
Bait + pitfall	0.750	0.001	0.924	0.001	0.995	0.001
Pitfall + winkler	0.729	0.001	0.954	0.001	0.946	0.001

4. Discussion

An important issue in devising an effective protocol for ant surveys is to evaluate if the extra information gathered with the use of more than one sampling technique is worth the financial costs and scientist-hours spent. Our results showed that pitfall traps were effective in estimating ant species richness and captured the

Table 6
Summary of the relative effort (cost and time) required for each technique used for collecting ground-dwelling ants and for their respective combinations in relation to the total effort using all three sampling techniques.

Techniques	Cost (%)	Time (%)
Bait	11	14
Pitfall	41	43
Winkler	48	43
Bait + pitfall	52	57
Bait + winkler	59	57
Pitfall + winkler	89	86
Bait + pitfall + winkler	100	100

relationships with environmental variables across different forest types in Amazonia, saving time and money in relation to the use of combined techniques. We did not try to detect all species in each site, because attempts to list all ant species in such large areas may be an impossible task. However, our results can be used as baseline information for management decisions related to biotic complementarity and habitat specificity.

The choice of sampling method and the number of samples to be collected is dependent on what proportion of the fauna is the target of the survey (Delabie et al., 2000). Many authors have suggested that Winkler extraction is the most effective technique, sampling more species per sampling unit, in areas of dense forest with abundant humid leaf litter (Olson, 1991; Fisher, 1999; King and Porter, 2005; Gotelli et al., 2011). A similar pattern was detected for cocoa plantation in the tropics, where Winkler extraction plus pitfall traps was considered the most effective combination for surveying litter-dwelling ant species (Delabie et al., 2000). In contrast, in temperate forests and open environments, such as savannas and managed-forest areas, the use of pitfall traps has been suggested as the most effective technique for ant biodiversity studies, although association with other sampling techniques is often recommended (Delabie et al., 2000; Parr and Chown, 2001; Wang et al., 2001; Lopes and Vasconcelos, 2008; Tista and Fiedler, 2010). In six plant physiognomies in the Brazilian Cerrado biome, pitfall traps collected more species in the open physiognomies (grasslands and savanna) and in gallery forest subjected to flooding, whereas the Winkler sampling detected more species in the semideciduous forest and gallery forest not subjected to flooding (Lopes and Vasconcelos, 2008).

Surprisingly, our results are more in line with findings for open environments than for dense forests. The pitfall traps sampled proportionally more species in Ducke (89%) and Maracá (94%) where all plots were installed in forested environments, comparable with the proportion of species collected in Viruá (86%), which encompasses open forests and savannas. These patterns hold even when differences in sampling intensity between techniques are taken into account. The accumulation curves for Pitfall traps were similar to accumulation curves using all methods combined. For all sites, pitfalls sampled more species per plot. If the objective is to sample more ant species at lower cost, our results suggest that use of pitfall traps is the best option in Amazonia, even for densely forested areas.The higher efficiency of pitfall traps compared with previous studies in tropical forests may have resulted from a variety of factors. Pitfall traps may have captured more species because they were in operation during the night when the humidity is usually higher. In contrast, litter samples for Winkler extraction are usually collected only during daylight hours. Low humidity may have affected the efficiency of Winkler extraction, especially in Viruá and Maracá, since the collections in all areas were made at the end of the dry season. A study in dry tropical forests showed that the efficiency of Winkler extraction may be affected during periods of drought and that pitfall traps should also be used to evaluate the local ant fauna (Delsinne et al., 2008). As ants are frequently reported to be affected by differences in microhabitat moisture levels, litter sifting during the rainy season may capture more ants than in the dry season (Kaspari and Weiser, 2000).The diameter of pitfall traps may also affect the efficacy of this technique (Adis, 1979). In our study, the diameter of the pitfall traps (95 mm) was larger than those commonly used in previous studies, such as 18 mm (Olson, 1991; Fisher, 1999), 18 and 62 mm (Parr and Chown, 2001), 58 mm (Wang et al., 2001) and 65 mm (Lopes and Vasconcelos, 2008). Larger pitfall diameter results in larger sampling areas, but additional factors may be operating. For example, Fisher (1999) suggested that larger ants where either absent or were relatively smaller in Madagascar, but they may not have been adequately sampled with 18 mm diameter vials. Large species, which were very common in our study, may avoid small traps or, in some cases, pass over them. As sampling area and season were similar in many previous studies, the size of the trap may have been the factor that most influenced the overall performance of pitfalls in relation to other techniques in our study.

We do not question the value of using more than one sampling technique in some ant surveys in order to capture the maximum species in an area, as sampling techniques may be complementary (Olson, 1991; Delabie et al., 2000; Parr and Chown, 2001; Lopes and Vasconcelos, 2008), even in humid tropical forest in eastern Amazonia (Souza et al., 2007). Winkler extraction should be more efficient at collecting smaller, more cryptic ants, while Pitfall trapping is thought to favor large mobile species (Olson, 1991; Parr and Chown, 2001). However, previous studies evaluated the sampling-technique only in relation to the number of species collected (e.g. Olson, 1991; Ivanov and Keiper, 2009; Tista and Fiedler, 2010), and not the efficiency of the techniques for revealing data useful to support decisions about land management (e.g. Santos et al., 2008). Given the roles of ants in ecosystem functioning, the scale of our study (25 km^2) captures more landscape variation than most studies (Costa and Magnusson, 2010) and is comparable to the scales at which most land-management decisions are made.

Pitfalls take little time to install and operate (Bestelmeyer et al., 2000), but this technique cannot be used in areas that are too wet, too steep, too rocky, or experience high human and domestic animal traffic as they disturb the soil (Gotelli et al., 2011). The advantage of Winkler extraction is that it can be used to provide an indication of ant density (Parr and Chown, 2001) and, unlike pitfall traps, does not require a second visit to the field for recovery. However, in other respects, Winkler extraction is much more time-consuming and labor intensive than pitfall trapping (Parr and Chown, 2001). Especially in Amazonia, financial costs limit the amplitude of biodiversity studies (Costa and Magnusson, 2010). As land-use decisions are usually made on complementarity rather than species richness (Grove, 2003), the possibility of investing financial resources economized by not using all techniques to allow surveys of other areas must be considered.

This study was one of the first to investigate how reduction in the number of sampling techniques affects the time and monetary costs of surveying Neotropical ant assemblages. Congruency and RDA analyses indicated that pitfall trapping is the best single technique to be used in each area to retrieve the main ecological patterns, and that it is generally as efficient as any other combination of techniques. Although it is not the cheapest technique, pitfall trapping revealed more than 86% of the total number of species recorded and retrieved the main ecological patterns found by use of all techniques simultaneously in the three forests. Pitfall trapping compensates the extra cost, compared with sardine baits, by being more prone to detect ecological patterns when used alone. The overall advantage of pitfall trapping, saving 48% in monetary cost and 43% in time, makes it a powerful tool for biodiversity studies. In addition, the technique provided data that were suitable for detecting the responses of the ant assemblage to environmental variables. Therefore, where time and economic costs limit the number of techniques applied, such as in most Amazonian-forest biodiversity-monitoring programs, the use of pitfall traps alone may be a good option.

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