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Litter fauna communities and litter decomposition in a selectively logged and an unmanaged pine-oak forest in Mexico

Comunidades de fauna y descomposición de la hojarasca en un bosque de pino-encino con tala selectiva y un bosque sin manejo en México

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SUMMARY

We analyzed the effect of selective logging on litter fauna parameters (abundance, richness and diversity) and litter decomposition (remaining dry mass) over time in a temperate pine-oak (*Pinus* spp.-*Quercus* spp.) forest in central México. An unmanaged and a managed forest were compared using a litter bag field experiment. Litter fauna was quantified to the levels of families and morphospecies. Litter fauna abundance, richness and diversity were higher in the unmanaged forest. The remaining dry mass of litter and the decomposition rates were statistically different between the two forests, suggesting that selective logging practices reduce decomposition processes. The remaining dry mass of litter was negatively correlated with fauna richness in the managed forest, and with both morphospecies richness and diversity at the unmanaged forest; indicating that as biodiversity increases, more litter might be decomposed. Both litter fauna diversity and the litter decay processes were better preserved in the unmanaged site, as compared with the selective logged forest. Our study reveals that leaving some pine-oak forest patches unmanaged is important for the protection of their biodiversity.

Key words: Mexican temperate forests, selective logging, soil fauna diversity, litter remaining dry mass.

RESUMEN

Se analizó el efecto del manejo silvícola en la abundancia, riqueza y diversidad de la fauna de invertebrados, así como en la tasa de descomposición de la hojarasca en un bosque templado de pino (*Pinus* spp.) y encino (*Quercus* spp.) del centro de México. Se comparó un bosque manejado (tala selectiva) y otro sin manejo, empleando un experimento de bolsas de malla plástica (*litterbags*). El bosque sin manejo tuvo mayor abundancia, riqueza y diversidad de morfoespecies de invertebrados que el bosque donde se aplicó tala selectiva. Se encontraron diferencias significativas en la hojarasca remanente y en la tasa de descomposición entre bosques: la hojarasca en el bosque sin manejo se descompuso más rápidamente que en el que se aplica tala selectiva. La hojarasca remanente correlacionó de forma negativa con la riqueza de invertebrados en el bosque manejado y con la riqueza y diversidad en el bosque sin manejo. Estos resultados indican que a mayor diversidad de fauna, más hojarasca puede descomponerse. El estudio muestra que las prácticas silviculturales pueden afectar los patrones de diversidad de invertebrados del suelo y los procesos de descomposición de los que forman parte. Se propone como medida de conservación dejar fragmentos de bosque sin manejo en localidades donde se aplica tala selectiva para mantener la diversidad y los procesos ecosistémicos en estos bosques templados.

Palabras clave: bosques templados mexicanos, tala selectiva, diversidad de fauna de suelo, peso seco remanente de hojarasca.

INTRODUCTION

Soil is one of the most important components in terrestrial ecosystems (Ashford *et al*. 2013). Many studies have evidenced that the fauna that inhabits soil and litter drive litter decomposition rates at global and biome scales (Yang *et al*. 2007, García-Palacios 2013). Litter decay is controlled by the composition of the decomposer communities (Moore *et al*. 1988) and by the diversity and abundance of soil fauna because it digests and breaks down litter, and also because it stimulates the activity of microorganisms (Maraun and Scheu 1996). Meso- and macrofauna are the biotic regulators of litter decomposition in the initial stages of the process. They cause chemical changes in litter compounds, which facilitate the leaching and mobilization of several nutrients, and increase the surface area for bacterial and fungal activities (Verhoef and Brussaard 1990, Couteaux *et al*. 1995). Litter decay has been positively linked with litter fauna (Hutchens and Wallace 2002). For example, large litter-feeding animals, along with litter species richness, determine rates of litter decomposition in a temperate forest ecosystem (Hättenschwiler and Gasser 2005). Despite the important roles of soil and litter fauna in ecosystem functioning, many ecological relations remain poorly understood (Ashford *et al*. 2013).

The structure of soil and litter fauna communities partially depends on the composition of plant communities, which determines litter composition (Ball *et al*. 2009). Hence, it is expected that changes in vegetation affect litter fauna communities, and in turn the processes of litter decomposition (Brown *et al*. 2001, Pietikäinen *et al*. 2003, Mayer *et al*. 2005, Negrete-Yankelevich *et al*. 2007). In temperate forests, litter manipulation changed the arthropod community composition (Osler *et al*. 2006).

Logging management can have short- and long-term impacts on the below-ground subsystem. In a Mexican cloud forest, Negrete-Yankelevich *et al*. (2007) reported that total macroinvertebrate abundance, taxa richness, diversity and the individual mean abundances of Chilopoda and Coleoptera larvae were lower in the litter of recently logged sites than in pristine sites. Thinning is a common forest management that removes surplus trees to concentrate timber production on a limited number of the best trees in the plantation, but the process of harvesting disturbs the litter layer. In a Douglas-fir forest both abundance and diversity of litter-dwelling arthropods decreased as thinning intensity increased (Yi and Moldenke 2008).

Pine-oak (*Pinus* spp.-*Quercus* spp.) temperate subhumid forests have enormous biological and economic importance in Mexico (Challenger 1998). The remaining areas of these forests are distributed over the mountain ranges. The country hosts between 50 and 70 pine species (Romeu 1995, 54 species according to the National Commission for the Knowledge and Use of Biodiversity, CONABIO), over 150 species of oak (Nixon 1993), and noteworthy numbers of endemic species of different biological groups associated with pine-oak forests. In spite of their biological value, pine-oak forests in Mexico are poorly protected, largely due to their economic value, soil fertility and climate. The major threats to these forests include timber extraction, clearing for agriculture and cattle grazing, fire and urbanization (Challenger and Dirzo 2009). More than 60 % of the Mexican pines have a commercial use, and more than 80% of pine and oak products are obtained by extraction from unmanaged forests. In order to develop sustainable forestry, alternative timber exploitation strategies have been implemented to slow down the rate of deforestation of Mexican temperate forests. In some areas of central Mexico selective tree logging is applied, which is supposed to be less aggressive to soil because only 10% of trees are harvested. Vigorous healthy trees are left standing as seed sources, providing a continuous arboreal stratum, allowing the maintenance of radiation and humidity more similar to those occurring in natural forests without wood extraction. Moreover, contrary to the common assumption that biodiversity loss results from human activities, selective logging has been found to increase the abundance, richness and diversity of litter fauna, as compared to that of unmanaged Mexican pine-oak forests (Moreno *et al*. 2008).

In order to test the hypothesis that selectively logged forests have higher litter fauna diversity generating a more efficient litter decomposition process than in unmanaged forests, in this paper we compare managed and unmanaged areas in terms of: a) meso- and macrofauna morphospecies abundance, richness and diversity; b) litter decomposition, measured as total remaining dry mass and decay rates; and c) the relationships between litter fauna parameters (abundance, richness and diversity) and litter decomposition (remaining dry mass) over time. We predict that: (1) managed areas will contain higher values of litter fauna abundance, richness and diversity than those found in unmanaged areas, as found using the direct search method for litter fauna in the same area (Moreno *et al*. 2008); (2) consequently, decomposition rates will also be higher in the managed stand than in the unmanaged forest; and 3) litter decay will be correlated with the abundance, richness and diversity of litter fauna only in the initial stages of the decomposition process.

METHODS

Study site. The study was carried out in a private property called “Rancho Santa Elena”, located in the state of Hidalgo, Mexico (between 20°06’07” and 20°09’50” N, and 98°30’04’’and 98°32’06’’ W). Climate is temperate-semi humid with cold winters. The monthly average temperature is 15.1 °C, with January and May the coldest and warmest months (12.1 and 18.0 °C, respectively). Total annual rainfall is 787.6 mm, with December and September the driest and wettest months (11.2 and 148.3 mm, respectively). The main vegetation type are pine-oak forest, and the dominant species are *Pinus teocote* Schltdl. *et* Cham., *P. patula* Schiede *et* Deppe, *P. montezumae* Lamb., *Quercus laurina* Humb. *et* Bonpl., *Q. crassifolia* Humb. *et* Bonpl. and *Q. rugosa* Née.

Most of the total area of the property (944 ha; 90 %) is covered by pine-oak forest, 89 ha are used for agriculture or cattle ranching activities, and the remaining 11 ha are covered by water bodies. Four hundred and twenty ha of the forest is currently used for timber extraction, 305 ha include areas recovering from fire and stands that are being reforested, and the remaining 219 ha have been set aside for nature conservation with eco-tourism activities, camping and countryside biking.

Our experiment was set in a 25 ha forest fragment subject to selective logging (managed forest) and in a 28 ha area of forest conservation (unmanaged forest). Both areas have the same topographical conditions and type of soil. No fires have been recorded for at least 40 years. In the managed area, thinning is carried out with the removal of 10 % of the trees. There has been no tree extraction in the unmanaged area over the last 40 years. The two forests are 400 m apart.

Litter bag experiment. This study was conducted using a litter bag experiment. First, in order to represent the mixture of leaf species in the same proportion as their representation in natural litterfall at each forest, we calculated the proportion of pine and oak leaves in litter within 10 plots measuring 50 x 50 cm at each forest. A sample of 150 leaves of each species was measured. Afterward, we filled litter bags with 20 g (fresh weight) of recently fallen pine and oak leaves. In the managed forest we set up 14 g of oak leaves and 6 g of pine needles, and in the unmanaged forest site we used 10 g of each species, as those were their natural proportions at each site. Oak leaves used for the experiment varied from 5 to 9 cm in length, and pine needles had an almost uniform size of ca. 8 cm. We took care to choose only leaves with no parasites or fungi.

Plastic litter bags (20 x 20 cm) were of large (6 mm) and small (1 mm) mesh sizes. Eighty litter bags of each mesh size were placed and secured to the soil with a nylon cord at each forest (160 per forest type), separated from each other by at least 20 m. The experiment lasted 315 days. Over that time, we collected litter bags on 16 sampling times. The first eleven samples were taken every 15 days, and the last five every month. On each sampling occasion, we randomly selected and retrieved five litter bags of each mesh size in both the managed and the unmanaged forests. However, in order to simplify the main objective of this paper, we will not include mesh size as a factor in our analyses. Thus, we will focus on the comparison between areas using a total of 10 litter bags retrieved each sampling occasion. The collected bags were labeled and placed in hermetic plastic bags for transportation.

Litter fauna collection and data analyses. We directly searched for meso-fauna (0.2 to 10 mm length) and macrofauna (over 10 mm length) in each litter bag sample. In addition, the leaves were washed with alcohol and cleaned manually with brushes to remove all the organisms. We made permanent plates for collembols and acarids. All litter fauna was preserved in 70 % alcohol and identified into family and morphospecies (larvae and other immature stages were also included as morphospecies in analyses). We separated morphospecies considering adults and larvae with the help of a taxonomist that kindly checked the specimens; see acknowledgments. The use of morphospecies as a surrogate for taxonomic species has been successfully used to describe biodiversity and some ecological patterns in highly diverse communities (Krell 2004).

In each forest, we quantified abundance as the number of individuals found, richness as the number of litter fauna morphospecies, and diversity as the effective number of morphospecies, calculated with the formula of true diversity of order 1 (Jost 2006), which equals the exponential of the Shannon entropy index.

To compare cumulative morphospecies richness between forests, we plotted rarefaction curves with standard errors, using the Species Diversity and Richness III v. 3.02 software (Henderson and Seaby 2002). A generalized linear model (GLM) was used to detect differences in abundance of morphospecies between sites and sampling time. We used Poisson error distribution to construct the model and checked for over-dispersion of the data (Crawley, 2007). GLM was carried out using R 6.1. (Crawley 2007, R Development Core Team 2012). We also compared the number of families between sites of three orders (Acari, Araneae and Coleoptera) that have the highest number of families using Mann-Whitney test.

Litter decomposition. We determined initial leaf litter dry mass using ten randomly selected samples from each site, dried in an oven at 90 °C for 48 h to a constant weight. Subsequently, litter decomposition was assessed for each time period by measuring the dry weight of oven-dried litter bag leaves after the extraction of fauna. The remaining dry mass was expressed as percentage of the initial sample dry mass (Martínez-Yrízar *et al*. 2007). Remaining dry mass values were transformed into square roots (Zar 1999) to determine differences in leaf decomposition between sites and among sampling times, using a multifactor analysis of variance. The relationships between remaining litter mass and time (days) were tested by fitting it to negative exponential decomposition models (Martínez-Yrízar *et al*. 2007, Adair *et al*. 2010). Total decay rate (*k*-value) for each forest was calculated by the negative exponential regression of $\ln(X_0/X_1)$ vs. time, where X_0 is the original dry mass, X_1 is the percentage of leaf litter remaining after time 1 (time in days). We used analyses of covariance (ANCOVA) to compare differences among decomposition rates, in decay constants, testing the assumption of equal slopes (i.e., testing for a significant interaction between sites with time, when time is used as a covariate). All leaf litter analyses were performed with the statistical program G-Stat (Letón and Pedromingo 2004).

Relationships between litter fauna and decomposition. Relationships between fauna abundance and remaining percentage of dry mass of litter were tested with Pearson correlations for each forest over the first 120, 165 and 315 days in order to detect if these relationships occur at different stages in the decomposition process. The same procedure was done with morphospecies richness and diversity data, using the Sigma Stat program (Systat 2006).

RESULTS

Litter fauna communities. We recorded 3,702 individuals of meso- and macrofauna belonging to 197 morphospecies and 60 families (appendix 1). In the managed forest the ant *Iridomyrmex* sp. was the most abundant, followed by *Zygoribatula* sp. and the acarid *Haplozetidae* sp. In the unmanaged forest, *Zygoribatula* sp. and *Haplozetidae* sp. dominated the community, while ants were much lower in abundance. Araneae, Acari and Coleoptera presented the highest numbers of families.

Total abundance was moderately higher in the managed than in the unmanaged forest (1,983 and 1,719 individuals, respectively). However, cumulative morphospecies richness was higher in the unmanaged forest (151 morphospecies) than in the managed forest (118 morphospecies). Rarefaction curves (figure 1) show that this difference prevailed even when both forests were compared at a standardized size of 1,700 insects: richness was higher in the unmanaged than in the managed forest, 150 and 110 morphospecies, respectively. We found the same pattern when we compared diversity taking into account species frequencies, though the difference was even higher: diversity was more than two times higher in the unmanaged forest (25.68 effective species) than in the managed one (12.29 effective species, figure 1).

Morphospecies abundance, richness, and diversity varied among sampling occasions (figure 2), with low values at the beginning and at the end of the study. Abundance was very high in the managed forest on two occasions: day 105 (349 individuals) and day 285 (638 individuals). As observed with the cumulative richness and diversity values, in most of the sampling occasions, morphospecies abundance, richness and diversity were higher in the unmanaged than in the managed forest (figure 2). The abundance of morphospecies differed significantly between habitats (x^2 = 26.37, $P < 0.001$) and in time (x^2 = 135, $P < 0.001$). We detected differences in the number of families of Acari between sites (U = 24878.50, $P < 0.001$), though not in the number of Araneae (U = 27655, P = 0.98) and Coleoptera (U = 28037, P = 0.56) families.

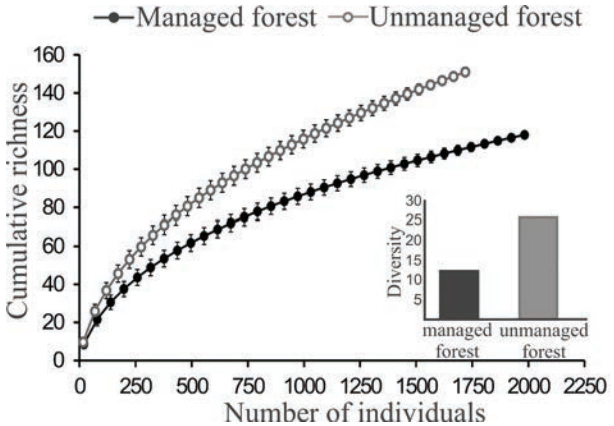

Figure 1. Rarefaction curves of litter fauna morphospecies richness for managed and unmanaged pine-oak temperate forests in central Mexico. The inner graphs show the morphospecies diversity (effective number of morphospecies) for these communities.

Curvas de rarefacción para la riqueza de morfoespecies de fauna de hojarasca en bosques templados con y sin manejo forestal en el centro de México. Las figuras internas muestran la diversidad de morfoespecies (número efectivo de morfoespecies) para estas comunidades.

Litter decomposition. A major proportion of the litter was decomposed in the unmanaged forest, given that in most sampling occasions the remaining litter dry mass was higher in the managed that in the unmanaged forest (figure 3). The remaining dry mass of litter was statistically different between the two forests ($F_{1,328}$ = 23.28, $P < 0.001$), and sampling occasions ($F_{16,328}$ = 20.96, $P < 0.0001$). The interaction between forest type and time was also significant ($F_{16,328}$ = 1.90, P = 0.02).

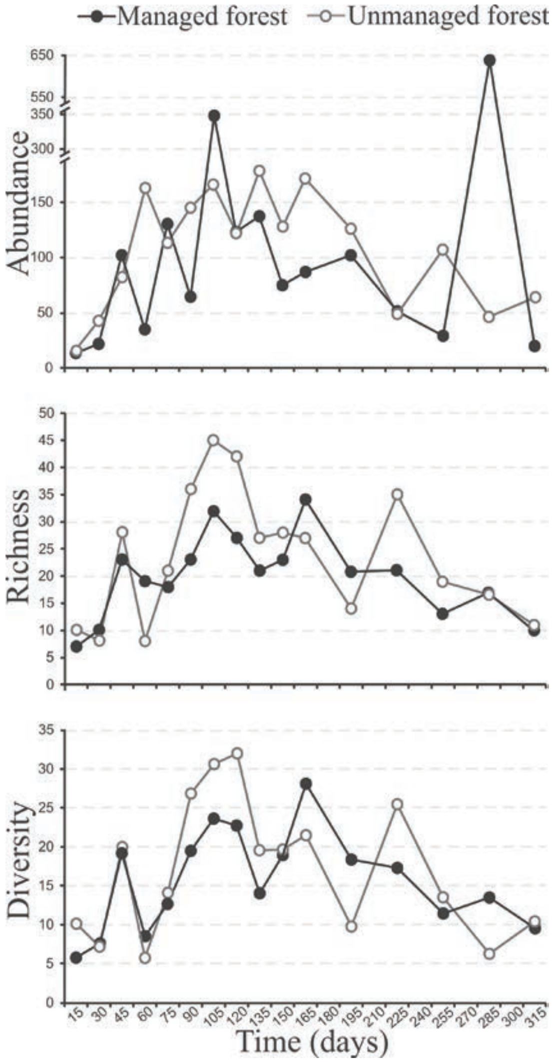

Figure 2. Abundance, morphospecies richness and diversity of litter fauna over the first 315 days of decomposition in plastic litterbags (total cumulative values from 10 litterbags retrieved each sampling occasion), in pine-oak temperate forests.

Abundancia, riqueza y diversidad de morfoespecies de fauna de hojarasca durante los primero 315 días de descomposición en bolsas de malla plástica (valores totales acumulados para 10 bolsas recolectadas cada ocasión de muestreo) en bosques templados de pino-encino.

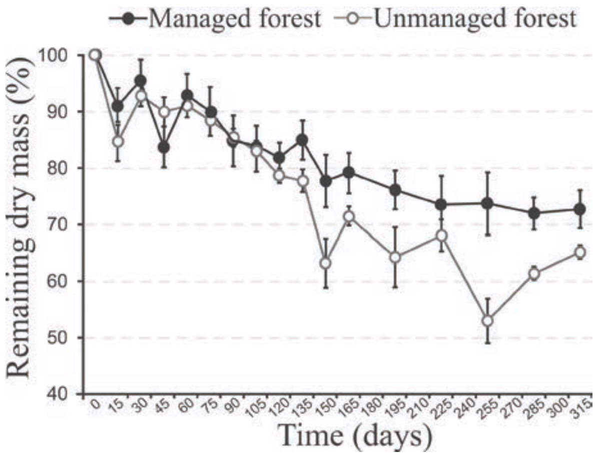

Figure 3. Remaining dry mass (percentage of original mass) in the decomposition of *Pinus* and *Quercus* leaves over time for managed and unmanaged pine-oak temperate forests.

Peso seco remanente de la hojarasca (porcentaje del peso original) en la descomposición de hojas de *Pinus* y *Quercus* a través del tiempo en bosques templados de pino-encino con y sin manejo forestal.

Moreover, the velocity of the decomposition process was higher in the unmanaged than in the managed forest: total decomposition rate was 0.0018 g per day in the unmanaged forest (negative exponential model: $F_{1,162} = 232.85$, $P < 0.001$), and 0.0014 g per day in the selective managed forest ($F_{1,162} = 66.25$, $P < 0.001$). The ANCOVA detected significant differences in decay rates between the two forests ($F = 248.08$, $P < 0.001$), with a faster litter decomposition in the unmanaged forest than in the managed one.

Relationships between litter fauna and litter decomposition. As expected, there were statistically significant correlations between litter fauna community parameters and the decomposition process only for the first sampling occasions. When we used data from the first eight sampling occasions (first 120 days of the experiment), the remaining dry mass of litter was negatively correlated with fauna richness in the managed forest, and with both morphospecies richness and diversity in the unmanaged forest (table 1). When we repeated the analysis for the first 165 days, fauna richness and diversity in the managed site were also negatively correlated with the remaining dry mass (table 1). We did not find statistically significant correlations between community parameters and the decomposition process when the complete datasets covering 315 days were taken into account in the analysis (figure 3; table 1).

DISCUSSION

Forest management generates perturbations in soil conditions that alter the structure of soil fauna communities. In spite of the potential conservation benefits derived from selective logging, which include the permanence of an arboreal stratum where other forestry practices would leave clear areas, our results show that the unmanaged forest preserves a richer and more diverse community of litter fauna. Unmanaged areas were left as conservation zones and have not been subjected to forestry or any other exploitation of natural resources, and our results confirm the success of management practices in the area, which include the protection of remnant stands as reservoirs of biodiversity. In contrast, timber extraction has modified litter

Table 1. Pearson correlation analysis of the litter fauna community and the percentage of litter remaining (dry mass), over the first 120 (n = 8), 165 (n = 11), and 315 days (n = 16) of the decomposition process in litterbags. * = $P < 0.05$; ns = non significant results.

Correlaciones de Pearson entre las comunidades de fauna de hojarasca y el porcentaje de hojarasca remanente (peso seco), durante los primeros 120 (n = 8), 165 (n = 11), y 315 días (n = 16) del proceso de descomposición en bolsas de malla plástica. * = $P < 0{,}05$; ns = no significativo.

	Managed forest	Unmanaged forest
First 120 days		
Abundance	$R = -0.587$, $P = 0.126$ ns	$R = -0.227$, $P = 0.589$ ns
Richness	$R = -0.821$, $P = 0.012$ *	$R = -0.727$, $P = 0.041$ *
Diversity	$R = -0.480$, $P = 0.229$ ns	$R = -0.730$, $P = 0.039$ *
First 165 days		
Abundance	$R = -0.367$, $P = 0.267$ ns	$R = -0.389$, $P = 0.238$ ns
Richness	$R = -0.786$, $P = 0.004$ *	$R = -0.399$, $P = 0.225$ ns
Diversity	$R = -0.607$, $P = 0.047$ *	$R = -0.586$, $P = 0.058$ ns
First 315 days		
Abundance	$R = -0.271$, $P = 0.310$ ns	$R = 0.068$, $P = 0.801$ ns
Richness	$R = -0.156$, $P = 0.564$ ns	$R = 0.013$, $P = 0.962$ ns
Diversity	$R = -0.339$, $P = 0.199$ ns	$R = 0.072$, $P = 0.791$ ns

composition and has decreased the richness and diversity of morphospecies. In the managed forest the disturbance of litter may affect soil moisture, by increasing evaporation as a result of more solar radiation an air movement (Yi and Moldenke 2008). Temperature is another factor that may be altered by selective harvesting (Negrete-Yankelevich *et al*. 2007). Unfortunately we do not have fine measures of abiotic factors to explore further relationships between these parameters and the litter fauna communities.

Besides leaving unmanaged patches for nature conservation, some strategies such as leaving residues from logging in the field may also promote a higher biodiversity and activity of litter fauna communities. Also, future studies with a landscape perspective would be required in order to explore the influence of landscape composition and configuration in both litter fauna and ecosystem processes. For example, studies designed to assess the influence of patch size, or the spatial arrangement of landscape components that combine logging and conservation purposes. Such a landscape approach may allow for a better understanding of the role of remnant stands as reservoirs of biodiversity in central Mexico, where this type of practice is common in private ranches, and represent a real conservation scenario, at least for certain groups. Mature forest patches are left for lot of reasons, one of them is because they are inaccessible. Most of the Mexican territory does not have a protection status; hence the conservation outside reserves or parks is highly important and valued for preserving forests. There are several pressures for the conservation of temperate forests in central Mexico, thus the results of this research constitute a novel step in exploring how logging practices affect the litter fauna and ecosystem processes.

Another research line for future prospect is the relationship between the taxonomical diversity and the ecological role they carry out. A fine analysis of functional traits of litter fauna would be needed to examine their potential implications in the ecosystem functioning. In order to accomplish this task, a careful revision of morphological and behavioral traits is needed, because the approach based on broad guilds may not be helpful to study the biodiversity-functioning relationship and its impact of ecosystem benefits.

The ant *Iridomyrmex* sp. was abundant principally in the managed forest. Ants have been reported as a dominant order in different ecosystems; for example, in a lowland tropical rainforest 29 % from of total individuals (2496) were ants (Ashford *et al*. 2013), and in a Mexican cloud forest ants represented 16.3 % of soil fauna (Negrete-Yankelevich *et al*. 2007). Ants were not dominant in the unmanaged forest probably because they prefer open areas and this mature forest has less open areas than the managed one. Also, these ants are considered highly aggressive and invaders, consequently forest management may promote their abundance. In the unmanaged forest *Haplozetidae* sp. was abundant, and mites (Acari) contribute to decomposition and nutrient cycling processes because of their interactions with the microbial community (Moore *et al*. 1988, Lindo and Winchester 2007).

In the same study area, Moreno *et al*. (2008) found a high soil fauna diversity in the managed forest. They used different sampling methods to study the litter fauna communities, including pitfall traps, Winkler funnels and direct searching. In their direct searching results, selectively logged areas presented higher richness and diversity than that observed in unmanaged areas. Such different results might be caused by temporal variations in environmental conditions, and thus in community structure. Litter fauna communities may vary notably in time: the samples of Moreno *et al*. (2008) differ from ours; taken 1.5 years later at the same site, and varied between the rainy and the dry seasons. Here we show variations through the first 315 days in the litter decomposition process, with less diverse communities at the beginning and at the end of this period. This coincides with the findings of Oliver (1981), who reported higher faunal diversity before the final stages of succession. As litter decays, the litter community undergoes succession from microbes to invertebrates, because the former make the substrate more palatable to arthropods (Wall and Moore 1999), and after that, other biochemical processes can decompose the litter more rapidly than do invertebrates.

Resembling their diverse faunal communities, both the decomposition rate and the percentage of decomposed litter were higher in the unmanaged forest than in the selectively logged site. Thus, if we compare the two types of forests, our results may point toward the hypothesis that ecological processes such as litter decomposition are more effective and rapid in highly diverse ecosystems than in less diverse ones. Also, abiotic factors such as leaching and photodegradation by exposure to ultraviolet radiation are recognized as important forces that account for a significant part of litter decomposition (Brandt *et al*. 2007). Thus, the factors affecting litter degradation in this temperate forest can be viewed as a sequence of filters likely including some degree of litter fauna diversity, the presence of certain idiosyncratic species, consumer-resource interactions and abiotic factors that limit and promote the decomposition process.

The rates of litter decomposition in our study sites are lower than the rate of 0.0044 g per day reported by Coleman *et al*. (2004) for temperate sites. Gholz *et al*. (2000) estimated that *k* values of litter decomposition rate ranged from 0.032 to 3.734, from arctic tundra to tropical rainforest after 5 years. However, we must be aware that the complete decay process of litter in this pine-oak forest was not revealed in our study because 73 and 65 % of the original mass remained at the end of 135 days (for the managed and the unmanaged forests, respectively). Longer term studies, recording mass loss over several months, will be needed to elucidate later stages of the litter decomposition process in these temperate ecosystems.

According to our prediction, litter meso- and macrofauna richness and diversity were correlated with the amount of decomposed litter only in the initial stages of the process, but not over the entire study. Meso- and macrofauna perform important roles as soil engineers because of their influence on soil and litter physical and chemical properties, including the creation of macropores, litter chewing, transformation and distribution of organic matter (Bignell *et al*. 2012). Therefore, during the first sampling occasions morphospecies richness and diversity increased while litter mass began to decay. Then, as meso- and macrofauna activity facilitates the establishment of bacteria and fungi, microbiota continues the processes of nutrient leaching and mobilization (Couteaux *et al*. 1995). As a degenerative succession, biodiversity decreased in the last steps, and this may explain the absence of significant correlations between meso- and macrofauna and the remaining dry mass of litter when we used data from the entire study.

The permanent protection of well conserved forest patches of this highly diverse ecosystem should be a target for conservation planning at the landscape level, especially because the natural distribution of pine-oak forests in Mexico coincides with high densities of human populations which pressure these systems with their ever increasing land requirements.

When studying the relationship between biodiversity and ecosystem functions, diversity is considered a driver of ecosystem processes, and a main objective of many research agendas is to understand the consequences of diversity changes in ecosystems. Human related disturbances supposedly decrease biodiversity, which in turn is supposed to negatively impact ecosystem processes, although there is still considerable debate on the magnitude and scope of this impact (Carpenter *et al*. 2009, Perrings *et al*. 2011). We support the idea that litter fauna is related to litter decomposition at the initial phase of the process. However, experimental studies are required to directly test the influence of biodiversity on this ecosystem process, and whether different forest management practices affect the system. Also, further research into both litter fauna communities and litter decomposition processes in pine-oak forests should explore the importance of variables such as litter quality and composition, plant biodiversity, the intensity of timber extraction and other external factors such as climate.

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Appendix 1. Abundance of litter fauna morphospecies in logged and unlogged areas of a pine-oak forest in México.

Abundancia de morfoespecies de fauna del mantillo en áreas explotadas y no explotadas de un bosque de pino-encino en México.

Class	Order	Family	Morphospecies	Logged	Unlogged
Arachnida	Acari	Bdellidae	*Bdella longicornis*	26	15
		Camisidae	*Camisia* sp.1	0	2
		Damaedidae	Damaeidae sp. 1	0	1
			Epidamaeus sp.1	0	4
		Dermanyssoidea	*Laelaspis* sp.1	0	1
		Erythraeidae	Erythraeidae sp. 1	0	1
		Haplozetidae	Haplozetidae sp. 1	137	363
		Nothridae	*Nothrus discifer*	1	0
		Opiidae	Oppiidae sp. 1	6	30
		Oribatulidae	*Zygoribatula* sp.1	201	461
		Phthricaridae	Phthricaridae sp. 1	9	4
		Phytoseiidae	*Amblyseus sp.1*	0	1
		Rhodacaridae	*Gamasellus* sp. 1	0	1
		Trhypochthoniidae	*Thrypochthonius* sp.1	5	1
			Mesostigmata (suborden) sp. 1	0	1
	Araneae		Araneae sp. 1	3	18
		Agelenidae	*Agelenopsis* sp. 1	1	0
		Anyphaenidae	Anyphaenidae sp. 1	21	28
		Araneidae	Araneidae sp. 1	0	1
		Clubionidae	*Clubiona* sp.1	1	0
		Erigonidae	Erigonidae sp. 1	0	2
		Gnaphosidae	Gnaphosidae sp. 1	4	0
		Hahniidae	Hahniidae sp. 1	3	1
		Linyphiidae	*Lepthyphantes* sp.1	0	5
			Lyniphidae sp. 1	0	1
			Lyniphidae sp. 2	0	1
		Liocranidae	*Scotinella sp.* 1	15	8
		Lycosidae	Lycosidae sp. 1	2	0
		Philodromidae	Philodromidae sp. 1	1	0
		Salticidae	Salticidae sp. 1	2	3
		Theridiidae	Theridiidae sp. 1	3	5
			Theridiidae sp. 2	0	2
			Theridiidae sp. 3	0	1
			Theridiidae sp. 4	0	1
			Theridiidae sp. 5	0	1
		Thomisidae	Thomisidae sp. 1	8	1
			Thomisidae sp. 2	1	0
	Opilionida	Phalangidae	Phalangidae sp. 1	0	3
			Phalangidae sp. 2	1	0
			Phalangidae sp. 3	0	1

Continue

Appendix 1 Continued

Class	Order	Family	Morphospecies	Logged	Unlogged
			Phalangidae sp. 4	0	2
			Laniatore sp. 1	0	1
	Pseudoscorpionida		Pseudoscorpionida sp. 1	3	0
			Pseudoscorpionida sp. 2	4	0
			Pseudoscorpionida sp. 3	1	0
Chilopoda	Geophilomorpha		Geophilomorpha sp. 1	1	3
			Geophilomorpha sp. 2	0	1
			Geophilomorpha sp. 3	1	0
	Lithobiomorpha	Lithobiidae	Lithobiidae sp. 1	65	71
			Lithobiidae sp. 2	38	31
			Lithobiidae sp. 3	0	1
			Lithobiidae sp. 4	2	1
Diplopoda	Julida		Julida sp. 1	8	5
			Julida sp. 2	2	1
			Julida sp. 3	2	1
			Julida sp. 4	1	1
	Platydesmida		Platydesmida sp. 1	0	2
			Platydesmida sp. 2	0	1
	Polydesmida		Polydesmida sp. 1	0	4
			Polydesmida sp. 2	0	1
	Polyxenida		Polyxenida sp. 1	1	6
			Polyxenida sp. 2	0	1
	Siphonophorida		Siphonophorida sp. 1	0	1
			Siphonophorida sp. 2	0	1
	Spirobolida		Spirobolida sp. 1	0	1
	Stemmiulida		Stemmiulida sp. 1	1	0
Hexapoda (superclase)	Collembola	Entomobryidae	*Americabrya* sp. 1	1	0
			Entomobrya sp. 1	19	51
			Entomobrya sp. 2	26	25
			Entomobrya sp. 3	5	10
			Lepidocyrtus sp. 1	6	5
			Orchesella sp. 1	4	9
			Pseudosinella sp. 1	8	3
			Seira sp. 1	15	37
			Willowsia sp. 1	4	6
		Neanuridae	Neanuridae sp. 1	0	3
		Sminthuridae	Sminthuridae sp. 1	0	3
		Tomoceridae	*Tomocerus* sp. 1	35	10
	Zygentoma		Zygentoma sp. 1	0	1
Insecta	Blattodea	Blattidae	Blattidae sp. 1	34	29
	Coleoptera		Coleoptera sp. 1	1	0

Continue

Appendix 1 Continued

Class	Order	Family	Morphospecies	Logged	Unlogged
			Coleoptera sp. 2	0	1
			Coleoptera sp. 3	0	7
			Coleoptera sp. 4	1	0
			Coleoptera sp. 5	1	0
			Coleoptera sp. 6	1	0
			Coleoptera sp. 7	1	1
			Coleoptera sp. 8	0	1
			L. Coleoptera sp. 1	1	1
			L. Coleoptera sp. 2	0	5
			L. Coleoptera sp. 3	2	0
			L. Coleoptera sp. 4	1	0
			L. Coleoptera sp. 5	1	7
			L. Coleoptera sp. 6	1	1
			L. Coleoptera sp. 7	1	0
		Brentidae	Apioninae (Subfamilia) sp. 1	2	2
		Cantharidae	Cantharidae sp. 1	0	1
		Cerylonidae	Cerylonidae sp. 1	5	9
			Cerylonidae sp. 2	3	5
			L. Cerylonidae sp. 1	44	2
		Chrysomelidae	Chrysomelidae sp. 1	0	1
			Chrysomelidae sp. 2	0	1
		Corylophidae	Corylophidae sp. 1	1	0
		Curculionidae	Curculionidae sp. 1	0	1
			Curculionidae sp. 2	0	1
			Curculionidae sp. 3	5	0
			Curculionidae sp. 4	0	2
			Curculionidae sp. 5	0	1
			Curculionidae sp. 6	1	0
			Curculionidae sp. 7	0	1
		Nitidulidae	Nitidulidae sp. 1	0	2
			Nitidulidae sp. 2	0	1
			Nitidulidae sp. 3	0	6
			Nitidulidae sp. 4	1	0
		Ptilidae	Ptilidae sp. 1	2	1
		Scolytidae	Scolytidae sp. 1	0	8
		Scydmaenidae	Scydmaenidae sp. 1	3	17
		Staphylinidae	Staphylinidae sp. 1	0	1
			Staphylinidae sp. 2	0	1
			Pselaphinae (subfamilia) sp. 1	1	5
			Sepedophilus sp. 1	2	0
			Paederinae (subfamilia) sp. 1	1	1

Continue

Appendix 1 Continued

Class	Order	Family	Morphospecies	Logged	Unlogged
			Philontus hoegei	1	0
			Heterothops sp. 1	2	0
			Trichophya sp. 1	0	2
			Xantholinini (tribu) sp. 1	0	1
			Aleocharinae (subfamilia) sp. 1	0	2
			Aleocharinae (subfamilia) sp. 2	0	2
			L. Staphylinidae sp. 1	1	0
	Dermaptera		Dermaptera sp. 1	1	0
			L. Desconocida sp. 1	0	1
			L. Desconocida sp. 2	0	1
			L. Desconocida sp. 3	2	2
			Pupa desconocida sp. 1	0	1
	Diptera		Diptera sp. 1	1	1
			Diptera sp. 2	0	1
			Diptera sp. 3	0	1
			Diptera sp. 4	0	1
			L. Diptera sp. 1	6	2
			L. Diptera sp. 2	2	13
			L. Diptera sp. 3	1	0
			L. Diptera sp. 4	2	1
	Hemiptera		Hemiptera sp. 1	0	1
			Hemiptera sp. 2	2	0
			Hemiptera sp. 3	0	1
		Achilidae	Achilidae sp. 1	1	0
		Anthocaridae	Anthocaridae sp. 1	0	2
			Anthocaridae sp. 2	13	0
		Aphididae	Aphididae sp. 1	2	0
			Aphididae sp. 2	2	0
			Aphididae sp. 3	0	7
		Cicadellidae	Cicadeliidae sp. 1	0	1
		Largidae	Largidae sp. 1	0	1
		Lygaeidae	Lygaeidae sp. 1	12	4
			Lygaeidae sp. 2	5	1
			Lygaeidae sp. 3	1	1
			Lygaeidae sp. 4	3	0
		Reduvidae	Emesinae (subfamilia) sp. 1	1	10
			Reduvidae sp. 1	1	3
			Reduvidae sp. 2	7	1
			Reduvidae sp. 3	1	0
	Hymenoptera	Chalcidoidea (superfamilia)	Chalcidoidea sp. 1	1	0
		Braconidae	Braconidae sp. 1	1	1

Continue

Class	Order	Family	Morphospecies	Logged	Unlogged
			Braconidae sp. 2	0	2
			Braconidae sp. 3	1	0
			Braconidae sp. 4	0	1
		Eulophidae	Eulophidae sp. 1	0	1
		Formicidae	*Iridomyrmex* sp. 1	998	1
			Iridomyrmex sp. 2	0	1
			Lepthothorax sp. 1	1	3
			Lepthothorax sp. 2	6	0
		Mymaridae	Mymaridae sp. 1	0	9
			Mymaridae sp. 2	1	0
		Pteromalidae	Pteromalidae sp. 1	4	2
			Pteromalidae sp. 2	1	0
	Lepidoptera		Lepidoptera sp. 1	0	1
			Lepidoptera sp. 2	0	1
			L. Lepidoptera sp. 1	5	9
			L. Lepidoptera sp. 2	0	3
			L. Lepidoptera sp. 3	1	0
			L. Lepidoptera sp. 4	2	0
			L. Lepidoptera sp. 5	1	11
	Neuroptera		L. Neuroptera sp. 1	0	6
	Orthoptera	Nemobiinae	Nemobiinae (subfamilia) sp. 1	6	1
	Psocoptera		Psocoptera sp. 1	7	37
			Psocoptera sp. 2	21	35
			Psocoptera sp. 3	10	9
			Psocoptera sp. 4	0	2
			Psocoptera sp. 5	1	5
			Psocoptera sp. 6	2	10
			Psocoptera sp. 7	1	1
			Psocoptera sp. 8	0	1
	Thysanoptera		Thysanoptera sp. 1	1	6
			Thysanoptera sp. 2	4	5
			Thysanoptera sp. 3	1	0
Malacostraca	Isopoda	Armadillidae	Armadillidae sp. 1	1	1
Oligochaeta	Haplotaxida	Lumbricidae	Lumbricidae sp. 1	14	97
Total				1,983	1,719