

Functional consequences of realistic extinction scenarios in Amazonian soil food webs

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Abstract. Global biodiversity loss is creating a more urgent need to understand the role organisms play in ecosystem functioning and mechanisms of control. Decomposition of dead organic matter is a key ecological process that ensures soil formation, nutrient availability, and carbon sequestration. To gain understanding of how biodiversity and ecosystems function together to control leaf-litter decomposition processes in a tropical rain forest (Yasuní National Park, Ecuador), we predicted the consequences of the decomposition process using a protocol in which we systematically disassemble the structural functionality of the soil macrofauna communities. We (1) describe the structure and function of the edaphic communities in detail and (2) explore the functional consequences of structural changes in these communities using a non-random exclusion experiment to simulate body size-related extinctions. To do this, we manipulated access of five size classes of soil invertebrates to eight types of plant leaf-litter resources. After measuring and identifying about 4400 soil individuals belonging to 541 morphospecies, 12 functional groups, and following the fate of about 2000 tree leaves in a 50-ha plot, we showed that (1) soil invertebrate communities were composed of a few common and many rare morphospecies that included mostly leaf-litter transformer groups, with the most morphospecies and the greatest abundance coming from Hymenoptera, Collembola, and Coleoptera; (2) our survey captured 63–74% of the total soil biodiversity of the study area (meaning there may be up to 860 morphospecies); (3) litter transformers covered the widest range of body volume, and all groups were evenly distributed at small and large spatial scales (i.e., we found no patterns of spatial aggregation); (4) changes in food web structure significantly altered biomass loss for only three of the eight leaf-litter treatments, suggesting the decomposition process was highly resistant to drastic changes such as size-biased biodiversity loss independent of resource quality. We conclude organic matter decomposition may depend on all non-additive effects that arise from multi-species interactions, including facilitation, interspecific interference competition, and top-down control that predators exert over detritivores at all body size ranges.

Key words: belowground; biodiversity and ecosystem functioning; brown food webs; decomposers; Ecuador; extinction order; invertebrates; leaf-litter decomposition; Yasuní National Park.

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INTRODUCTION

Biodiversity loss directly disrupts ecosystem functioning, undermining ecosystem services and ultimately affecting human well-being (Díaz et al. 2006, Cardinale et al. 2012). Biodiversity and ecosystem functioning research (BEF) seeks to determine how species diversity is related to the magnitude and stability of ecosystem processes (Griffin et al. 2009, Hooper et al. 2012). There is a great deal of ecological debate about three tenets of BEF, which are that biodiversity is likely to (1) improve productivity (Cardinale et al. 2007, Hooper et al. 2012), (2) increase ecosystem stability (Tilman et al. 2006), and (3) enhance the magnitude of a variety of ecosystem processes (Hooper et al. 2005, Balvanera et al. 2006, Wagg et al. 2014). However, the effects of changes in biodiversity on ecosystem functioning may vary across ecosystem types and study groups, and depend on the trophic relationships involved (Huston 1997, Smith and Knapp 2003, Wardle et al. 2008, Schmid et al. 2009). This has raised the question: Does the relationship between biodiversity and ecosystem functioning apply in the real world (across trophic levels), outside of controlled experiments? To answer this, new studies must look at the entire food web within an ecosystem (Tylianakis et al. 2008, Thompson et al. 2012). Future conservation strategies require an understanding of the reciprocal nature of relationships between food web structure and the functioning of a given ecosystem (Thompson et al. 2012, Poisot et al. 2013).

Decomposition of dead organic matter (OM), categorized as a supporting service in the Millennium Ecosystem Assessment (2005), is a key ecosystem function that ensures soil formation, nutrient availability for plants, and carbon sequestration (Swift et al. 1979, Chapin et al. 2002). OM processes are influenced by factors such as climate (Wall et al. 2008, Powers et al. 2009), the physical and chemical properties of dead OM (Kaspari et al. 2008, Hättenschwiler et al. 2011), the sequential action of soil invertebrates, fungi, and bacteria (Ingham et al. 1985, Pramanik et al. 2001, Mulder 2006), and the functional diversity of both dead OM (e.g., plant litter) and soil consumers (Hättenschwiler and Gasser 2005, Gessner et al. 2010, Dangles et al. 2012, Handa et al. 2014). A significant part of BEF research has focused on

the role of invertebrate fauna (primarily detritivores) on leaf-litter decomposition in both aquatic and terrestrial habitats (Lavelle et al. 2006, Gessner et al. 2010, García-Palacios et al. 2016). Detritivore biodiversity has proven to be critical to the biogeochemical and ecological functioning of terrestrial ecosystems, with consequences for fertility, plant growth, environmental structure, and carbon storage (Brussaard 1998).

We know little about how loss of detritivore biodiversity affects leaf-litter decomposition and other ecosystem processes, particularly when species in a focal community differ in key functional attributes (Bardgett and Wardle 2010, Wall et al. 2010). There is ample evidence that soil communities are adapted to specific environmental conditions and resource types; therefore, any changes in either factor could negatively affect species richness, with potential to severely impair ecosystem functioning (Wall and Nielsen 2012, Lavelle et al. 2016). A recent global review of experiments that have explored the relationship between carbon cycling and soil biodiversity concluded that although species richness, on average, led to better ecosystem functioning—measured as greater biomass, decomposition rates, and/or respiration, especially in species-poor communities—the relationship was neither linear nor redundant (Nielsen et al. 2011). However, Handa et al. (2014) conducted a first concerted set of experiments across five terrestrial locations (from the subarctic to the tropics), and found that functional biodiversity loss of both soil fauna and litter types slowed cycling of litter carbon and nitrogen. They suggest that documented differences in the effects of biodiversity loss on decomposition across global spatial scales may at least partly arise from variation in experimental protocols, plant species, and types of decomposers studied in a given experiment. Moreover, in ecosystems with high natural community evenness, stress or disturbances are unlikely to impair all species' contributions to an ecosystem service, making these communities more resistant and/or resilient to disturbances (Andrén et al. 1995). Communities with low evenness may lose dominant species due to stress or a disturbance. Dominant species tend to play a significant role in local ecosystem processes (the mass ratio hypothesis states that ecosystem processes are determined by the functional traits of the dominant species; Grime 1998, Smith and

Knapp 2003), and their loss impacts ecosystem functioning (Dangles et al. 2004, Wall and Nielsen 2012). Understanding detritivore community functional structure under natural settings will be key to understanding relationships between biodiversity and ecosystem functioning in complex, real-world systems.

Cárdenas and Dangles (2012) conducted an experiment using mesh bags to exclude both macro- and meso-detritivores from leaf litter, and found about a 50% decline in leaf-litter decomposition rates in an Ecuadorian cloud forest. Using the similar methodology to exclude macro-detritivores, Coq et al. (2010) found a 17.4% decline in leaf-litter decomposition rates in French Guiana and Yang and Chen (2009) found a 40% decline in tropical China. Although macro- and meso-detritivore fauna have been shown to play a crucial role in fragmenting dead OM in the tropics (Swift et al. 1979), studies that have manipulated the effects of detritivore diversity loss on leaf-litter decomposition in real field conditions (e.g., non-random extinction scenarios; Gross and Cardinale 2005) are still very scarce (Schmid et al. 2009). Furthermore, factors such as land use, nitrogen enrichment, acidification, and climate change have been reported to alter soil and stream detritivore diversity (Gessner et al. 2010).

Experiments that manipulate invertebrate diversity in natural ecosystems are extremely important for understanding the consequences of potential extinctions on decomposition and nutrient cycling. However, one specific problem in soil biology, and particularly in the tropics, is with how to deal with diverse and complex groups such as soil fauna (Giller 1996)—especially in these megadiverse systems where most species (>80% of all invertebrates of tropical forests) have yet to be described by science and almost nothing is known of the remainder's ecology (Primack and Corlett 2005, Wall et al. 2010). Ecosystem processes are a product of multiple biological and environmental variables (Petchey et al. 1999), underscoring the need for more realistic experiments under natural conditions that consider non-random loss of assemblages in local extinctions (e.g., Zavaleta and Hulvey 2004, O'Connor and Crowe 2005).

Community ecologists need tractable metrics that can serve as surrogates of interaction strength to better evaluate effects of biodiversity

loss on ecosystem stability and functioning. One potential surrogate is body size (a proxy to body mass and body volume). Body size is a key functional trait of species that is correlated with many life-history characteristics, and therefore, it is a good surrogate for a large amount of the biological information embedded within an ecological network (Emmerson and Raffaelli 2004, Woodward et al. 2005, Reiss et al. 2011). Body size could reflect the mass-dependent metabolic needs of an individual or a species community, predicting the impact of a drastic change in natural abundance of either on a given ecosystem functioning (Reiss et al. 2009). Size-dependent consumption and processing rates appear to be linked to energy flow (Dossena et al. 2012, Lang et al. 2014) and may even compromise stability of complex food webs (Otto et al. 2007). This is extremely important given that larger species are especially vulnerable to environmental perturbations such as global warming and changes in precipitation patterns (Salazar et al. 2007, Smith et al. 2009, Sheridan and Bickford 2011), habitat fragmentation (Klein 1989), or land use (McCracken and Bignal 1998). Moreover, recent research has shown that smaller species are not simply miniature copies of larger ones (due in part to mass-specific metabolic constraints, Reiss et al. 2011), suggesting that a range of animal size classes is needed to maintain ecosystem functioning (Dangles et al. 2012). In addition, larger-bodied invertebrates can directly or indirectly influence the diversity of smaller-sized organisms by promoting dispersal and modifying the soil habitat (Wardle 2006). For example, fragmentation by large detritivores could facilitate the ingestion/colonization of OM particles by smaller detritivores (including microflora; Lavelle et al. 1997, Jonsson et al. 2002, Yang et al. 2012). Or, larger detritivores, due to their needs to grow and higher mobility in the forest floor (e.g., giant annelids or cockroaches), could modify the accessibility to phosphorous, which may decrease locally and in the long term the biomass of small invertebrates relative to the larger ones (Mulder and Elser 2009). Finally, documenting the differential contribution of faunal size classes may help demonstrate how much redundancy and specialization is actually found in soil detritivore communities (Setälä et al. 2005, Bezemer et al. 2010). Size-biased, non-random species loss

therefore has important implications for the risk of cascading secondary extinctions and the loss of functional diversity from ecosystems (Solé and Montoya 2002, Ebenman et al. 2004).

Using the megadiverse invertebrate soil communities of Yasuní National Park (northwestern Amazonia, Ecuador) as a model system, our study aimed to answer two general questions: (1) What is the overall structural and functional organization of soil invertebrate communities in terms of taxa diversity, relative abundance, functional traits (based on trophic guilds, and biovolume as a proxy of biomass), and the diversity–area relationship? (2) How does non-random extinction within the soil invertebrate food web affect the leaf-litter decomposition process, and does such an effect depend on resource quality? These questions arise from (1) the “mass ratio hypothesis” that states that ecosystem processes are overwhelmingly determined by the functional traits of the dominant species. These dominant species may contribute most of the biomass, which actively controls fluxes of energy and matter through the ecosystem (Grime 1998, Smith and Knapp 2003). Therefore, we first need a detailed assessment of the relationship between species diversity, abundance, and body mass of the different functional groups present in the soil fauna of our study area—an elementary first step to understanding ecosystem functioning and the role and impact of species in the food chain (Jonsson et al. 2005); (2) larger soil species in the Amazon are more prone to extinction in the current climate change conditions (Salazar et al. 2007, Smith et al. 2009, Sheridan and Bickford 2011).

Given how little is known about soil biodiversity and functional diversity in Amazonian tropical ecosystems (Primack and Corlett 2005, Moreira et al. 2008), we followed the following steps to evaluate the realistic effect of biodiversity loss on leaf-litter decomposition: (1) We describe the soil invertebrate communities in detail, to understand how they are organized and distributed at the taxonomic, functional (including body size classes), and spatial levels; (2) we used a non-random exclusion experiment in which we manipulated the accessibility of five size classes of soil detritivore to eight types of plant leaf-litter resources (analogous to a removal experiment where we tested the influence of the dominant species, as explained by the mass ratio hypothesis; Díaz et al.

2003) to understand the potential implications of detritivore fauna extinction on the leaf-litter decomposition process in this ecosystem.

Here, we evaluate six hypotheses: (1) Amazonian soil invertebrate fauna biodiversity is dominated by the leaf-litter transformer (detritivore) functional group (in number of species, abundance, and biovolume); (2) leaf-litter transformer species encompass the largest range of body volume found in the forest floor; (3) there are no patterns of spatial aggregation, meaning that soil functional diversity does not increase with increased area based on the fact that most plant species in Yasuní follow the negative density dependence hypothesis (Metz et al. 2010), and therefore, they show a “random” distribution within our 50-ha plot (Valencia et al. 2004), which should be reflected by a leaf-litter diversity (and quality) homogeneity in this forest (Cárdenas et al. 2014, not shown); (4) leaf litter exposed to the smaller food web community may decompose at significantly lower rates than that exposed to larger soil fauna; (5) smaller species do not compensate for the loss of the larger ones in terms of leaf-litter transformation (there is a positive relationship between decomposition rates and detritivore diversity), suggesting that some size classes facilitate the effectiveness of others and that detritivore extinction may disrupt the decomposition process in this ecosystem; and (6) the effect of non-random soil fauna extinction on leaf-litter decomposition is independent of resource quality.

MATERIALS AND METHODS

Study site

Yasuní National Park (YNP) and the adjacent Waorani Indigenous territory cover 1.6 million ha of forest. Together they form the largest protected area in Amazonian Ecuador (~17.7% of the Ecuadorian Territory, Valencia et al. 2004) and harbor the world’s most diverse tropical forest (Bass et al. 2010). YNP is a wet evergreen lowland forest ranging in altitude from 200 m to 300 m above sea level. It has a 15- to 30-m canopy with some emergent trees reaching 50 m (Valencia et al. 2004). Rainfall and temperature are aseasonal; there are no clear patterns of dry/rainfall and warm/cold seasons during the year. Over 53 months of records at the research station, the longest rainless period was three weeks and the

least rainy month was August. The mean annual rainfall was 2826 mm, and no calendar months averaged less than 100 mm (Valencia et al. 2004). Over 742 days between 2008 and 2011, mean temperature at the research station was $24.9^{\circ}\text{C} \pm 3.9$ (ranging from 22° to 32°C ; min: 16.9°C ; max: 38.9°C ; warmest months: November–March; coldest months: April–October), and a mean humidity was $88.4\% \pm 13.9$ (data obtained from Yasuní Research Station meteorological station of the Pontificia Universidad Católica del Ecuador, <http://www.yasuni.ec>). The study area was in the vicinity of Yasuní Research Station in the 50 ha of the Yasuní Forest Dynamics Plot (see <http://www.ctfs.si.edu/site/Yasuni> for a detailed description of the area). Soils in the study area are mostly clay-like, acidic, udult ultisols with an average pH of 4.6 (John et al. 2007) and a texture dominated by silt (Tuomisto et al. 2003).

Soil detritivore biodiversity survey

We sampled invertebrate communities within the study area, including only those that may be involved in the fragmentation of leaf-litter material from the humic leaf-litter layers using two well-known and complementary sampling methods: pitfall traps and Winkler extractions (see Appendix S1). Our survey designs for both methodologies were conceived to evaluate the effect of the spatial area on soil food web structure and functionality. We are conscious that our sampling methodology is not suitable for collecting few important groups of invertebrates such as earthworms or nematodes, which are not considered as litter shredders (except probably for some omnivore nematodes) and are mainly collected in the soil below the leaf-litter layer (see Cares and Huang 2008 for nematodes soil sampling and extraction).

For the pitfall traps, we set a nested rectangular grid of six different spatial scales across the forest floor (smallest scale: 10×5 m; largest scale: 1000×500 m; each scale doubled the length and width of the previous). At each of these scales, we sampled four plots (one in each corner of each scale) for a total of 69 plots (Appendix S1: Fig. S1a). Each plot consisted of at least three pitfall traps (up to five in some cases), which remained opened for 24 h. Pitfall traps consisted of plastic cups that were 5 cm in diameter and 10 cm deep and buried to soil level.

A total of 40 Winkler extractions (from 1 m^2 of soil leaf litter) were analyzed. Twenty samples, each 10 m apart along a 200-m transect, were analyzed using the ALL protocol (Ants of the Leaf Litter, see Agosti and Alonso 2000 for details). The remaining 20 were distributed along 10, 20-m transects that followed the diagonal of the 1000×500 m plot. Each transect was set in 10, 100×50 m subplots where two samples, 5–20 m apart, were extracted and analyzed (Appendix S1: Fig. S1b).

Species identification and allocation to functional groups

Specimens were examined under the stereoscope at $0.68\times-50\times$ (Leica M275, Leica Microsystems AG, Wetzlar, Germany). They were counted and identified to the finest possible taxonomic group using specialized literature (see Appendix S2: Table S1 for a complete list of all identified specimens). When a morphospecies was recognized for the first time, lateral, dorsal, and ventral images were taken using an adaptable digital camera (Future Optics Science and Technology, 1.3 MP, MEM1300 model, Hangzhou, China). This image served for comparison for all subsequent, similar specimens in the collection. Larvae of holometabolous insects could not be associated with any adult species, so they were classified into different morphospecies. Nymphs of hemimetabolous insects that differed structurally (but not by color) from any adult morphospecies were assumed to be new morphospecies. This level of taxonomic resolution has been found to be sufficient for detecting significant patterns of community composition in temperate and tropical systems (Timms et al. 2013, Lamarre et al. 2016). Moreover, family-level identification has provided ecologically adequate surrogates for species in studies of functional diversity (see also Cardoso et al. 2011 for both temperate and tropical systems). Length, width, and depth were measured for up to 10 specimens of the same morphospecies to improve accuracy of morphometric dimensions. Finally, one or more functional group categories were assigned to each morphospecies based on the classification by Moreira et al. (2008): herbivores, ecosystem engineers (Jones et al. 1994, Lavelle et al. 1997, Boze et al. 2012, Jones 2012), litter transformers, decomposers, predators, microregulators, and soil-borne pests, diseases, and parasites (primary producers,

microsymbionts, and prokaryotic transformer categories were not included in our collection target). An extra functional group category, so-called mesoregulators, was assigned to encompass the mesofauna that regulates nutrient cycles through grazing and other interactions with decomposer microorganisms (analogous to microregulators, but at larger scale). Feeding habits were determined using specialized literature and Internet resources (e.g., Gillot 2005, Triplehorn and Jonson 2005, Brandão et al. 2011, <http://soilbugs.massey.ac.nz/index.php>, <http://www.collembola.org/>). Scolytines (Coleoptera) were considered ecosystem engineers because of their hole-digging behavior that physically changes the surrounding environment and creates access for subsequent decomposers (Muller et al. 2002). Although the taxonomic order Acari represents an important group in the soil food web, we were unable to discriminate specimens at the morphospecies level and accurately assign them to any of their many potential functional groups. Appendix S3, however, shows independent analyses of the distribution of body size and body width in this rich and complex group (Appendix S3: Fig. S1). Acari were excluded from this and further analyses that include morphospecies identity. 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 realistic approach based on what is known in the literature. Appendix S4 shows examples of soil invertebrate morphospecies, separated by functional groups and body dimensions that were found in both pitfall and Winkler samples.

Leaf-litter collection

Leaves are the most important component of litterfall in Amazonian forests (Chave et al. 2010). Most above-ground production comes from angiosperm trees (Kurokawa and Nakashizuka 2008). In a previous 11-month survey, Cárdenas et al. (2014) found that forest floor was mainly covered with leaf litter from 53 common tree species belonging to 21 plant families (rare species were not considered in that survey). Based on this list, species and families chosen for the present study aimed to represent a wide range of intrinsic chemical traits (Appendix S5: Table S1). Leaves were collected from adult and

sub-adult trees of eight common angiosperm species belonging to eight different families: *Matisia malacocalyx* (A. Robyns & S. Nilsson) W.S. Alverson (Malvaceae), *Inga capitata* Desv. (Fabaceae), *Nectandra viburnoides* Meisn. (Lauraceae), *Miconia "purpono"* [nomen nudum] (Melastomataceae), *Siparuna decipiens* (Tul.) A. DC. (Monimiaceae), *Pseudolmedia laevis* (Ruiz & Pav.) J.F. Macbr (Moraceae), *Neea "comun"* [nomen nudum] (Nyctaginaceae), and *Leonia glycyarpa* Ruiz & Pav. (Violaceae). Leaves were collected by shaking two to seven trees from the trunk or branches 5–20 times. Leaves fell on white fabric sheets (cotton, 1.5 m × 3.5 m) that were tied 1 m above the forest floor. Leaves that were characteristically young (presenting bright green or reddish colors and/or soft lamina), too old (rotten or presenting large amounts of necrosis), or presented evident fungal infection or insects galleries were discarded. For the experiment, we collected only senescent leaves with herbivore damage covering less than 30% of the leaf area (visually calculated in situ).

Soil fauna food web exclusion and decomposition experiments

To assess whether a sub-group of species disproportionately influences leaf-litter decomposition, we designed an exclusion experiment in *terra firme* using 20 cm diameter plastic and polyester fabric leaf litterbags. As a general rule, metabolism depends on body size (Brown et al. 2004), so this experiment aimed to simulate microcosms where the soil fauna that has access to litter resources is filtered sequentially as a function of body size. So, at one extreme, we excluded everything except microfauna (e.g., micro-detritivores, predators, omnivores). At the other extreme, we allowed all size groups of soil fauna. This is also in line with paleontological analyses showing that burrowing invertebrates such as beetles, bees, spiders, wasps, ants, and cicadas of the Paleocene–Eocene Thermal Maximum shrank in size by 50–75% (Smith et al. 2009). Salazar et al. (2007) analyzing future models of the Amazonian forest climate suggest that temperatures rising (2–6°C through year 2100) may induce larger evapotranspiration in tropical regions. Over time, these ecological and other factors may lead to evolutionary responses favoring smaller individuals (Sheridan and Bickford

2011). Microcosms were constructed by slightly folding and sewing together top and bottom meshes to form a bag. The resulting oval-shaped litterbags prevented the litter from flattening, and allowed it to retain a natural, three-dimensional structure. Five different mesh sizes that allowed the access/exit of different-sized invertebrate groups were used (see Swift et al. 1979 for soil microflora and fauna size classification): 268.8 mm² (15.2 × 17.7 mm; micro-, meso-, macro-, and megafauna), 118 mm² (10 × 11.8 mm; micro-, meso-, and macrofauna), 16.1 mm² (3.2 × 5.1 mm; micro-, meso-, and macrofauna), 2.7 mm² (1.1 × 2.5 mm; micro- and mesofauna), and <0.01 mm² (~0.1 × 0.1 mm; microfauna). Our non-random experimental design was conceived to ensure the accessibility of all species of the smallest size class (those that were dominant in terms of abundance) at all richness levels (microcosm treatments), emulating what would be found in nature, where dominant species are less likely to be lost from communities unless they are vulnerable to particular catastrophic events (Smith and Knapp 2003). This experimental design also aimed to detect facilitation in litterbags. Previous research has shown that the design does not confound access with “leakiness,” has quantified the assumption that increasing mesh size leads to greater soil fauna access, and has ruled out microclimate effects across different mesh sizes (Milton and Kaspari 2007). Besides, Bokhorst and Wardle (2013), after examining the microclimate effects of three litterbags of different mesh sizes on litter mass loss and leaching in the absence of soil animals, concluded that studies can use different mesh sizes to reliably quantify the role of soil animals in litter mass loss from litterbags. This methodology may furthermore allow us to decouple diversity effects—niche complementarity—from those of sampling effect (Huston 1997), because we considered naturally uneven species abundance, including those from dominant groups across the trophic web (Smith and Knapp 2003).

Finally, we removed the *petiolum* of every leaf and placed the leaves to dry at 40°C for 48–72 hours in cotton fabric bags (containing no more than 10 leaves per bag) and weighed to 0.001 g precision. The leaves were remoistened using rainwater to make them pliant and were enclosed in the litterbags.

The experiment consisted of testing the leaf decomposition rate of the eight species over the same period of time and area, but in different litterbag types in an area covering about 4000 m² of the forest floor in “ridge-slope”-type microhabitat (see Valencia et al. 2004 for a detailed description of microhabitat designation). In total, we analyzed the decomposition process of 8 (plant species) × 5 (mesh treatments) × 10 (replications) × 2–5 (leaves per bag, with the number of leaves depending on leaf size), for a total of 400 leaf litterbags and up to 2000 leaves placed randomly in the study area (Fig. 1). Each litterbag was filled with 2.78 ± 1.04 g of leaf-litter material, excluding the petioles. The large difference in litter mass added to the litterbags resulted from interspecific differences in leaf size (mean ± SD: 108.6 cm² ± 50.3; min.: 55.6 cm²; max.: 195.3 cm²) and leaf volume (leaf size × thickness; 1.84 cm³ ± 0.8; min.: 0.8 cm³; max.: 3.1 cm³; data of specific mean leaf size taken from Kraft and Ackerly 2010). We did not collect the largest leaves (e.g., from *M. malacocalyx* or *N. viburnoides* species), as we wanted to avoid having litterbags with dramatically higher leaf-litter mass with a comparable number of leaves (two to five). Litterbags were set in groups of five treatments, each with a randomized set of species, in a 50 × 80 m grid-type plot (see Appendix S6: Fig. S1 for details). Mesh bags were collected for analyses after 104 days of decomposition (mass loss of ~58% on average for the same eight species after 103 days, see Cárdenas 2013). In the laboratory, leaves from each litterbag were gently cleaned to remove soil particles, adhering debris, and invertebrates; dried at 40°C for 48–72 h; and weighed at 0.001 g precision.

Data analyses

Soil functional group cluster analysis.—Groups of organisms in the soil food web overlap in terms of feeding habits and body sizes, and therefore in their functional role and extent of their impact on soil ecological processes. A cluster analysis was first performed to statistically classify the different functional groups found in the forest floor. This classification was used for all subsequent analyses in our study. For this, we used morphospecies body length, width, and depth, and 0-1 binary data of the eight functional group categories. Twelve groups of species were defined using Gower’s distance (minimum spanning tree) and Ward’s linkage

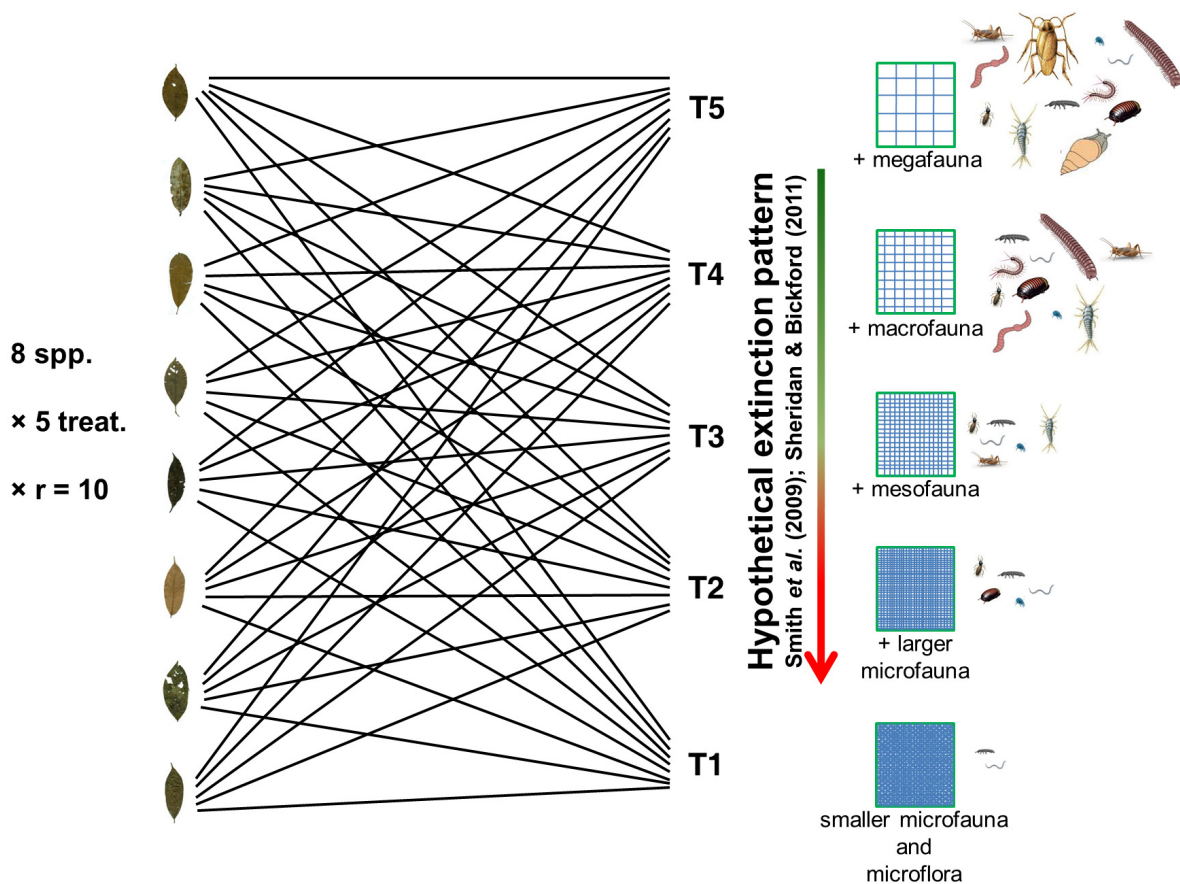


Fig. 1. Experimental design of the leaf-litter decomposition test in a hypothetical extinction scenario where bigger invertebrates may be more (and first) susceptible to extinction as a consequence of current climate change. Blue grids represent the five different mesh sizes used to gradually exclude the access of groups of invertebrates. treat. = treatments; r = replicates; + refers to the additional accessibility of larger invertebrates to coarser meshes. Leaves packed in plastic mesh bags were randomly distributed on the forest floor in an area that covered about 4000 m², and let decompose for 104 d.

(minimum variance). We chose Gower's distance as it allows mixed-scale types of data (quantitative, interval, nominal or ordinal, ratios, and/or missing values) and has proven to consistently provide the most reliable results and to minimize tree dissimilarity (Mouchet et al. 2008). Ward's method was chosen as it has been shown to produce more clearly defined clusters than does average linkage (Pla et al. 2012). Cluster analysis was performed using InfoStat v.2012 software (InfoStat Group, Córdoba, Argentina) with default program data standardization (Di Rienzo et al. 2012).

Description of the structural and functional organization of soil invertebrate communities.—Using data from all samples combined, we first used

rank plots (Magurran 2004) to describe the community structure of Yasuní soil fauna in relation to abundance (Appendix S2) at the levels of Order and morphospecies. Morphospecies rank plots were also used to compare, in detail, the relative abundance of the different functional groups of soil fauna that make up the invertebrate community. Additionally, following Preston's (1948) boundaries of octaves as a measure of the degree of commonness, we classified the number of species per functional group in relation to its abundance in eight categorical ranges. Finally, data were fitted to lognormal (equations of the form $y = a \times e^{(-0.5(\ln(x/b)/c)^2)}$, where a is the intersection with the y -axis and b and c are

parameters of the slope expression) and logarithmic (for mesoregulators only) distributions using Table Curve 2D software v.5.01 (Systat Software Inc., San José, California, USA).

Rarefaction “sample-based” accumulation curves were used to compare the efficacy of different sampling methods used in the same area (Sanders 1968, Longino et al. 2002, Ellison et al. 2007) and to assess whether pitfall traps and Winkler extractions reached an asymptote for species richness and functional groups. For this, we used Past v.3.07 software (Oslo, Norway; Hammer et al. 2001) that implements the analytical solution in which standard errors are transformed in $\pm 95\%$ confidence intervals. This is known as “Mao tau” following Colwell et al. (2004). Sample-based rarefaction curves implicitly reflect empirical levels of within-species aggregation of individuals by considering only incidence, providing a realistic estimate of the number of species found in sets of real-world samples (Gotelli and Colwell 2001). To assess whether soil fauna diversity was aggregated, we compared both individual- and sample-based rarefaction curves by plotting them together (Appendix S7: Fig. S1). Gotelli and Colwell (2001) explain that when the sample-based curve lies below the individual-based curve, one can assume there is species aggregation. An estimation of the total soil fauna biodiversity was evaluated using Jackknife 1 and Jackknife 2 (employing incidence data) and Chao 1 (employing abundance data) species richness estimators (Gotelli and Colwell 2001, details in Appendix S7).

Biovolume distribution of the clusterized functional groups was plotted to visualize the spread of mass volume and body width in the soil food web community. Finally, radar charts were plotted to compare the potential accessibility of the six functional groups of soil fauna to the five types of microcosms (mesh bags T1–T5) in terms of their accumulated biovolume and the relative number of species.

Species–area relationship (soil fauna and leaf litter).—We compared content of each collection unit (pitfall traps and Winkler extraction sites) to one another using similarity indexes and Euclidean distances to evaluate whether there is a patchy or uniform distribution of soil fauna within the communities of functional groups. Sørensen’s similarity coefficient was used for the species–area analysis using binary presence–absence data. Further

analyses of similarity indexes for the total number of collected morphospecies, their relative abundance, biovolume, and functional groups identity are detailed in Appendix S8. Analyses were performed using Past v. 3.07 (Hammer et al. 2001).

Sørensen’s similarity coefficient was similarly used to analyze the spatial heterogeneity in species composition of the leaf litter from 28 common species found in the study area using data from Cárdenas et al. (2014).

Mesh size-dependent litter decomposition.—Shapiro–Wilk normality tests for the residuals of each treatment showed normal distribution (with all W 's > 0.96 and all P 's > 0.14) for four species: *I. capitata*, *L. glycyarpa*, *N. viburnoides*, and *S. decipiens*, and non-normal distribution (with all W 's < 0.94 and all P 's < 0.015) for the remaining four species: *M. malacocalyx*, *M. “purpono,”* *N. “comun,”* and *P. laevis*. The percentage of mass loss of the leaf-litter material of the eight plant species in each of the five mesh-bag treatments was compared using analysis of variance (ANOVA, for those species presenting normal distributions of their residuals) and Kruskal–Wallis tests (for those species presenting non-normal distributions of their residuals). Significance of the differences between treatments was assessed using Tukey’s post hoc tests and Dunn’s z post hoc, respectively. ANOVAs, Kruskal–Wallis, and Shapiro–Wilk tests were performed using Past v. 3.07 (Hammer et al. 2001).

In order to analyze the factors controlling decomposition of the pool of our studied species, the differences in the percentage of averaged leaf-litter mass loss between the mesh treatments were analyzed using a generalized linear model (GLM). For this analysis, mesh sizes (mm) and chemical traits of the different species were used as independent variables. Prior to GLM, a principal components analysis (PCA) of nutrient content of all species (22 chemical traits, see Appendix S5 for details) was performed in order to evaluate which elements better explain the quality differences between our resource treatments. A previous study on these same plant species has shown that condensed tannins, lignin:N ratio, and Mn:Cu ratio significantly explain OM decomposition (Cárdenas et al. 2015); hence, we also included these traits in the PCA and GLM. PCA was performed using Past v. 3.07 (Hammer et al. 2001), and GLM was analyzed using R (R Development Core Team 2015).

Table 1. Functional group (FG) categories (Category 1) and sub-categories (Category 2) showing the total number of species (S), abundance (N), and biovolume (B; $N \times \text{mm}^3$; calculated from averaged volume per species).

| Category 1 | FG | Category 2 | S | N | B |
|---|--------------|---|------------|-------------|-----------------|
| Litter transformers | LT1 | | 48 | 127 | 75,322.9 |
| | LT2 | Ecosystem engineers and mesoregulators | 57 | 294 | 7798.3 |
| | LT3 | Microregulators | 57 | 347 | 155.2 |
| | Total | | 162 | 768 | 83,276.4 |
| Omnivores | O1 | + mesoregulators | 26 | 128 | 892.7 |
| | O2 | + predators | 85 | 398 | 4795.4 |
| | Total | | 111 | 526 | 5688.1 |
| Mesoregulators | Me | | 38 | 145 | 339.9 |
| | Total | | 38 | 145 | 339.9 |
| Herbivores | H1-Pd1 | Soil-borne pests, diseases, and parasites | 24 | 58 | 310.4 |
| | H2 | | 32 | 95 | 4340 |
| | Total | | 56 | 153 | 4650.4 |
| Predators | P1 | Ants | 30 | 161 | 1743 |
| | P2-Pd2 | Soil-borne pests, diseases, and parasites | 26 | 79 | 36.3 |
| | P3 | | 64 | 250 | 1308.3 |
| | Total | | 120 | 490 | 3087.6 |
| Soil-borne pests, diseases, and parasites | Pd3 | | 29 | 68 | 27.9 |
| | Total | | 29 | 68 | 27.9 |
| | Total | | 516 | 2150 | 97,070.3 |

Notes: Omnivores (O1 and O2) correspond to herbivores and/or litter transformers, including guilds in Category 2. Acari are not considered in this analysis.

To compare the effect of the five different mesh size treatments on the decomposition process, we calculated the weighted mean of the final:initial ratio of leaf dry mass for the eight plant species. We used the diagonal size of the grid holes for each of the five meshes (mm) as the weight (w) parameter. Because data elements with a high weight contribute more to the weighted mean than do elements with a low weight, we expected the coarser mesh bags to contribute more to decomposition. The averaged weighted means of the eight species were compared to the arithmetic means using a two-sample t -test with Past software v. 2.17 (Hammer et al. 2001, Shapiro-Wilk normality test: $W_{\text{weighted}} = 0.912$, $W_{\text{arithmetic}} = 0.869$, $P > 0.05$ in both cases; details in Appendix S9).

Body width is probably the most important morphometric parameter that discriminates access to the leaf-litter resource in each mesh litterbag treatment (width:height average ratio \pm SD of the litter transformer + omnivore communities = 1.28 ± 0.89). We assessed the biovolume ($N \times \text{mm}^3$) of litter transformer and omnivore functional groups that potentially had access to the different mesh treatments, and plotted along with the leaf-litter mass loss of the pooled dataset as a

way to visually contrast the effect of larger biovolume accessibility with resource decomposition.

RESULTS

Characterization of functional groups of soil invertebrates

Cluster analysis discriminated six main functional group classes in the soil food web (cophenetic correlation = 0.628). Some were mainly related to dead plant resources (leaf litter and wood), while others were related to fungal resources: “litter transformers” (LT; mainly collembolans, diplopods, blattids, ants, staphylinids, and termites), “omnivores” (O; mainly gryllids, thysanopterans, staphylinids, isopods, and ants), and “mesoregulators” (Me; mainly Diptera larvae, mycetophilids, ptiliids, endomychids, and staphylinids). Others were predators or parasites: “predators” (P; mainly ants, arachnids, phorids, and chilopods), “soil-borne pests, diseases, and parasites” (Pd; mainly mymarids, sapygids, scelionids, braconids, and trychogrammatids), and “herbivores” (H; mainly cicadellids, orthopterous, and curculionids). These six groups were divided into 12 sub-categories (Table 1, Fig. 2). Of these, the most speciose and

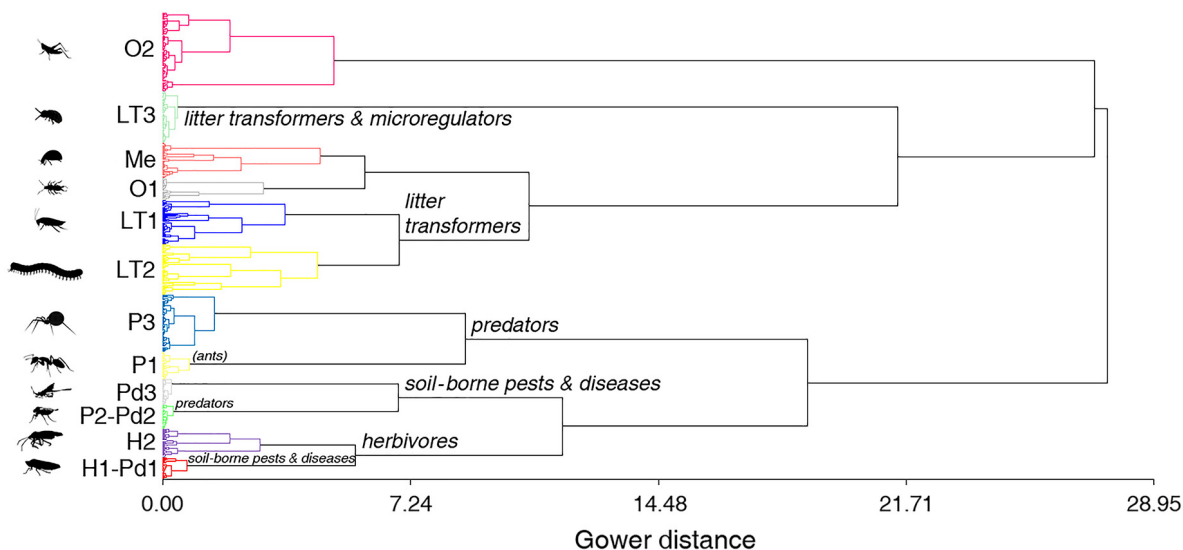


Fig. 2. Cluster analysis showing functional grouping of soil fauna communities. The Ward clustering method with Gower distance was used. Group abbreviations: litter transformers (LT), omnivores (O), predators (P), mesoregulators (Me), herbivores (H), and soil-borne pests, diseases, and parasites (Pd).

abundant were “omnivores + predators” (O2), represented by 85 morphospecies (16.5% from the total collected) and 398 individuals (18.5% from the total collected). The next most speciose were the “general predators” (P3), with 64 morphospecies (12.4%) and 250 individuals (11.6%), followed by “litter transformers, ecosystem engineers, and mesoregulators” (LT2) and “litter transformers and microregulators” (LT3), with 57 morphospecies in each group (11%) and 294 (13.7%) and 347 (16.1%) individuals, respectively (Table 1). The group “general litter transformers” (LT1) had the higher total biovolume with 75,322.9 mm³ (77.6%), followed by “litter transformers, ecosystem engineers, and mesoregulators” (LT2) with 7798.3 mm³ (8%; Table 1).

Soil invertebrate community structure

A total of 541 morphospecies were collected in our survey. In the soil fauna community, hymenopterans (predominantly ants; 1117 individuals), collembolans (mostly Hypogastruridae/Neaturidae, and Entomobryidae; 1101 individuals), and coleopterans (largely characterized by Staphylininae subfamily and other Curculionidae; 1083 individuals) were the most abundant groups. Chordeumids (Myriapoda), peripatids (Onychophora), lumbricids (Annelida), and scorpions

(Scorpiones) were the less-abundant groups (Fig. 3a; Appendix S2: Table S1). We have not found any specimen of nematode, confirming our sampling methodology is not suitable for collecting this important group of invertebrates. The morphospecies rank–abundance (SRA) plot showed the classic distribution of natural (pristine) environments: very few common species, some moderately common, and a great majority rare (Fig. 3b). This was also evident when plotting rank–abundance of the six functional groups separately. Data were fitted to lognormal equations, all with $P < 0.0001$ and all $R^2 > 0.93$ (Fig. 4). Finally, when SRAs were plotted into a Preston’s log₂ scale, data were adjusted to lognormal and logarithmic (for Me only) equations ($P_H = 0.034$; $P_P = 0.062$; $P_{LT} = 0.160$; $P_O = 0.037$; $P_{Me} = 0.087$; $P_{Pd} = 0.018$; with all R^2 s > 0.83 ; Fig. 5).

Sampling efficiency

Neither the pitfall trap nor Winkler extraction methodologies collected a sufficient number of species for rarefaction curves to reach an asymptote (Fig. 6a). Overall, Winkler collections were significantly more efficient—they captured more species per sample over a smaller area than did pitfall traps. The rarefaction curves and 95% confidence intervals for the two sampling methods

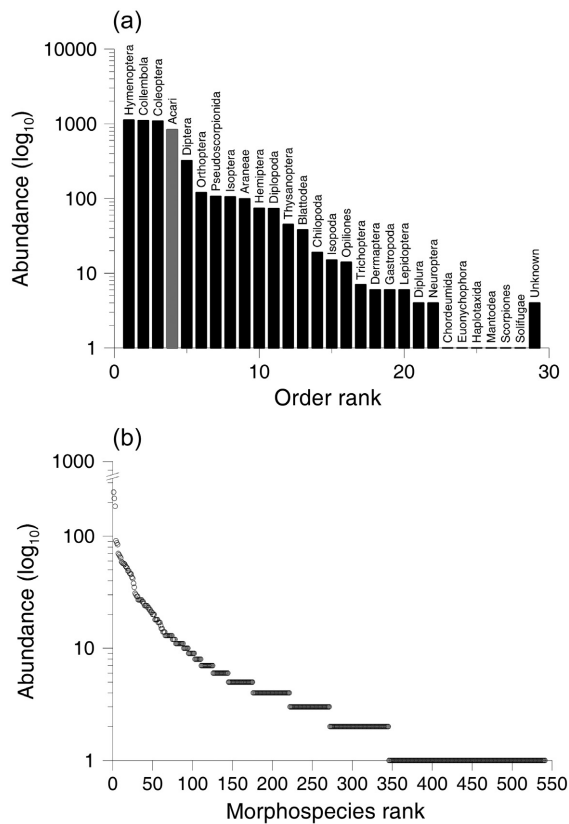


Fig. 3. Rank–abundance plots of the complete soil fauna survey showing (a) the relative distribution of the number of species for major soil animal groups and (b) the variation in the relative abundance of soil animal species ordered from most to least abundant. For detailed information on Acari morphometrics frequencies description, refer to Appendix S3.

still did not overlap at the minimum of 40 samples where the two methodologies are comparable. The pitfall and Winkler methods captured complementary invertebrate species sets. Five morphospecies were highly abundant in pitfall traps: Hypogastruridae/Neanuridae sp. 4, *Camponotus* sp. 1, Scolytinae sp. 1, Entomobryidae sp. 5, and Staphylininae sp. 1. A different set of morphospecies were highly abundant in Winkler extractions: *Solenopsis* sp. 1, *Strumigenys* sp. 2, *Isoptera* sp. 3, Pseudoscorpionida sp. 1, and *Hypoponera* sp. 1 (results not shown). Both methodologies needed relatively few samples (~15) to characterize the total number of functional groups (results not shown). When considering Winkler and pitfall collections together, the species accumulation

curve still did not reach an asymptote (Fig. 6b). Analyses of the potential total invertebrate biodiversity associated with soil estimated a range of 730–858 morphospecies (details in Appendix S7).

Soil invertebrate spatial heterogeneity

The Sørensen similarity index showed that species identity in the soil food web was heterogeneous at all spatial scales. In a range between 0 and 1, where 1 means full similarity, all functional groups showed values <0.165 (mean \pm SD): herbivores (H): 0.065 ± 0.18 ; predators (P): 0.057 ± 0.15 ; litter transformers (LT): 0.163 ± 0.16 ; Os: 0.135 ± 0.17 ; mesoregulators (Me): 0.111 ± 0.20 ; Pds: 0.04 ± 0.14 (Fig. 7). Fig. 7 shows that approximately the same levels of heterogeneity were found in small and large sampling areas, especially for litter transformers and omnivores. In Appendix S8, where we considered the full dataset, similarity indexes were plotted and analyzed using four different components of biodiversity: morphospecies identity, abundance, functional group allocation, and biovolume. Results showed that the soil food web was heterogeneous for all the components as well.

Finally, comparisons of sample- and individual-based rarefaction curves of both pitfall traps and Winkler extractions showed that species in the

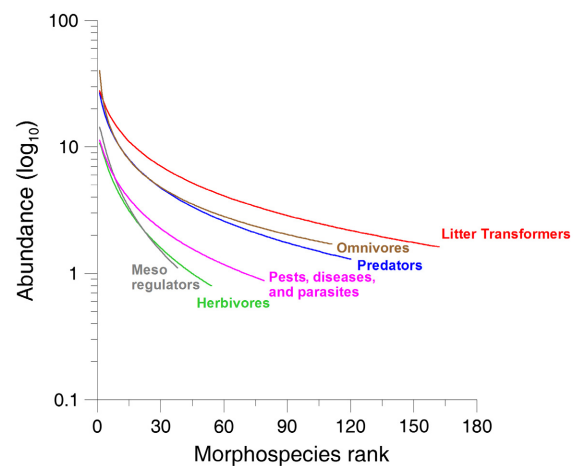


Fig. 4. Species rank–abundance curves of the six soil fauna functional groups as obtained from the Cluster analysis. All data were fitted to lognormal equations of the form $y = a \times e^{(-0.5(\ln(x/b))^2)}$, where all $P < 0.0001$ and all $R^2 > 0.93$.

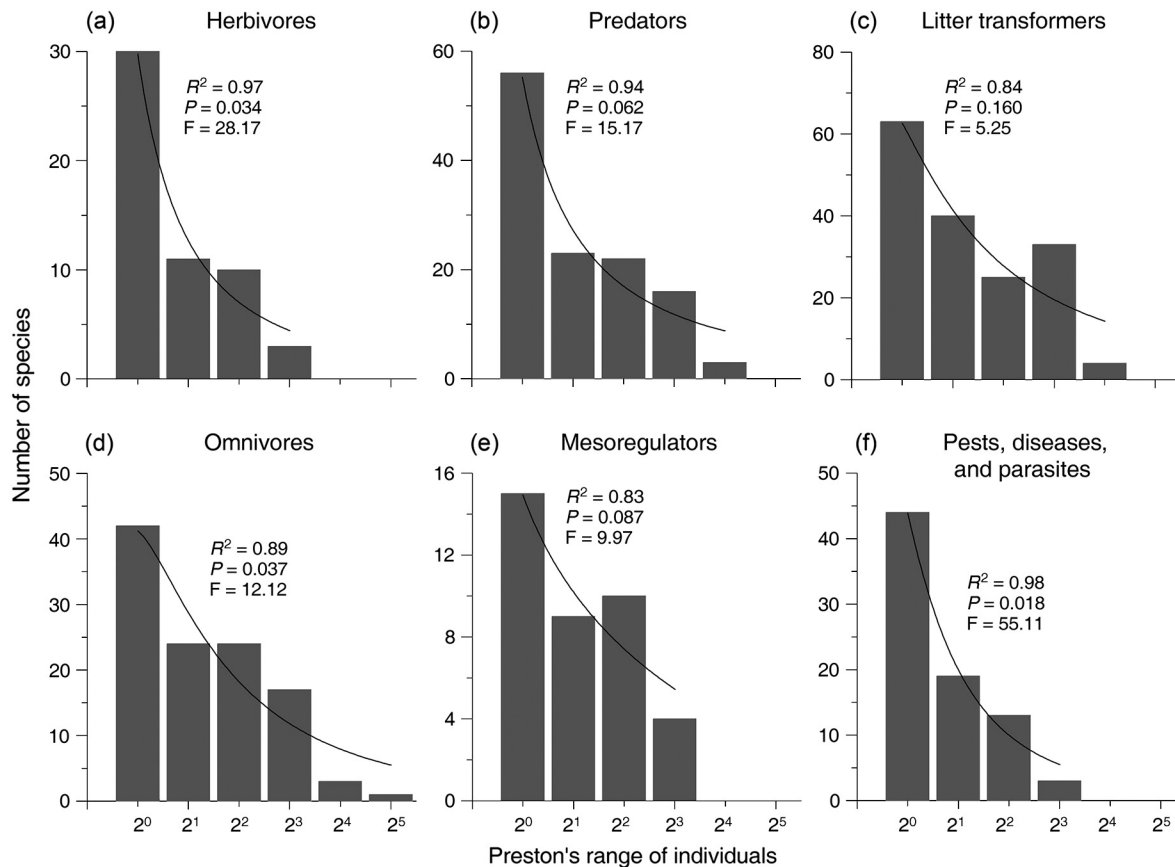


Fig. 5. Preston's plots of the number of species per log₂ abundance ranges for each functional group. Log₂ series followed Preston (1948) ranges: 2⁰ (1–2), 2¹ (2–4), 2² (4–8), 2³ (8–16), 2⁴ (16–32), 2⁵ (32–64). All data were fitted to lognormal equations of the form $y = a \times e^{(-0.5(\ln(x/b)/c)^2)}$, except for mesoregulators functional group that was fitted to a simple logarithmic equation of the form $y = a + b \ln x$ (simple lines in all cases). R², P, and F values correspond to the regressions fit to the curves. (a) represent herbivores; (b) predators; (c) litter transformers; (d) omnivores; (e) mesoregulators; (f) pests, diseases and parasites.

forest appeared to be aggregated at small sampling spatial scales, although this pattern did not persist at larger sampling scales (Appendix S7: Fig. S1).

Accessibility to mesh-bag treatments by the soil fauna community

Mass volume data showed a marked size distribution of different functional groups: The Pests, diseases and parasites (Pd), and predators (P) classes were frequently small-/medium-sized, the mesoregulators (Me) class was medium-sized, the herbivores (H) classes were medium-/large-sized, and litter transformers (LT) classes covered the whole size spectrum (Fig. 8). LT1 (general litter

transformers) and LT2 (litter transformers, ecosystem engineers, and mesoregulators) were the biggest classes in terms of volumetric mass, with an average of 569.9 mm³ and 101.8 mm³, respectively (results not shown). We found that for all functional communities, the great majority of individuals were "thin," or fit within the 1/15 of the total body width ranges (Fig. 9).

Different classes of litter transformers and omnivores biovolume had different access to OM resources through the five mesh treatments (Fig. 10; Appendices S10 and S11), except that the coarse meshes (T4 and T5) were accessible to virtually the same litter transformers and omnivores communities (Table 2). T1 accessibility was

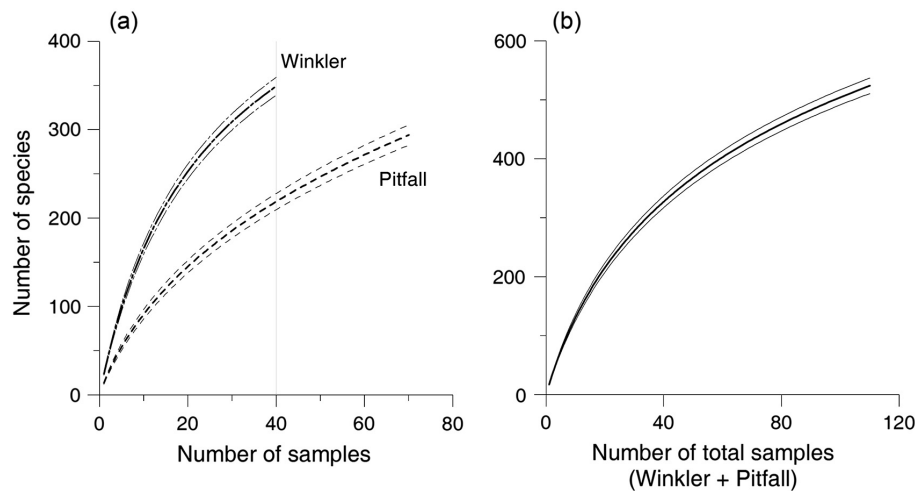


Fig. 6. Rarefaction curves (sample-based; bold lines) showing Winkler extraction and pitfall traps of the complete soil fauna collections in relation to the number of species. Vertical gray line in (a) indicates the number of samples where both methodologies are comparable. Smooth dashed and full lines correspond to $\pm 95\%$ confidence intervals. Considering Winkler + pitfall collections (b), analyses of the potential total biodiversity estimate a range of 730–858 morphospecies (details in Appendix S7).

2.2% of the species and 6% of the abundance of total litter transformers and omnivores, represented by LT3 (litter transformers and microregulators) and O1 (omnivores and mesoregulators) classes (mostly collembolans, Table 2). T2–T5 were accessible to both functional groups and by >86% of species and >93% of specimens (see Table 2 for details).

Leaf-litter mass loss across treatments

There was no difference between the five mesh-bag treatments in the percentage of mass loss in the leaf-litter material of the eight plant species (for *I. capitata*, *N. viburnoides*, and *S. decipiens*, all P values >0.05 and effect size $\omega^2 \leq 0.15$), except for *M. "purpono," M. malacocalyx*, and *L. glycy-carpa*; Fig. 11). For *M. "purpono,"* T4 differed significantly from T1 and T2, and T5 differed significantly from T1 (Dunn's P of the Kruskal–Wallis analysis for these treatments <0.029). For *M. malacocalyx*, T5 differed significantly from T2 (Dunn's P of the Kruskal–Wallis analysis for these treatments = 0.003). For *L. glycy-carpa*, T5 and T3 differed significantly from T1 and T2 (Tukey's P of the one-way ANOVA for these treatments <0.031; effect size ω^2 of this test = 0.39). There was one significant difference between mesh treatments when the averaged pooled dataset was analyzed

(Appendix S11). We found that mass loss was larger in the coarser mesh treatment T5 compared with the finer ones T1 and T2 (Dunn's $z_{T1vs.T5} = 2.57$, $P = 0.010$; Dunn's $z_{T2vs.T5} = 2.61$, $P = 0.001$; Appendix S11: Fig. S1). This is in line with GLM results that show a general positive and significant effect of mesh size treatments over leaf-litter decomposition (Table 4). Finally, t -test comparisons of weighted and arithmetic means for the eight species showed no significant differences ($P = 0.853$; Appendix S9).

Principal components analysis of 22 nutrient contents has shown that Ca, K, Mg, and S were the factors explaining most of the variance among species (PC1 = 69.57%; PC2 = 24.93%). In respect of the role of leaf-litter nutrient contents, we found that Ca, K, and S present a positive and significant effect over decomposition (Table 3). Mg and the Mn:Cu ratio present barely significant relationships, negative and positive, respectively, with decomposition. When analyzing nutrient contents interactions with the litterbag mesh sizes, we found that Mg, S, and condensed tannins are significant and negatively related to decomposition. Although not significant, lignin:N ratio alone surprisingly showed a positive relationship with decomposition and a positive and significant relationship when

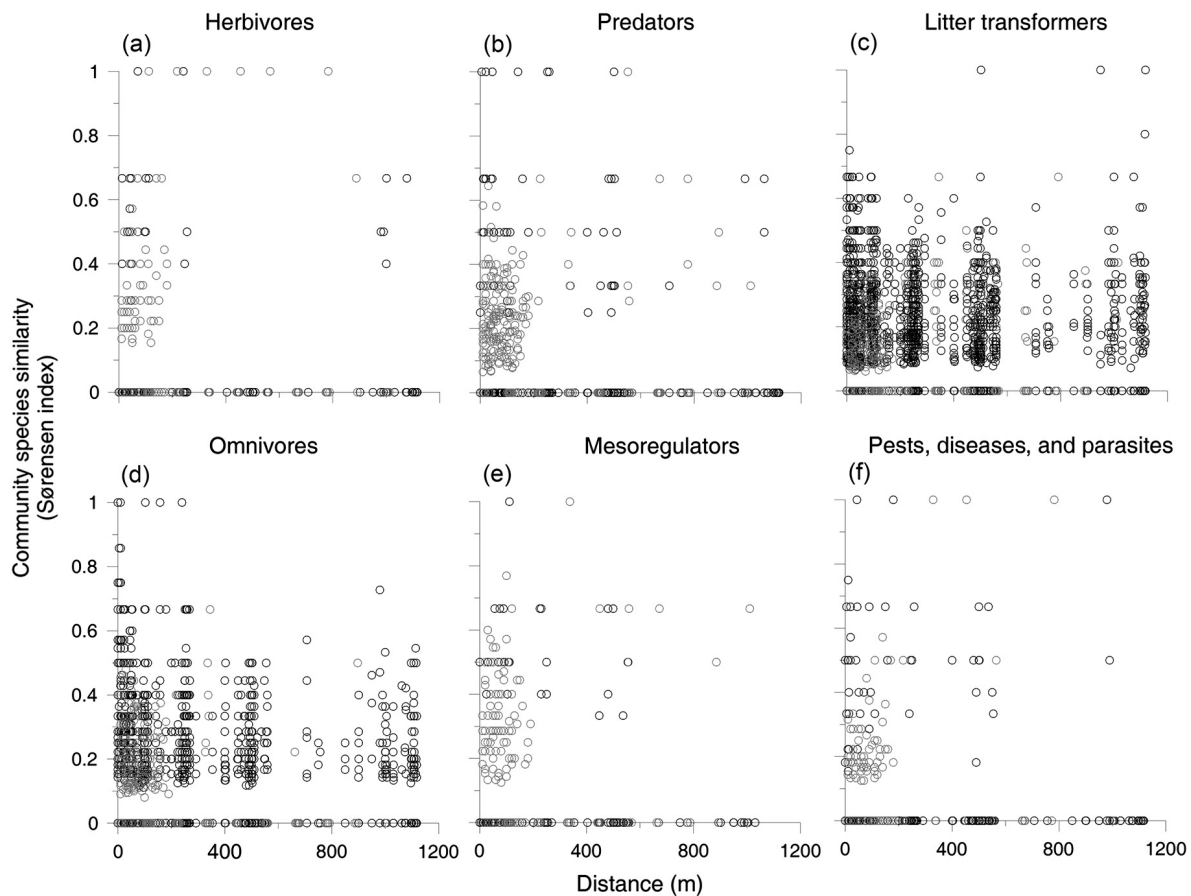


Fig. 7. Plots showing the effect of the geographical distance on the similarity of the species composition of six functional groups: (a) herbivores, (b) predators, (c) litter transformers, (d) omnivores, (e) mesoregulators, and (f) pests, diseases, and parasites, between Winkler extraction sites (empty gray circles) and pitfall traps (empty black circles). A value of 1 on the y -axis means full similarity.

considering the interaction with the mesh size (Table 3).

DISCUSSION

The soil invertebrate community

Soil organisms are essential for terrestrial ecosystems to function (e.g., nutrient cycling, soil formation, soil aeration). However, the functional role and importance of species diversity in tropical soils are yet to be discovered (Wall et al. 2010). Our results showed a predominant abundance of hymenopterans (mainly ants), collembolans, and coleopterans (mostly bark beetles and weevils). These three groups are heterogeneous in terms of feeding habits and may occupy a wide range of niches in the forest food web.

Ants represent one of the most diverse and ecologically dominant animal groups and are extremely important in terms of biomass and relative local abundance (Wilson and Hölldobler 2005). Nutritional biology of ants can be wide ranging—they can be predators, leaf cutters, fungus growers, sap feeders, pollinivorous, saprophytes, and generalists (Brandão et al. 2011). Recent studies suggest that niche diversity drives ant specialization and supports high species diversity in the Neotropics (Vasconcelos and Vilhena 2006, Ryder Wilkie et al. 2010).

Compared to ants, collembolans belong to less diverse niches that include saprophagic, fungivores, including some spore feeders; phytophages, including pollen feeders; and very rarely predators (Gillot 2005). However, they are

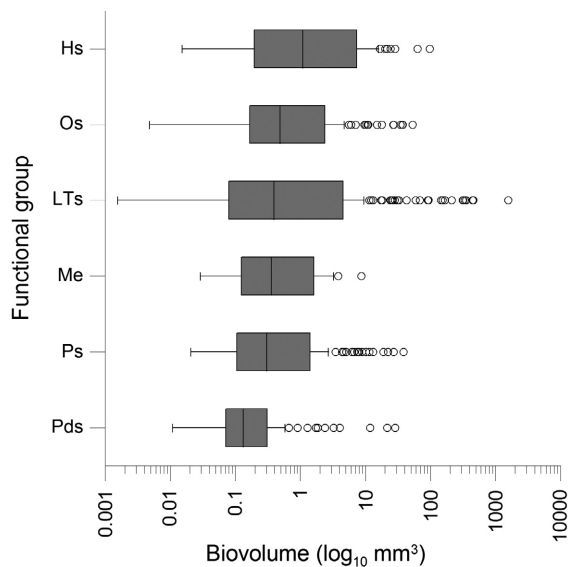


Fig. 8. Box plot showing the distribution of the biovolume of the six categories of functional groups. The black line inside the boxes represents the median, and empty circles are outliers.

also among the most globally abundant terrestrial arthropods, and despite their relatively low individual biomass, together they have a dramatic influence on soil structure (Hopkin 1997). They primarily contribute to regulation of fungal populations and enhancement of mycorrhizal function, improving plant growth (Hopkin 1997, Gange 2000).

Bark beetles live beneath the bark of trees typically constructing tunnels, facilitating fungal colonization in decaying wood (Muller et al. 2002), subsequent bacterial access (de Boer et al. 2005), and further OM decomposition. Weevils, on the other hand, are mostly phytophagous—both above- and belowground (i.e., leaves and roots)—and their diet may also include seeds and fresh and decaying fruits (Triplehorn and Jonson 2005).

These three abundant groups belong to the meso- and macrofauna classification of Swift et al. (1979). They fragment (ecosystem engineering) and ingest litter coated with microbial biomass, and produce large amounts of fecal material, which is more favorable for decomposition (Hopkin 1997, Lavelle et al. 1997). Our results agree with our first and second hypotheses—litter transformers were the most representative in

terms of number of species, abundance, and biovolume, and had the largest range of body volume found in the forest floor.

Structure and distribution of soil invertebrate communities

Neither Winkler nor pitfall collections reached an asymptote, and both methods were sufficient to characterize all functional groups with a relatively low sampling effort. The number of species per sample unit (the methods' efficiency) differed between the two methods, and the composition of species collected using each method was complementary. Using both methodologies together, the species accumulation curve still did not reach an asymptote ($S_{total} = 541$ morphospecies; Appendix S7: Fig. S1). Estimates of diversity based on Jackknife 1 and Jackknife 2 (using incidence data) and Chao 1 (using abundance data) showed that our samples may have covered 63.1–74.1% of the total soil biodiversity in the study area (Appendix S7). A more complete sampling effort (e.g., see Krell et al. 2005) is therefore necessary to reveal total soil food web biodiversity richness in Yasuní. The 26–37% of the soil fauna that was not collected likely includes mostly rare species that may have a minimal impact on forest ecosystem functioning because of low abundance, low accumulated biomass, or both (Grime 1998, Smith and Knapp 2003, Mokany et al. 2008). Although the two collection methodologies used in our study are not directly comparable, Winkler extraction seemed to be more efficient, capturing more species over a smaller area. This is in contrast with other tropical studies that found pitfall traps were more efficient in terms of abundance of the most representative taxa (e.g., Sabu and Shiju 2010). Our complementary species identity results may be explained by the particularities of the two methodologies. Pitfall traps target invertebrate taxa that are active nocturnally on the soil surface. Winkler extractions capture leaf-litter-inhabiting and fast, mobile invertebrates—particularly ants and beetles (Agosti and Alonso 2000, Moreira et al. 2008, Sabu and Shiju 2010).

A rapid assessment of functional groups intuitively suggests that the western Amazonian forest floor is carpeted with all kinds of taxa that represent a wide range of behaviors, strategies, and feeding habits, thereby suggesting high redundancy per unit of area. In this context,

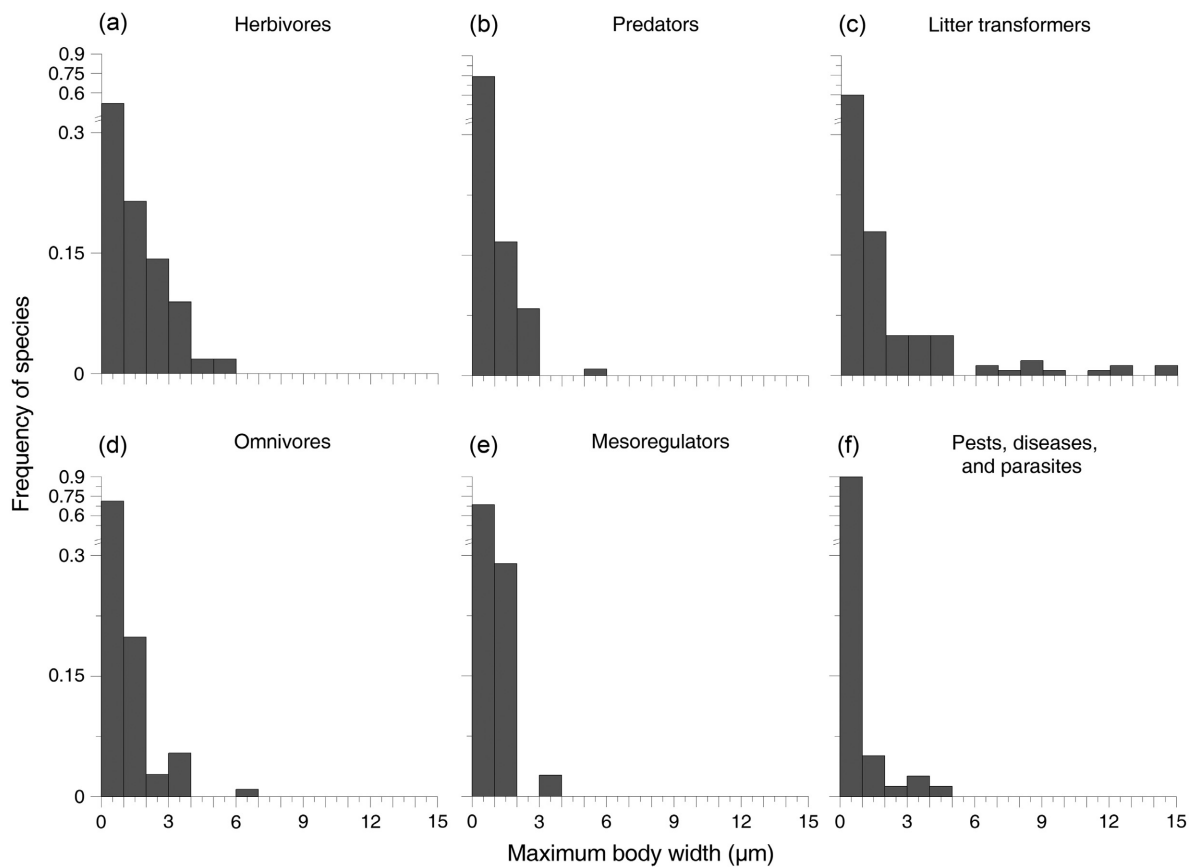


Fig. 9. Frequency distributions of the maximum body width of the soil fauna functional groups. In all cases, data correspond to the averages of width of the morphospecies. (a) represent herbivores; (b) predators; (c) litter transformers; (d) omnivores; (e) mesoregulators; (f) pests, diseases and parasites.

aggregation tests (similarity and distance indexes, and individual/sample rarefaction plots) showed consistent heterogeneity of soil fauna at all levels (species, abundance, functionality, and biovolume), especially at larger scales. This reinforces the idea that taxa and functionality are redundant at all spatial scales, agreeing with our third hypothesis that there is no spatial aggregation. This pattern persisted when only the litter transformer community was considered (results not shown).

The relationship between species and functional diversity remains poorly understood for most of the world's ecosystems (Micheli and Halpern 2005). Some studies, however, have shown low levels of redundancy in other highly diverse (aquatic) environments (Bellwood et al. 2003). Others have shown high functional redundancy, but low functional diversity (Strauß et al. 2010),

which has direct implications for how biodiversity loss might impact the resilience of ecosystems (Peterson et al. 1998, Reich et al. 2012). Finally, we do not yet know whether redundancy in the Yasuní tropical forest can only be predicted at small temporal and spatial scales, as stable coexistence might be incompatible with functional redundancy (Loreau 2004).

Soil invertebrate functional groups

Though we found a wide range of body sizes both within and between functional groups that had overlapping feeding habits, cluster analysis showed cophenetic correlation. This means that the results of the cluster analysis were a reasonable representation of pairwise differences between functional groups. We hypothesized (hypothesis 2) that leaf-litter transformer species would encompass the largest range of body volume

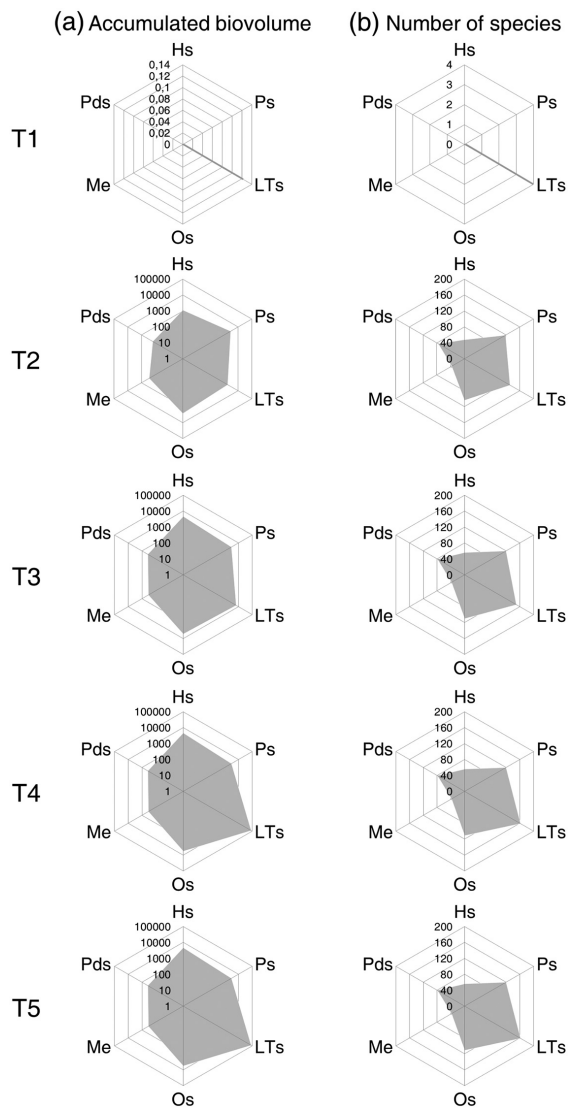


Fig. 10. Radar charts showing the potential accessibility of the soil fauna belonging to the six functional groups to the five types of mesh bags (T1–T5) in terms of (a) accumulated biovolume and (b) the relative number of species. Values on (a) column are the number of individuals per species multiplied by its averaged volume ($N \times \text{mm}^3$), and except for T1, they are \log_{10} -transformed for easier reading and interpretation. Values in (b) column are total number of species. Diagonal size of the mesh treatments: T1 = 0.14 mm; T2 = 2.73 mm; T3 = 6.02 mm; T4 = 15.47 mm; T5 = 23.33 mm.

found in the forest floor—and this is exactly what we found in our samples.

It was noteworthy that collembolans (included in the litter transformers and microregulators group, LT3) were statistically distant within the dendrogram in relation to the other litter transformer groups (general litter transformers and litter transformers, ecosystem engineers, and mesoregulators, LT1 and LT2, respectively). The biological interpretation could be that their ecological role and potential impact (relative to their feeding habits and biovolume) are well defined in the food web. Microarthropods such as collembolans can reasonably be generalized as predominately fungal feeders (mycophages; Seastedt 1984). Collembolans fragment organic matter such as leaf litter while feeding on the adhering microflora, thereby increasing leaf-litter decomposition rates by an average of 23% (based on numerous studies, Seastedt 1984). The remaining litter transformer groups were more compactly distributed in the tree and were closely related to other functional groups, such as omnivores and mesoregulators (e.g., LT1 and LT2 related to O1 and Me). This might be explained by overlapping feeding habits and the body size range of litter transformers (Fig. 8).

Predatory ants and general predators (P1 and P3) were all grouped together in a separate branch of the tree, illustrating their unique ecological position in the soil food web. More importantly, the cluster analysis kept ants (P1) separated from other predators (e.g., arachnids), highlighting the physiological and morphological characteristics that might delineate the unique role and position of ants in this ecosystem (Philpott et al. 2010, Brandão et al. 2011).

The omnivore groups (omnivores and mesoregulators, and omnivores and predators, O1 and O2, respectively) were evenly distributed across the branches of the tree related to consumers of the leaf-litter resources, wood and fungi.

Pest–diseases–herbivores–predators–parasites (Pd1 and Pd2, separated by their body size, Table 1) were all clustered at the base of the dendrogram (Fig. 2; closely related to herbivores H2 and other predators [P1 and P3]), which can be

Table 2. Details of the total accumulated biovolume (B ; $N \times \text{mm}^3$), species number (S), abundance (N), litter transformer and omnivore functional groups (FG), and representative groups that could be involved in the decomposition process of leaf-litter resources within the five different mesh-bag treatments.

| Variables | T1 ($\sim 0.1 \times 0.1$ mm) ($d = 0.14$ mm) | T2 (1.1×2.5 mm) ($d = 2.73$ mm) | T3 (3.2×5.1 mm) ($d = 6.02$ mm) | T4 (10×11.8 mm) ($d = 15.47$ mm) | T5 (15.2×17.7 mm) ($d = 23.33$ mm) |
|-----------------------|---|---|--|---|---|
| B | 0.001% | 3.9% | 12.1% | 74.4% | "100%" |
| S | 6 | 237 | 261 | 274 | 274 |
| N | 6.0% | 93.4% | 98.2% | 99.8% | "100%" |
| FG | LT3, O1 | All | All | All | All |
| Representative groups | Mostly collembolans | + isoptersans, staphylinoids, and smaller isopods | + larger isopods and gryllids | + large blattids and diplopods | + larger blattids and diplopods |

Note: d = diagonal size of grid holes; + = additional litter transformer groups.

explained by their overlapping feeding habits and body dimensions.

Body mass distribution in the Yasuní soil food web

Our mass volume species rank fitted significantly to a lognormal distribution, revealing that the size structure of species within the soil community included a few large species and many

small ones (Appendix S10: Fig. S1). Moreover, mass volume and body width abundance frequency distributions were slightly left-skewed and bell-shaped (and only the maximum body width was normally distributed; Appendix S10: Fig. S1). Peak species richness, therefore, occurred at the intermediate body size that led to the maximum number of individuals, consistent

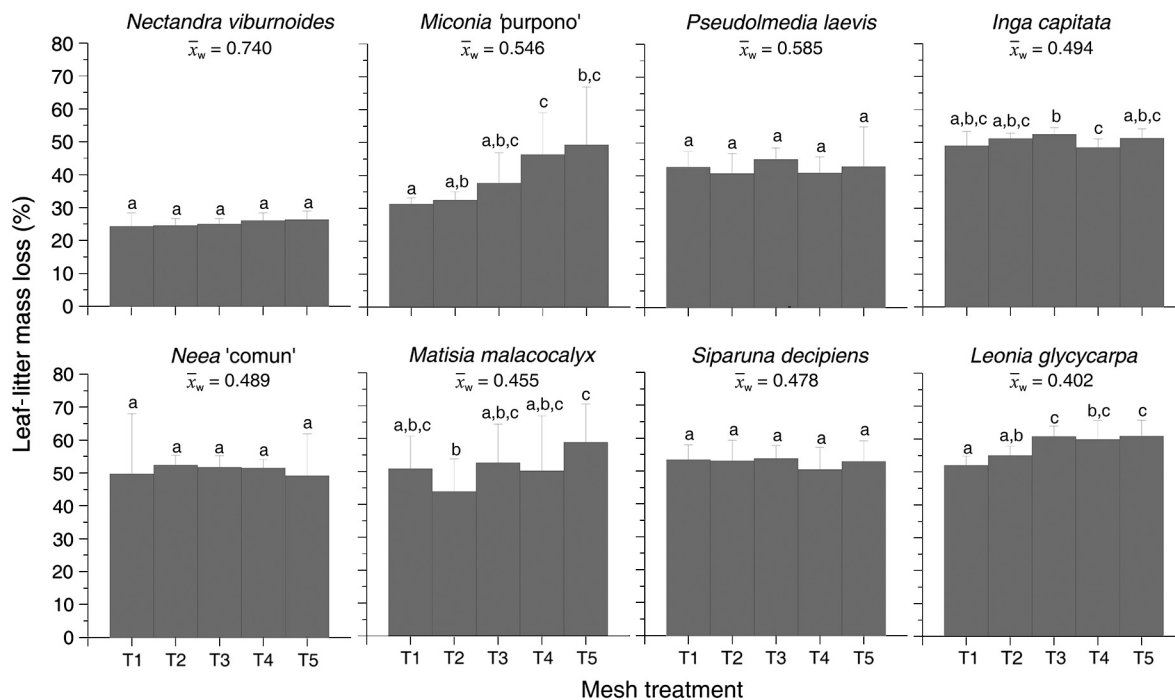


Fig. 11. Percentage of mass loss of the leaf-litter material of the eight plant species in relation to the five mesh-bag treatments. Tukey's and Dunn's post hoc (ANOVA and Kruskal–Wallis tests, respectively) mean difference significances are denoted using a, b, and c nomenclature. \bar{x}_w denote weighted means of the final:initial biomass ratio per species (see Appendix S9 for details). Error bars represent standard deviations. Diagonal size of the mesh treatments: T1 = 0.14 mm; T2 = 2.73 mm; T3 = 6.02 mm; T4 = 15.47 mm; T5 = 23.33 mm.

Table 3. Results of the generalized linear model (GLM) analysis of the leaf-litter decomposition of eight plant species as a function of (A) litterbag mesh sizes, seven leaf plant traits (Ca, K, Mg, S, condensed tannins, Mn:Cu ratio, and lignin:N ratio), and (B) their interactions.

| Effect | Estimate | SE | <i>t</i> | <i>P</i> |
|----------------------|------------|-----------|----------|------------------|
| (A) | | | | |
| Mesh size | 0.188 | 0.064 | 2.935 | 0.006 |
| Ca | 0.002 | 0.0002 | 8.167 | <0.001 |
| K | 0.001 | 0.001 | 2.500 | 0.018 |
| Mg | -0.001 | 0.001 | -1.988 | 0.056 |
| S | 0.012 | 0.003 | 4.097 | <0.001 |
| CT | -1.937 | 2.969 | -0.652 | 0.519 |
| Mn:Cu | 0.040 | 0.022 | 1.839 | 0.075 |
| Lignin:N | 0.457 | 1.050 | 0.436 | 0.667 |
| (B) | | | | |
| Mesh size × Ca | -3.453e-05 | 1.724e-05 | -2.003 | 0.057 |
| Mesh size × K | 6.567e-05 | 3.928e-05 | 1.672 | 0.108 |
| Mesh size × Mg | -1.165e-04 | 5.574e-05 | -2.090 | 0.047 |
| Mesh size × S | -9.792e-04 | 2.161e-04 | -4.531 | <0.001 |
| Mesh size × CT | -1.302 | 0.227 | -5.729 | <0.001 |
| Mesh size × Mn:Cu | 6.229e-03 | 1.672e-03 | 3.725 | 0.001 |
| Mesh size × lignin:N | 0.366 | 0.080 | 4.553 | <0.001 |

Notes: CT, condensed tannins. In boldface, all significant effects when $P \leq 0.05$.

with the results of other large-scale sampling efforts (e.g., Siemann et al. 1999, Jonsson et al. 2005). In an ecological food web context, Cohen et al. (1993) suggested that the “cascade model” can describe a lognormal distribution of body sizes of different animal species. The cascade model is a food web model that assumes hierarchical feeding along a single niche axis, with each species allocated a probability of feeding on taxa below it on the hierarchy (Cohen et al. 1993, Thompson et al. 2012). This lies in the fact that every species has an equal chance of being represented in a random sample of links (as predator or prey). Because animal predators generally consume animal prey smaller than themselves, body size can be assumed to be a natural order in the cascade model, at least for animal species. This model is likely to fit in the Amazonian soil food webs considering that predators like ants, which are extremely diverse and represent a significant amount of living biomass in these forests floor, might exert a significant impact on the detritivore communities and hence on the fragmentation and posterior decomposition of OM (Milton and Kaspari 2007, Kaspari et al. 2011, but cf. Mancinelli and Mulder 2015 for a hypothesis suggesting that microbes may disrupt trophic cascades in the brown food webs around the world). With this interpretation, the cascade

model provides a convenient tool to analyze the consequences of ordering trophic relationships by body size. To summarize, smaller predators eat smaller prey and larger predators consume a wider range of prey sizes (Cohen et al. 1993, Woodward et al. 2005). This may help understand the role of food web structure in the soil of our study area, where a size-structured food web is likely to contain small and abundant species that operate more locally than larger and less-abundant species (Mulder et al. 2005; discussed in the *Exclusion experiment* below).

Recent studies have suggested that diet breadth and foraging behavior of individual species are determined by who eats whom in a community, which in turn is determined by the physical constraints imposed by body mass (Jonsson et al. 2005, Loeuille and Loreau 2005). More importantly, it is now well accepted that community stability is critically dependent on body mass distribution within food webs, especially the distribution of predator:prey body mass ratios (Emmerson and Raffaelli 2004, Loeuille and Loreau 2005). Brose et al. (2006a) found that the average \log_{10} body mass ratios of terrestrial invertebrate predators in temperate ecosystems were among the smallest (a value of 0.6) when compared to terrestrial ectotherm and endotherm vertebrates (values of 2.08 and 2.91, respectively).

Our data showed that the combined biovolume of Yasuní soil invertebrate predator and prey was extremely low (\log_{10} body volume ratio of -1.46). We found two potential explanations for the large discrepancy between the cumulative biovolume of predators and prey in this Amazonian soil food web. (1) Ants may represent between one-third and half of the insect biomass in Central Amazonian soil (Fittkau and Klinge 1973). In our survey, predatory ants represented 10.1% of species, 44.7% of the individuals, and 6.7% of the cumulative biovolume within the total sample. Some voracious ant colonies, such as those of army ants, are patchily distributed, but have been described as episodic and chronic agents of disturbance in the tropical litter that are capable of reducing biomass of litter invertebrates by up to 25% (Kaspari et al. 2011). The patchiness of ant distribution was not considered in our survey; thus, our predator:prey body mass ratio might be underestimated due to a sampling effect. (2) Based on the conclusions of Brose et al. (2006a), we suggest that preys that are much smaller than predators may contain too little energetic reward to be worth the energetic costs of capture and consumption. Perhaps predators in Yasuní are highly efficient at harvesting a large number of small to large prey during periods of activity.

Studies based on model simulations have suggested that an increase in predator:prey body mass ratios in complex model food webs corresponds to an increase in food web stability (i.e., population persistence; Brose et al. 2006b). We have shown, however, that this relationship is not strong in the Yasuní forest floor ecosystem. However, the complex invertebrate soil food web in this ecosystem may exhibit specific structural features that convey high dynamic stability, such as (1) low variability in interaction strengths, (2) efficient predators with a wide range of focal prey species, and (3) species at a high trophic level feeding on multiple prey species, and species at an intermediate trophic level fed upon by multiple predator species (Gross et al. 2009). Overall, decomposition in this ecosystem appears to be highly resistant to drastic changes in food web structure such as size-biased biodiversity loss—only three of our eight leaf-litter treatments saw significant biomass loss in response to experimental treatments.

Exclusion experiment

We found that the T1 mesh size filtered out most of the biovolume, species, abundance, and functional groups of soil fauna. Although most of the litter transformers and omnivores groups were able to pass through all remaining mesh size treatments (T2–T5), it was noteworthy that the resource consumption potential of the species (measured as biovolume) found between T2 and T5 complemented each other.

Body size is one of the primary determinants of metabolism and, therefore, resource use (Brown et al. 2004). Larger individuals need and consume more resources, and the relationship between size and abundance (biovolume accessibility to resources in our set of experiments) may also reveal how resources are partitioned in ecological systems (Grime 1998, White et al. 2007, Bílá et al. 2014).

Our experiment highlighted how resources are exploited following non-random, gradual extinction of larger soil detritivores in a natural scenario. Results suggest that the different body size classes in a detritivore community (averaged across the pooled dataset) played a redundant rather than complementary role in fragmenting leaf litter for five of the eight plant species treatments (Andrén et al. 1995, cf. Nielsen et al. 2011).

Our pooled dataset also fitted to a linear regression ($P = 0.058$, with a slope of 0.19; results not shown). The potential presence of larger detritivore fauna did not drastically and significantly increase OM mass loss for most of our treatments (also revealed by the weighted-arithmetic means comparisons), contradicting our fourth hypothesis that leaf litter exposed to a smaller food web community would decompose at significantly lower rates than that exposed to larger soil fauna. We interpret our results in three ways:

First, it could be that detritivore species size classes contributed similarly to the performance of the decomposition process in the leaf-litter layer of the Yasuní forest floor (Naeem et al. 2009), which may be in conflict with the mass ratio hypothesis. However, this pattern was not common for all plant species used in this experiment. Of the eight plant species, three presented significant differences between the extremes of mesh size treatments: *M. "purpono"* *M. malacocalyx* and *L. glycyarpa*. Based on outlier mass loss values

(results not shown), we suggest that large-sized detritivore individuals, which are often rarer than small ones but can break down more dead OM, may be patchily distributed on the forest floor (Jiménez et al. 2001, Milton and Kaspari 2007). These large individuals might be exploiting resources sporadically, although our experimental design does not allow us to demonstrate this.

Second, because litter transformers and omnivores were represented across the size class continuum, there were some that could enter into all the mesh treatments. Of these, the tiny Collembola were particularly abundant and may have had a significant impact on leaf-litter decomposition rates in all mesh treatments (Seastedt 1984, Cragg and Bardgett 2001), especially in the absence of larger predators and potential competitors as in T1 (see *Discussion* below). According to the mass ratio hypothesis, it has been suggested that the dominant species—or those with the most frequent trait values in a community—would be the main drivers of litter decomposition (Bíla et al. 2014). This contradicts our fifth hypothesis—that there is a positive relationship between decomposition rates and detritivore diversity—because our results show that the smaller species that remained seemed to compensate for the loss of the larger ones in terms of leaf-litter transformation. Yang et al. (2012) showed that previous mechanical litter fragmentation by larger detritivores did enhance the contribution of smaller detritivore fauna (e.g., Collembola) in the decomposition process in a seasonal tropical ecosystem study. Our experimental approach was not able to demonstrate this kind of interspecific interaction, and our results suggest no facilitation between detritivore size classes. The redundancy found in leaf-litter processing in the study area may likewise be explained by the fact that leaf-litter diversity found in the study area was shown to be evenly heterogeneous in a distance scale of >600 m (Sørensen's similarity index mean \pm SD: 0.298 ± 0.19 ; Fig. 12). This means that the Yasuní forest floor is carpeted with a mosaic of diverse litter qualities, which would explain why soil fauna functionality is also significantly homogeneous at a distance scale. Because soil fauna are also taxonomically heterogeneous, this might suggest that the level of detritivore specialization may not be as low as previously thought (Muñoz-Upegui 2016, cf. Giller 1996). Lavelle et al. (2016) conclude that soil

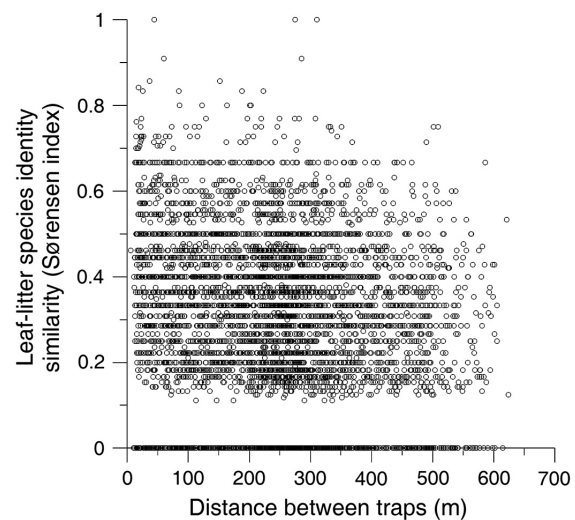


Fig. 12. Plot showing the effect of the geographical distance on the similarity of leaf-litter composition collected in traps, among 28 common plant species of the YFDP (data from Cárdenas et al. 2014). A value of 1 on the y -axis means full similarity.

heterogeneity properties may favor species coexistence and functional redundancy.

Third, PCA of 22 quality traits showed us that the nutrient contents that better explain the differences between species are those that are not usually significantly related to leaf-litter decomposition (Swift et al. 1979). This may suggest, in broad terms, that leaf litter is largely homogenous in those nutrients that have shown a larger effect on decomposition (e.g., positively such as Mn:Cu ratio, or negatively such as condensed tannins; Coq et al. 2010, Cárdenas et al. 2015, Keiluweit et al. 2015). This may suggest in part that soil detritivores in these forests are conditioned, and hence adapted, to exploit resources with a kind of “uniform” critical nutrient content. Interestingly, our GLM analysis showed how these kinds of critical traits such as condensed tannins, Mn:Cu ratio, and lignin:N ratio become significant when including the interaction with mesh size treatments. This suggests that for condensed tannins and Mn:Cu, larger detritivores are directly affected by the relative content of these traits (positive and negative relationships, respectively). Surprisingly, the lignin:N ratio, which systematically appears in the literature as negatively correlated with decomposition (Melillo et al. 1982,

Chapin et al. 2002, Talbot and Treseder 2012, Cárdenas et al. 2015), shows to be positively and significantly related to decomposition, suggesting in this particular case, that the smaller groups of detritivores and very probable, decomposers such as fungi and bacteria, are those that are directly and largely affected by higher proportions of lignin content face to N.

Rank–abundance plots are commonly used based on the assumption that loss of some species will have a greater impact on ecosystem that would others, especially those that make up a dominant part of the total community biomass. These species typically provide the major energy flow and the three-dimensional structure that supports and shelters other organisms (Power et al. 1996, Grime 1998, Bílá et al. 2014). Experimental tests of this assumption have produced mixed results. In a plant productivity experiment, Smith and Knapp (2003) found that reduced abundance of dominant species had direct negative effects on total aboveground net primary productivity. But because an increase in production of the dominant species is able to offset the negative effects of species loss, they concluded that dominant species can provide short-term resistance to reductions in ecosystem functioning in a non-random species loss scenario. In contrast, Lyons and Schwartz (2001) found an increase in the plant community's susceptibility to an exotic plant invasion when the least common species was excluded from a mountain meadow. Their results highlight the potential role of less common species in maintaining ecosystem functioning: in this case, protection against exotic invasive species.

In our study, the loss of the species with the highest biovolume (larger detritivore species) did not have a significant negative effect on the leaf-litter decomposition process. This agrees with Smith and Knapp (2003) in the sense that, in the short term, smaller-dominant species (in terms of abundance, e.g., Collembola) appear to offset the species loss of the larger and rarer species (e.g., giant cockroaches or millipedes). Likewise, Bardgett (2002) noted that most available evidence suggests no predictability in the relationship between diversity and function in soils, and that ecosystem properties are governed more by individual traits of dominant species and by the extraordinary complexity of biotic interactions that occur between components of soil food webs.

Future studies could measure the role of larger and smaller litter transformers in separate “natural” micro- or mesocosms to quantify the OM fragmentation impact separately and over the long term (e.g., Bradford et al. 2002). We also suggest that it will be important to follow the decomposition process over several time intervals to determine whether detritivory is actually more important in the first days of exposure to litter transformers, as has been shown in previous studies (see Imler 2000, Cárdenas and Dangles 2012).

We conclude that extinction of larger invertebrates could represent a challenge for the decomposition process of particular leaf-litter resources in Yasuní (in terms of chemical quality). However, nutrient cycling seems to be mostly guaranteed by the smaller detritivore fauna and most likely by the significant action of microflora (fungi and bacteria) that we did not test here. This is more significant if we consider that larger species loss could generate an increase in the diversity and abundance of the smaller species, as shown by Kunte (2008) after removal of the two dominant butterfly species in a tropical rain forest. However, our results might not mean that larger invertebrates have no essential role in the healthy function of this tropical ecosystem. They are consistent with the idea that changes in community composition, rather than richness, are most important for carbon dynamics (Nielsen et al. 2011). For example, loss of a few medium and large detritivore species may have a significant impact on specialized degradation processes, such as the decomposition of particular carbon sources such as lignin and cellulose (Cox et al. 2001, Hanson et al. 2008) or specific litter qualities such as those found in *M. purpono*, *M. malacocalyx*, and *L. glycyarpa*. The role of detritivores in forests goes far beyond their feeding habits, as they also serve as prey, and many aerate the soil or act as pollinators (Triplehorn and Jonson 2005). The food web changes with each successive extinction, making it difficult to predict the impact of potential detritivore extinction on ecosystem functioning and which remaining species will be able to compensate (Ives and Cardinale 2004). A more extensive experiment using more plant species that represents a wider spectrum of the mosaic of forest litter quality and integrates the concept of complementary use of resources (Vos et al. 2013) may reveal a more realistic pattern of leaf-litter decomposition as a

function of a gradual loss of body size biodiversity of soil detritivores in Yasuní.

Interspecific interactions in the soil food web affecting leaf-litter decomposition?

Non-significant differences in leaf-litter decomposition between mesh size treatments for five of the eight plant species in this experiment have generated several new questions.

1. Would there be an interference competition between small-, medium-, and large-sized detritivores for leaf litter from these plant species?

Bradford et al. (2002) found that meso- and macrofauna inhibited decomposition by microfauna, fungi, and bacteria by 11.5% through indirect effects. Nonetheless, the presence of larger invertebrates increased the rate of decomposition overall. These results may suggest that in the short term, larger invertebrates alone would functionally (over)compensate in the absence of the smaller ones—something that we cannot show with our study because we used different methodological approaches. Heemsbergen et al. (2004) did not find a significant net diversity effect of species (the sum of the per-capita effects of its component species) on the leaf-litter mass loss, potentially due to a wide range of negative (interspecific competition), neutral, and positive (facilitation) interactions among species. Although the role of competition in soil biotic communities is thought to be relatively weak (Setälä et al. 2005, Wardle 2006, Lavelle et al. 2016), increased species richness is also likely to increase interspecific competition, and in some cases, this may outweigh any positive effects of complementarity and/or the inclusion of highly influential species on carbon dynamics (Nielsen et al. 2011). Our data may thus be showing the total of all non-additive effects arising from multi-species interactions including facilitation and interspecific interference competition (Basset and Rossi 1990, Heemsbergen et al. 2004, Fox 2005, Ball et al. 2008, McKie et al. 2008). This would partly explain the neutral effect of our non-random species loss design on decomposition of most of the studied leaf-litter types.

2. To what extent are litter transformer and omnivore size assemblages functionally redundant, given that functional identity and divergence of species, rather than species diversity per se, promote ecosystem multifunctionality (Mouillot et al. 2011)?

At the soil food web level, different size classes of detritivores may consume resources in different ways (scraping, piercing, tearing) and amounts, and therefore, they may have had unexpected effects on litter fragmentation (Heemsbergen et al. 2004, Vilisics et al. 2012). For example, there was no evidence of ecosystem engineering, which usually occurs after fragmentation work of large detritivores that facilitate the ingestion/colonization of OM particles by smaller detritivores (including microflora; Lavelle et al. 1997, Jonsson et al. 2002, Yang et al. 2012). Future research should consider whether larger detritivores prefer fresh leaf litter of one or more plant species (not pre-treated by smaller detritivores, or already invaded by fungi and bacteria), which would also partly explain why there was so much variation in OM mass loss of *M. purpono* or *P. laevis* in T4 and T5 mesh treatments. This would make sense if smaller detritivores were more abundant than larger ones, and if early accessibility to “fresh” resources were hazardous.

3. Does the predator:prey biovolume ratio influence decomposition rates within each of the five size-biased microcosms?

Breadth and foraging behavior of organisms are determined by intrinsic predator–prey characteristics and interactions (Jonsson et al. 2005, Loeuille and Loreau 2005)—or consumer–resource relationships that shape food web structure—that may drive ecosystem processes such as nutrient cycling (Hättenschwiler and Gasser 2005). Predators that are harvesting in the forest floor of Yasuní may control detritivore activity in our coarser mesh size treatments. This could explain why, for most of the leaf-litter types, leaf-litter mass loss was not significantly different from finer mesh size treatments, which, consistent with other studies, suggests top-down control of decomposition (Milton and Kaspari 2007, Srivastava et al. 2009). By contrast,

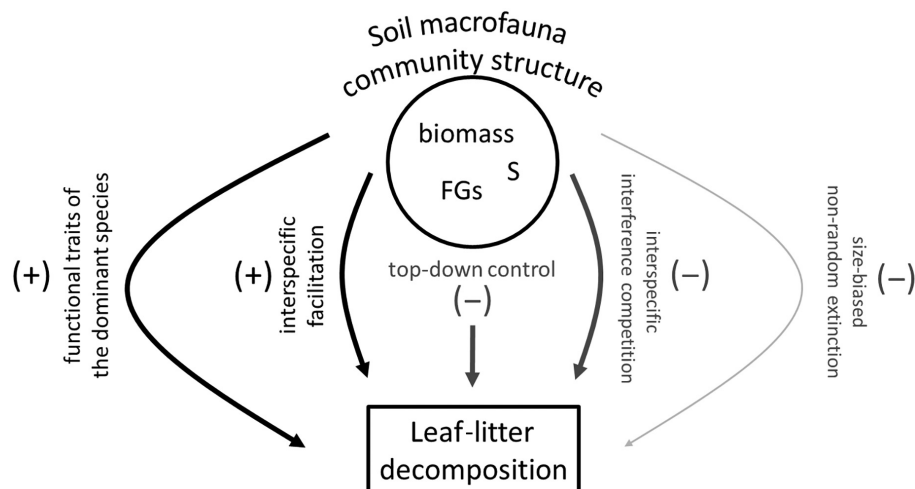


Fig. 13. Theoretical multi-species interactions at all macrofauna body size ranges of the potential mechanisms controlling leaf-litter decomposition in the Yasuní tropical rain forest. Biomass (based on biovolume calculations for this study); *S*: the number of species; FGs: functional groups; “top-down” refers to the effect of predators exerting pressure over detritivores; (+) = positive effect; (–) = negative effect.

the “self-organized systems framework” suggests that evolution may have favored cooperation (i.e., facilitation interactions) where competition and predation may act as secondary regulators of soil functioning (Lavelle et al. 2016). By which mechanisms inter- and intraspecific interactions at all levels of organization are driving soil processes is still a matter of study and debate.

CONCLUSION

The soil fauna in the forest floor of Yasuní is heterogenous in terms of species composition for all functional groups analyzed, but homogeneous with respect to functionality at all spatial scales. Heemsbergen et al. (2004) concluded that communities composed of functionally dissimilar species should have stronger effects on decomposition rates than communities consisting of functionally similar species. Considering the efficiency of the decomposition process in Amazonian ecosystems, it is therefore very likely that there is actually a very high level of functional dissimilarity at all body size ranges (not identified in this study) that ensure decomposition will proceed. Based on our results and results of other studies, we suggest OM decomposition may depend on all non-additive effects that arise from multi-species

interactions, including facilitation, interspecific interference competition, and top-down control that predators exert over detritivores at all body size ranges (Fig. 13).

However, it is important to note that short-term changes in soil biodiversity—those implemented in our study design—may not manifest their effects on the stability of soil processes for a long time after organisms are lost, suggesting that delayed responses may be an important legacy of changes in soil biodiversity (Bardgett 2002, Lavelle et al. 2016). Future studies in the Amazon should consider monitoring the decomposition process over a longer term (removal) under conditions where biodiversity has been fragmented and the complete soil food web has been modified, such as in gradients of land use (Díaz et al. 2003).

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LITERATURE CITED

- Agosti, D., and L. E. Alonso. 2000. The ALL protocol: a standard protocol for the collection of ground-dwelling ants. Pages 204–206 in D. Agosti, J. Majer, E. Alonso, and T. R. Schultz, editors. *Ants: standard methods for measuring and monitoring biodiversity*. Biological Diversity Handbook Series. Smithsonian Institution Press, Washington, D.C., USA.
- Andrén, O., J. Bengtsson, and M. Clarholm. 1995. Biodiversity and species redundancy among litter decomposers. Pages 141–151 in H. P. Collins, G. P. Robertson, and M. J. Klug, editors. *The significance and regulation of soil biodiversity*. Kluwer Academic, Dordrecht, The Netherlands.
- Ball, B. A., M. D. Hunter, J. S. Kominoski, C. M. Swan, and M. A. Bradford. 2008. Consequences of non-random species loss for decomposition dynamics: experimental evidence for additive and non-additive effects. *Journal of Ecology* 96:303–313.
- Balvanera, P., A. B. Pfisterer, N. Buchmann, J. S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters* 9:1146–1156.
- Bardgett, R. D. 2002. Causes and consequences of biological diversity in soil. *Zoology* 105:367–374.
- Bardgett, R. D., and D. A. Wardle. 2010. Above-ground-belowground linkages: biotic interactions, ecosystem processes, and global change. *Oxford series in ecology and evolution*. Oxford University Press, Oxford, UK.
- Bass, M. S., et al. 2010. Global conservation significance of Ecuador's Yasuní National Park. *PLoS One* 5:e8767.
- Basset, A., and L. Rossi. 1990. Competitive trophic niche modifications in three populations of detritivores. *Functional Ecology* 4:685–694.
- Bellwood, D. R., A. S. Hoey, and J. H. Choat. 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters* 6:281–285.
- Bezemer, T. M., et al. 2010. Divergent composition but similar function of soil food webs of individual plants: plant species and community effects. *Ecology* 91:3027–3036.
- Bíla, K., M. Moretti, F. Bello, A. T. Dias, G. B. Pezzatti, A. R. Van Oosten, and M. P. Berg. 2014. Disentangling community functional components in a litter-macrodetrivore model system reveals the predominance of the mass ratio hypothesis. *Ecology and Evolution* 4:408–416.
- Bokhorst, S., and D. A. Wardle. 2013. Microclimate within litter bags of different mesh size: implications for the 'arthropod effect' on litter decomposition. *Soil Biology and Biochemistry* 58:147–152.
- Boze, B. G. V., A. D. Hernandez, M. A. Huffman, and J. Moore. 2012. Parasites and dung beetles as ecosystem engineers in a forest ecosystem. *Journal of Insect Behavior* 25:352–361.
- Bradford, M. A., G. M. Tordoff, T. Eggers, T. H. Jones, and J. E. Newington. 2002. Microbiota, fauna, and mesh size interactions in litter decomposition. *Oikos* 99:317–323.
- Brandão, C. R. F., R. R. Silva, and J. H. C. Delabie. 2011. Neotropical ants (Hymenoptera) functional groups: nutritional and applied implications. Pages 213–236 in A. R. Panizzi and J. R. P. Parra, editors. *Insect bioecology and nutrition for integrated pest management*. CRC Press, Taylor & Francis Group, Boca Raton, Florida, USA.
- Brose, U., et al. 2006a. Consumer-resource body-size relationships in natural food webs. *Ecology* 87:2411–2417.
- Brose, U., R. J. Williams, and N. D. Martinez. 2006b. Allometric scaling enhances stability in complex food webs. *Ecology Letters* 9:1228–1236.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85:1771–1789.
- Brussaard, L. 1998. Soil fauna, guilds, functional groups and ecosystem processes. *Applied Soil Ecology* 9:123–135.
- Cárdenas, R. E. 2013. Plant and fauna functional trait diversity affecting leaf herbivory and decomposability in a Neotropical rainforest (Yasuní National

- Park Ecuador). Dissertation. Pierre and Marie Curie University (Paris 6), France.
- Cárdenas, R. E., and O. Dangles. 2012. Do canopy herbivores mechanically facilitate subsequent litter decomposition in soil? A pilot study from a Neotropical cloud forest. *Ecological Research* 27:975–981.
- Cárdenas, R. E., S. Hättenschwiler, R. Valencia, A. Argoti, and O. Dangles. 2015. Plant herbivory responses through changes in leaf quality have no effect on subsequent leaf-litter decomposition in a Neotropical rain forest tree community. *New Phytologist* 207:817–829.
- Cárdenas, R. E., R. Valencia, N. J. B. Kraft, A. Argoti, and O. Dangles. 2014. Plant traits predict inter- and intraspecific variation in susceptibility to herbivory in a hyperdiverse Neotropical rainforest tree community. *Journal of Ecology* 102:939–952.
- Cardinale, B. J., J. P. Wright, M. W. Cadotte, I. T. Carroll, A. Hector, D. S. Srivastava, M. Loreau, and J. J. Weis. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *Proceedings of the National Academy of Sciences* 104:18123–18128.
- Cardinale, B. J., et al. 2012. Biodiversity loss and its impact on humanity. *Nature* 486:59–67.
- Cardoso, P., S. Pekar, R. Jocqué, and J. A. Coddington. 2011. Global patterns of guild composition and functional diversity of spiders. *PLoS One* 6:e21710.
- Cares, J. E., and S. P. Huang. 2008. Soil nematodes. Pages 97–106 in F. M. S. Moreira, E. J. Huisling, and D. E. Bignell, editors. *A handbook of tropical soil biology: sampling and characterization of below-ground biodiversity*. Earthscan, London, UK.
- Chapin, F. S., P. A. Matson, and H. A. Mooney. 2002. *Principles of terrestrial ecosystem ecology*. Springer Verlag, New York, New York, USA.
- Chave, J., et al. 2010. Regional and seasonal patterns of litterfall in tropical South America. *Biogeosciences* 7:43–55.
- Cohen, J. E., S. L. Pimm, P. Yodzis, and J. Saldaña. 1993. Body sizes of animal predators and animal prey in food webs. *Journal of Animal Ecology* 62:67–78.
- Colwell, R. K., C. X. Mao, and J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85:2717–2727.
- Coq, S., J. M. Souquet, E. Meudec, V. Cheyrier, and S. Hättenschwiler. 2010. Interspecific variation in leaf litter tannins drives decomposition in a tropical rainforest of French Guiana. *Ecology* 91:2080–2091.
- Cox, P., S. P. Wilkinson, and J. M. Anderson. 2001. Effects of fungal inocula on the decomposition of lignin and structural polysaccharides in *Pinus sylvestris* litter. *Biology and Fertility of Soils* 33:246–251.
- Cragg, R. G., and R. D. Bardgett. 2001. How changes in soil faunal diversity and composition within a trophic group influence decomposition processes. *Soil Biology and Biochemistry* 33:2073–2081.
- Dangles, O., C. Carpio, and G. Woodward. 2012. Size-dependent species removal impairs ecosystem functioning in a large-scale tropical field experiment. *Ecology* 93:2615–2625.
- Dangles, O., M. O. Gessner, F. Guérold, and E. Chauvet. 2004. Impacts of stream acidification on litter breakdown: implications for assessing ecosystem functioning. *Journal of Applied Ecology* 41:365–378.
- de Boer, W., L. B. Folman, R. C. Summerbell, and L. Boddy. 2005. Living in a fungal world: impact of fungi on soil bacterial niche development. *FEMS Microbiology Reviews* 29:795–811.
- Di Rienzo, J. A., F. Casanoves, M. G. Balzarini, L. Gonzalez, M. Tablada, and C. W. Robledo. 2012. *InfoStat*. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Córdoba, Argentina. <http://www.infostat.com.ar>
- Díaz, S., J. Fargione, F. S. Chapin, and D. Tilman. 2006. Biodiversity loss threatens human well-being. *PLoS Biology* 4:e277.
- Díaz, S., A. J. Symstad, F. S. Chapin, D. A. Wardle, and L. F. Huenneke. 2003. Functional diversity revealed by removal experiments. *Trends in Ecology and Evolution* 18:140–146.
- Dossena, M., G. Yvon-Durocher, J. Grey, J. M. Montoya, D. M. Perkins, M. Trimmer, and G. Woodward. 2012. Warming alters community size structure and ecosystem functioning. *Proceedings of the Royal Society B* 279:3011–3019.
- Ebenman, B., R. Law, and C. Borrvall. 2004. Community viability analysis: the response of ecological communities to species loss. *Ecology* 85:2591–2600.
- Ellison, A. M., S. Record, A. Arguello, and N. J. Gotelli. 2007. Rapid inventory of the ant assemblage in a temperate hardwood forest: species composition and assessment of sampling methods. *Environmental Entomology* 36:766–775.
- Emmerson, M. C., and D. Raffaelli. 2004. Predator-prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology* 73:399–409.
- Fittkau, E. J., and H. Klinge. 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem. *Biotropica* 5:2–14.
- Fox, J. W. 2005. Interpreting the ‘selection effect’ of biodiversity on ecosystem function. *Ecology Letters* 8:846–856.

- Gange, A. 2000. Arbuscular mycorrhizal fungi, Collembola and plant growth. *Trends in Ecology and Evolution* 15:369–372.
- García-Palacios, P., B. G. McKie, I. T. Handa, A. Frainer, and S. Hättenschwiler. 2016. The importance of litter traits and decomposers for litter decomposition: a comparison of aquatic and terrestrial ecosystems within and across biomes. *Functional Ecology* 30:819–829.
- Gessner, M. O., C. M. Swan, C. K. Dang, B. G. McKie, R. D. Bardgett, D. H. Wall, and S. Hättenschwiler. 2010. Diversity meets decomposition. *Trends in Ecology and Evolution* 25:372–380.
- Giller, P. S. 1996. The diversity of soil communities, the 'poor man's tropical rainforest'. *Biodiversity and Conservation* 5:135–168.
- Gillot, C. 2005. *Entomology*. Third edition. Springer, Dordrecht, The Netherlands.
- Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4:379–391.
- Griffin, J. N., E. J. O'Gorman, M. C. Emmerson, S. R. Jenkins, A.-M. Klein, M. Loreau, and A. Symstad. 2009. Biodiversity and the stability of ecosystem functioning. Pages 78–93 in S. Naeem, D. E. Bunker, A. Hector, M. Loreau, and C. Perrings, editors. *Biodiversity, ecosystem functioning, and human wellbeing*. An ecologic and economic perspective. Oxford University Press, Oxford, UK.
- Grime, J. P. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology* 86:902–910.
- Gross, K., and B. J. Cardinale. 2005. The functional consequences of random vs. ordered species extinctions. *Ecology Letters* 8:409–418.
- Gross, T., L. Rudolf, S. A. Levin, and U. Dieckmann. 2009. Generalized models reveal stabilizing factors in food webs. *Science* 325:747–750.
- Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: Palaeontological statistics software package for education and data analysis. *Palaeontologica Electronica* 4:1–9. <http://folk.uio.no/ohammer/past/>
- Handa, I. T., et al. 2014. Consequences of biodiversity loss for litter decomposition across biomes. *Nature* 509:218–221.
- Hanson, C. A., S. D. Allison, M. A. Bradford, M. D. Wallenstein, and K. K. Treseder. 2008. Fungal taxa target different carbon sources in forest soil. *Ecosystems* 11:1157–1167.
- Hättenschwiler, S., S. Coq, S. Barantal, and I. T. Handa. 2011. Leaf traits and decomposition in tropical rainforests: revisiting some commonly held views and towards a new hypothesis. *New Phytologist* 189:950–965.
- Hättenschwiler, S., and P. Gasser. 2005. Soil animals alter plant litter diversity effects on decomposition. *Proceedings of the National Academy of Sciences* 102:1519–1524.
- Heemsbergen, D. A., M. P. Berg, M. Loreau, J. R. van Hal, J. H. Faber, and H. A. Verhoef. 2004. Biodiversity effects on soil processes explained by interspecific functional dissimilarity. *Science* 306:1019–1020.
- Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. I. O'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486:105–108.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Hopkin, S. P. 1997. *Biology of the springtails (Insecta: Collembola)*. Oxford University Press, New York, New York, USA.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110:449–460.
- Ingham, R. E., J. A. Trofymow, E. R. Ingham, and D. C. Coleman. 1985. Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. *Ecological Monographs* 55:119–140.
- Irmiler, U. 2000. Changes in the fauna and its contribution to mass loss and N release during leaf litter decomposition in two deciduous forests. *Pedobiologia* 44:105–118.
- Ives, A. R., and B. J. Cardinale. 2004. Food-web interactions govern the resistance of communities after non-random extinctions. *Nature* 429:174–177.
- Jiménez, J. J., J. P. Rossi, and P. Lavelle. 2001. Spatial distribution of earthworms in acid-soil savannas of the eastern plains of Colombia. *Applied Soil Ecology* 17:267–278.
- John, R., et al. 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences* 104:864–869.
- Jones, C. G. 2012. Ecosystem engineers and geomorphological signatures in landscapes. *Geomorphology* 157–158:75–87.
- Jones, C. G., J. H. Lawton, and M. Shachak. 1994. Organisms as ecosystems engineers. *Oikos* 69:373–386.
- Jonsson, T., J. E. Cohen, and S. R. Carpenter. 2005. Food webs, body size, and species abundance in ecological community description. *Advances in Ecological Research* 36:1–84.

- Jonsson, M., O. Dangles, B. Malmqvist, and F. Gue-
érol. 2002. Simulating species loss following per-
turbation: assessing the effects on process rates.
Proceedings of the Royal Society B 269:1047–1052.
- Kaspari, M., M. N. Garcia, K. E. Harms, M. Santana,
S. J. Wright, and J. B. Yavitt. 2008. Multiple nutri-
ents limit litterfall and decomposition in a tropical
forest. *Ecology Letters* 11:35–43.
- Kaspari, M., S. Powell, J. Lattke, and S. O'Donnell.
2011. Predation and patchiness in the tropical litter:
Do swarm-raiding army ants skim the cream or
drain the bottle? *Journal of Animal Ecology*
80:818–823.
- Keiluweit, M., P. Nico, M. E. Harmon, J. Mao,
J. Pett-Ridge, and M. Kleber. 2015. Long-term litter
decomposition controlled by manganese redox
cycling. *Proceedings of the National Academy of
Sciences* 112:E5253–E5260.
- Klein, B. C. 1989. Effects of forest fragmentation on
dung and carrion beetle communities in central
Amazonia. *Ecology* 70:1715–1725.
- Kraft, N. J. B., and D. D. Ackerly. 2010. Functional trait
and phylogenetic tests of community assembly
across spatial scales in an Amazonian forest. *Eco-
logical Monographs* 80:401–422.
- Krell, F.-T., A. Y. C. Chung, E. DeBoise, P. Eggleton,
A. Giusti, K. Inward, and S. Krell-Westerwalbesloh.
2005. Quantitative extraction of macro-invertebrates
from temperate and tropical leaf litter and soil: effi-
ciency and time-dependent taxonomic biases of the
Winkler extraction. *Pedobiologia* 49:175–186.
- Kunte, K. 2008. Competition and species diversity:
Removal of dominant species increases diversity in
Costa Rican butterfly communities. *Oikos* 117:69–76.
- Kurokawa, H., and T. Nakashizuka. 2008. Leaf
herbivory and decomposability in a Malaysian
tropical rain forest. *Ecology* 89:2645–2656.
- Lamarre, P., B. Hérault, P. V. Fine, V. Vedel, R. Lupoli,
I. Mesones, and C. Baraloto. 2016. Taxonomic and
functional composition of arthropod assemblages
across contrasting Amazonian forests. *Journal of
Animal Ecology* 85:227–239.
- Lang, B., B. C. Rall, S. Scheu, and U. Brose. 2014.
Effects of environmental warming and drought on
size-structured soil food webs. *Oikos* 123:1224–1233.
- Lavelle, P., D. Bignell, M. Lepage, V. Wolters, P. Roger,
P. Ineson, O. W. Heal, and S. Dhillion. 1997. Soil
function in a changing world: the role of inverte-
brate ecosystem engineers. *European Journal of
Soil Biology* 33:159–193.
- Lavelle, P., T. Decaëns, M. Aubert, S. Barot, M. Blouin,
F. Bureau, P. Magerie, P. Mora, and J.-P. Rossi.
2006. Soil invertebrates and ecosystem services.
European Journal of Soil Biology 42:S3–S15.
- Lavelle, P., et al. 2016. Ecosystem engineers in a self-
organized soil: a review of concepts and future
research questions. *Soil Science* 181:91–109.
- Loeuille, N., and M. Loreau. 2005. Evolutionary emer-
gence of size-structured food webs. *Proceedings of
the National Academy of Sciences* 102:5761–5766.
- Longino, J. T., J. Coddington, and R. K. Colwell. 2002.
The ant fauna of a tropical rain forest: estimating
species richness three different ways. *Ecology* 83:
689–702.
- Loreau, M. 2004. Does functional redundancy exist?
Oikos 104:606–611.
- Lyons, K. G., and M. W. Schwartz. 2001. Rare species
loss alters ecosystem function – invasion resistance.
Ecology Letters 4:358–365.
- Magurran, A. E. 2004. *Measuring biological diversity*.
Blackwell, Oxford, UK.
- Mancinelli, G., and C. Mulder. 2015. Detrital dynamics
and cascading effects on supporting ecosystem
services. *Advances in Ecological Research* 53:
97–160.
- McCracken, D. I., and E. M. Bignal. 1998. Applying the
results of ecological studies to land-use policies and
practices. *Journal of Applied Ecology* 35:961–967.
- McKie, B. G., G. Woodward, S. Hladysz, M. Nistorescu,
E. Preda, C. Popescu, P. S. Giller, and B. Malmqvist.
2008. Ecosystem functioning in stream assemblages
from different regions: contrasting responses to
variation in detritivore richness, evenness and den-
sity. *Journal of Animal Ecology* 77:495–504.
- Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982.
Nitrogen and lignin control of hardwood leaf litter
decomposition dynamics. *Ecology* 63:621–626.
- Metz, M. R., W. P. Sousa, and R. Valencia. 2010. Wide-
spread density-dependent seedling mortality pro-
motes species coexistence in a highly diverse
Amazonian rain forest. *Ecology* 91:3675–3685.
- Micheli, F., and B. S. Halpern. 2005. Low functional
redundancy in coastal marine assemblages. *Ecol-
ogy Letters* 8:391–400.
- Millennium Ecosystem Assessment. 2005. *Ecosystems
and human well-being: synthesis*. Island Press,
Washington, D.C., USA.
- Milton, Y., and M. Kaspari. 2007. Bottom-up and top-
down regulation of decomposition in a tropical for-
est. *Oecologia* 153:163–172.
- Mokany, K., J. Ash, and S. Roxburgh. 2008. Functional
identity is more important than diversity in influ-
encing ecosystem processes in a temperate native
grassland. *Journal of Ecology* 96:884–893.
- Moreira, F. M. S., E. J. Huising, and D. E. Bignell. 2008.
*A handbook of tropical soil biology. Sampling and
characterization of below-ground biodiversity*.
First edition. Earthscan, London, UK.

- Mouchet, M., F. Guilhaumon, S. Villéger, N. W. H. Mason, J.-A. Tomasini, and D. Mouillot. 2008. Towards a consensus for calculating dendrogram-based functional diversity indices. *Oikos* 117:794–800.
- Mouillot, D., S. Villéger, M. Scherer-Lorenzen, and N. W. H. Mason. 2011. Functional structure of biological communities predicts ecosystem multifunctionality. *PLoS One* 6:e17476.
- Mulder, C. 2006. Driving forces from soil invertebrates to ecosystem functioning: the allometric perspective. *Naturwissenschaften* 93:467–479.
- Mulder, C., J. E. Cohen, H. Setälä, J. Bloem, and A. M. Breure. 2005. Bacterial traits, organisms mass and numerical abundance in the detrital soil food web of Dutch agricultural grasslands. *Ecology Letters* 8:80–90.
- Mulder, C., and J. J. Elser. 2009. Soil acidity, ecological stoichiometry and allometric scaling in grassland food webs. *Global Change Biology* 15:2730–2738.
- Muller, M. M., M. Varama, J. Heinonen, and A. Hallaksela. 2002. Influence of insects on the diversity of fungi in decaying spruce wood in managed and natural forests. *Forest Ecology and Management* 166:165–181.
- Muñoz-Upegui, D. A. 2016. Diversity of soil invertebrates associated to six spatially aggregated plant species in the Yasuní National Park, Amazonian Ecuador. Dissertation. Pontificia Universidad Católica del Ecuador, Quito, Ecuador.
- Naeem, S., D. E. Bunker, A. Hector, M. Loreau, and C. Perrings. 2009. Introduction: the ecological and social implications of changing biodiversity. An overview of a decade of biodiversity and ecosystem functioning research. Pages 3–13 in S. Naeem, D. E. Bunker, A. Hector, M. Loreau, and C. Perrings, editors. *Biodiversity, ecosystem functioning, and human wellbeing. An ecologic and economic perspective*. Oxford University Press, Oxford, UK.
- Nielsen, U. N., E. Ayres, D. H. Wall, and R. D. Bardgett. 2011. Soil biodiversity and carbon cycling: a review and synthesis of studies examining diversity-function relationships. *European Journal of Soil Science* 62:105–116.
- O'Connor, N. E., and T. P. Crowe. 2005. Biodiversity loss and ecosystem functioning: distinguishing between number and identity of species. *Ecology* 86:1783–1796.
- Otto, S. B., B. C. Rall, and U. Brose. 2007. Allometric degree distributions facilitate food-web stability. *Nature* 450:1226–1229.
- Petchey, O. L., P. T. McPhearson, T. M. Casey, and P. J. Morin. 1999. Environmental warming alters food-web structure and ecosystem function. *Nature* 402:69–72.
- Peterson, G., C. R. Allen, and C. S. Holling. 1998. Ecological resilience, biodiversity and scale. *Ecosystems* 1:6–18.
- Philpott, S. M., I. Perfecto, I. Armbrrecht, and C. L. Parr. 2010. Ant diversity and function in disturbed and changing habitats. Pages 137–156 in L. Lach, C. L. Parr, and K. Abbott, editors. *Ant ecology*. Oxford University Press, New York, New York, USA.
- Pla, L., F. Casanoves, and J. Di Rienzo. 2012. *Quantifying functional biodiversity*. Springer, Lexington, Kentucky, USA.
- Poisot, T., N. Mouquet, and D. Gravel. 2013. Trophic complementarity drives the biodiversity–ecosystem functioning relationship in food webs. *Ecology Letters* 16:853–861.
- Power, M. E., D. Tilman, J. A. Estes, B. A. Menge, W. J. Bond, L. S. Mills, D. Gretchen, J. C. Castilla, J. Lubchenco, and R. T. Paine. 1996. Challenges in the quest for keystones. *BioScience* 46:609–620.
- Powers, J. S., et al. 2009. Decomposition in tropical forests: a pan-tropical study of the effects of litter type, litter placement and mesofaunal exclusion across a precipitation gradient. *Journal of Ecology* 97:801–811.
- Pramanik, R., K. Sarkar, and V. C. Joy. 2001. Efficiency of detritivore soil arthropods in mobilizing nutrients from leaf litter. *Tropical Ecology* 42:51–58.
- Preston, F. W. 1948. The commonness and rarity of species. *Ecology* 29:254–283.
- Primack, R., and R. Corlett. 2005. *Tropical rainforests: an ecological and biogeographical comparison*. Blackwell, Oxford, UK.
- R Development Core Team. 2015. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>
- Reich, P. B., D. Tilman, F. Isbell, K. Mueller, S. E. Hobbie, D. F. B. Flynn, and N. Eisenhauer. 2012. Impacts of biodiversity loss escalate through time as redundancy fades. *Science* 336:589–592.
- Reiss, J., R. A. Bailey, D. A. Perkins, A. Pluchinotta, and G. Woodward. 2011. Testing effects of consumer richness, evenness and body size on ecosystem functioning. *Journal of Animal Ecology* 80:1145–1154.
- Reiss, J., J. R. Bridle, J. M. Montoya, and G. Woodward. 2009. Emerging horizons in biodiversity and ecosystems functioning research. *Trends in Ecology and Evolution* 24:505–514.
- Ryder Wilkie, K. T., A. L. Mertl, and J. F. A. Traniello. 2010. Species diversity and distribution patterns of the ants of Amazonian Ecuador. *PLoS One* 5:e13146.
- Sabu, T. K., and R. T. Shiju. 2010. Efficacy of pitfall trapping, Winkler and Berlese extraction methods

- for measuring ground-dwelling arthropods in moistdeciduous forests in the Western Ghats. *Journal of Insect Science* 10:1–17.
- Salazar, L. F., C. A. Nobre, and M. D. Oyama. 2007. Climate change consequences on the biome distribution in tropical South America. *Geophysical Research Letters* 34:L09708.
- Sanders, H. L. 1968. Marine benthic diversity: a comparative study. *American Naturalist* 102:243–282.
- Schmid, B., P. Balvanera, B. J. Cardinale, J. Godbold, A. B. Pfisterer, D. Raffaelli, M. Solan, and D. S. Srivastava. 2009. Consequences of species loss for ecosystem functioning: meta-analyses of data from biodiversity experiments. Pages 14–29 *in* S. Naem, D. E. Bunker, A. Hector, M. Loreau, and C. Perings, editors. *Biodiversity, ecosystem functioning, and human wellbeing: an ecologic and economic perspective*. Oxford University Press, Oxford, UK.
- Seastedt, T. R. 1984. The role of microarthropods in decomposition and mineralization processes. *Annual Review of Entomology* 29:25–46.
- Setälä, H., M. P. Berg, and T. H. Jones. 2005. Trophic structure and functional redundancy in soil communities. Pages 236–249 *in* R. D. Bardgett, M. B. Usher, and D. W. Hopkins, editors. *Biological diversity and function in soils*. Cambridge University Press, Cambridge, UK.
- Sheridan, J. A., and D. Bickford. 2011. Shrinking body size as an ecological response to climate change. *Nature Climate Change* 1:401–406.
- Siemann, E., D. Tilman, and J. Haarstad. 1999. Abundance, diversity and body size: patterns from a grassland arthropod community. *Journal of Animal Ecology* 68:824–835.
- Smith, J. J., S. T. Hasiotis, M. J. Kraus, and D. T. Woody. 2009. Transient dwarfism of soil fauna during the Paleocene-Eocene thermal maximum. *Proceedings of the National Academy of Sciences* 106:17655–17660.
- Smith, M. D., and A. K. Knapp. 2003. Dominant species maintain ecosystem function with non-random species loss. *Ecology Letters* 6:509–517.
- Solé, R. V., and J. M. Montoya. 2002. Complexity and fragility in ecological networks. *Proceedings of the Royal Society B* 268:2039–2045.
- Srivastava, D. S., B. J. Cardinale, A. L. Downing, J. E. Duffy, C. Jouseau, M. Sankaran, and J. P. Wright. 2009. Diversity has stronger top-down than bottom-up effects on decomposition. *Ecology* 90: 1073–1083.
- Strauß, A., E. Reeve, R.-G. Randrianiaina, M. Vences, and J. Glos. 2010. The world's richest tadpole communities show functional redundancy and low functional diversity: ecological data on Madagascar's stream-dwelling amphibian larvae. *BMC Ecology* 10:12.
- Swift, M. J., O. W. Heal, and J. M. Anderson. 1979. *Decomposition in terrestrial ecosystems*. Blackwell, Oxford, UK.
- Talbot, J. M., and K. K. Treseder. 2012. Interactions among lignin, cellulose, and nitrogen drive litter chemistry-decay relationships. *Ecology* 93:345–354.
- Thompson, R. M., et al. 2012. Food webs: reconciling the structure and function of biodiversity. *Trends in Ecology and Evolution* 27:689–697.
- Tilman, D., P. B. Reich, and J. M. H. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature* 441:629–632.
- Timms, L. L., J. J. Bowden, K. S. Summerville, and C. M. Buddle. 2013. Does species-level resolution matter? Taxonomic sufficiency in terrestrial arthropod biodiversity studies. *Insect Conservation and Diversity* 6:453–462.
- Triplehorn, C. A., and N. F. Jonson. 2005. *Borror and De Long's introduction to the study of insects*. Seventh edition. Thomson Brooks/Cole, Belmont, California, USA.
- Tuomisto, H., A. D. Poulsen, K. Ruokolainen, R. C. Moran, C. Quintana, J. Celi, and G. Cañas. 2003. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecological Applications* 13:352–371.
- Tylianakis, J. M., T. A. Rand, A. Kahmen, A. M. Klein, N. Buchmann, J. Perner, and T. Tschardtke. 2008. Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *PLOS Biology* 6:947–956.
- Valencia, R., R. B. Foster, V. Gorky, R. G. Condit, J. C. Svenning, C. Hernandez, K. Romoleroux, E. C. Losos, E. Magard, and H. Balslev. 2004. Tree species distributions and local habitat variation in the Amazon: large forest plot in eastern Ecuador. *Journal of Ecology* 92:214–229.
- Vasconcelos, H. L., and J. M. S. Vilhena. 2006. Species turnover and vertical partitioning of ant assemblages in the Brazilian Amazon: a comparison of forests and savannas. *Biotropica* 38:100–106.
- Vilicis, F., S. Szekeres, and E. Hornung. 2012. Size dependent differences in litter consumption of isopods: preliminary results. *ZooKeys* 176:247–259.
- Vos, V. C. A., J. van Ruijven, M. P. Berg, E. T. H. M. Peeters, and F. Berendse. 2013. Leaf litter quality drives litter mixing effects through complementary resource use among detritivores. *Oecologia* 173: 269–280.
- Wagg, C., S. F. Bender, F. Widmer, and M. G. A. van der Heijden. 2014. Soil biodiversity and soil community composition determine ecosystem multifunctionality. *Proceedings of the National Academy of Sciences* 111:5266–5270.

- Wall, D. H., R. D. Bardgett, and E. F. Kelly. 2010. Biodiversity in the dark. *Nature Geoscience* 3:297–298.
- Wall, D. H., et al. 2008. Global decomposition experiment shows soil animal impacts on decomposition are climate-dependent. *Global Change Biology* 14:2661–2677.
- Wall, D. H., and U. N. Nielsen. 2012. Biodiversity and ecosystem services: Is it the same below ground? *Nature Education Knowledge* 3:8.
- Wardle, D. A. 2006. The influence of biotic interactions on soil biodiversity. *Ecology Letters* 9:870–886.
- Wardle, D. A., A. Lagerström, and M. C. Nilsson. 2008. Context dependent effects of plant species and functional group loss on vegetation invasibility across an island area gradient. *Journal of Ecology* 96:1174–1186.
- White, E. P., S. K. Morgan Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. *Trends in Ecology and Evolution* 22:323–330.
- Wilson, E. O., and B. Hölldobler. 2005. Eusociality: origin and consequences. *Proceedings of the National Academy of Sciences* 102:13367–13371.
- Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. Body size in ecological networks. *Trends in Ecology and Evolution* 20:402–409.
- Yang, X., and J. Chen. 2009. Plant litter quality influences the contribution of soil fauna to litter decomposition in humid tropical forests, southwestern China. *Soil Biology and Biochemistry* 41: 910–918.
- Yang, X., Z. Yang, M. W. Warren, and J. Chen. 2012. Mechanical fragmentation enhances the contribution of Collembola to leaf litter decomposition. *European Journal of Soil Biology* 53:23–31.
- Zavaleta, E. S., and K. B. Hulvey. 2004. Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science* 306: 1175–1177.

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