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Diversity of soil invertebrates associated to six spatially aggregated plant species in the Yasuní National Park, Amazonian Ecuador.

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1. ABSTRACT

Amazonian tropical rainforests harbor the largest biodiversity on Earth. Over the past decade, there has been increasing interest in understanding how such diversity can coexist in small areas. One broadly accepted explanation is the Negative Density Dependence hypothesis (NDD) that promotes species coexistence through a spacing mechanism that prevents species from becoming locally abundant. This may happen due to seedling mortality caused by intraspecific competition, or the attack of natural enemies. However, there are organisms such as particular plant tree species that are adapted to live in aggregation. How does this particular group of plants cope with the above mentioned survival constraints? A potential mechanism would be the efficient use of nutrients mainly coming from their own litter resources that are invested by plants in growing and defense. If that is so, one would expect detritivore communities within the sites of plants aggregation to be different from what is found outside these microhabitats. Here, using two different sampling methodologies, we provide a detailed description of soil fauna community diversity in areas of aggregation of six common tree species in the Yasuní National Park (Amazonian Ecuador). We hypothesized that (i) both capture methodologies used in our survey (i.e. Winkler extraction and pitfall traps) are complementary between them in terms of species composition; (ii) the 'litter transformers' guild represents the largest portion of the soil invertebrate fauna in both, the number of species and abundance; and (iii) soil fauna communities in areas of plants aggregation are significantly different in terms of the number of species, composition, abundance and functionality, compared to the sites where the focal plant species are absent. Agreeing with our hypotheses, our results showed that Amazonian soil fauna are predominantly represented by species included within the litter transformers functional group (65 % of total collection), and they are clustered in small-scale patches and

specific to the areas of aggregation of our focal plant species. This suggests that plant species living in aggregation may create microhabitats that promote the association of particular soil fauna species that may be adapted to exploit specific combinations of nutrients in the Yasuní forest floor.

Key words: biodiversity, functional groups, litter transformers, negative density dependence (NDD), soil species, Pitfall trap, small scales, Winkler extraction.

2. RESUMEN

Los bosques tropicales amazónicos albergan la mayor diversidad de vida en la Tierra. En efecto, durante la última década se ha incrementado el interés por comprender cómo tal diversidad puede coexistir en áreas relativamente pequeñas. En este sentido, una explicación ampliamente aceptada es la hipótesis de dependencia negativa de la densidad (NDD, por sus siglas en inglés) la cual promueve que por presiones selectivas como por ejemplo competencia intra-específica o ataque de los enemigos naturales se regula la población de especies comunes y abundantes en un área determinada favoreciendo la coexistencia de varias especies. Sin embargo, en la naturaleza algunas especies de árboles se han adaptado a vivir en áreas de agregación espacial. ¿Cómo logran estas especies sobrevivir en un ecosistema tan competitivo? Una posible explicación sería el uso eficiente de los recursos nutritivos de su propia hojarasca, con lo cual se esperaría que la comunidad detritívora en los sitios de agregación espacial de plantas difiera de las comunidades fuera de estos micro-hábitats. El presente estudio ofrece una descripción detallada de la diversidad de fauna del suelo en las áreas de agregación de seis especies de árboles comunes en el Parque Nacional Yasuní (Amazonía de Ecuador). Las hipótesis planteadas son (i) los métodos de captura usados en este estudio (extractores Winkler y trampas de caída) son complementarios entre sí en cuanto a composición de especies (ii) el grupo funcional transformadores de hojarasca representa la mayor parte de la diversidad de invertebrados del suelo en cuanto al número de especies y su abundancia relativa; y (iii) las comunidades del suelo en las zonas de agregación espacial de plantas son significativamente diferentes en términos del número de especies, la composición, la abundancia y la funcionalidad, en comparación con los sitios donde no se encuentran agregadas. Los datos mostraron que la macrofauna del suelo amazónico está representada principalmente por especies del grupo funcional

‘transformadores de hojarasca’ (65 % del total de la colección) y que estas especies se agrupan en parches pequeños y específicos en las áreas de agregación espacial de plantas. Esto sugiere que las especies de plantas que viven en agregación podrían crear micro-hábitats que promueven la asociación de determinadas especies de fauna del suelo idóneas para descomponer combinaciones específicas de nutrientes en el suelo del bosque Yasuní.

Palabras clave: biodiversidad, grupos funcionales, transformadores de hojarasca, dependencia de la densidad negativa (NDD), fauna edáfica, trampas Pitfall, extracción de Winkler.

3. INTRODUCTION

The Amazon rainforest has the greatest diversity of life on Earth (Gillison *et al.* 2003). For example, in one hectare of the Yasuní National Park in Ecuador there are about 655 species of plants (Valencia *et al.* 2004a), more than are native to the continental United States and Canada combined (Elias 1980). Insects may be represented by at least 100,000 species (Wilkie *et al.* 2010) approximately the same number of insect species as is found throughout all United States (Evans 2007). These comparisons illustrate how extremely diverse is Yasuní at local scales. Numerous mechanisms (e.g., species interactions, environmental and stochastic fluctuations, among others; Wright 2002) have been proposed to explain the coexistence of high species diversity (e.g. within a single hectare). In this context, the negative density dependence (NDD) suggests that selective pressures such as intraspecific competition or transmission of parasites may regulate the common and abundant species population, promoting the viability of rare species (Wright 2002). This may be influenced by the biotic variety (density and identity) of neighboring species (e.g. Metz *et al*. 2010). For instance, individual seedling species show increased mortality at high densities or in the proximity of conspecific adult neighbors (Peters 2003; Packer & Clay 2000). In contrast, some plant species are adapted to live together in spatial aggregation in the tropical forest (i.e. sharing small spaces with their conspecifics). This spatial aggregation of species determines the interactions overall the ecosystem (De Boeck *et al.* 2006) and affects growth and reproduction of plants (Stoll & Prati 2001).

How do species defy the NDD and live in aggregation within natural ecosystems? One potential mechanism could be an efficient use of soil nutrients via an accelerated rate of decomposition process of their own leaf litter driven by specialized soil organisms (Gholz *et al*. 2000). Such efficient nutrient uptake could probably allow plants to invest more in

defenses against pathogens and avoid inter- and intraspecific competition for resources (Ayres *et al*. 2009a and b). This may be in line with the home field advantage hypothesis (HFA). It predicts that, litter may decompose faster in an area dominated by the plant species from which it is derived (i.e. at home) than in an area dominated by other plant species (i.e. away), because local detritivores and decomposers are more efficient (specialized) at degrading 'home' litter (Gholz *et al*. 2000; Austin *et al.* 2011; Ayres *et al*. 2009a). In this sense, plant species may be influencing the soil fauna community and their identity may operate as an important driver of soil food webs (Wardle *et al.* 2003). Plant species that live in aggregation in tropical forests may therefore be creating a microhabitat that attracts specific decomposers (Austin *et al.* 2011) suggesting that litter quality and/or quantity could influence the decomposer community and trajectory of decomposition (Manzoni *et al*. 2010; Laosii *et al.* 2007).

Invertebrate soil bio- and functional-diversity is practically unexplored in the Amazonian tropical ecosystems (Primack & Corlett 2005, Moreira *et al*. 2008). In this study we aimed to evaluate whether plant species that live in aggregation show a significantly different soil fauna species composition (at home) comparing to away of their spatial distribution. For this, we present a detailed description of the soil fauna diversity within the area of aggregation of six common tree species in the Yasuní National Park (Amazonian, Ecuador). We hypothesized that (i) both capture methodologies (i.e. Winkler extraction and pitfall traps) used in our survey are complementary between them (ii) the soil invertebrate fauna under aggregated plant species is significantly represented by litter transformers both, in number of species and abundance; (iii) soil fauna communities in aggregated areas are significantly different, in terms of the number of species, abundance and functionality, compared to sites where our focal plant species are not present.

4. MATERIALS AND METHODS

4.1 STUDY AREA

Yasuní National Park (YNP) and the adjacent Waorani Indigenous territory cover 1.6 million hectares of forest being the largest protected area in continental Ecuador, and one of the most biodiverse places on Earth (Albuja 2011; Bass *et al.* 2010). YNP is an evergreen lowland wet forest ranging in altitude from 200 to 300 m above sea level. It has a 15–30 m canopy with some emergent trees reaching 50 m (Valencia *et al.* 2004b). Rainfall and temperature are aseasonal, with a mean annual rainfall of 2826 mm and a mean monthly temperature ranging from 22 to 32 °C (Valencia *et al.* 2004a; for detailed information visit www.yasuni.ec).

The Yasuní Forest Dynamic Plot (YFDP; southwest corner coordinates 76° 23' 72'' W; 00° 41' 14''S) is located ~700 m south the Yasuní Research Station of the Pontificia Universidad Católica del Ecuador (YRS-PUCE coordinates: 76° 24' 1.8''W; 00° 40' 16.7''S). YFDP has been catalogued as one of the most biodiverse places on Earth with ca. 1200 plant species coexisting in 50 ha (Valencia *et al.* 2004a). Since its establishment in 1995, the plot is part of a worldwide network of permanent forest dynamics plots whose primary objective is to describe the long-term demography of thousands of plant species, and explain their dynamics with ecological theories (e.g. Bagchi *et al.* 2011; Metz *et al.* 2010; Kraft *et al.* 2008).

4.2 PLANT SPECIES SELECTION

Prior to choose the species of plants to use in this study we calculated the degree of spatial aggregation of individuals in the YFDP using scalewise variances and moment equations – i.e. the spatial distribution variance as a function of spatial scale– calculated with wavelet kernel functions as developed by Detto & Muller-Landau (2013). This procedure determinates the probability distribution of independently observed scalewise variances for a given expectation, including complete spatial randomness. This technique provides an analytical test of the null model of spatial randomness to understand at which scales, if any, the variance departs significantly from randomness. It also derives the likelihood function that is needed to estimate parameters of spatial models and their uncertainties from observed patterns (Detto & Muller-Landau 2013). Using the 2002 and 2007 plot census data (Valencia *et al.* 2004; Valencia *unpublished data*), the test clearly identified six common plant species living in spatial aggregation: *Acalypha cuneata*, *Acidoton nicaraguensis*, *Macrolobium* 'yasuni', *Matisia oblongifolia*, *Rinorea apiculata* and *Rinorea viridifolia* (see Appendix 1 for spatial aggregation analysis). Using 2D Kernel density estimation analysis, we furthermore mapped plant density distribution to identify the aggregated sites within the plot from where we chose five different sites per plant species (i.e. 30 sites; see maps in Appendix 2).

In the field, we checked that each selected site had at least two adult trees of the focal species and that the ground was covered, or at least showing presence of its own leaf-litter (no less than 20 % cover in our field of vision, DM and RC personal observation). Then, we marked the sites with plastic tubes and field tape to recognize them easily within the plot. When the chosen site did not meet these minimal characteristics, another site was chosen in its place.

4.3 SOIL FAUNA COLLECTION

Our soil fauna sampling design was focused within the above-mentioned sites of plant aggregation. However, we used previous random data (Cárdenas 2013; Appendix 3) to compare soil fauna composition and diversity between aggregated and random sites inside the plot. Hereinafter these surveys will be referred as 'aggregated' and 'control' sites, respectively. We made sure that aggregated and control sites did not overlap (see Appendix 4 for details).

For both, aggregated and control sites, Winkler extractors and pitfall traps were used (see protocols in Moreira *et al.* 2008 and decryptions below). Both methodologies have shown to be complementary in terms of soil macrofauna diversity composition and functional structure (Cárdenas 2013; Hopp *et al.* 2011; Parr & Chown, 2001; Agosti & Alonso 2000).

4.4 SOIL-FAUNA BIODIVERSITY SURVEY

Pitfall traps consisted of a ~15 cc cup buried in the ground with its rim at surface level and were used to trap mobile animals. Each trap contained 75 % ethanol as immobilizing agent. We set two pitfall traps in each sampling site (2 m NE and 2 m SW of the centroid of the chosen site) during two periods of 24 hours. The experimental design for Pitfall traps consisted on 6 spp × 2 traps × 5 sites × 2 sample days (120 samples in total).

For Winkler extractions (see Agosti & Alonso, 2000 for more details about this collecting method), we used a plastic frame to delimitate an area of $1m^2$ and collect litter at each sampling site (1.5 m N and 1.5 m S of the centroid of the chosen site). Then, we sieved

the litter and temporally deposited the resulting material in plastic bags. In the laboratory, we put the contents of the bags into a cloth mesh (holes of 2.5 mm^2) placed inside the Winkler extractors for a period of 72 hours at a constant temperature of 20 °C inside the laboratory. At the bottom of each extractor, we tied up a plastic cup (~6 cc) with 75 % ethanol and collect soil invertebrates that fell into it. This procedure was repeated twice at each sampling site. The experimental design for Winkler extractions consisted on: 6 spp × 2 extractions × 5 sites × 1 sample day (60 samples in total).

In control sites, the experimental design was different. For the Pitfall collection methodology, a nested rectangular grid of six different spatial scales was established across the forest ground. While for Winkler extractions, a 200 m transect was done following the ALL-protocol (Ants of the Leaf Litter, see Agosti & Alonso 2000 for details) and 10 transects of 20 m that followed the diagonal of the 1000 × 500 m plot were also distributed. See Appendix 3 for details on soil fauna biodiversity in control sites.

4.5 SOIL MACRO-FAUNA IDENTIFICATION AND FUNCTIONAL GROUPS ASSIGNMENT

Samples were brought to the laboratory, cleaned from soil particles and the specimens were quantified and identified up to the highest taxonomic resolution possible using a stereoscope at 0.68X–50X magnification (Wild *Heerbrugg* Ltd., Stereomicroscope *Wild M3 model,* Heerbrugg, Switzerland). All individuals were classified into Class, Sub-Class and Order, and when possible, up to Family and/or subfamily or Genus, and separated into morphospecies (Cárdenas, 2013; Zerbino *et al.* 2008). For this, we used a previous soil macrofauna database from YFDP (Cárdenas 2013) and specialized bibliography (e.g.

Brandão *et al.* 2012; Urbani & de Andrade 2007; Borges *et al.* 2004). When a morphospecies was recognized for the first time, we took lateral, dorsal and ventral pictures using an adaptable digital camera (Future Optics Sci. & Tech Co., 1.3 MP, MEM1300 model, Hangzhou, China). These images were useful to compare if any similar specimen appeared in the collection updating the previous database. Larvae of holometabolous insects were always classified as different morphospecies. In the case of hemimetabolous insects, when nymphs showed structural differences from the adult morphospecies, we classified them as different morphospecies.

All morphospecies were classified into functional groups based on Moreira's *et al.* (2008) classification: herbivores, ecosystem engineers, litter transformers, decomposers, predators, microregulators and soil borne pest and diseases. Primary producers, microsymbionts and prokaryotic transformers categories were not part of our collection target. In addition, we included 'mesoregulators' as a new functional group category in order to consider meso-fungivores as animals that regulate nutrient cycles. Although Acari taxonomic genus represents an important group in the soil food web, we were unable to discriminate specimens at morpho-species level and accurately assign them into any of the many functional groups.

Most of the specimens belonged to more than one functional group in relation to their feeding habits, which were determined consulting specialized literature and internet resources (e.g. Brandão *et al.* 2012; Bolton *et al.* 2006; http://www.collembola.org). A full list of the collected morphospecies and the functional groups where they were assigned is shown in Appendix 5. Finally, we classified litter transformers into five groups (LT1, LT2, LT3, LT4 and LT5) considering their complementary functional role with other functional groups. For instance, LT1 represented only litter transformers, LT2 litter transformers and ecosystem engineers, LT3 litter transformers and meso-regulators, LT4 litter transformers,

ecosystem engineers, herbivores and predators, and LT5 litter transformers and soil borne pest & diseases. We recognize that the functional traits assigned in our study may still be a simplistic representation of insect ecological niches; however, we believe this is a novel and a realistic approach based on what is known in the literature, and it is useful for investigating invertebrate community patterns and function.

4.6 STATISTICAL ANALYSES

4.6.1 EVALUATION OF SAMPLING EFFICIENCY

In order to evaluate whether there are differences on the diversity composition of soil communities, of both aggregated and control sites, we used the rarefaction technique to compare the efficiency of sampling methods in terms of the number of individuals collected per sample (Gotelli & Colwell 2001), and to infer total richness at each site (Magurran 2004). We used sample-based (incidence data) and individual-based (abundance data) rarefaction curves to provide a realistic estimation of the number of species in sets of real-world samples (Colwell *et al.* 2012; Gotelli & Colwell 2001). For this, we used Past v.2.17 software (Hammer *et al.* 2001) which implements Mao tau analytical solution, where standard errors are transformed in ± 95 % confidence intervals (CI). Two sampling methods are considered differently efficient in terms of species richness when rarefraction curves and their CI do not overlap. With the intention of revealing whether soil fauna diversity was spatially heterogeneous or not, we compared both individual- and sample-based rarefaction curves by plotting them together. Gotelli and Colwell (2001) explain that when the sample-based curve lies below the individual-based curve one can assume spatial aggregation of species.

4.6.2 ANALYSES OF SOIL MACROFAUNA COMMUNITIES

We described the community structure of soil macrofauna in the aggregated sites using rank-abundance plots (Magurran 2004) at the Order and morphospecies levels. Then, following Preston's (1948) boundaries of octaves as a measure of commonness degree, we classified the number of species in relation to their abundance in nine categorical ranges, and finally, fitted data to a lognormal distribution ($y = 1238{,}73\ e^{(-0{,}5(\ln(x/-8{,}062)/8{,}397)^2)}$) using Table Curve 2D software v.5.01. In addition, we compared both macro fauna communities (aggregated and control sites) to determine similarities on their structure using a Mann Whitney test.

We used an Analysis of Similarity (ANOSIM) which is a statistical permutation test of faunal similarities between groups, and a Nonmetric Multidimensional Scaling analysis (NMDS) to evaluate whether soil macrofauna species composition were dissimilar within all aggregated sites and between aggregated and control sites. Following Cárdenas (2013), we chose Bray Curtis as an abundance-sensitive distance measure because it provides a robust estimate of difference in the structure between communities (e.g. Faith *et al.* 1987). We also performed a similarity percentage test (SIMPER) to reveal the relative contribution of each taxa to the differences between groups (Sallan & Coates 2010; Zerbino *et al*., 2008).

5. RESULTS

5.1 SOIL FAUNA SAMPLING EFFICIENCY

Winkler extraction and Pitfall traps together collected 8171 individuals and 597 morphospecies for both aggregated and control sites. The amount of individuals and morphospecies collected with Winkler extractions was 5978 and 456, respectively, while Pitfall traps collected 2193 individuals and 302 morphospecies, with an overlap of 24.58 % between the two methods in terms of species composition (Figures 1A and 1B). In addition, for both Pitfall traps and Winkler extractions the sample-based curves lie below the individual-based curves when considering aggregated and control sites together.

For both Winkler and Pitfall collecting methodologies, rarefaction curves showed that the number of collected species was not enough to reach an asymptote (Figure 1A). Instead, species richness estimators Jackknife 1 and Jackknife 2 (using incidence data) and Chao 1 (using abundance data) revealed that our samples may cover 75.2 % – 78.3 % of the total soil biodiversity of the study area (results not shown). Overall, Winkler extractions collected 34 % more morphospecies in a smaller sampling area than Pitfall traps. Comparing the number of samples of both aggregated and control sites at 40 samples stop vertical line, species rarefaction curves and their 95 % confidence intervals did not overlap (Figure 2A). While, Pitfall traps showed that their confidence intervals crossed all over the rarefaction curves (Figure 2B). Our results revealed that both methodologies were different in terms of invertebrate identity. For example, Pitfall traps were highly represented by *Isoptera* sp.1, *Camponotus* sp. 1, *Isoptera* sp.7, *Phoridae* sp. 11 and *Hymomirma* sp. 1, while Winkler

extractions were better represented by *Camponotus* sp.1, *Pheidole* sp. 9 and sp. 5, *Nylanderia* sp. 2, *Pheidole* sp. 3 and *Wasmania* sp. 1 (results not shown).

5.2 SOIL INVERTEBRATE COMMUNITY ASSEMBLY: CONTROL AND AGGREGATED SITES

Our survey within the aggregated sites showed that Hymenoptera was the insect group better represented in terms of the total number of individuals (1117 individuals, about 33 % of total collection; predominantly represented by Formicidae), followed by Collembola (1101 individuals, about 20 %; mostly Hipogatruridae-Neanuridae group) and Coleoptera, (1084 individuals, 15 % of total collection; largely characterized by Staphylinidae). In the control sites, the most abundant groups were the same in the same order: hymenopterans with 1910 individuals (23 % of total collection), collembolans with 797 individuals (10 % of total collection) and coleopterans with 419 individuals (5 % of total collection) (Figure 3A). When comparing the soil macrofauna communities for both aggregated and control sites at order resolution, our data showed similarities in their composition (ANOSIM, $P = 0.464$). At the morphospecies resolution, the species rank abundance plot (SRA) fitted to a lognormal distribution showing that few species were common, some were moderately common and a great majority were rare (Figure 3B; regression fit not shown). When the SRA was plotted in a $\log_2$ scale, data fitted significantly to a lognormal distribution as well ($P = 0.0001$; $R^2 = 0.991$; F = 152.22 Figure 3C).

5.3 TOTAL SOIL FAUNA DIVERSITY: CONTROL VS. AGGREGATED SITES

NMDS and similarity indexes showed that the invertebrate communities were significantly different in terms of morphospecies composition between aggregated and control sites (ANOSIM; $P < 0.001$; Figure 4A; overall *P* values for each treatment are shown in Table 1). Dissimilarity was about 85 % between both treatments (aggregated and control) and the morphospecies driving these differences were represented by *Hipogatruridae-Neanuridae* sp.4 and sp.1, *Wasmania* sp.1, *Pheidole* sp.1, and *Strumigenys* sp.1. Likewise, within the aggregated sites, soil fauna communities differed in 78 % (ANOSIM; $P = 0.00177$; Figure 4B). While, *Camponotus* sp.1, *Isoptera* sp.4, *Pheidole* sp.9, *Pheidole* sp.5 and *Wasmania* sp.1 were the species that contributed more to this dissimilarity.

5.4 LITTER TRANSFORMERS FUNCTIONAL GROUP DIVERSITY: CONTROL VS. AGGREGATED SITES

Considering the litter transformers functional group only, the 'litter transformers and regulators' (LT3) and the 'litter transformers and ecosystem engineers' (LT2) sub-groups were the most abundant in both treatments (830 and 93 individuals for LT3 and LT2, respectively, in the aggregated sites, and 539 and 102 individuals for LT3 and LT2, respectively, in the control sites). When comparing the litter transformer communities composition between aggregated and control sites, our data revealed similarities in terms of abundance (ANOSIM, $P = 0.583$; Figure 5). However, at the species diversity level our data showed differences between both types of treatments (ANOSIM, $P < 0.001$; Figure 6A) *Entomobryidae* sp. 1, *Oxyteline* sp.1, *Gryllidae* sp.4 and *Scolytinae* sp. 1 were the species that contributed most to this dissimilarity (sum of the contribution percentages = 98.16 %).

At the functional sub-groups level NMDS and similarity indexes showed that litter transformers communities were different between the aggregated and control sites (ANOSIM, $P = 0.0015$; Figure 6B). Within the aggregated sites, NMDS and similarity indexes showed that litter transformer communities were also dissimilar at the species diversity level (ANOSIM, $P < 0.001$;; see *P* values for each treatment in Table 1) as well as at the functional sub-groups level (ANOSIM, $P < 0.0001$; Figure 7). Figure 7 clearly shows that litter transformers are grouped in two noticeable assemblages: those in the areas of *A. cuneata, A. nicaraguensis* and *M. '*yasuni*'* distribution, and those in the areas of *M. oblongifolia, R. apiculata* and *R. viridifolia*. Species composition in both *Rinorea* soil surface are practically identical (ANOSIM, $P = 0.992$).

6. DISCUSSION

6.1 CAPTURE METHODS

Even though Winkler and pitfall collections by their own particularities were not enough to characterize soil fauna assemblages, our samples covered 75.2 % – 78.3 % of the total soil biodiversity in YFDP (according to species richness estimators Jackknife 1 and 2 and Chao 1). A higher sampling effort (i.e. for at least three continuous days; e.g. Krell *et al.* 2005) is hence necessary for revealing the total soil fauna biodiversity richness in Yasuní.

Our results also revealed that Winkler extraction was more efficient for capturing more species in a smaller area, contrasting with other tropical studies that found pitfall traps were ideal for capturing most taxa in Indian moist-deciduous forest comparing to Winkler extraction methodology (e.g. Sabu and Shiju 2010). Even though, both collection methodologies (Winkler and pitfall) differed in terms of sampling efficiency (i.e. number of species per sample unit), they were complementary concerning species composition, agreeing with our first hypothesis, and collected all the functional groups with a relatively small sampling effort. Complementary results of both collection methodologies may be explained by their own particularities. Pitfall traps estimate relative activity rather than density, reflecting individual abundances of species and movement rates of nocturnal invertebrates on the soil surface (Cheli & Corley 2010), while Winkler extractions are more suitable for capturing leaf litter-inhabiting and rapidly mobile invertebrates (particularly ants and beetles) (Agosti & Alonso 2000, Moreira *et al.* 2008, Sabu & Shiju 2010).

6.2 THE SOIL INVERTEBRATE COMMUNITY

Our results showed a predominant abundance of hymenopterans (mostly ants), collembolans and coleopterans in aggregated and control sites. These three abundant groups differ in their feeding habits and may occupy a wide range of niches in the forest food web. It is known that ants are important components of ecosystems (especially in tropical regions) not only because they constitute a great part of the animal biomass but also because they act as ecosystem engineers (Folgarait 1998; Jones *et al.* 1994). They represent one of the most diverse animals and ecologically dominant groups in terrestrial habitats (Stock & Eggleton 1992). The nutritional biology of ants could be wide-ranging including: predators, leaf cutters, fungus growers, sap feeders, pollinivorous, saprophytes and generalists (Brandão *et al.* 2012). Less known, is the importance of native ants in regulating the population of other soil invertebrates (Stock & Eggleton 1992). In this respect, Kaspari *et al.* (2011) demonstrated that swarm-raiding army ants (agents of disturbance) reduce the biomass of litter invertebrates in a neotropical rain forest. Nevertheless, studies in Yasuní suggest that niche diversity has driven ants' specialization and may be the actual factor supporting their high diversity in the neotropics (e.g. Wilkie *et al.* 2010). Meanwhile, collembolans play an important role in plant litter decomposition processes and in forming soil microstructures such as soil pores and bioturbation (Rusek 1998). Collembolans represent one of the most abundant terrestrial arthropods globally, and regulate fungal populations and enhance micorrizal functioning, improving plant growth (Gange 2000; Hopkin 1997). Conversely, coleopterans in the soil surface (highly represented by Staphylinidae family in our survey) are principally predators and saprophagous. They are usually located in a variety of environments (e.g. wooden logs,

dung and carrion; Marquez & Navarrete 1994) and some of them typically construct tunnels facilitating fungal colonization in decaying wood (e.g. bark beetles are principally woodborers; Muller *et al.* 2002), subsequent bacterial access (de Boer *et al.* 2005), and further organic matter decomposition (Marquez & Navarrete 1994). These three abundant groups play an important direct or indirect role in the decomposition process in the forest floor (see Swift *et al.* 1979).

Further, in the analysis of diversity, our ranked abundance plots fitted significantly to lognormal distributions, agreeing with other large-scale invertebrate's samplings in the neotropics indicating very few abundant species and many rare species (e.g. Longino *et al.* 2002; Wilkie *et al.* 2010). This lognormal model has been used to describe the distribution patterns of biological communities in natural ecosystems, based on the assumption that resources (e.g. food, space and time) drive species abundance in an ecological community (i.e. niche partitioning; Magurran 2004). The compact and heterogeneous nature of the soil matrix provides unrivalled potential for niche partitioning, thus allowing high levels of local diversity. This heterogeneity is itself strongly increased by the omnipresent activity of ecosystem engineers that generate patchiness at a range of spatio-temporal scales (Decaëns 2010).

6.3 STRUCTURE AND DISTRIBUTION OF SOIL INVERTEBRATE COMMUNITIES

Cárdenas (2013) suggested that the Yasuní forest floor is upholstered of taxa representing multiple behaviors, strategies and feeding habits, suggesting a high rate of functional redundancy per unit area. This has also been suggested in other tropical studies where plant identity failed in predicting soil fauna diversity (Donoso *et al.* 2010). However, our

results showed that this might not always be true. The relationship between functional diversity and species composition remains poorly understood for most of the ecosystems (Lavelle *et al.* 2006). When considering specific areas of plant species aggregation we found significant differences in functional diversity within all the aggregated sites, and between aggregated and control sites. This same pattern was found when analyzing the litter transformers communities only.

In terms of abundance, litter transformers represented 65 % of the total collection (results not shown), agreeing with our second hypothesis. Overall, these invertebrates normally ingest purely organic material and build organic structures that serve as incubators for microbial activities (Lavelle 1997). Within litter transformer communities, our survey revealed that LT3, LT2 and LT1 were, in that order, the most abundant groups over all the study area. These three subgroups (LT1-meso-regulators-, LT2-ecosystem engineers- and LT3-litter transformers-) may be closely related with micro-fauna activity during the decomposition process. For example, collembolans and mites (represented in LT3) act as litter transformers and micropredators (grazers of fungal and bacterial), thus, contributing to smaller-scale organic comminution processes and exerting a strong regulatory role within soil biota (Swift *et al.* 1979). LT4 and LT5, which may act as biological controls on litter transformer communities, demonstrated to be similar in terms of composition between aggregated and control sites, and within all aggregated sites.

Even though, previous studies suggest that soil fauna is homogeneously distributed in the Yasuní forest and other tropical ecosystems (e.g. Cárdenas 2013; Donoso *et al.* 2010) our comparisons of sample- and individual-based rarefaction curves, of both Pitfall traps and Winkler extractions considering aggregated and control sites, suggest that species in the forest are aggregated at smaller sampling spatial scales. In this context, our survey suggests that while soil fauna might be aggregated in patches at small

scales at larger scales this pattern could be unnoticed in terms of their ecological functionality. These results partially agree with our third hypothesis weakening the idea of redundant taxa and functionality at all spatial scales. However, functional complementary, which allows different species to partly exploit different resources (Loreau 2004), may explain the coexistence of many different species in natural environments such as Yasuní at small scales in areas of high plant aggregation.

6.4 INFLUENCE OF SPATIALLY AGGREGATED PLANTS ON SOIL FAUNA COMMUNITIES

Our analyses showed significant differences between aggregated and control sites for total soil fauna and litter transformers communities. Litter quality differences may create microhabitats that promote the association of particular soil fauna and specific combinations of nutrients in sites dominated by aggregated species (Etterma & Wardle 2002; Giller 1996). *Rinorea* species, which harbor the highest abundance of soil fauna within their distribution sites (i.e. 33.9 % of the total collection), present low values of leaf litter tannin content (Cárdenas *et al*. 2015; Montiel 1991). This particular characteristic may explain their similarities in terms of species composition because it is widely known that soil fauna avoids litter rich in polyphenols, and particularly tannin-protein complexes (Cárdenas *et al.* 2015; Loranger *et al*. 2007; Harbone 1997; Tian *et al.* 1993; Satchell and Lowe 1967). Therefore, factors such as total leaf litter biomass, quality and chemistry may explain soil fauna species composition patterns in sites of plants aggregation (Austin *et al*. 2014; Manzoni *et al*. 2010; Pérez-Harguindeguy *et al*. 2000). Future studies should analyze the quality of leaf litter to explain differences or similarities in the soil fauna diversity patterns. Conversely, other surveys such as Laosii *et al*.´s (2007)

suggested that plant biomass has a positive effect on the diversity and density of soil macrofauna independent of plant diversity. It suggested that plants could create microcosms that may affect belowground diversity through the quantity rather than the diversity of organic matter produced in Amazon pastures (Laosii *et al.* 2007). Therefore, we suspect that the totality of soil resources and particular characteristics of *Rinorea* litter quantity and quality, should dictate the persistence of decomposer organisms that are better able to take advantage of the specific suite of those available resources (Austin *et al.* 2014; Laosii *et al.* 2007).

Soil fauna composition may also be influenced by abiotic factors such as daily temperatures and precipitation (Vossbrink & Wooley 1979). Although, most tropical forests experience continually warm climates, they vary greatly in the amount and seasonal distribution of precipitation (Dewar & Wallis 1999). During our sampling, we faced periodic rains and floods particularly in valleys (valleys represented 20 % of our habitat samples) inside the plot. These factors may have influenced our results. We recognize that additional data are needed to provide a conclusive evidence of soil fauna composition and diversity in the aggregated sites inside the YFDP. A second sampling effort using the same methodology was performed in October 2015, which has not been considered for analyses in this Master dissertation.

6.5 THE IMPORTANCE OF SOIL FAUNA FOR CONSERVATION IN YASUNÍ

Soil organisms play a vital role in the production and maintenance of healthy soils (Stock & Eggleton 1992). Their contributions on ecosystem services types (i.e. production,

support and regulation) are well-described. Nevertheless, the exact functional role and importance of most of these environmental goods and services are yet to be discovered in tropical soils (Wall *et al.* 2010; Lavelle *et al.* 2006). Several soil organisms (e.g. earthworms, ants and collembolans) have been used as bioindicators (Fiera 2009; Bruyn 1999; Paoletti 1999). Since they have shown to be sensitive to detect important environmental changes (i.e. caused by pollutants and other degradation factors; Gillet and Ponge, 2003; Bruce *et al.*, 1997) that may affect soil functioning (e.g. Cenci & Jones 2009; Van Straalen 1998). For instance, the relationships of soil collembolan fauna with their ecological niches and the stability of community composition at a specific site provide good starting points for bioindication of changes in soil properties and impact of human activities (Fiera 2009).

Despite threats related to oil exploitation (e.g. unsustainable hunting along oil companies access roads, habitat fragmentation and deforestation; Bass *et al.* 2010) and human colonization, Yasuní is probably still home to a largely intact assemblage of top predators, seed dispersers, herbivores and seed predators (Franzen 2006; Zapata-Ríos *et al.* 2006). Studies have shown that biodiversity has positive effects on the provision of services (e.g. primary productivity, erosion control, nutrient cycling, regulation of biological diversity and stability) and that further biodiversity loss can be expected to compromise service delivery (Gibson *et al.* 2011; Balvanera *et al.* 2006; Wardle *et al.* 2003). Although our results revealed a great diversity of soil fauna in Yasuní, the continuous anthropogenic threats could be driving insidious, long-term changes in the composition and structure of plants (Peres & Palacios 2007; Terborgh *et al.* 2008). This could affect soil trophic network and the availability of environmental goods and services (Wagg *et al.* 2014; Gibson *et al.* 2011), because plants are the basis of energy and nutrient turnover in food webs. Therefore, they are the primary determinants of terrestrial

ecosystem structure including microhabitat conditions for other organisms at secondary and tertiary trophic levels (i.e. soil macrofauna; Gillison *et al.* 2003). In addition, soils represent a necessary substrate for a large part of global biodiversity (Decaëns *et al.* 2006). The majority of animals in terrestrial habitats are soil inhabitants for at least one stage of their life cycle (Andrén *et al.* 1999). Therefore, bioindicators of soil health such as soil fauna (Pankhurst *et al*. 1997), which are key aspects of soil quality, could be used as a tool to establish sustainable land management strategies and promote conservation initiatives to prevent environmental degradation (Fiera 2009; Gillet & Ponge, 2003).

6.6 CONCLUSION

Even though, previous studies in tropical forests suggested that plant species do not predict soil fauna diversity (Donoso *et al.* 2010), and that the Amazonian forest floor is homogeneously upholstered with a bunch of macro-organisms with similar characteristics (i.e. in terms of species functionality; Cárdenas 2013), our results have shown that this pattern is not valid at the scale of the habitats created by plant species living in aggregation. Whether our findings reflect, any kind of soil organisms' specialization to exploit particular resources in these specific microhabitats is yet to be investigated. One first step should consider analyzing the physical and chemical quality of leaf litter to correlate with the soil fauna composition at these microhabitats scales.

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8. FIGURES

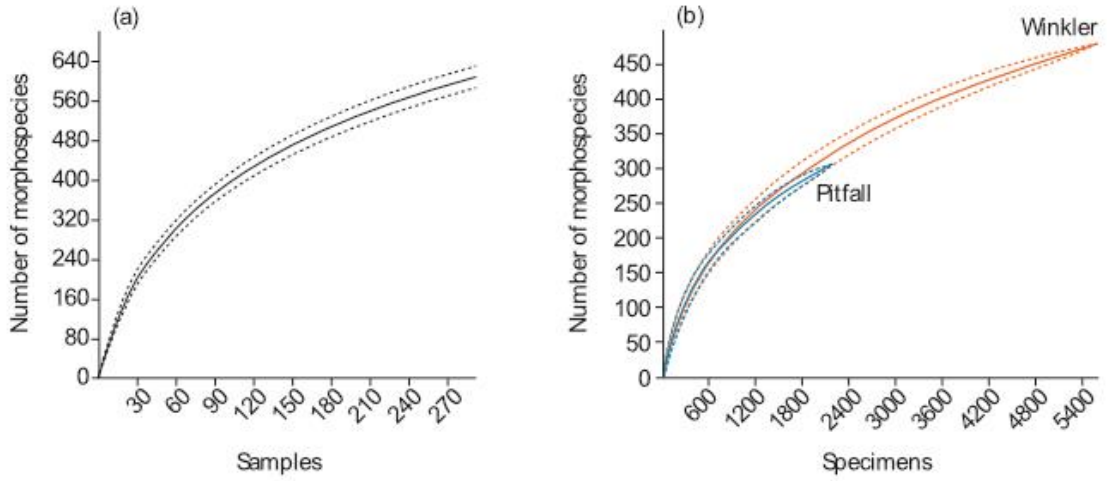

Figure 1. Rarefaction curves showing the whole sampling collection, including aggregated and control sites in a single dataset. (a) Sample-based rarefaction curve for both collecting methodologies, Winkler extraction and Pitfall traps, together in one single dataset. Dashed lines correspond to ±95 % confidence intervals based on Mao tau analytical solution. (b) Individual-based rarefaction curves revealing the number of morphospecies collected using Winkler extraction (red) and Pitfall traps (blue). Dashed lines correspond to ±95 % confidence.

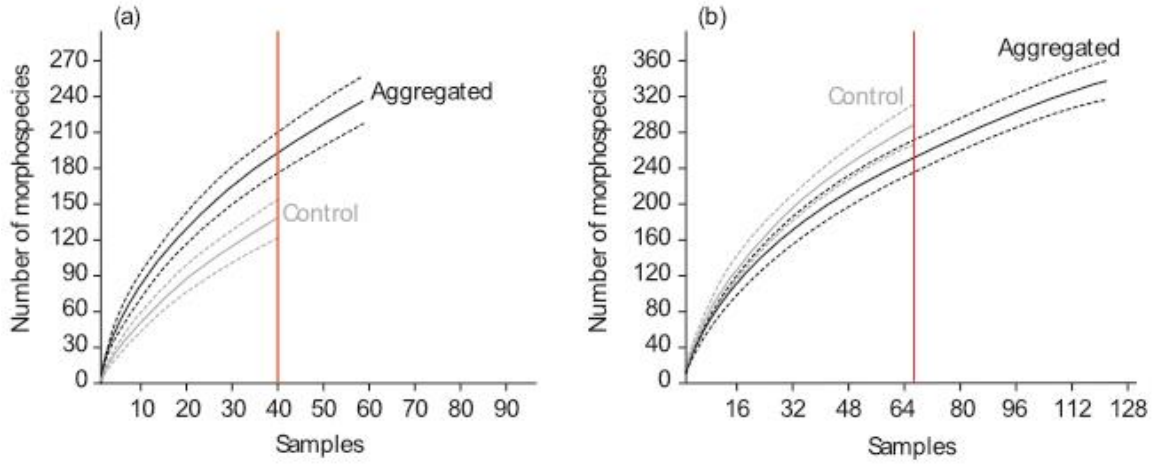

Figure 2. Sample-based rarefaction curves (solid lines) between aggregated and control sites in relation to the number of soil fauna species of (a) the Winkler extraction and (b) Pitfall traps methodologies. The vertical red line indicates the number of samples where both sites are comparable. Dashed lines correspond to ± 95 % confidence intervals.

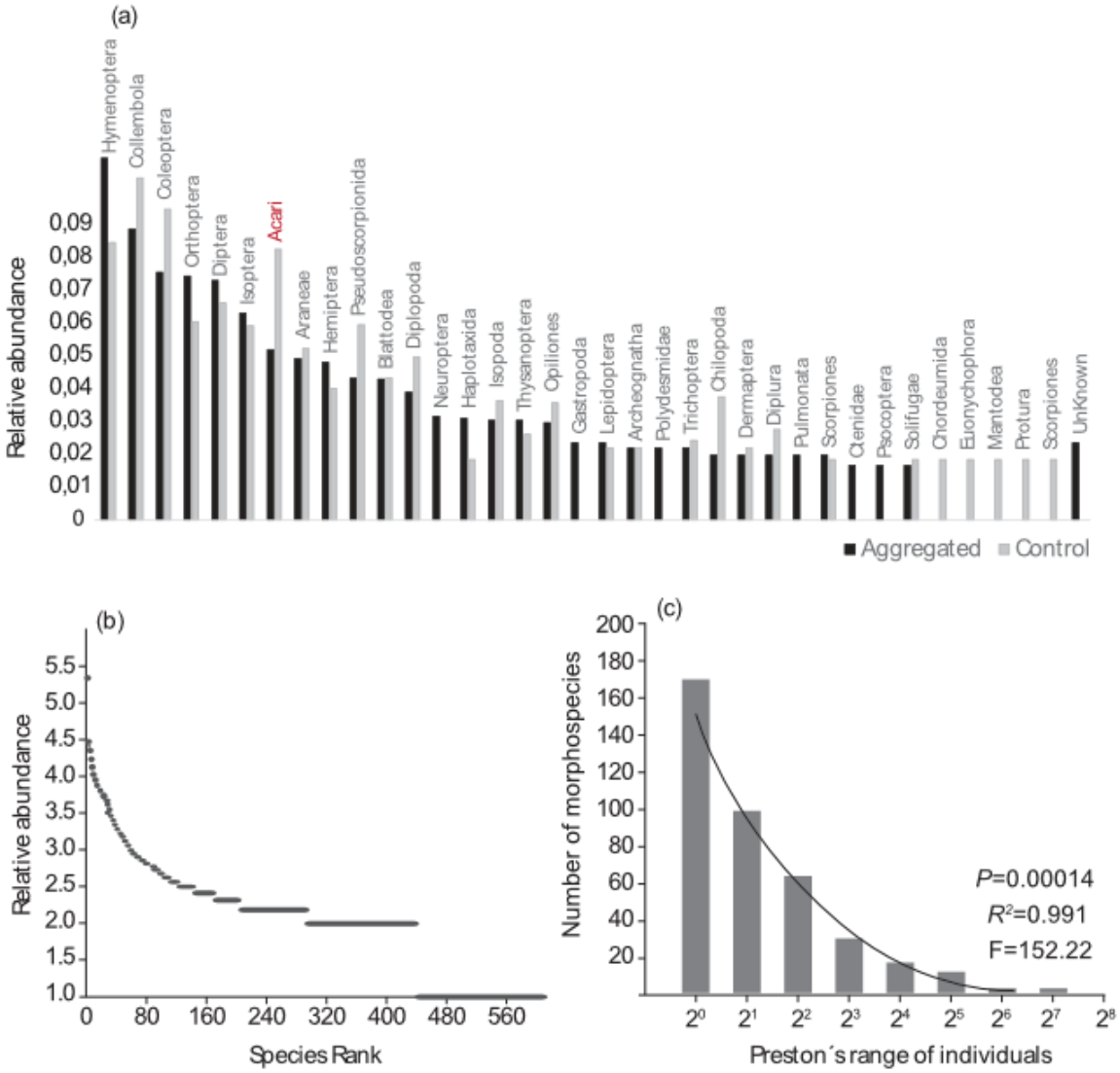

Figure 3. Rank abundance plots showing (a) the relative abundance of the number of species for major order soil animal groups, (b) the variation in the relative abundance of soil animal species ordered from most to least abundant, and (c) the Preston's plot of the number of species per $\log_2$ abundance ranges. On (c), log2 series followed Preston (1948) ranges: 2^0 (1–2), 2^1 (2–4), 2^2 (4–8), 2^3 (8–16), 2^4 (16–32), 2^5 (32–64), 2^6 (64–128), 2^7 (128–256). *P*, R^2 and *F* values in (c) correspond to the statistical values of the fit of the lognormal regression curve.

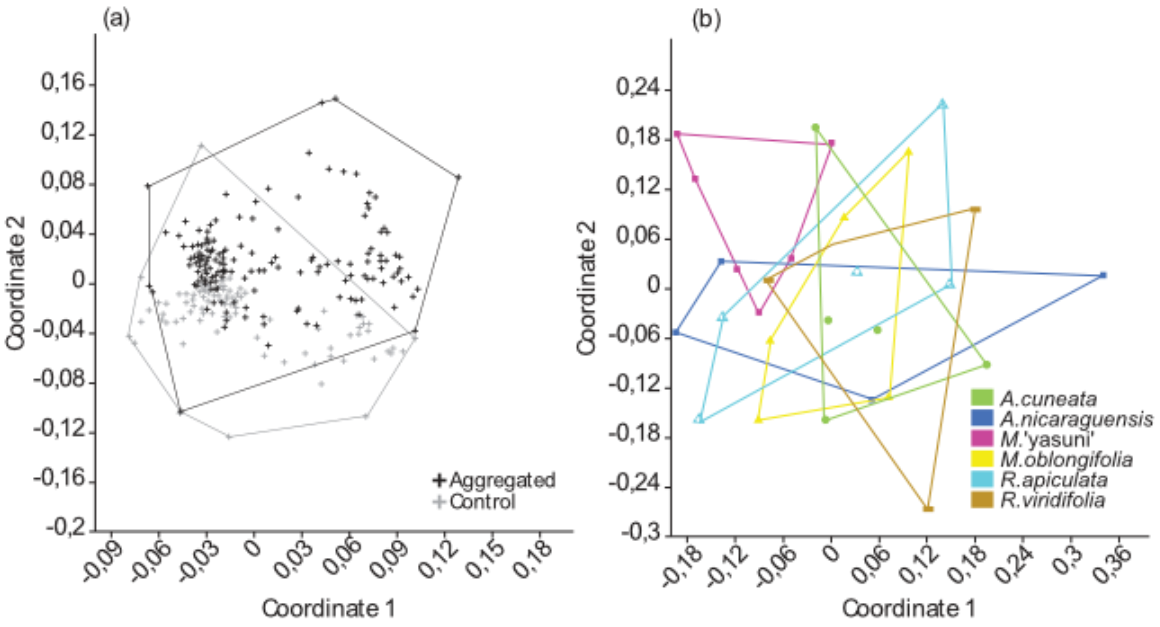

Figure 4. NMDS plots showing the differences of soil fauna communities between aggregated and control sites (a), and plant species aggregation sites (b) analysis showed that soil fauna communities were significantly different in terms of species composition (a) between aggregated (black polygon) and control (grey polygon) sites ($P < 0.001$) and (b) within all aggregated sites ($P = 0.00177$). Colored polygons represent aggregated plant species.

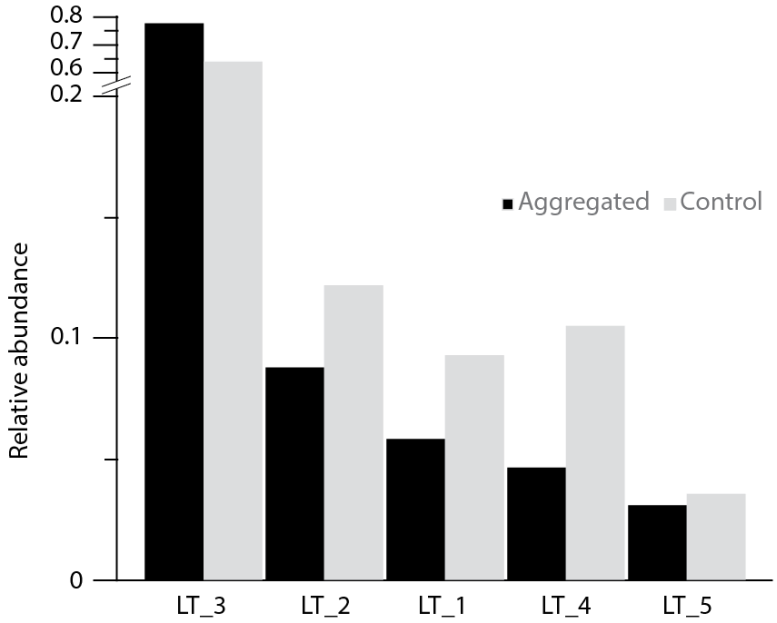

Figure 5. Rank abundance plot of the sites of plants aggregation showing the relative abundance of the five groups of litter transformers between aggregated (black) and control (grey) sites.

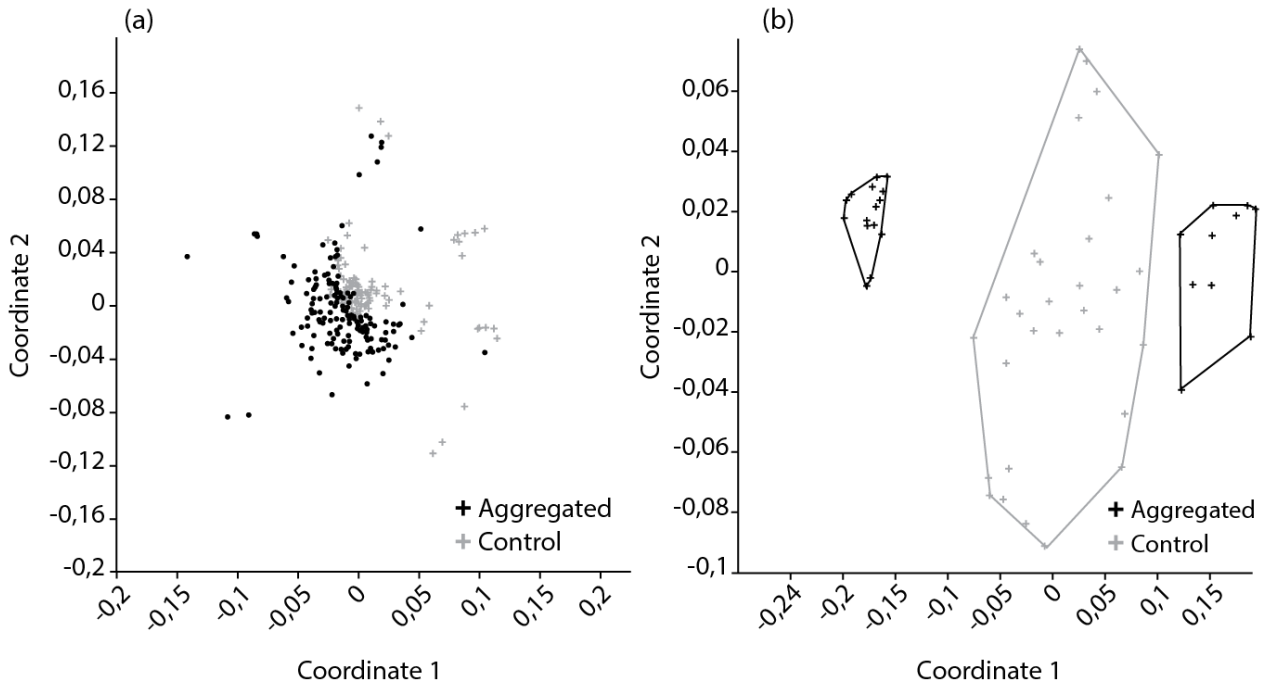

Figure 6. NMDS plots showing litter transformers dissimilarities at (a) species diversity level, ($P < 0.002$) and (b) at functional groups level ($P < 0.001$) level between aggregated (black polygon) and control (grey polygon) sites.

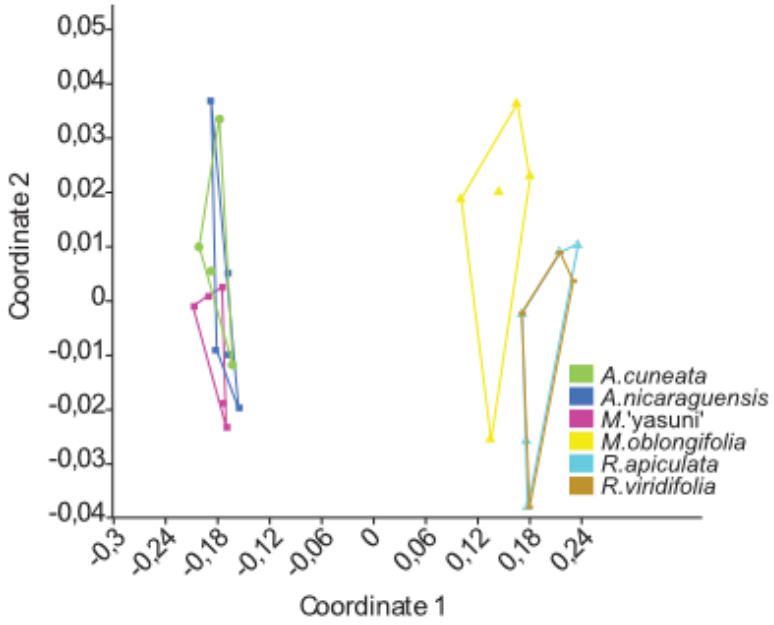

Figure 7. NMDS plots showing litter transformers dissimilarities in aggregated sites at functional groups ($P < 0.0001$) level within all the sites of plants aggregation. Colored polygons represent aggregated plant species.

9. TABLES

Table 1. *P* values from ANOSIM analyses within aggregated sites showing dissimilarities in the composition of a) soil fauna diversity and b) litter transformers species diversity. Grey diagonal dashed line separates *P* values.

	A. cuneta	*A. nicaraguensis*	*M.* 'yasuni'	*M. Oblongifolia*	*R. Apiculata*	*R. viridifolia*
A. cuneta	a b	0.6202	0.0020	0.0010	0.0000	0.0000
A. nicaraguensis	0.4994		0.0099	0.0004	0.0001	0.0000
***M.* 'yasuni'**	0.0218	0.0177		0.0000	0.0000	0.0000
M. Oblongifolia	0.7220	0.2342	0.0419		0.4712	0.0620
R. Apiculata	0.0075	0.0776	0.0141	0.0089		0.1585
R. viridifolia	0.3620	0.7436	0.4536	0.8583	0.5600	

10. APPENDIX

Appendix 1. Spatial aggregation analysis of six tropical tree species in the 50-ha plot of the YFDP, in Yasuní National Park Ecuador.

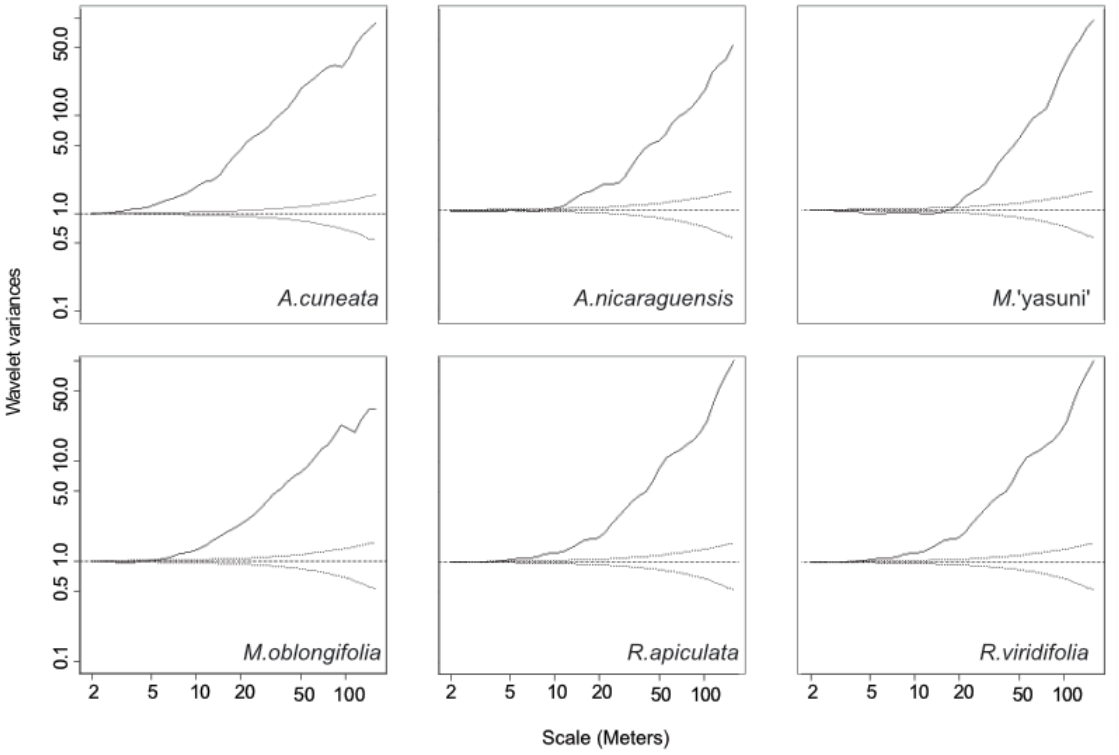

Figure 1. Wavelet variances of six tropical tree species in the 50-ha plot of the YFDP, in Yasuní National Park, Ecuador. Spatial aggregation was defined using scalewise variances and moment equations. This procedure determines the probability distribution of independently observed scalewise variances for a given expectation, including complete spatial randomness providing an analytical test of the null model of spatial randomness to understand at which scales the variance depart significantly from randomness. This technique also derives the likelihood function that is needed to estimate parameters of spatial models and their uncertainties from observed patterns (Detto & Muller-Landau 2013). The observed wavelet variances (solid lines) are comparable with

95 % confidence intervals for a complete spatial randomness process (dot lines). Species are aggregated when both wavelet variances (observed and random) start to separate at certain distance

References

Detto, M. and Muller-Landau, H. C. 2013. Fitting ecological process models to spatial patterns using scalewise variances and moment equations. The American Naturalist 181: E68-E82.

Appendix 2. Spatial distribution of six tropical tree species in the 50-ha plot of the YFDP, in Yasuní National Park Ecuador, considering its topography.

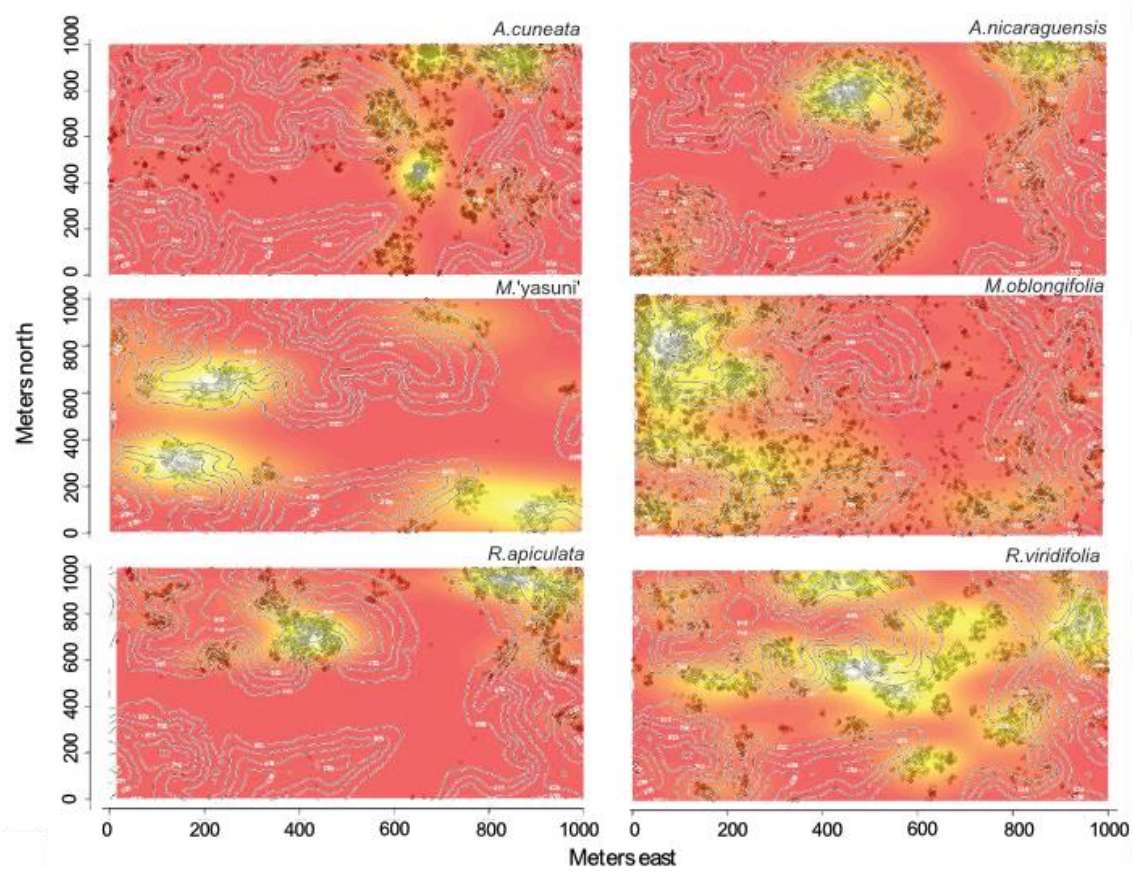

Figure 2. Topographic map of the 50-ha plot, with 2-m contour intervals. Numbers marking each line are metres above sea level. Six habitats are indicated: valley, low-slope, high-gully, upper-slope and ridge-top. Axes are marked in metres; north is up (based on Valencia *et al.* 2004 data). The red-orange-yellow-white color gradient shows the density levels of trees presence where the white color represents the sites with the highest individuals' density.

References

Valencia, R., Foster, R.B., Villa, G., Condit, R.G., Svenning, J.C., Hernandez. C., Romoleroux, K., Losos, E.C., Magard, E. & Balslev, H. 2004 Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. Journal of Ecology 92: 214–229.

Appendix 3. Soil fauna biodiversity survey in control sites.

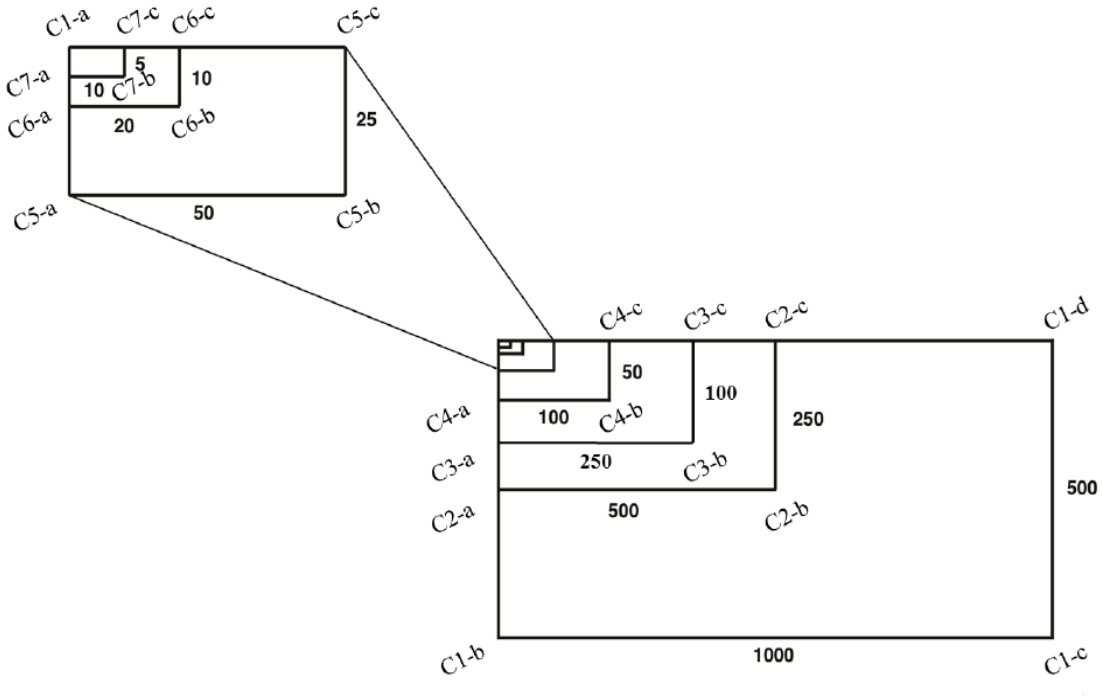

Figure 3A. For the Pitfall collection methodology, a nested rectangular grid of six different spatial scales was established across the forest floor (smallest scale: 10 × 5 m; largest scale: 1000 × 500 m; each scale doubled the length and width of the previous). Four plots (one in each corner of each scale) for a total of 69 plots were sampled at each of these scales. Each plot consisted of three pitfall traps (up to five in some cases) which remained opened for 24 hours. Pitfall traps consisted of plastic cups of 5 cm in diameter and 10 cm in depth and were buried to soil level.

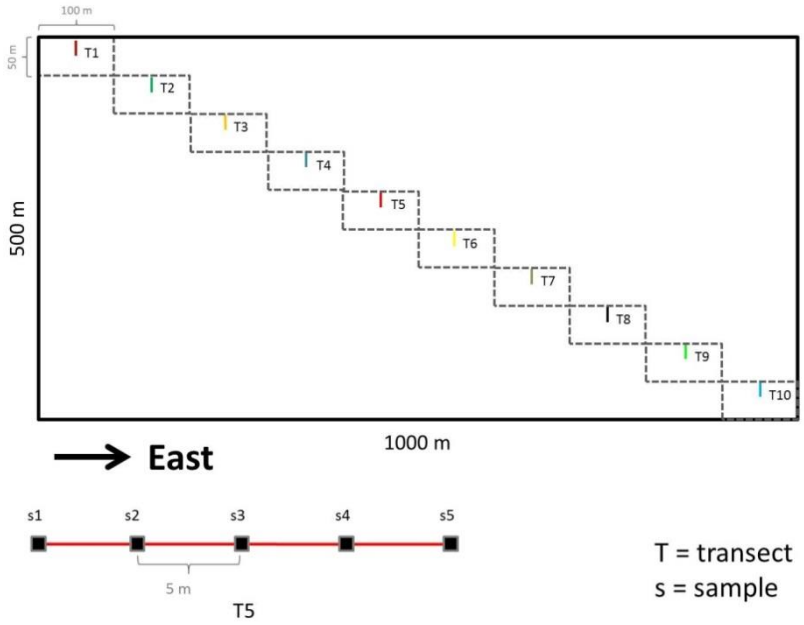

Figure 3B. For the second method, a total of 40 Winkler extractions (from 1 m^2 of soil leaf litter) were analyzed. Twenty of them were performed in a 200 m transect separated by 10 m between each other following ALL-protocol (Ants of the Leaf Litter, see Agosti & Alonso 2000 for details). The remaining 20 were distributed in 10 transects of 20 m that followed the diagonal of a 1000 × 500 m plot. Each transect was set in 10 subplots of 100 × 50 m, where two samples separated by 5–20 m were extracted and analyzed.

References

Cárdenas, R.E. 2013. Plant and fauna functional trait diversity affecting leaf herbivory and decomposability in a Neotropical rainforest (Yasuní National Park – Ecuador). PhD thesis, Pierre and Marie Curie University (Paris 6), France.

Appendix 4. Soil fauna sampling collection inside YFDP, in Yasuní National Park Ecuador

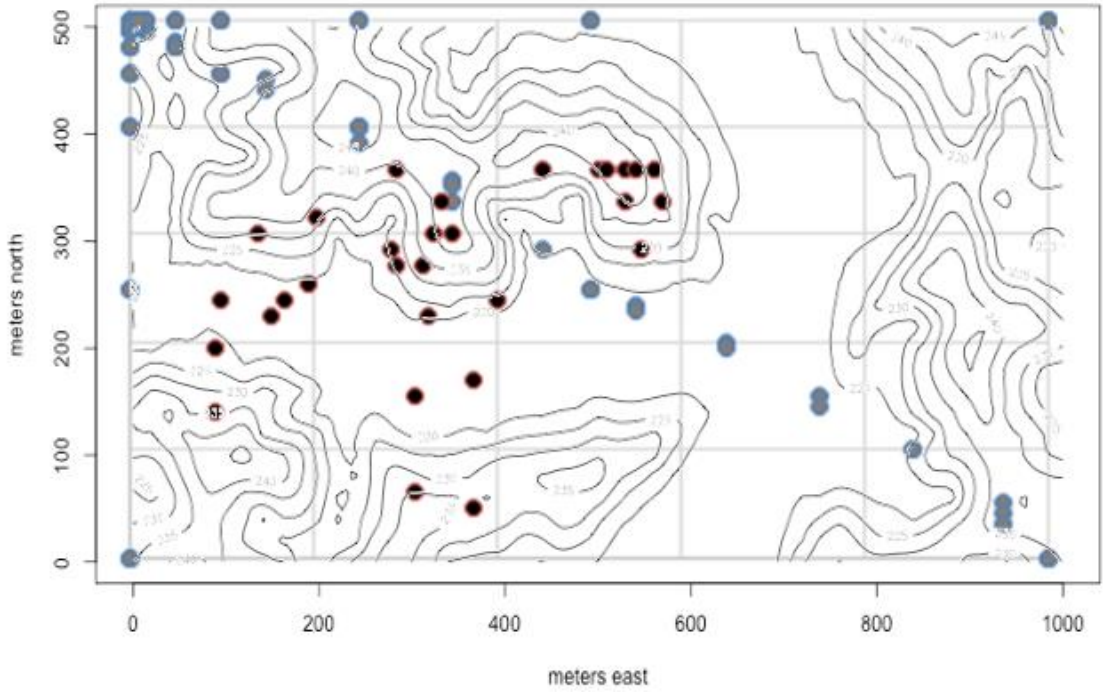

Figure 4. Topographic map of the YRS-PUCE sub-plot and the location of the collection sites, aggregated (black) and control (grey) used for this assessment (coordinates X: 50–700; Y: 100–500). Lines represent 4m contour interval. Image modified from Metz *et al*. (2010).

References

Metz, M.R., Sousa, W.P. and Valencia, R. 2010. Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rain forest. Ecology 91: 3675–3685.

Appendix 5. Functional groups assignment for each collected specie inside YFDP, in Yasuní National Park Ecuador. Functional groups represented by (1) Primary producers, (2) Herbivores, (3) Ecosystem engineer, (4) Litter transformers, (5) Decomposers, (6) Predators, (7) Microregulators, (9) Soil born pest and disease and (11) Mesoregulators. Acari are not considered in this analysis.

Specie	Funtional Group
Aleocharinae_1	2,4,6,11
Aleocharinae_3	2,4,6,11
Aphodinae_1	3,4
Arrhopalitidae_1	4,7
Arrhopalitidae_10	4,7
Arrhopalitidae_12	4,7
Arrhopalitidae_13	4,7
Arrhopalitidae_14	4,7
Arrhopalitidae_15	4,7
Arrhopalitidae_3	4,7
Arrhopalitidae_4	4,7
Arrhopalitidae_5	4,7
Arrhopalitidae_6	4,7
Arrhopalitidae_7	4,7
Arrhopalitidae_8	4,7
Arrhopalitidae_9	4,7
Arthropoda/Myriapoda_3	4,6,9
Arthropoda/Myriapoda_8	4,6,9
Blattellidae_1	4
Blattellidae_10	4
Blattellidae_11	4

Specie	Funtional Group
Blattellidae_12	4
Blattellidae_2	4
Blattellidae_3	4
Blattellidae_5	4
Blattellidae_7	4
Blattellidae_9	4
Blattidae_2	4
Blattidae_3	4
Blattidae_4	4
Blattidae_6	4
Blattidae_8	4
Blattodea_1	4
Camponotus_1	2,3,4,6
Cecidomyiidae_1	2,4,11
Cecidomyiidae_2	2,4,11
Cecidomyiidae_3	2,4,11
Coleoptera/larva_1	2,4,6
Coleoptera/larva_10	2,4,6
Coleoptera/larva_11	2,4,6
Coleoptera/larva_12	2,4,6
Coleoptera/larva_13	2,4,6

Specie	Funtional Group
Coleoptera/larva_14	2,4,6
Coleoptera/larva_15	2,4,6
Coleoptera/larva_16	2,4,6
Coleoptera/larva_17	2,4,6
Coleoptera/larva_20	2,4,6
Coleoptera/larva_21	2,4,6
Coleoptera/larva_22	2,4,6
Coleoptera/larva_23	2,4,6
Coleoptera/larva_24	2,4,6
Coleoptera/larva_25	2,4,6
Coleoptera/larva_26	2,4,6
Coleoptera/larva_27	2,4,6
Coleoptera/larva_5	2,4,6
Coleoptera/larva_7	2,4,6
Coleoptera/larva_8	2,4,6
Coleoptera/larva_9	2,4,6
Curculionidae/Dorytosomimus_1	4
Curculionidae/Rhina_barbirostris_1	4
Curculionidae_2	2,4
Curculionidae_4	2,4
Curculionidae_5	2,4

Specie	Funtional Group
Curculionidae_6	2,4
Dermaptera_3	2,4,6
Diplopoda_1	3,4,9
Diplopoda_2	3,4,9
Diplopoda_3	3,4,11
Diplopoda_4	3,4,11
Diplopoda_5	3,4,11
Diplopoda_8	3,4,11
Diptera/larva_1	4,6,9,11
Diptera/larva_10	4,6,9,11
Diptera/larva_11	4,6,9,11
Diptera/larva_12	4,6,9,11
Diptera/larva_13	4,6,9,11
Diptera/larva_14	4,6,9,11
Diptera/larva_3	4,6,9,11
Diptera/larva_4	4,6,9,11
Diptera/larva_6	4,6,9,11
Diptera/larva_7	4,6,9,11
Diptera/larva_8	4,6,9,11
Drosophilidae_1	4,11
Drosophilidae_2	4,11
Drosophilidae_3	4,11
Drosophilidae_4	4,11
Drosophilidae_5	4,11
Drosophilidae_6	4,11
Entomobryidae_1	4,7
Entomobryidae_10	4,7

Specie	Funtional Group
Entomobryidae_11	4,7
Entomobryidae_14	4,7
Entomobryidae_16	4,7
Entomobryidae_17	4,7
Entomobryidae_18	4,7
Entomobryidae_19	4,7
Entomobryidae_2	4,7
Entomobryidae_20	4,7
Entomobryidae_22	4,7
Entomobryidae_23	4,7
Entomobryidae_24	4,7
Entomobryidae_25	4,7
Entomobryidae_26	4,7
Entomobryidae_3	4,7
Entomobryidae_4	4,7
Entomobryidae_5	4,7
Entomobryidae_6	4,7
Entomobryidae_7	4,7
Entomobryidae_8	4,7
Entomobryidae_9	4,7
Gastropoda_1	2,4
Gastropoda_2	2,4
Gryllidae_1	2,4,6
Gryllidae_10	2,4,6
Gryllidae_11	2,4,6
Gryllidae_12	2,4,6
Gryllidae_13	2,4,6

Specie	Funtional Group
Gryllidae_14	2,4,6
Gryllidae_15	2,4,6
Gryllidae_16	2,4,6
Gryllidae_17	2,4,6
Gryllidae_18	2,4,6
Gryllidae_2	2,4,6
Gryllidae_20	2,4,6
Gryllidae_21	2,4,6
Gryllidae_22	2,4,6
Gryllidae_23	2,4,6
Gryllidae_24	2,4,6
Gryllidae_25	2,4,6
Gryllidae_26	2,4,6
Gryllidae_27	2,4,6
Gryllidae_28	2,4,6
Gryllidae_29	2,4,6
Gryllidae_3	2,4,6
Gryllidae_30	2,4,6
Gryllidae_31	2,4,6
Gryllidae_32	2,4,6
Gryllidae_33	2,4,6
Gryllidae_34	2,4,6
Gryllidae_35	2,4,6
Gryllidae_36	2,4,6
Gryllidae_37	2,4,6
Gryllidae_4	2,4,6
Gryllidae_5	2,4,6

Specie	Funtional Group
Gryllidae_6	2,4,6
Gryllidae_8	2,4,6
Hypogastruridae/Neanuridae_10	4,7
Hypogastruridae/Neanuridae_4	4,7
Hypogastruridae/Neanuridae_7	4,7
Hypogastruridae/Neanuridae_8	4,7
Hypogastruridae/Neanuridae_9	4,7
Isoptera_1	3,4,5
Isoptera_4	3,4,5
Isoptera_5	3,4,5
Isoptera_7	3,4,5
Isotomidae/Oncopoduridae_2	4,7
Lumbricidae_1	3,4
Lumbricidae_2	3,4
Meinertellidae_1	2,4
Meinertellidae_2	2,4
Nylanderia_1	2,3,4,6
Nylanderia_2	2,3,4,6
Oxysternon_conspicillatum_1	3,4
Oxytelinae_1	2,4,6
Oxytelinae_10	2,4,6
Oxytelinae_11	2,4,6
Oxytelinae_12	2,4,6
Oxytelinae_14	2,4,6
Oxytelinae_2	2,4,6
Oxytelinae_3	2,4,6
Oxytelinae_5	2,4,6

Specie	Funtional Group
Oxytelinae_6	2,4,6
Oxytelinae_7	2,4,6
Oxytelinae_8	2,4,6
Oxytelinae_9	2,4,6
Oxytelinae-Aleocharinae_1	2,4,6,11
Pheidole_1	2,3,4,6
Pheidole_10	2,3,4,7
Pheidole_11	2,3,4,8
Pheidole_2	2,3,4,9
Pheidole_3	2,3,4,10
Pheidole_4	2,3,4,11
Pheidole_5	2,3,4,12
Pheidole_7	2,3,4,13
Pheidole_8	2,3,4,14
Pheidole_9	2,3,4,15
Phlaeothripidae_1	2,4,6
Phlaeothripidae_10	2,4,6
Phlaeothripidae_2	2,4,6
Phlaeothripidae_5	2,4,6
Phlaeothripidae_6	2,4,6
Phlaeothripidae_8	2,4,6
Polydesmidae_2	3,4,9
Polydesmidae_3	3,4,9
Pulmonata_1	2,4
Scaphidiidae_1	4,11
Scarabaeinae_1	3,4
Scarabaeinae_10	3,4

Specie	Funtional Group
Scarabaeinae_11	3,4
Scarabaeinae_2	3,4
Scarabaeinae_4	3,4
Scarabaeinae_5	3,4
Scarabaeinae_6	3,4
Scarabaeinae_7	3,4
Scatopsidae_1	2,4
Scolytinae_1	3,4
Scolytinae_2	3,4
Scolytinae_4	3,4
Scolytinae_6	3,4
Scolytinae_7	3,4
Scolytinae_8	3,4
Scolytinae_9	3,4
Solenopsis_1	3,4,6
Solenopsis_2	3,4,7
Solenopsis_3	3,4,8
Solenopsis_4	3,4,9
Staphylinidae/larva_1	4,6
Staphylinidae/Larva_2	4,6
Staphylinidae/Larva_5	4,6
Staphylinidae/Staphylininae_6	2,4,6
Staphylinidae_15	2,4,6
Staphylinidae_5	2,4,6
Staphylininae_1	2,4,6
Staphylininae_10	2,4,6
Staphylininae_11	2,4,6

Specie	Funtional Group
Staphylininae_12	2,4,6
Staphylininae_13	2,4,6
Staphylininae_2	2,4,6
Staphylininae_3	2,4,6
Staphylininae_4	2,4,6

Specie	Funtional Group
Staphylininae_5	2,4,6
Staphylininae_6	2,4,6
Staphylininae_7	2,4,6
Tenebrionidae_1	4
Tettigoniidae_2	2,4,9

Specie	Funtional Group
Thysanoptera_2	2,4,6
Thysanoptera_7	2,4,6
Tipulidae_1	4,6
Trichoptera/Larva_1	2,4,6
Trichoptera_1	2,4,6

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DECLARACION Y AUTORIZACION

Yo, Dolly Amparo Muñoz Upegui, CI. 171663125-2 autora del trabajo de graduación intitulado: "Diversity of soil invertebrates associated to six spatially aggregated plant species in the Yasuní National Park, Amazonian Ecuador", previa a la obtención del grado académico de **MAGISTER EN BIOLOGIA DE LA CONSERVACION** en la **Facultad de Ciencias Exactas y Naturales**:

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