

Geographic position of sample grid and removal of uncommon species affect multivariate analyses of diverse assemblages: The case of oribatid mites (Acari: Oribatida)



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ABSTRACT

In view of the rapid loss of biodiversity, large-scale environmental monitoring programs are urgently needed, over a range of local, regional and global scales. These programs can be made more efficient and cost-effective through shortcuts such as reduction of sampling effort and the use of low-cost surrogates. We revisited a large-scale dataset composed by 161 species recorded in 72 plots of 250 m, distributed over an 8 m × 8 m sampling grid in the tropical rainforest. Samples of litter and soil were collected and oribatid mites were extracted with a Berlese–Tullgren apparatus. Using a “moving window” procedure, we delimited smaller 5 km × 5 km grids in 16 possible positions within the larger grid. We first evaluated which fraction was more important to explain environmental and spatial patterns in the species composition: known environmental or spatial filters representing unknown causes of aggregation, and the confounded variance that might be associated with either or both. We used soil clay content, litter quantity, soil pH, number of trees, and distance to the nearest stream as environmental predictors. The spatial filters were generated using Moran Eigenvector mapping through the Principal Coordinates of Neighbor Matrices technique. To evaluate the influence of these fractions on the species composition, we used partial Redundancy Analysis. Using Principal Coordinates Analysis for abundance and presence/absence data, we evaluated if reduced matrices, discarding sets of less-frequent species, could identify the relationships captured with the complete dataset. All smaller grids contained more than 100 species. The effect of environmental variables on oribatid-mite community composition was always low, and each smaller grid position produced different results. Soil clay content and pH were the main factors associated with oribatid-mite distributions. The effects of unknown spatial patterns were greater than the environmental ones. Independently of the grid position, similar results were obtained for analyses with all oribatid-mite species, to the results obtained from analyses of only the most frequent species. Sets of more frequent and easily identifiable species proved to be a reliable surrogate for the complete assemblage. Omitting identifications of most species will improve the cost-effectiveness of monitoring programs. More emphasis should be placed on investigating the role of spatial heterogeneity and the effects of grid position in relation to patterns in species associations. Efficient biomonitoring could target surrogate species, to enable rapid tracking of environmental change while enlarging the sampling area to provide data for conservation strategies.

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1. Introduction

1.1. Landscape variability influences assemblages recorded in large-scale surveys at smaller spatial scales

Although more tests and research are needed, the simplification of biomonitoring assessment and the use of surrogates are

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suggested as necessary shortcuts for conservation planning (Landeiro et al., 2012a; Rodrigues and Brooks, 2007; Sebek et al., 2012). Large-scale, long-term and integrated biodiversity monitoring programs must be implemented over a range of local, regional and global scales (Costa and Magnusson, 2010; Sebek et al., 2012). One of the impediments to biodiversity measurements is their dependence on the sampling effort and the size of the area measured (Margules et al., 2002; Vane-Wright et al., 1991). The relative importance of spatial and environmental factors for influencing abundance and diversity has been the subject of studies involving plants (Landeiro et al., 2012a; Li et al., 2011), several groups of aquatic organisms (Landeiro et al., 2012b; Soininen et al., 2007), ants (Baccaro et al., 2012), and oribatid mites (Borcard and Legendre, 1994; Caruso et al., 2011; Lindo and Winchester, 2009; Minor, 2011). However, complete surveys are not a practical option because they depend on field data and the availability of experts, and require substantial investments of financial resources and time, especially in hyperdiverse groups (Margules et al., 2002; Moraes et al., 2011; Santos et al., 2008). Fisher (1999) reviewed the literature up to the end of the 20th century and showed that effective and practical methods to survey hyperdiverse groups are possible.

The number of replicates influences the ability to detect ecological responses of invertebrates (Santos et al., 2008; Souza et al., 2009), but the positioning of the sample sites in the landscape might also be important. Moraes et al. (2011) investigated the edaphic oribatid-mite assemblage in an 8 km × 8 km grid with 72 250-m long permanent plots arranged regularly across a landscape covered by dense Amazon rainforest. The soil clay content, litter quantity and pH generated microhabitat variability associated with patterns in the mite assemblage, but we do not know to what extent the environmental variability across the landscape influences the assemblage at smaller spatial scales.

Oribatid mites are small (150–2000 μm in length), characterized by high density and diversity (Norton and Behan-Pelletier, 2009) and low dispersal capacity (Berthet, 1964; Minor, 2011). These mites feed on fungi, algae, amorphous detritus or other soil animals, thereby functioning as microherbivores, herbivores, detritivores/litter transformers and predators (Norton, 1986; Scheu, 2002). Oribatid mites occur in aggregations of individuals (Berthet, 1964; Usher, 1975); this tendency has been attributed to several environmental factors, including water availability, temperature, time of day, season, food source, microflora vegetation, soil clay content, litter quantity and soil pH (Erdmann et al., 2012; Moraes et al., 2011), as well as endogenous factors, such as clustering of eggs (Usher, 1975). Biological activity is extremely important for decomposition processes and release of nutrients in tropical forests (Luizão and Schubart, 1987). The conservation of meso-invertebrate assemblages will depend on the conservation of the vegetation structure and plant diversity.

Changes in the invertebrate assemblage composition alter the action of primary decomposing agents in terrestrial soils (Crowther et al., 2011), and positive correlations have been detected between plant species richness and meso-invertebrates, including oribatid mites (Eisenhauer et al., 2011). Although litter decomposition is mainly the result of microbial and invertebrate activities (Coleman et al., 2004; Luizão and Schubart, 1987), in tropical forests oribatid mites account for a large portion (50%) of the known biodiversity of detritivores, and decomposition of litter is mainly due to the activities of fungi, termites, springtails and oribatid mites (Braganeto et al., 2011; Fonseca et al., 2009; Moraes et al., 2011).

Different oribatid assemblages occur on tree trunks and in the soil (Lindo and Winchester, 2009), in different forest types (Erdmann et al., 2012; Sylvain and Buddle, 2010), in exposed grassy and sheltered shrubby sites (Kallimanis et al., 2002), in beech forest and grassland (Caruso et al., 2011), and in forest fragments and the surrounding savanna matrix (Ferreira et al., 2012). Gross

differences in assemblages between distinct habitat categories are to be expected; however, more-subtle variations may also occur in the oribatid assemblage within a single forest type.

1.2. Selecting potential surrogate species

Invertebrate sampling is relatively fast, but requires extensive laboratory work to sort and identify specimens (Santos et al., 2008; Souza et al., 2009). We attempted to reduce time required in sorting by reducing the number of species and the high frequency of rare species that are often represented in quantitative samples of oribatid mites in tropical forests (Ferreira et al., 2012; Moraes et al., 2011; Santos et al., 2008). The numbers of soil oribatid-mite species recorded in large-area surveys in the Amazon region range from 91 in savanna (Santos et al., 2008), 143 in semi-deciduous forest fragments (Ferreira et al., 2012) to 161 in dense Amazon rainforest (Moraes et al., 2011). The percentages of singletons and doubletons in these forests were 33%, 34% and 16%, respectively. Based on our experience with Amazonian oribatid mites, identification of rare species (singletons and doubletons) accounts for about 50% of laboratory time. About 50–61% of these rare species are undescribed. In contrast, in the Amazon region, the majority of the most frequent oribatid-mite species have been described (see Ferreira et al., 2012; Moraes et al., 2011; Santos et al., 2008), and are easily recognizable after short periods of taxonomic training. Researchers undertaking multivariate analyses, such as Borcard et al. (1992), Borcard and Legendre (1994) and Minor (2011) often discard the less-frequent oribatid-mite species from their analyses. Caruso and Migliorini (2006) used higher taxonomic groups of oribatid mites, at family and genus levels. We therefore assumed that, if common species are sufficient to describe turnover along spatial and environmental gradients, sets of less-frequent species can be discarded from the analyses.

Comprehensive assessment of patterns can be obtained by revisiting existing data (see Rodrigues and Brooks, 2007). In this investigation we used the maximum set of oribatid-mite species recorded by Moraes et al. (2011) within a large and original 8 km × 8 km grid with 72-plots. A “moving window” scheme was produced to evaluate the possible results that we would obtain if we established a smaller 5 km × 5 km grid with 30 plots each. There are 16 possible positions for grids of this size within the 8 km × 8 km grid. The size of 5 km × 5 km was chosen because this is the standard size RAPELD grid in many Amazonian sites (Costa & Magnusson, 2010). We investigated whether differences in assemblage–environment associations across sampling grids were due to changing environmental heterogeneity in space. Because of the continuous gradient within the same type of forest, we expected that differences in the oribatid-mite assemblage among smaller grids would be subtle or not detectable. If this proved to be so, the geographical positioning of the smaller grids would not be the most important factor for understanding oribatid-mite distribution. If this did not prove to be the case, we first evaluated which fraction was more important to explain environmental and spatial patterns in the species composition: known environmental or spatial filters representing unknown causes of aggregation, and the confounded variance that might be associated with either or both. We then evaluated if alternative and simplified matrices derived by successively discarding of the less-frequent oribatid-mite species could still retrieve the ecological signal captured with the maximum set of species. We also looked for the minimum set of species that would still retain the ecological signal captured with the complete data set. If a similar pattern persists for successively reduced sets of species, time and money can be saved, and this procedure can be a reliable shortcut to increase sampling efficiency and expand sampling intensity.

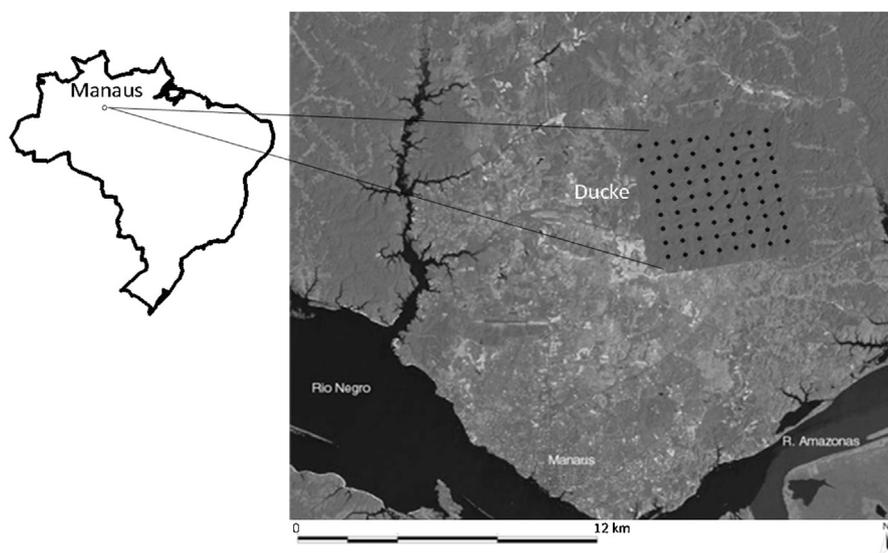


Fig. 1. Location of the Reserva Ducke adjacent to the city of Manaus in the Brazilian Amazon. Points indicate 1-km equidistant sample plots (image: Landeiro et al., 2012a).

2. Material and methods

2.1. Study site

Fieldwork was conducted from September 2001 through May 2002 in the Reserva Ducke, a protected area situated 25 km north-west of Manaus (3°01' S, 59°59' W). The climate is characterized by a rainy season from November to May and a dry season during the rest of the year (Marques-Filho et al., 1981). Mean daily annual temperature and mean annual rainfall between 1992 and 2002 were 26.7 °C and 2479 mm (Coordenação de Pesquisas em Clima e Recursos Hídricos, CPRH, INPA). The dense ombrophilous tropical rain forest has topographic and edaphic variations typical of many areas in central Amazonia, and has a total area of 10,000 ha. It has moderately uneven terrain (about 39–109 m.a.s.l. in the study area). The nutrient-poor soils are classified as yellow clay latosol (Xanthic Hapludox) in the higher areas, clay-sand (Typic Epiaquods) on the slopes, and sandy soils (Typic Endoaquods) in the valleys. The vegetation consists of relatively uniform dense rain forest that is not subject to seasonal flooding by large rivers. The only special type of vegetation recognized is locally called “campinarana” (low-canopy forests adapted to extremely poor sandy soil). The undergrowth includes abundant sessile palms, such as *Astrocaryum* spp. and *Attalea* spp. (Chauvel et al., 1987; Ribeiro et al., 1999). There are approximately 1200 species of trees (Costa et al., 2009) with a canopy height of 30–37 m, and some emergents reaching 40–45 m (Ribeiro et al., 1999).

2.2. Sampling design

The basic sampling design is based on the RAPELD system (Costa and Magnusson, 2010; Magnusson et al., 2005). The RAPELD grid in the reserve is an 8 km × 8 km containing 64 km² of trails connecting 72 uniformly distributed plots separated by a minimum distance of 1 km (Fig. 1). The smallest distance between the trails and the edge of the forest is 1 km. The largest RAPELD grids in most other areas are 5 km × 5 km. Each plot is 250 m long and 6 m wide, and follows the altitudinal contours to minimize within-plot soil variation. The shortest distance between the trails and the edge of the forest is 1 km. Width of the plot depends on the type of organism. Edaphic mites are sampled in soil cores distributed along the entire 250 m center line of the plot. Sampling and identification procedures for mites were described by Moraes et al. (2011). Voucher specimens

were deposited in the Entomological Collection of INPA, Manaus, Brazil.

2.3. Data analysis

We analyzed the dataset of oribatid mites (Moraes et al., 2011) available at <http://ppbio.inpa.gov.br/knb/metacat/fecosta.95.6/ppbio>. We used soil clay content, litter quantity, soil pH, number of trees in the plot, and distance to the nearest stream as environmental predictors of the oribatid-mite distributions. We used a “moving window” within the existing dataset of oribatid mites for the larger 8 km × 9 km grid, to evaluate the possible results that we would obtain if we had surveyed smaller 5 km × 5 km 30-plot grids in each of the 16 possible positions within the larger grid. The complete datasets containing these environmental predictors and the geographical coordinates (space) are available at <http://ppbio.inpa.gov.br/knb/style/skins/ppbio/> where the sampling protocols for each of these variables are described in detail.

To evaluate environmental and spatial patterns in the oribatid species composition, we used partial Redundancy Analysis (pRDA; Peres-Neto and Legendre, 2010) and the variation partitioning technique (Peres-Neto et al., 2006). The species-abundance dataset was transformed using the Hellinger transformation as recommended when running pRDA. The spatial filters (i.e., spatial predictors) were generated using Moran Eigenvector mapping through the technique called Principal Coordinates of Neighbor Matrices (PCNM; Borcard and Legendre, 2002). For the complete dataset, 37 PCNM filters were generated, and for the 30-plot grids, 16 PCNM filters were used. To avoid the use of many spatial variables in the pRDA model, we used the forward-selection procedure recommended by Blanchet et al. (2008). The forward selection procedure was also run to select only the most important environmental variables that had the strongest simple linear relationships with densities of each species. Therefore, our final pRDA model was composed by the environmental variables retained in the forward selection plus the spatial filters retained. Then we decomposed the explained variance into three fractions: the fraction explained exclusively by the environmental variables included [Env]; the fraction explained exclusively by spatial filters [Spat] that represent spatial clumping of any cause that can be represented by sinusoidal decomposition; and the confounded variance that may be due to either or both [EnvSpat].

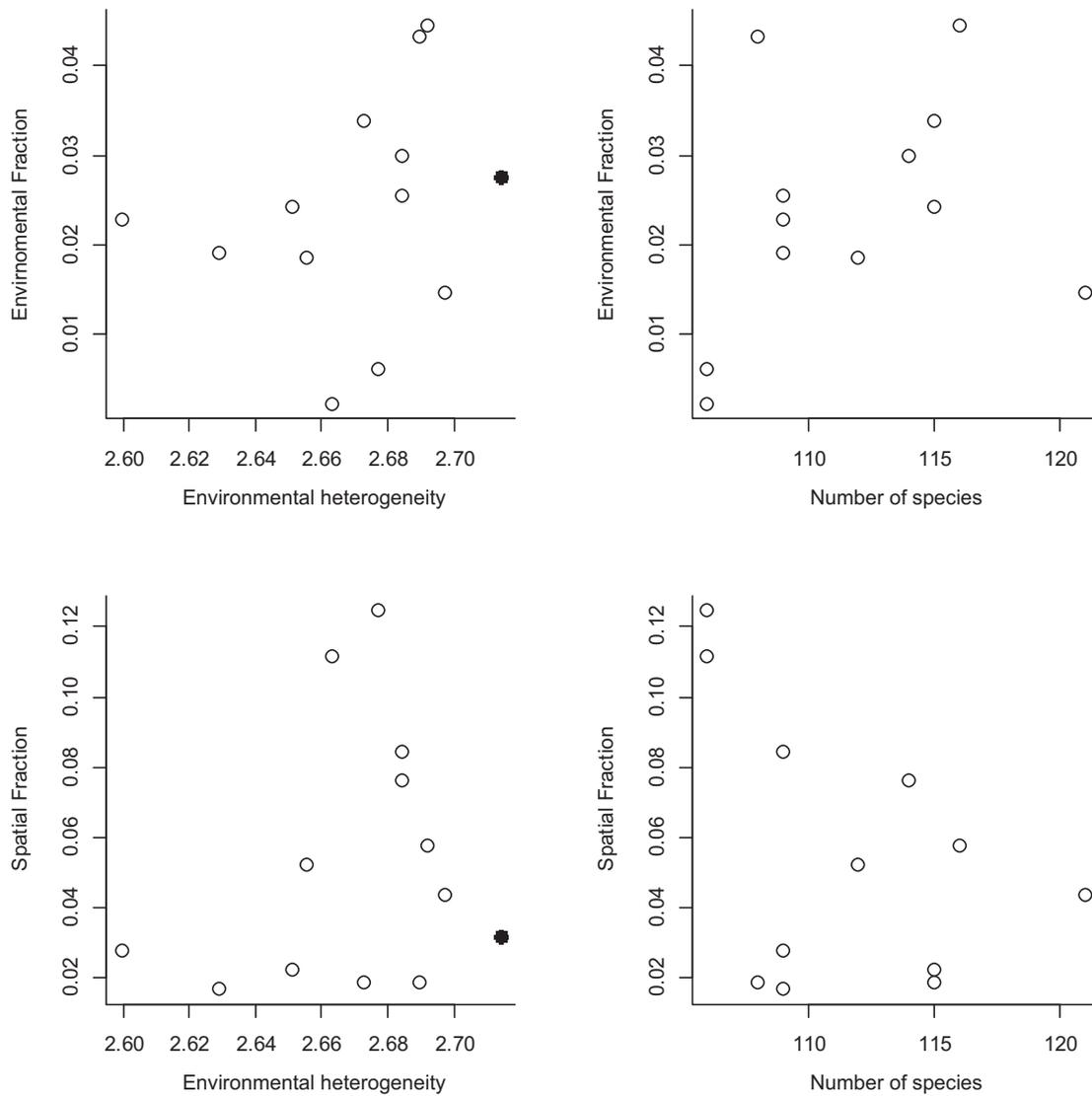


Fig. 2. Relationship between variance fractions associated with known environmental factors (upper graphs) and spatial filters that are surrogates for unknown factors that cause spatial clumping (lower graphs) obtained from pRDA analyses with environmental heterogeneity (left graphs) and species richness (right graphs). The open circles are for the 12 grid positions where the pRDA had significant values (see Table 1). The black circle on left plots represents the values for the larger grid (72 plots).

The procrustean correlations between the complete dataset of species recorded in the 72-plot grid and the reduced datasets showed that the exclusion of the rarest species (occurring only in four or fewer plots) did not cause loss in the ordination patterns; for the four dissimilarities indices (Bray–Curtis, Sørensen, Jaccard and Simpson–Baselga) Procrustes correlation remained near 1 (Fig. 3). At this point, 87 (54%) species could be discarded, remaining only 74 species to be used for the analysis. In fact, correlation values began to decline only when the community was reduced to species that occurred in only 11 of the 72 plots. In general, species occurring in fewer than 11 plots contributed little to the ordination. Of the 43 species that occurred in at least 11 plots, 30 (69.8%) had been described species, and 13 were recorded as morphospecies (Appendix A). Exclusion of rare species caused little change in the ordination analysis for any of the dissimilarity indices used (Fig. 3a–d). The Simpson dissimilarity described by Baselga et al. (2007) accounts for differences in species richness; for this index, the rate of decrease in Procrustes correlations was lowest, indicating that the differences in the other indices may have been due to their confounding similarity in species composition and similarity in number of species in the sample. Overall, matrices resulting from the successive discarding of less-frequent species

from the analysis performed similarly to the original matrix, and showed that reduced datasets of species were able to generate the ordination pattern observed with the original matrix.

4. Discussion

As far as we are aware, no other investigation of an oribatid-mite community in the Amazon region has encompassed the broad spatial scale of the Moraes et al. (2011) and Santos et al. (2008) oribatid-mite surveys undertaken in plots distributed in 30,000 ha and 10,000 ha, respectively. Because we were not studying gross differences in assemblages between distinct habitat categories (e.g., primary forest × secondary forest), and there are no geographical barriers among the 16 smaller grids that we investigated, we expected that the variations within the same type of forest would result in more subtle variation in the oribatid community. Despite this, the results depend on the geographical positioning of the sampling. After successively discarding sets of less-frequent species from the analysis, we have also shown that small and incomplete datasets of species identify similar ecological pattern as the complete dataset composed of 161 species.

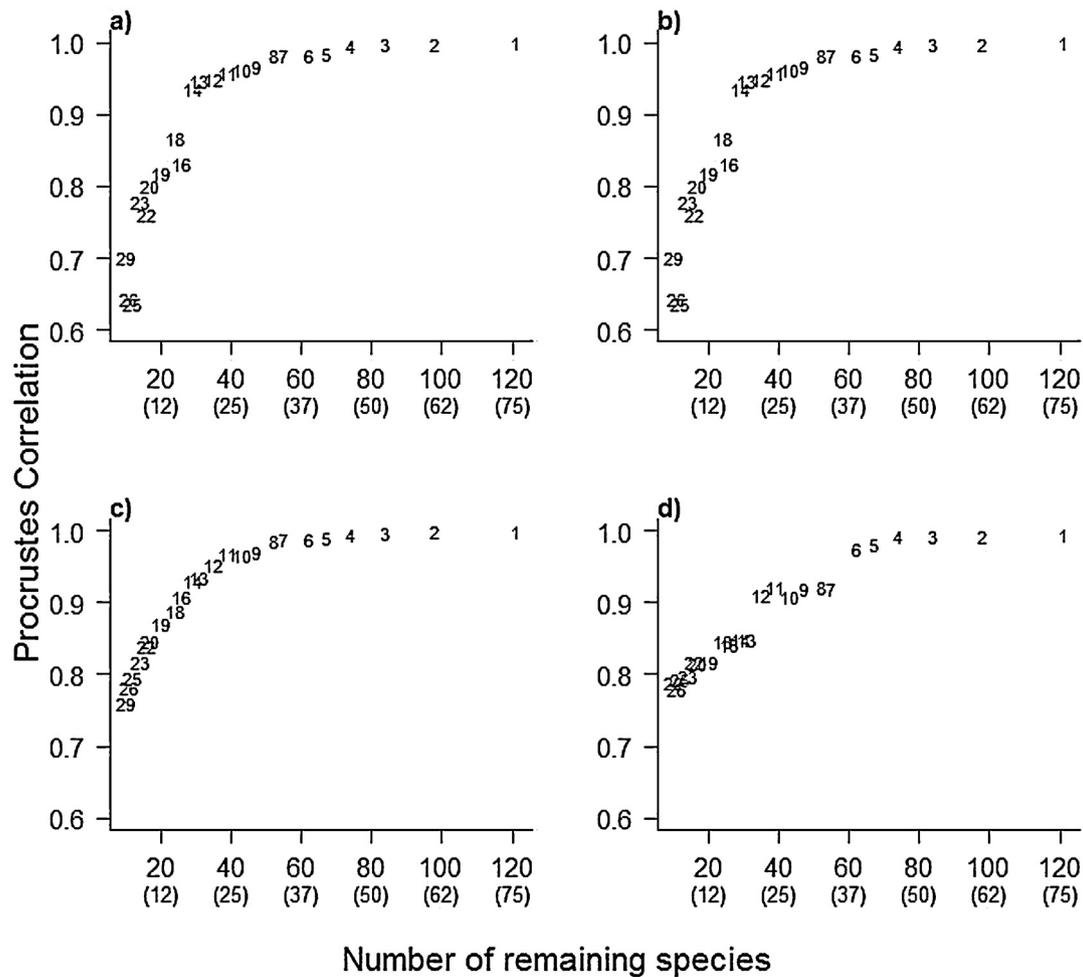


Fig. 3. Procrustes correlations between the maximum set of 161 oribatid-mite species with species data excluding uncommon species. The proportions in relation to the maximum set of species are represented in parenthesis. Numbers in the plot indicate the number of plots in which excluded species occurred (e.g., number 2 indicates that we excluded all species that occurred in only one or two plots). Ordinations used in the Procrustes analysis were constructed on the following dissimilarities: (a) Bray–Curtis; (b) Sørensen, (c) Jaccard, (d) Simpson–Basella.

4.1. The effects of grid position in the landscape

The low variance explained by spatial and environmental predictors for the different grid positions is an indication that oribatid mites are largely randomly distributed, with little patchiness at this scale in the Amazon. However, changing the grid position by 1 km to 4 km might result in very different ecological patterns. The environmental and spatial patterns generated by unknown causes are very different in different grid positions. Moving the grid from one position to another caused a decrease in the variance associated with spatial patterns of unknown causes from 0.11 with a non-significant contribution of the included environmental predictors to 0.035 with a significant contribution of the environmental predictors.

The number of locations sampled affects the number of species encountered (Fisher, 1999). Reducing the number of sample locations from 72 to 30 resulted in a loss of at least 43 species. The different grid positions resulted in a maximum difference of 15 species, which might not be a drastic difference for survey purposes. However, the geographical location must be considered in order to understand the environmental and spatial patterns of oribatid-mite assemblages. We suggest that environmental monitoring programs should evaluate the possible effects of grid position in relation to the expected results. Despite the apparent natural homogeneity, the tropical rainforest contains a mosaic distribution of soil texture,

which is correlated with forest architecture and linked to the altitudinal gradient (Costa and Magnusson, 2010; Guillaumet, 1987). Clay texture is associated with the variations of herb, palm (Costa and Magnusson, 2010), ant (Souza et al., 2012), and oribatid-mite (Moraes et al., 2011) assemblages. However, the capacity of the analyses to detect the association depends on the grain of variation in the landscape in relation to the size of the sampling units. Presumably, the same factors affect mites throughout the reserve, but the magnitude of the effect on the pattern seen depends on the landscape configuration.

4.2. The set of potential surrogate species

Although the reduction from 72 to only 30 250-m long plots caused loss of species from the original matrix, all 16 smaller 30-plot grids had rich oribatid-mite faunas (>100 species). In all cases, the simplified matrices after discarding less-frequent species produced results comparable to those obtained using the maximum set of species. In fact, the geographical coverage of sampling was much more important than the subset of mites analyzed. Therefore, reducing the sorting effort and increasing the area surveyed will increase confidence in the generality of the patterns revealed.

Because of the large area and the large sampling effort of this study, we can be confident that the less frequent species have effectively very low population densities in the forest, compared to other

species (see Manté et al., 1995). The most frequent oribatid-mite species are habitat generalists (Schneider et al., 2004; Schneider and Maraun, 2005), and are able to persist in a wide range of humus types and vegetation types (Osler et al., 2006). Despite this, our results showed that even the most broadly distributed oribatid-mite species do not occur homogeneously across the landscape. Franklin and Woas (1992) postulated that we are far from having a complete survey of oribatid mites from the Brazilian Amazon, because most taxa remain undescribed. Twenty years later, the situation has changed little, and the goal of identifying all of the species for conservation and monitoring purposes is unrealistic.

The exclusion or inclusion of comparatively rare or less-frequent species from a community-level analysis has been controversial. Some authors have argued for inclusion, because rare species are thought to be more sensitive to disturbance than are abundant species, which are widely distributed and probably have high tolerance to a variety of environmental conditions (e.g., Cao and Williams, 1999; Novotný and Basset, 2000). Other authors have argued for exclusion, because ordination results using subsets of aquatic macroinvertebrate species or reducing the taxonomic resolution almost exactly reflected those obtained with the full database (Marchant et al., 1994; Marchant, 1999). For hyperdiverse aquatic assemblages, studies on biodiversity and ecosystem functioning focused on indices and statistical methods to select the most representative species, to improve cost-benefit ratios in the field and laboratory (e.g., Heino and Soininen, 2010; Lavoie et al., 2009; Manté et al., 1995; Siqueira et al., 2011; Stephenson and Cook, 1980). Caruso and Migliorini (2006) found that grouping oribatid mites to family or genus level was equally efficient for detecting the effects of disturbance, with little loss of information in relation to the full species dataset.

The novelty of our statistical procedure is that we did not arbitrarily decide which criteria could define a set of rare species (see Manté et al., 2003), which can work well for one group, but not for another. In contrast, to investigate how a reduction in the number of species differs from the results obtained with the maximum set of species, we simplified the original matrix of 161 species with successive cutoff levels of species discarded, based on their frequency in the larger 72-plot grid. This alternative procedure can be tested for other hyperdiverse organisms.

We believe that a detailed survey of species must be done at the beginning of an environmental monitoring program (see Kallimanis et al., 2002), and the species identified, despite the costs, in order to justify the use of a subset of species. However, the costs are enormous (see Santos et al., 2008) and the real decision is between using surrogates or excluding mites from the monitoring. It is possible that rare species could become locally endangered or extirpated in the course of a long-term monitoring program. However, this would not be noticed in the ordination analyses even though the complete assemblage of species was used, because our results showed that rare species contributed very little to the ordination results. Intensive studies would have to be done to monitor the apparently rare species using methods that allow for detectability and occupancy (see Coddington et al., 2009; Manté et al., 2003). Although the public may be willing to pay for such expensive studies for uncommon vertebrates known to have restricted distributions, it is unlikely that they would be willing to pay such costs for locally rare mites that may occur over the whole Amazon basin. It will be a long time before we have enough information on Amazonian mites to determine which are rare and of conservation concern and which are just locally relatively infrequent.

It is possible that we will continue to detect and monitor ecological changes without noticing that rare species are being extirpated. However, it has been shown that common and rare species often react similarly to environmental gradients, and the use of common and easily surveyed species can be more efficient in the context

of environmental assessment (Heino and Soininen, 2010; Lavoie et al., 2009; Siqueira et al., 2011). Also monitoring programs aimed at protecting the most frequent and widely distributed species will indirectly protect the less-frequent species (Siqueira et al., 2011; Vane-Wright et al., 1991). These arguments support our assumption that less-frequent oribatid-mite species can be discarded from the analysis because they are more difficult to find and will not affect the results obtained with the most representative species (“monitoring species”; Sebek et al., 2012).

The percentage of described species among the 43 most frequent species which occurred in at least 11 plots, includes a large proportion (73%) of described and easily identifiable species, which will facilitate future analyses. Additionally, parataxonomists can be trained by specialists to sort and identify the species. These most-frequent species are representative of the soil and litter oribatid-mite assemblage in dense Amazon rainforest, because they respond mainly to conspicuous environmental variables (see Lennon et al., 2011; Siqueira et al., 2011). The less-frequent species that are not used for the purpose of a rapid survey for biodiversity monitoring will provide biological material for improving knowledge of taxonomy and phylogeny.

Our results are not general for all types of forests and all groups of organisms. Oribatid mite species are sensitive to forest type; for instance, large differences were found between the oribatid-mite assemblage structures in semi-deciduous forest fragments and the surrounding savanna matrix in eastern Amazonia (Ferreira et al., 2012). Similar analyses conducted on each dataset from both forest types may select different sets of oribatid-mite species. However, the results of this study are likely to apply to most oribatid-mite assemblages in dense Amazonian rain forest. This type of forest covers 42% of the Amazon Biome in Brazil (MMA, 2007). Therefore, the most representative oribatid-mite species that we indicated for the dense rain forest can be used in most of the Amazon region. Poos and Jackson (2012) showed that the removal of rare species from an assemblage may produce an impact as large as other methodological choices in multivariate analyses, but they studied an assemblage composed by only 67 species of fishes. Because of these differences, and as also suggested by species discarding must be thoroughly justified case by case.

5. Conclusions

The variance in species associations associated with spatial patterns of unknown origin was greater than that associated with the environmental variables included in the analysis, but the results were dependent on the position of the sampling grid in the landscape. Nonetheless, independent of geographical position, information on species dissimilarity across space can be recovered from sets of easily identifiable species, which are reliable surrogates for the broader set of oribatid-mite species in this forest. Traditional biodiversity surveys are usually presented as checklists of species that are assumed to be as complete as possible. Although the procedure is costly and time consuming, intensive data collection and sorting must be undertaken in each forest type, and the collections processed with taxonomic rigor. However, for rapid tracking of environmental change, the area studied needs to be surveyed at frequent intervals, and continued intensive sorting is generally not feasible. Our results showed that subsets of frequent, easily-identified species or morphospecies are as effective to identify ecological relationship as analyses based on all individuals collected. We suggest that sampling and identification efforts should be reduced when the primary objective is to describing ecological relationships to support and improve management, and the use of surrogates is a less-expensive solution. Rare species should be discounted from the estimates of species only for monitoring

purposes. This simplification would allow reallocation of resources from sample processing and identification to sampling of larger or additional areas, which is important to make general conclusions because the perceived relationships depend heavily on the local landscape configuration, even in continuous rainforest that appears superficially homogeneous. This will increase the rate of knowledge acquisition about soil invertebrate species and allow studies of biotic complementarity in the mega diverse Amazonian region.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2013.04.024>.

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