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ORIGINAL PAPER

Effectiveness of genera as a higher-taxon substitute for species in ant biodiversity analyses is not affected by sampling technique

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Abstract

Survey costs and a lack of taxonomists are often the main impediments to biodiversity inventories. The use of a higher-taxon approach that is efficient in representing species patterns within a short period of time is one way to overcome these constraints, especially if these responses are consistent at various spatial scales and sampling techniques. Here, we evaluated whether the use of pitfall trapping or Winkler extraction influenced the utility of genus as a surrogate to predict patterns of species richness and composition related to environment. The study sites were spread along 10 degrees of latitude, covering phytophysiognomies with different topographic characteristics. We recorded 450 ant species/morphospecies distributed in 70 genera. Pitfall-traps captured a larger proportion of species (77–98%) and genera (71–100%) per site. Genus was efficient in predicting variations in richness, and assemblage composition detected at the species level, using pitfall-traps or Winkler extractors. The higher-taxon approach saved approximately 40% of the surveys costs. The negative effect of the species-genus ratio was detected only on species composition, but it did not affect the quality of predictions using genera. The results are consistent with the hypothesis that genus can be used as a proxy for broader sets of species independent of sampling technique or environmental heterogeneity. The use of pitfall-traps or Winkler extractors for genus-level identification proved to be cost-efficient and time-efficient and should work well in other regions requiring conservation effort and monitoring programs.

Keywords Amazon · Ants · Beta diversity · Standardized sampling protocol · Surrogate · Tropical forest

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Introduction

Complete biodiversity inventories are costly and difficult to obtain (Whittaker et al. 2005), leading to a growing demand for faster and more efficient techniques for monitoring actions (Ugland et al. 2008; Mandelik et al. 2010; Tulloch et al. 2011; Kessler et al. 2011). Higher-taxon surrogacy, the use of taxonomic levels other than species, is a common approach for rapidly assess biodiversity (Gaston and Williams 1993; Oliver and Beattie 1993, 1996; Andersen 1995, 2002; Longino and Colwell 1997; Souza et al. 2009, 2016). Taxonomic surrogacy is widely used in biodiversity monitoring of aquatic environments (Ellis 1985; Heino and Soininen 2007; Carneiro et al. 2010), but it is less often used in terrestrial environments (Caruso and Migliorini 2006; Van Rijn et al. 2015). There is no consensus on which taxonomic level to use as a surrogate (Jones 2008; Neeson et al. 2013), but this approach has been widely used by researchers in conservation planning (Cardoso et al. 2004b) and biodiversity monitoring (Nakamura et al. 2007; Bevilacqua et al. 2012) in the last 20 years. These studies often use surrogates without testing their suitability either by pilot studies or based on what is already known about taxonomic diversity and community structure for a group and area of interest (Bevilacqua et al. 2012; Neeson et al. 2013; Van Rijn et al. 2015).

Several authors have postulated that genus resolution is a good candidate as a surrogate for species-level identification (Pik et al. 1999; Heino and Soininen 2007; Gallego et al. 2012). Indeed, the ecological patterns revealed by genus level often mirror the ecological patterns of species locally (dos Ribas and Padial 2015) and over large areas (Souza et al. 2016). However, other studies indicate that the use of genus as a surrogate failed to retrieve species-level information (Andersen 1995; Rosser and Eggleton 2012). This can occur due to reduced sample size, or an elevated number of rare species in the assemblages, resulting in inventories that do not reach the asymptote of the species accumulation curves (Neeson et al. 2013). Another factor that seems to affect surrogates' performance is the variation of number of species per genus (Bevilacqua et al. 2012; Neeson et al. 2013; Van Rijn et al. 2015; Driessen and Kirkpatrick 2017). These contradictory results call into question the usefulness of genus as surrogates (Van Rijn et al. 2015). Nevertheless, the use of higher-taxon surrogacy remains attractive due to the possibility of economical taxonomic identification (Gaston and Williams 1993; Williams and Gaston 1994; Gotelli 2004) and reducing the financial costs of biodiversity surveys (Souza et al. 2016). The cost (time and money) of biodiversity monitoring is a crucial factor for its viability (Margules et al. 2002) and this is particularly important for taxonomic groups that are extremely diverse and have small body sizes, such as arthropods (McGeoch 1998; Hodkinson and Jackson 2005).

Many strategies have been used to reduce labor and costs associated with sorting and identifying invertebrates. Investigators have used ecological responses based on predictive variables that are correlated with assemblage composition (de Souza et al. 2012; Porto et al. 2016; Graça et al. 2017), sample rarefaction (Santos et al. 2008) and sets of more-frequent species (Franklin et al. 2013) to validate the reduction of sampling effort. Other studies used functional traits to predict changes in community structure in response to environmental variation (French and Picozzi 2002; Gallego et al. 2012; Graça et al. 2016).

Ants constitute a hyper-diverse group that can usually be easily collected (Folgarait 1998; de Souza et al. 2012), and can be used in management, monitoring and conservation programs (Kaspari and Weiser 2000; Underwood and Fisher 2006). Pitfall traps and Winkler litter extraction are the most used sampling methods for ground-dwelling ants in ecological studies (Agosti et al. 2000a, b; Bestelmeyer et al. 2000). For most environments, these techniques can be complementary (Olson 1991; Fisher 1999; Souza et al. 2007), but often show some degree of redundancy (Parr and Chown 2001; Lopes and Vasconcelos 2008; de Souza et al. 2012), suggesting that the reduction in the number of sampling techniques may be a cost-efficient decision (de Souza et al. 2012). The most efficient sampling protocol should satisfy taxonomic, ecological and financial aspects of the investigations. For ants, environmental factors, such as topography (altitude and slope) and soil texture, generate microhabitat variability that can affect spatial patterns of ground-dwelling-ant assemblages at local scales (Vasconcelos et al. 2003; Oliveira et al. 2009; Mezger and Pfeiffer 2011) and can be used to validate the use of surrogate taxa or reduced-sampling methods.

In this study, we investigated the effects of two sampling techniques for ground-dwelling ant species on the efficiency of genus as a higher-taxa surrogate over 1000 km in the Brazilian Amazon. We documented differences in species composition between the two sampling methods, and then measured the degree of congruence of the richness and composition data between species-level and genus-level identification. We hypothesized that, regardless of the chosen sampling technique, the coarser level of taxonomic information (genus) could be used as an efficient surrogate for species-level identification and that the use of genus-level identification would be able to retrieve information on species richness and composition in the gradient studied. We tested whether results based on genus-level identification revealed similar responses of the assemblages to local environmental gradients to those detected with species. We also tested whether the responses obtained with genus in this study were affected by the number of species per genus, as some recent studies have suggested (Lovell et al. 2007; Bevilacqua et al. 2012; Neeson et al. 2013; Van Rijn et al. 2015; Driessen and Kirkpatrick 2017; Rosser 2017). Finally, we estimated the monetary and time costs to use genus and species data to compare the cost-efficiency of using these two types of data in biodiversity-monitoring programs.

Methods

Study sites

We investigated the distribution patterns of ground-dwelling-ant assemblages in eight sites associated with the Brazilian Biodiversity Research Program (PPBio) along a gradient of 1000 km (~10 degrees latitude), covering phytophysiognomies with different topographic and soil characteristics (open and dense rainforests, deciduous and semi-deciduous forests, and forested, seasonal and shrubby white-sand areas). Maracá Ecological Station (Maracá) and the Viruá National Park (Viruá) are situated in Roraima State (extreme north of Brazil). Reserva Ducke (Ducke), the Amazonas University Experimental Farm (UFAM), Manaquiri, Orquestra, Campanã and Jari are located in Amazonas State (Online Resource 1). All sites have seasonal rainfall, with rain concentrated from October to March in sites located in the Amazonas State (De Marques-Filho et al. 1981), and from July to September in Maracá and Viruá. Ducke was sampled in September 2006, Viruá and Maracá in February 2007, Manaquiri in November 2009, Orquestra, Campanã and Jari in November 2010 and UFAM in September 2011, all during their respective dry seasons. The coordinates, vegetation type, elevation range, rainfall and spatial layout of the study sites are summarized in Table 1.

Table 1 Vegetation, rainfall, elevation range, number of samples and sampling techniques in eight sites in the Brazilian Amazon

Sites	Maracá	Viruá	UFAM	Ducke	Manaquiri	Orquestra	Campanã	Jari
Coordinates	3°22′56.73″N 61°27′52.31″W	1°27′49.28″N 61°1′30.59″W	2°38′26.51″S 60°5′44.55″W	2°57′51.69″S 59°56′27.26″W	3°41′31.25″S 60°14′51.60″W	4°59′2.39″S 61°34′30.00″W	5°36′36.00″S 62°12′0.00″W	5°58′11.99″S 62°29′24.00″W
Vegetation type (number of 250-m long plots)	Open ombrophilous forest (14), Deciduous forest (7), Semi-deciduous forest (8), Campinarana seasonal forested (1)	Open ombrophilous forest (12), Campinarana seasonal forested (8), Seasonal campinarana (6), Seasonal campinarana shrubby (4)	Dense ombrophilous forest (27)	Dense ombrophilous forest (30)	Open ombrophilous forest (10)	Dense ombrophilous forest (5)	Dense ombrophilous forest (5)	Dense ombrophilous forest (5)
Elevation range (m.a.s.l.)	54–85	43–130	42–130	46–110	30–36	36–61	70–72	70–72
Mean rainfall (mm)	1718	1682	2362	2507	2200	2200	2200	2200
Sampling-grid area (km^2)	25	25	24	25	5	5	5	5
Number of plots with Pitfall traps	30	30	27	30	10	5	5	5
Number of plots with Winkler extractor	30	14	16	25	10	5	5	5
Total of samples	600	440	430	550	200	100	100	100
Sampling date	February/2007	February/2007	September/2011	September/2006	November/2009	November/2010	November/2010	November/2010

Table 1 (continued)

Sites	Maracá	Viruá	UFAM	Ducke	Manaquiri	Orquestra	Campanã	Jari
Responsible organization	ICMBIO—Chico Mendes Institute for Biodiversity Conservation	ICMBIO—Chico Mendes Institute for Biodiversity Conservation	UFAM—Federal University of Amazonas	INPA—National Institute for Amazon Research	Private	Private	ICMBIO—Chico Mendes Institute for Biodiversity Conservation	ICMBIO—Chico Mendes Institute for Biodiversity Conservation

Sampling design

Ants were sampled in permanent plots with ten samples per sampling method. Some sites also had a smaller number of 250-m plots sampled with Winkler due to soil and/or litter being soaked at sampling time. In total, we took 2520 samples from 252 plots (Table 1). We used the RAPELD sampling design (Online Resource 2), which is based on a system of trails and permanent plots where a diverse range of taxa can be sampled (Magnusson et al. 2005, 2013; Costa and Magnusson 2010). The permanent plots are 250-m long and positioned to follow terrain contours to minimize the effects of topographical variation within plots. In each site, plots were 1 km distant from each other and had the same standardized spatial design between-plot. Due to the area of each site studied, the number of 250-m long plots varied.

Ant sampling

Ground-dwelling ants were collected using pitfall traps and litter samples that were processed in Winkler extractors. Litter-dwelling ants were sampled from 1 m^2 litter in ten sampling stations located at 25 m intervals along the center line of each plot. Using a Winkler extractor with a 1 cm^2 mesh sieve, the ants were extracted from the sifted litter hung in a mesh bag inside a cotton bag for 48 h. As a behavioral response to litter drying, the ants migrate from the suspended sample and fall into a container partially filled with alcohol at the bottom of the bag (Agosti et al. 2000a; Bestelmeyer et al. 2000). The litter-sampling procedures were undertaken between 8:00 am and 5:00 pm. A pitfall trap (diameter of 95 mm, depth of 8 cm, volume of 500 ml) without bait, was partially filled with water and detergent, and placed in each station after litter collection, and remained open for 48 h without interruption (see de Souza et al. 2012 for sampling details).

Pitfall traps are fast and easy to install (Bestelmeyer et al. 2000), but this technique does not work properly in overly humid, steep, or rocky areas (Gotelli et al. 2011). The advantage of Winkler extractor is that it can provide an indication of ant density (Parr and Chown 2001) and, unlike pitfall traps, does not require a second field visit for trap removal. The Winkler extractor samples proportionally more smaller and cryptic ants, while pitfall trapping is more useful to capture large and active species (Olson 1991; Parr and Chown 2001).

All ants were first identified to genus using the taxonomic keys provide by Baccaro et al. (2015), and then sorted to species. We used available taxonomic keys and comparisons with specimens in collections previously identified by experts. A unique identification was given to each morphospecies based on morphological differences from related species. The morphotyping was the same for all collection sites. Undescribed species were also sorted into morphospecies. Voucher specimens are deposited in INPA's Entomological Collection. The raw data used here are available in Online Resource 3 and PPBio's web site (http://ppbio.inpa.gov.br/repositorio/dados). The species list by sampling technique and study site is available in Online Resource 4.

Data analysis

Prior to analyses, the information of each sampling station was combined per plot. All analyses were run in the R environment for statistical computing (R Core Team 2017, version 3.4.3), using the vegan package 2.4-6 (Oksanen et al. 2018) and nlme package 3.1-131 (Pinheiro et al. 2017).

Redundancy in sampling techniques

To determine the proportion of variance in the ant species composition patterns that was common to different sampling techniques, we used permutational multivariate analysis of variance (PERMANOVA) to compare the species compositions between sampling methods (Anderson 2001). The study sites were included as a random factor in the PERMANOVA model to control the possible spatial autocorrelation of the data. To avoid giving more weight to species sampled in large numbers, relative-frequency data (i.e. the number of sampling stations in a plot in which a species was collected) were used when constructing the taxa-composition matrix (Gotelli et al. 2011). Therefore, the relative frequency of a given species per plot varied between zero and ten for each method. We reduced the dimensionality of each species-data matrix (pitfall and Winkler) using nonmetric multidimensional scaling-NMDS (Minchin 1987), based on the Bray–Curtis dissimilarity index (Legendre and Legendre 2003), based on the best ordination from 999 permutations.

Surrogate and richness

To estimate whether genus richness can predict species richness, we calculated the correlation between the number of genera and the number of species found in each site studied by sampling technique. The number of species and genera were calculated by plots and correlations were measured within each study site. To measure the congruence between number of genera and number of species in the entire environmental gradient studied, we used a linear mixed-effects model (Laird and Ware 1982) and included the site as a random effect to control the effect of spatial autocorrelation in this analysis.

Surrogate and composition

To evaluate the congruence between the matrices of genus and species sampled with each sampling technique by site ($n = 8$), we initially reduced the dimensionality of each species-data and genus-data matrix (pitfall-trap and Winkler extractor separately) using NMDS (Minchin 1987), based on the Bray–Curtis dissimilarity index of relative-frequency data (Legendre and Legendre 2003). The congruence between the species- and genus-level NMDS ordinations for each sampling method was quantified by Procrustes correlation, with 999 Monte Carlo permutations to test for statistical significance (Peres-Neto and Jackson 2001). In this analysis, NMDS ordinations based on the matrices of species and genera were compared using a rotational-fit algorithm that minimizes the sum of squared residuals between the ordinations. The statistic, called m^2 (the goodness-of-fit statistic that measures the level of congruence between two ordination configurations) was transformed to the Procrustes correlation coefficient (r) using the following equation: $r = \sqrt{(1 - m^2)}$ (Oksanen et al. 2018). We used paired *t* test to test whether there was difference in Procrustes correlation coefficient between the two sampling techniques.

Relationships with environmental gradients

We investigated whether the use of genus as a surrogate for species maintains the same relationships detected between ant assemblages and environmental variables (altitude, slope, and percentage of soil clay content). The datasets and details of the sampling protocols (metadata) for each used variable are available in Online Resource 5 and the PPBio website (http://ppbio.inpa.gov.br/repositorio/dados). We selected these variables because they were sampled in a standardized way in the eight study sites and their effects on the richness and composition of the ant assemblages in the Brazilian Amazon were known from earlier studies (Vasconcelos et al. 2003; Oliveira et al. 2009; de Souza et al. 2012; Souza et al. 2016; Gomes et al. 2018).

We used redundancy analysis (RDA) to evaluate how much variance in the dependent variable (species or genus composition matrix) could be explained by the independent variables. RDA combines regression and principal component analysis (Borcard et al. 2011). We used the site scores weighted by species (SSWS) of the first RDA axis to indicate how sites are ordered along the main axis of the RDA (Legendre and Legendre 2003). We calculated a Pearson correlation between the SSWS axes of genus and species for each sampling technique. High correlations between SSWS axes of species and genus data for each sampling technique indicate that the assemblages respond in a similar way to the environmental gradient.

The effect of species-genus ratio on surrogate responses

To evaluate if there is loss of information when using genera as surrogate of ant species due to differences in the number of species per genus, we used the species-genus ratio. The value of the correlation coefficient (between genus and species-level) of each metric evaluated (richness, composition, and SSWS axes) was correlated with the values of the species-genus ratio.

Time and financial resources

We estimated the absolute and relative (%) time and financial costs for species- and genus-level identifications for each sampling technique used. We considered the costs as expenses with field and laboratory materials, field sampling and salary of team members. We considered the laboratory costs as those related to the sorting, mounting, and identification of ant specimens, as well as chemicals used for the conservation of the voucher specimens. To calculate the cost of salaries, we took into account the time of activities in the field and in the laboratory. All costs were measured for each sampling technique by site, the salary and scholarships were based on current Brazilian federal government payments. To estimate the costs in US dollars we used the average value of the currency conversion rates for Brazilian currency (Real = R$), which was US $ 1 = R$ 1.94 (average annual resources from 2006 to 2013; source: Central Bank of Brazil). Costs of laboratory equipment and accommodation buildings for field staff were not included, as there is no qualitative change in total cost (Gardner et al. 2008).

Results

A total of 70,273 specimens belonging to 450 species/morphospecies of ants distributed in 10 subfamilies and 70 genera were collected using pitfall traps and Winkler extractor combined (Table S2). The greatest number of species was detected by pitfall traps in Ducke (208), followed by Maracá (196) and UFAM (167) (Table 2). Only at Manaquiri and Orquestra were more species and genera captured in Winkler extractors than in pitfall traps. The species-genus ratio was always higher in pitfall traps. The sites with the highest number of species per genus were UFAM and Ducke for both sampling techniques: the lowest ratios were in Orquestra and Jari with pitfall traps and Viruá and Orquestra with Winkler extractors (Table 2).

The species compositions (Fig. 1) differed among pitfall traps and Winkler extractors (PERMANOVA; $F_{1,250}=1088.98$; $r^2=0.96$; $P=0.001$). Genus richness predicted overall species richness for both pitfall traps ($r=0.93$) and Winkler extractors ($r=0.98$) (Fig. 2).

The Procrustes correlation coefficients were statistically significant in almost all comparisons between genus- and the species-level matrix (Table 3). The Procrustes correlation coefficients were similar for both sampling techniques at all sites except in Viruá, where there is some discrepancy in the values. The correlations with species-level data sampled by pitfall traps and Winkler extraction were 0.79 ± 0.15 and 0.81 ± 0.12, respectively. The Procrustes correlation coefficients were not statistically different between the two sampling techniques (paired t-test, $F_{1,7}=-0.0003$; $P=0.998$).

The correlation coefficients of SSWS axes did not differ between two sampling techniques (ANOVA, $F_{1,14}=0.013$; $P=0.911$), indicating that there was little or no difference in response between the sampling techniques. The correlation analyses of SSWS values indicated that the ant-assemblage composition was significantly related to environmental variables within sites, and genera and species had similar responses to the environmental gradients. In most cases, a significant correlation was detected (Table 4). Similar results were found with the r^2 values of RDA, where genera and species responded similarly to the environment within each sampling technique. When a RDA result was significant for the species level, it was also significant for the genus level for a given sampling technique at a given study site. Statistically non-significant results were also congruent between sampling techniques. That is, all relationships detected from the species matrices of a given sampling technique against environmental variables were also retrieved using genus resolution (Table 4).

The correlation analyses between species-genus ratios and richness correlation coefficients were not significant (Fig. 3a). The correlation analyses between species and genus ratios and Procrustes correlation coefficients were significant, indicating an effect of species–genus ratio on differences in assemblage composition. However, all predicted correlations (calculated by Procrustes between species- and genus-level matrices; i.e., x-axis values) were significant and higher than 0.7, even for those with the highest species-genus ratio (Fig. 3b). There was no detectable effect of species-genus ratio on SSWS values; the correlation analyses between species-genus ratio and correlation coefficients of SSWS values were not statistically significant (Fig. 3c). The responses of the correlations between the species-genus ratio and the richness, composition and SSWS values were similar for both collection techniques.

Use of genus-level identification saved about 40% of the time and financial resources when compared to species-level identifications in both sampling techniques. Winkler extractors have a higher monetary cost when compared to pitfall-traps. Regardless of

Table 2 Absolute and relative richness values of species, genus and species-genus ratio of ground-dwelling ants in eight sampling sites across the Brazilian Amazon

Identification levels	Techniques	Sites															
		Ducke		UFAM		Manaquiri		Maracá		Viruá		Orquestra		Campanã		Jari	
		N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Species	Pitfall	208	90	167	89	111	65	196	98	131	97	64	53	98	74	92	63
	Winkler	109	47	86	46	132	77	36	18	22	16	75	63	55	41	73	50
	Combined	230	100	187	100	171	100	199	100	135	100	120	100	133	100	145	100
Genus	Pitfall	51	93	39	100	32	71	48	100	39	98	25	58	34	87	33	75
	Winkler	32	58	25	64	41	91	17	35	12	30	38	88	26	67	32	73
	Combined	55	100	39	100	45	100	48	100	40	100	43	100	39	100	44	100
Species-Genus ratio	Pitfall	4.08		4.28		3.47		4.08		3.36		2.56		2.88		2.78	
	Winkler	3.40		3.44		3.22		2.12		1.83		1.97		2.12		2.28	
	Combined	4.18		4.79		3.80		4.15		3.38		2.79		3.41		3.30	

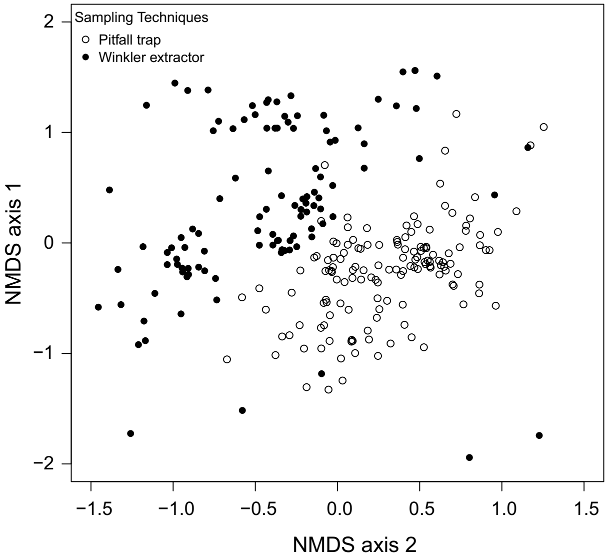

Fig. 1 An NMDS ordination plot indicating differences in ground-dwelling ant species associations between sampling methods (pitfall trap and Winkler extraction) in 268 plots distributed over eight study sites across the Brazilian Amazon

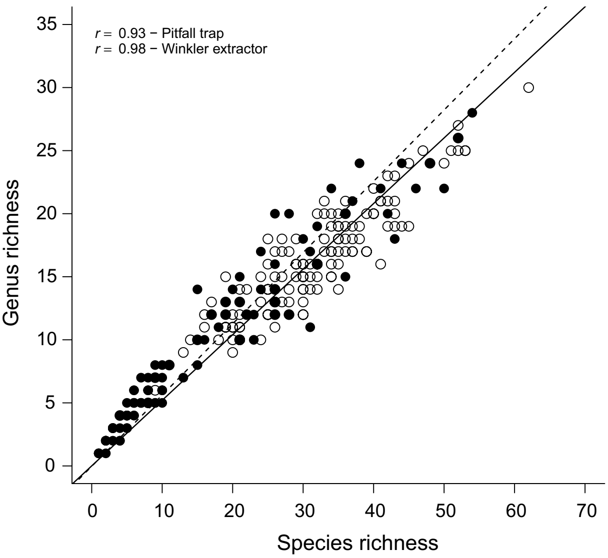

Fig. 2 Correlation between the numbers of genera and species of ground-dwelling ants for pitfall-trap and Winkler-extraction data used in eight study sites in the Brazilian Amazon. The statistical significance of models was tested using 1000 permutations. Both correlations were significant at $P < 0.001$. Open symbols and the continuous trend line refer to the pitfall-trap data, closed symbols and the dashed trend line refer to Winkler-extractor data

the level of identification used, pitfall trapping had the lowest monetary and time costs (Table 5).

Discussion

An important step before proposing the use of genus level as a surrogate of species level for ant-survey protocols is to assess whether the information attained changes depending on the sampling technique used, because the sampling method is often related to the

Table 3 Values of Procrustes correlation coefficients for comparisons between ant species- and genus-level matrices for the eight sites in the Brazilian Amazon

Sites	Procrustes coefficient between species and genus matrices	
	Pitfall	Winkler
Ducke	0.749***	0.708***
UFAM	0.699***	0.707***
Manaquiri	0.800***	0.823***
Maracá	0.734*	0.842***
Viruá	0.809***	0.624
Orquestra	0.800	0.965**
Campanã	0.937*	0.815*
Jari	0.810	0.853*
Average	0.7945	0.8098

Significance levels: P ≤ 0.05*; P ≤ 0.01**; P ≤ 0.001***

Table 4 Values of correlation coefficients for comparisons between site scores weighted by species (SSWS) of the first axis of RDA for matrices of species and genus levels of ant identification, and the proportion of variance in the ant-assemblage composition jointly explained by the environmental variables in redundancy analysis (RDA) for models within each site sampled by pitfall traps and Winkler extractors in eight sites in the Brazilian Amazon

Site	*r* of SSWS	*r* of SSWS	r^2 of RDA Pitfall		r^2 of RDA Winkler	
	Pitfall	Winkler	Species	Genus	Species	Genus
Ducke	0.936***	0.925***	0.2196**	0.2978**	0.1549	0.1865
UFAM	0.922***	0.727***	0.1429**	0.1471*	0.1568	0.1477
Manaquiri	0.094	0.076	0.4745	0.4123	0.4783	0.4833
Maraca	0.948***	0.980***	0.1924**	0.2890**	0.1802	0.2035
Virua	0.900***	0.978***	0.2171**	0.2513**	0.4206**	0.4636*
Orquestra	0.978**	0.975**	0.5057	0.5257	0.4196	0.3452
Campanã	0.571	0.980**	0.7523	0.9115	0.7371	0.8635
Jari	0.392	0.239	0.7877	0.8380	0.7164	0.6570
Mean	0.7175	0.7375				

Significance levels: P ≤ 0.05*; P ≤ 0.01**; P ≤ 0.001***

assemblage composition sampled. Using a comprehensive ant survey of two sampling techniques that collect different ant assemblages, we showed that use of genus was efficient in predicting the information about richness, composition and ecological patterns detected at the species level over a gradient of 1000 km in the Brazilian Amazon and across different vegetation types in the Brazilian Amazon.

There are different suggestions about the use of surrogates to replace the use of species-level identifications for conservation planning. Several authors suggest that surrogates work well (Williams and Gaston 1994; Andersen 1995; Pik et al. 1999; Ricketts et al. 2002; Su et al. 2004; Cardoso et al. 2004a; Sætersdal et al. 2005; Bhusal et al. 2014; Alves et al. 2016), while others claim that they do not (Bilton et al. 2006; Lawler and White 2008; Gaspar et al. 2010; Neeson et al. 2013). These contradictory results may be due to differences between the number of species within the genera (Andersen 1995; Lovell et al.

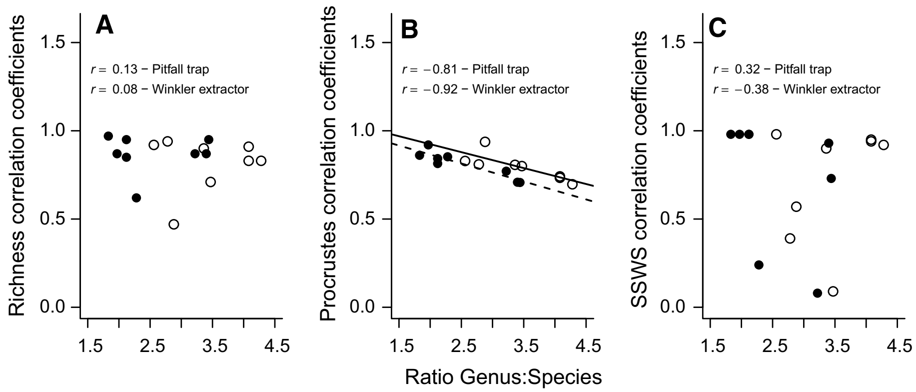

Fig. 3 Relationships between matrix correlation coefficients and the number of ant species per genus measured by each sampling technique. **a** Richness correlation coefficients; **b** Procrustes correlation coefficients and **c** SSWS correlation coefficients. Open symbols and continuous trend lines refer to the pitfall-trap data, closed symbols and dashed trend lines refer to Winkler-extractor data

2007; Rosser 2017). Probably because of the taxonomic hierarchy, the species and higher-taxa data have a nested structure and must have some degree of correlation (Gaston 2000). Likewise, the studies were undertaken at different spatial scales, using various methods, statistical tests and surrogate groups, which makes it difficult to make comprehensive conclusions (Lawler and White 2008). To gain more consistent overall trends at meso or large spatial scales, standardized sampling methods are useful to describe biodiversity patterns (Andersen 1999; Reyers et al. 2000). It may be easier to reach a consensus on which surrogates are best by evaluating studies conducted on meso or large scales (Balmford et al. 1996; Rosser and Eggleton 2012), using standardized methods for data sampling and covering a wide environmental heterogeneity (Souza et al. 2016).

The use of taxonomic classification to genus proved to be reliable in predicting richness and composition patterns of species distributions independent of sampling technique, sampling area, geographic sites and vegetation type. Furthermore, the high congruence between the SSWS of RDA values obtained with species and genera of ants indicate that these two taxonomic classifications share similar ecological patterns. In all analyses, genus can be rated as a "good" or "excellent" surrogate (i.e. able to predict > 70% of the variation in species data with significant relationships), according to the criteria used by Leal et al. (2010), dos Ribas and Padial (2015) and Souza et al. (2016). Thus, genus-level data proved robust to major concerns raised in the literature.

To evaluate limitations of identification to genus as a higher-taxon approach, we used the species-genus ratio, which has often been reported (Bevilacqua et al. 2012; Neeson et al. 2013; dos Ribas and Padial 2015; Van Rijn et al. 2015; Driessen and Kirkpatrick 2017; Rosser 2017), and has been singled out as an important statistic to take into account for higher-taxa surrogacy studies (Prance 1994; Andersen 1995). Unlike other studies (Rosser and Eggleton 2012; Rosser 2017), we detected a weak influence of the number of species per genus on the correlation coefficient for species richness between sites, and the same low influence of species-genus ratio was also apparent in the comparisons with the correlation coefficients for SSWS values. Together, these results indicate that the predictions of genus level for species richness and environmental responses of Amazonian ants are little influenced by the species–genus ratio. This may be explained

Table 5 Absolute and relative values of time and monetary costs for species- and genus-level identifications of ants for each site and sampling technique

Identification level	Technique	Cost types	Categories	Maracá	Viruá	UFAM	Ducke	Manaquiri	Orquestra	Campanã	Jari	Average of relative costs
Species	Winkler extractor	Monetary	Field-laboratory material (US$)	197.94	197.94	206.18	197.94	31.8	31.8	31.8	31.8	
			Staff costs (US$)	4651.55	4651.55	5592.78	4651.55	902.06	902.06	902.06	902.06	
			Relative monetary cost (%)	100	100	100	100	100	100	100	100	100
		Time	Time consuming (days)	159	159	165	159	24	24	24	24	
			Relative time cost (%)	100	100	100	100	100	100	100	100	100
	Pitfall trap	Monetary	Field-laboratory material (US$)	169.07	169.07	176.08	169.07	27.2	27.2	27.2	27.2	
			Staff costs (US$)	3973.20	3973.20	4776.23	3973.20	770.36	770.36	770.36	770.36	
			Relative monetary cost (%)	100	100	100	100	100	100	100	100	100
		Time	Time consuming (days)	136	136	165	136	24	24	24	24	
			Relative time cost (%)	100	100	100	100	100	100	100	100	100

Table 5 (continued)

Identification level	Technique	Cost types	Categories	Maracá	Viruá	UFAM	Ducke	Manaquiri	Orquestra	Campanã	Jari	Average of relative costs
Genus	Winkler extractor	Monetary	Field-laboratory material (US$)	124.71	124.51	117.52	124.51	18.21	18.21	18.21	18.21	
			Staff costs (US$)	2930.48	2930.48	3187.88	2930.48	514.17	514.17	514.17	514.17	
			Relative monetary cost (%)	63	63	62	63	61	61	61	61	61.9
		Time	Time consuming (days)	86	86	95	86	14	14	14	14	
			Relative time cost (%)	54	54	57	54	57	57	57	57	55.9
	Pitfall trap	Monetary	Field-laboratory material (US$)	106.59	106.59	100.36	106.59	15.55	15.55	15.55	15.55	
			Staff costs (US$)	2502.63	2502.63	2722.45	2502.63	439.10	439.10	439.10	439.10	
			Relative monetary cost (%)	63	63	57	63	57	57	57	57	59.3
		Time	Time consuming (days)	86	86	95	86	14	14	14	14	
			Relative time cost (%)	54	54	57	54	57	57	57	57	55.9

by the use of standardized sampling techniques throughout the study (Andersen 1999; Reyers et al. 2000), standard morphotypes throughout the database (e.g. de Souza et al. 2012), the spatial scale used (Souza et al. 2016), and the variance in the distribution of individuals among species (Neeson et al. 2013), which minimized bias. On the other hand, we detected the effect of the number of species within genera on species composition (dos Ribas and Padial 2015; Rosser 2017), which could restrict the applicability of genus as a higher-taxon approach (Balmford et al. 1996). However, even with this effect of the species-genus ratio, all significant correlations between genus and species composition were higher than 0.7, so genus could still be considered useful for representing information about species composition in this database. Similar results were also found in communities from aquatic environments (dos Ribas and Padial 2015). This further highlights the robustness of genus-level data to known sources of bias.

Even with some studies indicating different results between regions (Andersen 1997; Heino 2014) or even weakening surrogate predictive power with increasing spatial scale (Cardoso et al. 2004a), our results are consistent across the spatial and environmental range studied. Regardless of the sampling technique used, we did not detect changes or reductions in the predictive capacity of genus as a surrogate for species, indicating that the congruence of these relationships is powerful enough to remain stable even with the environmental heterogeneity of the Amazon region. In the Brazilian Amazon, many different ant genera show convergent levels of variation in species richness and composition. That is, the mechanisms affecting ground-dwelling ant assemblages (species sorting and filtering) may be similar for species of different genera. A similar pattern was previously reported for Brazilian savannas as well (Vasconcelos et al. 2014). Genus has been shown to be an effective surrogate of species in several previous studies (Pik et al. 1999; Bilton et al. 2006; Heino and Soininen 2007; Mazaris et al. 2010; Gallego et al. 2012; Alves et al. 2016; Souza et al. 2016), but the assessment of the maintenance of surrogate responses between sampling techniques is still poorly explored. The consistency in the results of this study is important, in places such as the Amazon basin where funding limits biodiversity studies (Costa and Magnusson 2010; Magnusson et al. 2013). Brazilian science is facing one of its worst crises, with large cuts in research funding directly affecting capacity building and research (Escobar 2015; Angelo 2016, 2017). Financing cuts is even more pervasive in places with costly logistics like the Amazon. In this context, some studies are already beginning to include cost analyses and suggest alternatives to save already scarce resources (e.g. de Souza et al. 2012; Souza et al. 2016; Graça et al. 2017). The use of genus as a higher taxon substitute can save up to 40% of time and money, which is a substantial value, especially in times of low budgets for science.

The two techniques most used for sampling ground-dwelling ants showed congruent results for the use of genus in higher-taxon approaches. Identification to genus instead of species collected using these sampling techniques can potentially reveal ecologically important patterns while reducing time and costs for monitoring ecosystem health. Conservation and monitoring programs need data that can support management at mesoscales (100–100,000 km^2). Thus, the time and money saved employing this protocol can be used to sample other areas, or include other strata (i.e. vegetation, subsoil or canopy) and to repeat monitoring of the same area. Taking into consideration the large spatial scale of our study (1000 km; ~ 10 degrees of latitude), the use of solely pitfall traps or Winkler extractors and genus-level identification proved to be cost-efficient and time-efficient and should work well in other regions requiring conservation efforts and monitoring programs. The results that we documented are especially important for the vast Amazon region, which holds an iconic status in global conservation (dos Santos et al. 2015) and where a large sampling effort of invertebrates is required.

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