

Assessing the efficacy of higher-taxon approach for ant species surveys to improve biodiversity inventories

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Abstract

Understanding the distribution of species is essential for the conservation and management of biodiversity. But the availability of this kind of information is still scarce for the most diverse regions. The higher-taxon approach (i.e. use of coarser taxonomic levels to represent species) as an easier and efficient method in representing species patterns can be one way to overcome these constraints. However, there is a general lack of information about the taxonomic stability of surrogate taxa across space and time. We investigated the predictive power and stability of taxonomic identification at the genus level as a predictor of ant species (Hymenoptera: Formicidae) distribution throughout ~1000 km along the Amazon Basin, using taxonomy over the past 120 years. Using intervals of 10 years, from 1900 to 2020 we generated a genus and species matrix based on actual data from our sampling sites for each decade over a total of 120 years. We tested the predictive power of genera as a surrogate of species for approximating species-level richness, composition and distribution-based measures along topographic gradients at local (within site) and regional (between sites) scales. We detected a strong correlation between genera and ant species richness in the current database. There was also high congruence between genera and ant species composition over the time period studied. Genera were also efficient at detecting patterns of species distribution along topographic gradients. Despite changes in ant taxonomy over the past 120 years, our data indicate that such revisions did not affect the ability of ant genera to predict general patterns of ant species in our study area within the Amazon Basin. This reinforces the potential of genera to serve as surrogates for ant species elsewhere, which may significantly decrease the cost of surveying ants in environmental monitoring programs because of the time saved from identifying collected specimens to genus rather than species level.

Introduction

It is widely acknowledged that we are witnessing vast losses to global biodiversity (Ceballos *et al.* 2017), mainly caused by modification of natural environments by anthropic activities, such as hunting, deforestation, agricultural expansion, increase in carbon emissions and urbanization (Laurance *et al.* 2012). Biodiversity loss is still increasing even with the policies and targets created around the globe to prevent it (Ripple *et al.* 2019). Therefore, we need information on the distribution of organisms to generate better biodiversity conservation and management outcomes (Margules *et al.* 2002). Even with the recent advances, the supply of accurate species distribution maps is still restricted, especially for

highly diverse areas (Barlow *et al.* 2011; Gibson *et al.* 2011), thus resulting in the so-called ‘Wallacean shortfall’ (Whittaker *et al.* 2005). The use of surrogates or higher taxa as species substitutes is one approach to minimize this shortfall (Landeiro *et al.* 2012).

There are many types of species substitutes and a range of applications for them as environmental, ecological or biodiversity indicators (McGeoch, 1998); however, to be effective, these surrogates must suitably represent the target group (Souza *et al.* 2016). Generally, organisms are more easily and rapidly identified at higher taxonomic levels, which could act as surrogates for species-level identification (Olsgard *et al.* 2003). The use of coarse taxonomic identification as a surrogate for species-level identification is more

common in highly diverse groups such as invertebrates (Gaspar *et al.* 2010; Gallego *et al.* 2012) and plants (Ramsay *et al.* 2006). However, many invertebrate groups are being taxonomically reassigned with the increasing use of genetic information (e.g. Inward *et al.* 2007). Therefore, incorporating a time scale in surrogate species research is essential to predict the success of higher-taxon approaches over time (Favreau *et al.* 2006). Understanding the effectiveness of higher-taxon surrogates over time may have two main implications: (1) to explicitly include the temporal dynamics in surrogates assessments, something that earlier studies have already done (e.g. Magierowski & Johnson, 2006; Lentini & Wintle, 2015; Souza & Fernandes, 2021); and (2) to investigate the effect of taxonomic changes over time on surrogate responses, something which remains poorly explored (e.g. Heterick & Majer, 2018) and largely unknown. The latter implication directly affects the use of past inventories which are of increasing interest to investigate the responses of biodiversity to climate change (Zettler & Daunys, 2007; Dornelas *et al.* 2014).

Genus-level identification is often presented as a surrogate candidate for species-level identification (Pik *et al.* 1999; Gallego *et al.* 2012). However, the efficiency of the genus as a surrogate appears to be affected by the species-genus ratio. The use of the genus as a surrogate works best for groups with a species-genus ratio close to 1:1, while groups that have more species tend to have more conflicting results (Van Rijn *et al.* 2015; Driessen & Kirkpatrick, 2019). Spatial scale may also affect the effectiveness of the genus as a surrogate for species identification. In some cases, the ecological patterns detected using the genus generally reflect the ecological patterns of species on both smaller and larger scales (dos Ribas & Padiál, 2015; Souza *et al.* 2016), but in other cases genus as a surrogate may fail to retrieve species-level information at larger scales (Rosser & Eggleton, 2012). These idiosyncratic outcomes could undermine the usefulness of the genus as a surrogate (Van Rijn *et al.* 2015). Despite these drawbacks, the surrogate approach remains attractive due to faster and more accurate taxonomic identification (Williams & Gaston, 1994; Gotelli, 2004) and a consequent reduction in biodiversity research costs (Souza *et al.* 2016). Time and money spent on biodiversity surveys are critical factors (Margules *et al.* 2002), especially for taxonomically diverse groups with small body sizes such as invertebrates (McGeoch, 1998; Hodkinson & Jackson, 2005).

During the past decade, the higher taxonomic classification of ants (Hymenoptera: Formicidae) has received significant attention (Schmidt & Shattuck, 2014; Blaimer *et al.* 2015; Ward *et al.* 2015). Due to careful reassessments of morphological variation (Schmidt & Shattuck, 2014) and molecular phylogenetic studies (Ward *et al.* 2015), the higher classification of the subfamilies of Formicidae is now relatively stable. Within those subfamilies, however, uncertainty remains in terms of the relationships within and between major ant genera. This taxonomic instability also affects different taxa in different ways, where more diverse groups tend to have fewer problems with reclassifications of species already described (Thomson *et al.* 2018). However, the effect of such taxonomic uncertainties on studies with surrogates

has been little debated (Morrison *et al.* 2009; Strand & Panova, 2015).

Here, we investigated the effect of spatial scale and taxonomic changes on the efficiency of genera as surrogates of ant species in the Brazilian Amazon. We hypothesized that, regardless of taxonomic adjustments (affecting the status of genera or species) or spatial scale, the coarser taxonomic level (genus) could be used as an efficient surrogate for species-level identification. Specifically, we evaluated whether the taxonomic changes over the last 120 years and/or the spatial scale have an effect on the diversity metrics, that is number of species (richness) and species composition. Richness is probably the simplest and most often used measurement for diversity. However, this metric gives the same weight to rare and abundant species, and unsurprisingly the distribution patterns of assemblage composition and species richness often produce different results (Oliveira *et al.* 2009). We also assessed whether patterns of a genus-level resolution against key environmental variables maintain responses similar to using species-level data. Finally, we tested whether the results obtained at the genus-level (richness, composition and distribution along topographic gradients) in this study were affected by the species-genus ratio.

Materials and methods

Study sites

The research was carried out at nine sites maintained by the Brazilian Biodiversity Research Program (PPBio). The sites cover phytophysiognomies with different topographic and soil characteristics that naturally occur along ~10 degrees of latitude (~1000 km) in the Amazon Basin (see Table 1 and Fig. S1 for additional geospatial information pertinent to the study).

Sampling design

Ground-dwelling ants were sampled using the RAPELD sampling design, which is based on a system of trails and permanent plots where a diverse range of taxa can be sampled (Magnusson *et al.* 2013). The RAPELD system can be applied at a variety of spatial scales. Smaller modules (combinations of trails and plots) were used for rapid cross-site assessments. The acronym RAP was coined by Conservation International for rapid biological surveys. Larger grids were used to investigate the ecological processes in more accessible sites. These are often long-term ecological research sites (LTER or PELD in Portuguese). The permanent plots were 250-m long and positioned to follow the terrain contours to minimize the effects of topographical variation within plots. The number of 250-m long plots varied from 5 to 30 per site, were located at a distance of 1 km from each other and had the same standardized spatial design (Table 1).

Ant sampling

Ground-dwelling ants were collected using pitfall traps, sardine baits and Winkler extractors. One to three sampling

Table 1 Vegetation, elevation range, rainfall, spatial sampling design and sampling techniques in nine sites in the Brazilian Amazon

Sites	Coordinates	Vegetation type (number of plots)	Elevation range (m.a.s.l.)	Mean rainfall (mm)	Sampling area (km ²)	Number of plots	Number of samples per plot	Technique used	Total of samples	Sampling date
Maracá	3°22'56.73"N 61°27'52.31"W	Open ombrophilous forest (14), Deciduous forest (7), Semi-deciduous forest (8), Campinarana seasonal forest (1)	54–85	1718	25	30	10	Bait, Pitfall & Winkler	900	February/ 2007
Cauamé	2°52'12.00"N 60°38'24.00"W	Open savannas (12)	67–85	1650	5	12	10	Bait & Pitfall	240	February/ 2011
Virúá	1°27'49.28"N 61°1'30.59"W	Open ombrophilous forest (12), Campinarana seasonal forest (8), Seasonal campinarana (6), Seasonal shrubby campinarana (4)	43–130	1682	25	30	10	Bait, Pitfall & Winkler	900	February/ 2007
UFAM	2°38'26.51"S 60°5'44.55"W	Dense ombrophilous forest (21)	42–130	2362	24	21	10	Pitfall	210	September/ 2011
Ducke	2°57'51.69"S 59°56'27.26"W	Dense ombrophilous forest (30)	46–110	2507	25	30	10	Bait, Pitfall & Winkler	850	September/ 2006
Manaquiri	3°41'31.25"S 60°14'51.60"W	Open ombrophilous forest (10)	30–36	2200	5	10	10	Pitfall & Winkler	200	November/ 2009
Orquestra	4°59'2.39"S 61°34'30.00"W	Dense ombrophilous forest (5)	36–61	2200	5	5	10	Pitfall	50	November/ 2010
Campanã	5°36'36.00"S 62°12'0.00"W	Open ombrophilous forest (5)	70–72	2200	5	5	10	Pitfall	50	November/ 2010
Jari	5°58'11.99"S 62°29'24.00"W	Open ombrophilous forest (5)	70–72	2200	5	5	10	Pitfall	50	November/ 2010

techniques were used per site. In each plot, 10 sampling stations were established at 25-m intervals (Table 1). At each sampling station, the ants were extracted from 1 m² of sifted litter in a Winkler extractor through a 1 cm² mesh sieve and placed in Winkler sacks. The sieved litter was placed in a mesh bag suspended inside a cotton bag for 48 h. Pitfall traps and sardine baits were placed at the same stations after the litter was collected. The pitfall traps were 8-cm deep and 9.5 cm in diameter and were buried with the rim at ground level and left open for 48 h. After the pitfall traps were removed, approximately 5 g of canned sardine was placed on a plastic card on the litter surface. All ants on the plastic card were collected after 45 min and preserved in 90% ethanol (Souza *et al.* 2012).

All the ants were first identified to genus-level using the taxonomic keys provided by Baccaro *et al.* (2015), and then sorted according to species. We used available taxonomic keys and comparisons with specimens in collections previously identified by experts. A unique identification code 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 have been deposited in INPA's Invertebrate Collection. The data used here are available in Table S1.

Environmental variables

Environmental variables were measured in the same permanent 250 m plots in which the ants were sampled at each study site. The slope of the terrain was measured with an inclinometer. Six measurements were taken along the plot, spaced 50 m apart. The measurements were taken perpendicularly to the plot, 2 m away from the center line. Soil clay content (%) was determined from physical-chemical analysis of soil samples collected from six points spaced at every 50 m along the plot. The soil samples were collected at the depth of up to 20 cm after removal of the leaf litter and large roots. The individual soil samples were mixed, yielding a sample representing the plot, of which 500 g was separated for particle size analysis. After dispersion with sodium pyrophosphate, the clay percentage of the soil samples was determined by drying 20 mL of the suspension in an oven at 105°C (for more details and metadata, please visit PPBio website <https://ppbio.inpa.gov.br/manuais>).

Data analysis

Before analyses, the information of each sampling station (Winkler, pitfall and sardine baits) was combined per plot to provide the most comprehensive species list possible. We

used two approaches in this study, one using the complete database with taxa identified to species and morphospecies, and another using only the taxa formally identified to species called hereafter the reduced dataset. We evaluated two granularity levels in this study: one coarse, considering variation at the site level ($n = 9$), and one fine-grained at the plot level ($n = 158$), along the entire topographic gradient. The two-grain level analysis may produce different results due to differences in species sampling coverage. In addition, the usual biodiversity metrics (species richness, composition, productivity and genetic variability) are highly dependent on the spatial scale (Costa & Magnusson, 2010). All analyses were run in the R environment for statistical computing (R Core Team, 2021, version 4.1.0), using the *vegan* 2.5-7 (Oksanen *et al.* 2020), *lme4* 1.1-27.1 (Bates *et al.* 2015) and *MuMIn* 1.43.17 (Barton, 2020) packages. We built all graphics using the *ggplot2* 3.3.5 (Wickham, 2016) and *gridExtra* 2.3 (Auguie, 2017) packages.

Taxonomic modification surveys over 120 years

We obtained information about the taxonomic modifications of Formicidae over 120 years from the Hymenoptera Name Server (<https://hns.osu.edu>). The Hymenoptera Name Server organizes and keeps track of species taxonomy modification since 1900 providing key information about when a new taxa combination was established or synonymized. We used the unique code attributed to each taxon of the Hymenoptera Name Server to create our current database looking back at the data in intervals of 10 years. Thereby, for the reduced data set, the number of species and genus increased over time, following the taxonomy history. For the complete dataset, we assumed that changes in a particular genus were applied to all species in that genus. In this way, we have created a database with valid species and genus identification from the year 1900 to 2020 using only species formally described (reduced database), and all entities, species and morphospecies (complete database). We aimed to reproduce the valid taxonomic identification corresponding to the respective time period, and so we constructed Table S2 according to the dates of the taxa descriptions. Therefore, genera or species not officially described in a given decade were left as empty cells.

Higher-taxon and richness

We calculated the correlation between the number of genera and the number of species found in each studied site to estimate whether genus richness can predict species richness. The associations between the numbers of species and genera were calculated within each study scale (fine or coarse) from 1900 to 2020 at decade intervals. We used generalized linear mixed-effects models (Bates *et al.* 2015) and included location as a random factor in the models, respecting the hierarchy of the data for each spatial scale studied. We built figures to show the trend of genera predictions over the 120 years. We adjusted the significance levels for multiple

tests of the same hypothesis with the Bonferroni correction. We used a local polynomial regression (locally estimated dispersion plot smoothing - LOESS) to fit a smoothed line in the figure and show the general trend of the regression coefficients (Marginal R GLMM2 or R2m) over the decades. We chose this regression class because there is no necessary linear prediction about the response of genus surrogates over time. The 95% confidence interval was calculated based on the Student's *t*-distribution for each adjusted *y*-value.

Higher-taxon and composition

To calculate the association between the genus and species composition matrices by each spatial scale studied (coarse and fine), we used permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001). The study locations (sites or plots nested by sites) were included as strata in the PERMANOVA permutation structure to control the possible spatial autocorrelation of the data. We used relative-frequency data (i.e. the number of sampling stations in a plot in which a species was collected), to avoid giving more weight to abundant species when constructing the taxa-composition matrix (Gotelli *et al.* 2011). We estimated the statistical significance of the PERMANOVA tests based on 999 permutations. We adjusted the significance levels for multiple tests of the same hypothesis with the Bonferroni correction. We used a LOESS to fit a smoothed line in the figure and show the general trend of the PERMANOVA regression coefficients over the decades. We calculated the 95% confidence interval based on the Student's *t*-distribution for each adjusted *y*-value.

Association with the environment

We evaluated whether a genus maintains the relationships detected between ground-dwelling ant species and the topographic variables (slope of terrain and percentage of soil clay content) over time. We chose these environmental variables because they are correlated with the richness and composition of ant assemblages in the Brazilian Amazon (Oliveira *et al.* 2009; Souza *et al.* 2016; Gomes *et al.* 2018). We also included vegetation type and location as variables in the analysis.

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 is a type of direct ordination that combines regression and principal component analysis (Borcard *et al.* 2011). We performed the RDA with species and genus matrices for each decade to test the effect of environmental variables on ant assemblages. To evaluate the consistency of the results, we checked whether the variance explained by the variables changed between taxa (species and genera) and between decades. We estimated the statistical significance of the RDA tests based on 999 permutations. We adjusted the significance levels for multiple tests of the same hypothesis with the Bonferroni correction. 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 & Legendre, 2003). High congruence between the SSWS species and the genus data for each decade interval indicates that the explanatory covariates have a similar power level. We then assume that this is an adequate approximation that assemblages are responding similarly to environmental variables, independent of the taxonomic identification used at the time. We measured the Pearson correlation between the SSWS axes of genus and species for each time interval. We used a LOESS to fit a smoothed line in the figure and show the general trend of the SSWS correlation coefficients over the decades. The 95% confidence interval was calculated based on the Student's *t*-distribution for each adjusted *y*-value.

Species-genus ratio and the effect on higher-taxon responses

We used the species-genus ratio to evaluate if there is a loss of information when using genera as a surrogate of ant species due to differences in the number of species per genus. We correlated the values of the coefficients (between genus and species-level) of each metric evaluated (richness, composition and SSWS axes) with the species-genus ratio per decade.

Results

The smallest and largest number of taxa were detected at the two extremes of the time period, in 1900 and 2020, respectively, for both the complete (species + morphospecies) and reduced (without morphospecies) datasets based on the taxonomy in use at each respective time period. Between 1900 and 2020, the number of species and genera in the complete dataset increased by 1.4-fold (314–423) and 1.3-fold (58–73), respectively, and 1.7-fold (144–247) and 1.3-fold (52–65), respectively, in the reduced dataset (Table S3). The results of our analysis were also similar regardless of the spatial scale used (coarse vs. fine), and therefore, we present our results from the fine spatial scale analyses (see Table S3 for additional results). Genus richness adequately predicted species richness, regardless of the spatial grain or the database used, over the analyzed decades (Fig. 1; Table S3, column F). The values of the richness regression coefficient were ≥ 0.7 (Fig. 2a,b), and in general, the fine-scale had higher values than the coarse-scale. Regardless of the spatial scale, location explained a small part of the data variance, sometimes even having no effect (Table S3, column G).

The associations between the species- and genus-level compositions were similar for the two grains (coarse and fine-scale) and for complete and reduced databases over the studied decades (Fig. 2c,d, Table S3). In all cases, the PERMANOVA correlation coefficients were above ≥ 0.7 and statistically significant in all comparisons between the genus- and the species-level composition matrices. Regardless of the spatial scale, location explained a small part of the data variance (Table S3, column I).

Ant assemblage composition was significantly related to the environmental variables throughout the decades for the two grain levels and for the complete and the reduced databases (Table S3). With the complete database, the site scores weighted by species (SSWS) correlation values had a greater amplitude when compared to the reduced database (Fig. 2e, f). In addition, the genera and the species presented similar responses to the environmental variables, as the correlation values of the SSWS are high (≥ 0.7 ; Table S3, column T).

The effect of the species:genus ratio was detected only for the richness data with the reduced database (without morphospecies), at the fine spatial scale (reduced database: $r = 0.77$; $P \leq 0.01$; Fig. 3b). For the other metrics analyzed, there was no relationship detected between the species:genus ratio and species richness, assemblage composition or environmental variables (Fig. 3). At the fine spatial scale, we found no significant correlation between species:genus ratios and richness correlation coefficients (complete database: $r = 0.08$; $P = 0.803$), composition coefficients (complete database: $r = 0.35$; $P = 0.235$; reduced database: $r = -0.18$; $P = 0.547$) and SSWS coefficients (complete database: $r = 0.22$; $P = 0.478$; reduced database: $r = -0.09$; $P = 0.782$) in either database over time. Similarly, at the coarse scale, we found no significant correlation between species:genus ratios and richness correlation coefficients (complete database: $r = 0.27$; $P = 0.374$; reduced database: $r = 0.84$; $P \leq 0.01$), species composition coefficients (complete database: $r = 0.35$; $P = 0.235$; reduced database: $r = -0.18$; $P = 0.547$) and SSWS coefficients (complete database: $r = 0.24$; $P = 0.429$; reduced database: $r = -0.06$; $P = 0.862$) in either database over time.

Discussion

Surveys using the higher-taxon approach are generally focused on spatial variation. However, most of such research results would be used for biodiversity monitoring which usually involves time-series data. In this study, we add relevant information to considering the use of genera as surrogates for species identification that may substantially reduce the amount of time required for identification and, thus, reduce the resources needed for monitoring. The stability of the genus–species relationship throughout the 120 years of modern ant taxonomy, regardless of spatial scale, strongly indicates that the genus is a good and stable predictor of ant species diversity within the Amazon Basin.

The use of genus or other higher taxa to predict species diversity in monitoring has idiosyncratic outcomes. Some results support the use of higher taxonomic surrogates for various taxa (Williams & Gaston, 1994; Pik *et al.* 1999; Ricketts *et al.* 2002; Su *et al.* 2004; Alves *et al.* 2016), however, there are also reports showing that surrogates are a poor predictor of species-level patterns (Lawler & White, 2008; Gaspar *et al.* 2010). Two non-mutually exclusive hypotheses have been proposed to explain these idiosyncrasies. Some suggest that species proportions within genera or other higher taxa may show skewed distributions, especially if several monotypic taxa are present, inflating the relationship between genus and species

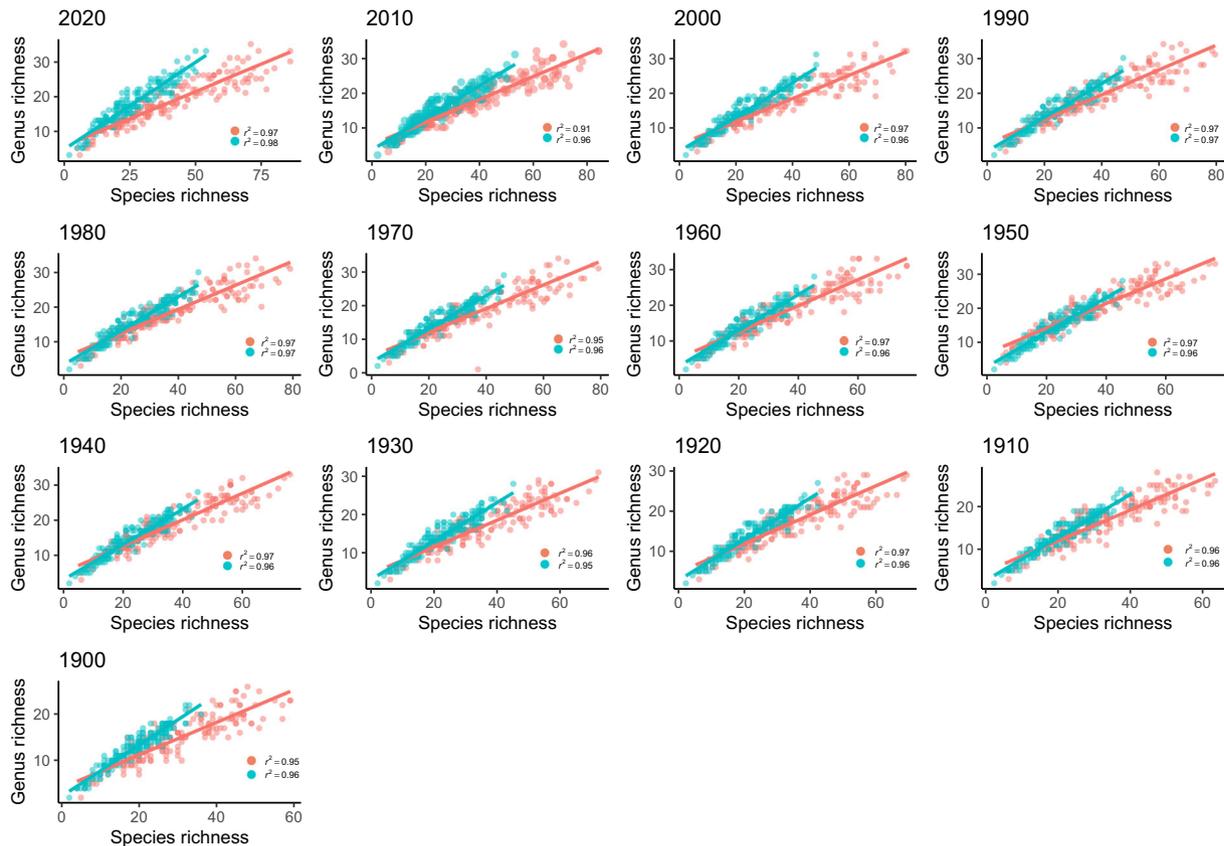


Figure 1 Regressions between the numbers of genera and species of ground-dwelling ants for complete (red circles) and reduced (green circles) database per plot, for nine study sites located in the Brazilian Amazon. The statistical significance of models was tested using 1000 permutations. All regressions were significant at $P < 0.001$.

metrics (Strand & Panova, 2015; Van Rijn *et al.* 2015; Rosser, 2017; Driessen & Kirkpatrick, 2019). Other researchers suggest that the lack of standardization of data collection and spatial scale could affect the ability of these taxa to be efficient as surrogates (Lawler & White, 2008). However, the use of genera as a taxonomic surrogate for species-level richness analyses seems to be a viable option, with vast support in invertebrate studies (Pik *et al.* 1999; Gallego *et al.* 2012; Alves *et al.* 2016), along with other relevant options like the use of indicator taxa (Lawton *et al.*, 1998) or models that mix the two previous categories (Groc *et al.*, 2010; Koch *et al.*, 2021). In the Amazon Basin, despite the high environmental heterogeneity or the sampling technique used, the ant genera were effective in detecting species richness, composition and distribution patterns along topographic gradients (Souza *et al.* 2016, 2018). Our results add a prominent facet to this pattern, showing that genus-level classification has consistent results over a century of modern ant taxonomy regardless of spatial resolution (plot or site) or database (reduced or complete). This stability using coarser taxonomic identification may be promising for organisms with taxonomic uncertainties at the species level. For example, parasitoid wasps are difficult to identify at the species level, and some beetle families are extremely diverse, making species identification more time-consuming.

Recently, the species:higher-taxon ratio variation was proposed as one of the main objections to surrogate analysis (Ribas & Padiál, 2015; Van Rijn *et al.* 2015; Rosser, 2017; Driessen & Kirkpatrick, 2019), even though this pattern and its effects had been reported years earlier (Prance, 1994). The species:higher-taxon ratio could be considered an indirect way of assessing the outcome of taxonomic changes on surrogate responses since this ratio is related to the number of described taxa. However, the studies that tested for the species:higher-taxon ratio were performed without explicitly assessing the effect over different spatial (most were conducted at smaller scales) or time scales (Rosser & Eggleton, 2012; Rosser, 2017). At the two-grain resolution, using both the complete and the reduced databases, our results did not detect a significant effect between the species-genus ratio and the metrics of taxon richness, taxon composition or distribution patterns of ant assemblages along environmental gradients. Deciding on the efficiency of surrogates using only the species-taxa ratio seems to be less cautious, whereas the use of various metrics to evaluate the usefulness of surrogates seems to be more parsimonious and less prone to conflicting conclusions (Rosser, 2017; Souza *et al.* 2018).

New processes using phylogenies, generic classifications and taxonomic descriptions could cast doubt on the quality

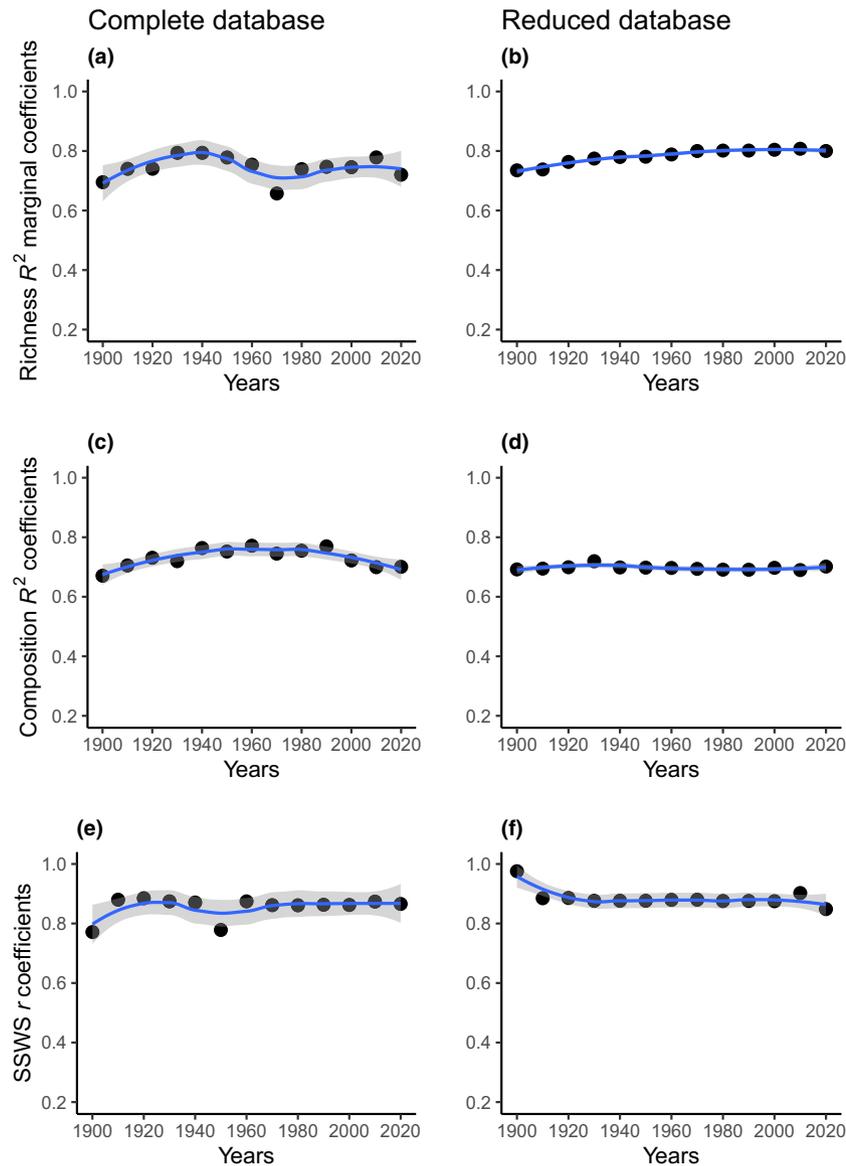


Figure 2 Distributions of regression and correlation coefficients between genera- and species-level taxonomy for taxon richness (a, b) and composition (c, d) and their correlations with the environment, or % clay, slope, vegetation type and locations (e, f) by decade over 120 years for both the complete (left) and reduced (right) datasets. Smooth curves have been fitted by LOESS and their respective 95% confidence interval (shaded area) for the correlation coefficients over decades are shown.

of surrogates over time, as many such works carried out profound reorganizations regarding the classification of particular groups (Brady *et al.*, 2014; Schmidt & Shattuck, 2014; Ward *et al.* 2015). However, in more than a hundred years of taxonomic modifications, regardless of the tools used by taxonomists, the results with genera as surrogates for ant species level remain stable as shown with our study area within the Amazon Basin. Biodiversity studies are undoubtedly among the most affected by uncertainties in the taxonomic lists. Much of the existing knowledge on biodiversity has been collected and organized using species (or higher taxa) names, and the growing need to evaluate and monitor

biodiversity demands efficient taxonomic identification (Strand & Panova, 2015), further highlighting the importance of work done by taxonomists.

The effect of taxonomic changes or taxonomic instability on biodiversity studies has received little attention (Morrison *et al.* 2009) or has even been overlooked (Strand & Panova, 2015), although this issue has recently regained momentum (Garnett & Christidis, 2017). Although its impact seems to be reduced in groups with greater diversity, such as ground-dwelling ants, taxonomic instability may have pronounced effects in bats, rodents and birds (Thomson *et al.* 2018). These taxa are often used as emblematic or umbrella species,

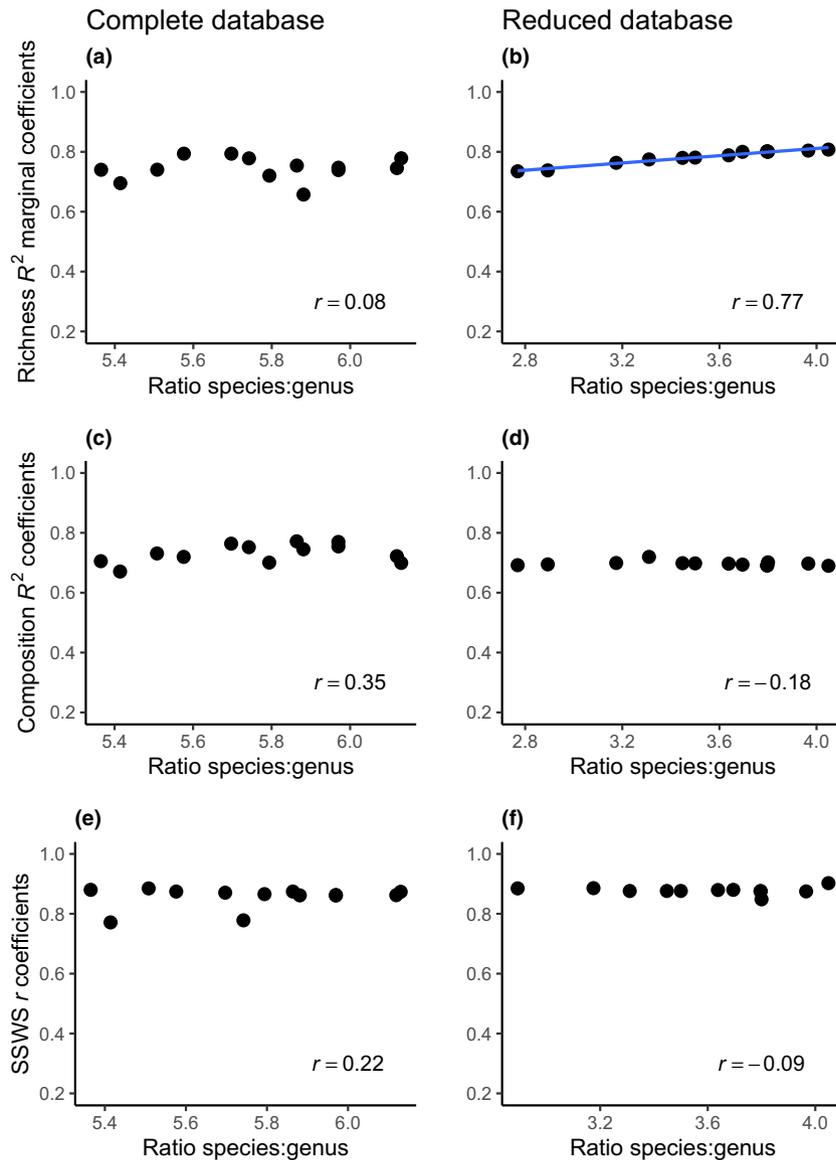


Figure 3 Relationships between matrix regression and correlation coefficients and the number of ant species per genus measured at fine spatial scale for taxon richness (a, b) and composition (c, d) and their correlations with the environment (e, f) for the complete (left) and reduced (right) datasets.

and could benefit from our results using the higher-taxon approach and thus minimize the effects of this instability. Our data confirm that surrogates of highly diverse groups may be less prone to inconsistencies, as through 120 years of taxonomic adjustments, genera satisfactorily retrieved information on ground-dwelling ant species distributed over a wide environmental gradient in the Amazon Basin. These results also reinforce the idea that genera can also possess part of the information on the evolutionary processes of their constituent species (Strand & Panova, 2015). It is also a considerable step for the use of genera as a taxonomic surrogate for species level inferences in environmental monitoring programs, as we are dealing with a cumulative effect of taxonomic adjustments that could be potentiated over the years.

There are few studies about surrogate responses over the years, with most having short intervals of less than two years (Magierowski & Johnson, 2006), or they group data over many time periods (Olsgard *et al.* 2003; Tulloch *et al.* 2016). This approach seems to overlook the effect of time on changes in the distribution of organisms and assume (often not explicitly) that the changes in biodiversity detected in samples collected from various locations and at different times are only related to spatial (environmental) variation.

Our results strongly suggest that the taxonomic adjustments made by experts over 120 years did not affect the ability of surrogates to reveal ecologically relevant patterns within our study system. It already has been shown that using the genus as a surrogate to species in the Amazon Basin can save up to

60% of resources in biodiversity inventories (Souza *et al.* 2016). These resources could be allocated to fund replication surveys over time (Mueller & Geist, 2016; Souza *et al.* 2018). It has been shown that the higher-taxon approach can produce relevant results in this kind of monitoring (Souza & Fernandes, 2021), and may be particularly important in situations where governmental science funding is seen as a burden or an unjustified cost by politicians or decision-makers (Magnusson *et al.* 2013; Escobar, 2015; Angelo, 2017). Although surrogates have long been used in ecological and monitoring studies (Ellis, 1985; Prance, 1994), examples of their use as effective protocols are still scarce, most likely due to the lack of tests showing their effectiveness over time (Favreau *et al.* 2006; Magierowski & Johnson, 2006) or the potential effect of taxonomic changes. Furthermore, the higher-taxon approach for organisms with difficulties in species determination seems promising since we did not detect any effects of taxonomic changes on the efficiency of genera as surrogates for ant species.

There is a growing need for longer monitoring time series to uncover biodiversity trends related to the changing climate (Dornelas *et al.* 2014). Revisiting sites with high-quality historic datasets is a predominant way to generate longer monitoring records. However, such high-quality datasets are rare for insects, especially in the tropics. Our results support the use of higher taxonomic resolution in biodiversity surveys, which can increase the number of monitoring sites and hence the spatial scale that can be used to compare with contemporaneous data. Whenever possible, future research on surrogates should prioritize detecting taxa responses over time, increasing the possibility of surrogates gaining their place in biodiversity monitoring studies.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Locations of the nine sites in the Brazilian Amazon.
Table S1. Frequency of ground-dwelling ant species sampled in nine sites located in the Brazilian Amazon.

Table S2. List with valid taxonomic identifications for ants in the Brazilian Amazon in each decade over 120 years of modern ant taxonomy.

Table S3. Values of species and genus richness; regression coefficients of richness, composition and environment and species:genus ratio for the two spatial scales and the two databases tested in nine sites located in the Brazilian Amazon.