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REGULAR ARTICLE

Species-specific characteristics of trees can determine the litter macroinvertebrate community and decomposition process below their canopies

Simoneta Negrete-Yankelevich · Carlos Fragoso ·
Adrian C. Newton · Graham Russell ·
O. William Heal

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Abstract This paper tests whether individual trees in a mature forest stand influence the process of litter decomposition and the macroinvertebrate communities in the soil underneath their canopies, as a result of species-specific characteristics. A field decomposition experiment was performed in a mature forest stand of tropical montane cloud forest in Mexico. The areas under the canopies of *Quercus laurina* Humbl. & Bompl., *Oreopanax xalapensis* (Kunth) Decne. & Planchon and *Beilschmedia ovalis* (Blake) C. K. Allen trees were used as experimental units. The natural soil and litter macroinvertebrate communities were monitored and compared to the community that invaded decomposition boxes with reciprocally transplanted leaf litter. The abundances of four macroinvertebrate taxa in natural litter differed among tree species independently of season. No differences were found in the soil community. The response to experimental litter by macroinvertebrate taxa suggests that the production of a specific quality of litter is an important mechanism by which a tree influences the litter macroinvertebrate community that develops under its canopy. However, not all differences in community composition naturally found between tree species can be explained by differences in litter quality during the first year of decomposition. Differences in nutrient release that occur after the first year, and physical properties of litter also probably play an important role. Independently of the canopy tree, the initial chemical quality (N, P, Ca, Mg and lignin) of experimental litter largely determined the decomposition rate and nutrient dynamics of decomposing leaves. However, it was found that under *O. xalapensis* trees the breakdown of lignin from the litter produced by the same species of tree was particularly effective. This suggests that a feedback has developed between this tree species and the decomposer community prevailing under its canopy.

Keywords Above-belowground relationship · Litter quality · Macrofauna · Nutrients · Single-tree influence circles · Tropical mountain cloud forest

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S. Negrete-Yankelevich (✉) · C. Fragoso
Departamento de Biología de Suelos,
Instituto de Ecología A.C.,
Apartado postal 63, Congregación El Haya,
91070 Xalapa, Veracruz, Mexico
e-mail: simoneta.negrete@inecol.edu.mx

S. Negrete-Yankelevich · G. Russell
School of Geosciences, University of Edinburgh,
Crew Building, The King's Buildings, West Mains Road,
Edinburgh EH9 3JN, UK

A. C. Newton
School of Conservation Sciences, Bournemouth University,
Talbot Campus,
Poole, Dorset BH12 5BB, UK

O. W. Heal
Department of Biological Sciences, University of Durham,
Durham DH1 3LE, UK

Introduction

The concept of “single-tree influence circles” was first used by Zinke (1962) to describe a mosaic of soil profiles that are spatially associated with individual trees. The influence of individual trees on soil biochemistry has scarcely been studied in mixed forests and only in temperate areas (Ayres et al. 2006; Dijkstra 2003; Turner and Franz 1985). However the mechanisms by which particular plant species create distinct chemical environments in the soil, resulting in bottom-up control of the decomposer food-web, have been demonstrated in a variety of field, laboratory and greenhouse settings (Bardgett et al. 1999; Wardle et al. 2003; Warren and Zou 2002). Below-ground, the roots of different plant species may produce different quantities of litter and release diverse sources of labile-C and molecular signals that promote distinct micro-organism community assemblages and patterns of nutrient cycling (Guevara and Romero 2007; Kourtev et al. 2002). Plants may also demonstrate differing capacities for nutrient uptake, which may induce changes in the community composition of microorganisms (Kaye and Hart 1997). Above-ground, neighbouring tree canopies can generate patches of contrasting litter qualities and quantities (Boettcher and Kalisz 1990) which are also a determinant of microbial community composition in both the litter itself and the soil below (Conn and Dighton 2000). Different combinations of microbes either in the soil or litter can exert bottom-up controls on the composition of organisms at higher levels of the food web, because they vary in palatability to microbial feeders and these in their turn vary in palatability to predators (Wardle et al. 2003). Finally, different canopy and root structures can promote particular microenvironmental conditions as a result of variation in light penetration and through-fall (Whelan and Anderson 1996). Microclimatic differences can also directly control the survival of organisms at all levels of the decomposer food-web (Lavelle et al. 1993).

The influence that single plants have on the environment and the food-web of the soil in which they are rooted is likely to be particularly pronounced under trees, given their relatively long life spans (Phillips and Marion 2004). An association between the dominant tree species in a forest and the soil community composition has been shown at different levels of the decomposer food-web (Migge et al. 1998; Widden 1985). Particularly large differences in macroinvertebrate communities have been found to develop under the influence of different tree species compositions in tropical areas (Vohland and Schroth 1999; Warren and Zou 2002).

In previous work, Negrete-Yankelevich et al. (2006, 2007a, b) found that in Tropical Mountain Cloud Forests (TMCF) of Oaxaca the diversities of trees, litter components and macroinvertebrate taxa increase with the age of the forest. Furthermore, the most common macroinvertebrate higher taxa displayed aggregated distributions more frequently in the oldest forests. This evidence suggests that in mature forest stands, not only do highly diverse communities develop below- and above-ground, but also that there is an explicit spatial framework in which they interact. A relevant question is whether this spatial framework is associated with a soil mosaic created by the influence of a highly diverse tree species assemblage. The present paper presents the results of a reciprocal transplant decomposition experiment in a *c.*100-year-old secondary cloud forest. The areas under the canopies of typical late successional trees (*Quercus laurina* Humbl. & Bompl., *Oreopanax xalapensis* (Kunth) Decne. & Planchon and *Beilschmedia ovalis* (Blake) C. K. Allen) were used as experimental units to determine if:

- Topsoil microenvironment conditions and macroinvertebrate communities are different under the canopies of contrasting species of trees.
- The macroinvertebrate community associated with a canopy tree species is exclusively related to the litter provided by the tree or if its characteristics prevail even if the decomposing litter belongs to a different species.
- Mass loss and nutrient release of decomposing leaves differ under the canopy of contrasting species of trees.

Material and methods

Study site

The research was carried out in El Rincón (Villa Alta District), in the Sierra Norte of Oaxaca, Mexico. The study site is an approximately 100-year-old secondary Tropical Montane Cloud Forest (Blanco-Macias 2001). The site is located between 17°19′ and 17° 20′ N and 96°16′ and 96°18′ W at an altitude of 1,500 m. The mean annual precipitation at the nearest meteorological station (≈16 km away) is 1,719 mm, with a rainy season in the summer (June–November) and a dry season in the winter (December–May). The mean annual temperature ranges between 20°C and 22°C (Anonymous 1999). The soil is rich in organic matter, poor in cations and very acidic (pH 4.1–4.6); it also has high porosity, and a high content in exchangeable aluminum (Bautista-Cruz and del Castillo 2005). Del Castillo and co-workers (Bautista-Cruz and del Castillo 2005; del Castillo 1996) were able to estimate that this forest is around 100-years-old by measuring the age of the few *Pinus chiapensis* (Martinez) trees left. *P. chiapensis* is a pioneer species that develops soon after the canopy is opened by logging and it is out-competed as a new canopy of tropical species develops.

Experimental set-up

The areas under twelve trees belonging to three typical late successional species (four *B. ovalis*, four *O. xalapensis* and four *Q. laurina*) were used as experimental units. All selected trees had a minimum DBH of 40 cm showing that they were at least 20-years-old. On 21–22 May 2001 four sets of litter boxes were buried under the litter layer 1.5 m away from the base of each tree trunk, facing north, south, east and west (Fig. 1). Each set consisted of four litter boxes (located on the corners of a 1 m^2 square). Each box in the set contained experimental litter from one of four species of trees (*P. chiapensis*, *B. ovalis*, *O. xalapensis* and *Q. laurina*), which are referred to as leaf species in this paper. Freshly fallen leaves collected from the forest floor were used as experimental litter. The leaves were dried in a herbarium drier until they reached constant mass. Each experimental box in a set contained a different leaf species and therefore all four leaf species were represented in each set (Fig. 1). Because *P. chiapensis* is a pioneer species, at the time this study was performed we could only locate one individual left in this old forest and therefore it was not possible to use it as a tree species treatment. However, it was included as an experimental leaf species as it is one of the most dominant components of litter for approximately 45 years of secondary succession. Further it has a high content of P, which is one of the most deficient nutrients in this forest (Negrete-Yankelevich et al. 2007b). One set of litter boxes was randomly selected for extraction from each experimental tree 28, 56, 112 and 210 days after placement (on 19–29/Jun/01, 17–18/Jul/01, 17–18/Oct/01 and 16–17/Jan/02), all dates being between early rainy and early dry seasons.

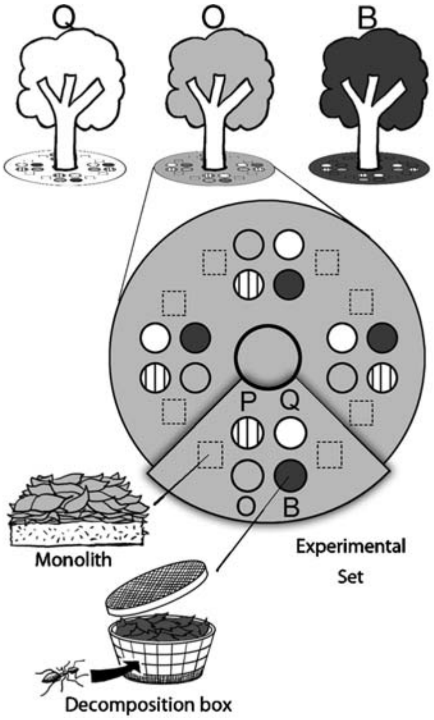

Fig. 1 The experimental design. The experiment was carried out under the canopy of 12 experimental trees (four *O. xalapensis* (*O*), four *B. ovalis* (*B*) and four *Q. laurina* (*Q*)). The litter used in decomposition boxes belonged to *O. xalapensis* (*O*), *B. ovalis* (*B*), *Q. laurina* (*Q*) and *P. chiapensis* (*P*) tree species. On each collection date a random experimental set (boxes and monoliths) was extracted from under each tree

The body of decomposition boxes was a kitchen colander made out of hard plastic mesh (7 mm openings, 25 cm top diameter × 15 cm bottom diameter × 10 cm depth). The lid and bottom of the boxes had a thin plastic mesh (1 mm openings) to prevent sample loss and new materials from entering the box. The boxes contained 30.000±0.025 g (d.w.) of loose experimental leaves (Fig. 1). The boxes were buried within the local litter until the box opening was level with the surface. Experimental boxes were hand-sorted *in situ* for macroinvertebrates. All handling of the experimental leaves was performed over wide white trays to ensure that no material was lost. Four experimental boxes per leaf species were carried to the field, placed and recovered immediately to assess mass loss as a result of handling. Every time a set of experimental boxes was collected, two monoliths were extracted with a box corer (1 m away on each side of the location of the experimental boxes). Monoliths extracted consisted of 25 cm×25 cm×5 cm depth of soil, plus the entire litter layer. This soil depth was chosen because the surface soil is known to be where most plant–soil biochemical interactions occur in forests (Hendrick and Pregitzer 1996). The litter and soil sample was hand sorted *in situ* for macroinvertebrates (all invertebrate animals larger than 3 mm in any dimension). All collected macroinvertebrates were preserved in 70% alcohol, and experimental leaves, litter and soil samples were dried to constant mass.

Each time a set of experimental boxes was retrieved, microenvironment conditions were measured under the canopy of the experimental tree. Soil temperature, volumetric soil water content, canopy cover (as a surrogate of solar radiation reaching the soil), soil bulk density and litter mass were considered as indicators of soil microenvironment conditions. Soil bulk density and litter mass were measured from the collected monoliths.

In the collection after 28 days soil temperature could not be measured as a result of a technical failure. For soil water content and temperature a Delta-T-Theta Probe soil moisture sensor attached to a Delta-T-HH1 meter (Delta-T Devices Ltd, Cambridge, UK) and a Taylor soil digital thermometer (model 9840; Taylor Precision Products LP, Oak Brook, USA) were used respectively. The final calculation of volumetric soil water content was based in a soil-specific calibration performed with soil cores obtained from the same forest. Both the temperature and humidity sensor probes were placed at a soil depth of 10 cm. Percent canopy cover was measured with a Convex Spherical Crown Densiometer (Forestry Suppliers Inc., Jackson, USA), facing north and holding the densiometer at breast height, above the location of the experimental area.

All macroinvertebrates collected were counted and classified into one of the following 25 higher taxa and groups of immature stages (from here on called Macroinvertrebrate taxa): Chilopoda, Diplopoda, Diplura, Arachnida, Opiliones, Pseudoescorpionida, Aranea, Ricinulei, Uropygi, Coleoptera, Orthoptera, Blattodea, Hemiptera, Dermaptera, Diptera, Hymenoptera (other than Formicidae), Formicidae, Thysanura, Diplura, Isopoda, Gasteropoda, Coleoptera larvae, Diptera larvae, Lepidoptera larvae and Other larvae and pupae.

Four random samples of undecomposed leaves per leaf species and leaves extracted from decomposition boxes were analysed for: (1) total N concentration with sulphuric acid digestion followed by distillation and titration (Anderson and Ingram 1993); (2) total P concentration using sulphuric acid digestion followed by colorimetric determination (Anderson and Ingram 1993) and (3) Ca^{++} and Mg^{++} concentration using atomic absorption spectroscopy (Allan 1971).

The lignin contents in experimental leaves were analysed with a sequential procedure of Neutral Detergent Fibre (NDF) and Acid Detergent Fibre (ADF) extractions (Van Soest 1994) followed by a 72% Sulphuric acid extraction through the Acid Detergent Lignin method extraction in beakers (ADL; ANKOM Technology, 2000). All this was performed in filter bags simultaneously for 15 samples at a time in an ANKOM^{200} Technology Fiber Analyzer (ANKOM Technology, Fairport, NY).

Statistical analysis

Generalized Linear Models (GLM) were used to test the effect of tree species (three levels) on environmental conditions and natural macroinvertebrate community variables (Shannon–Weiner index of diversity -*H*′-, taxa richness and most common taxa abundances) under the canopy of different tree species. The most common macroinvertebrate taxa were defined as those with a minimum mean abundance of 10 ind·m^{-2} either in the soil or litter under experimental trees. Tree individual (nested within tree species) and collection date (continuous covariate) were also included in the models to account for their effect. The abundances per taxon in the two monoliths extracted per tree per collection date were averaged.

Similar GLM were used to analyse the results of the decomposition experiment, but this time including leaf species (four levels) as an additional explanatory factor. Experimental response variables were in this case remaining litter mass, remaining nutrient and lignin contents and macroinvertebrate community variables of organisms that invaded experimental boxes. The minimal adequate models were found by removing non-significant terms and contrasting competing models with partial analyses of variance. In order to control for deviations from the normal distribution and overdispersion in the data we used Quasipoisson error distribution and logarithmic link functions for count data and Gaussian error distribution and logarithmic link functions for continuous variables with a skewed distribution. Normally distributed variables and the arcsin-transformed canopy cover were modelled with Gaussian error distribution and identity link functions. When a Quasiposson error distribution function was used, a χ^2 test was performed in the analysis of deviance (Crawley 2005). Modelling was performed in R 2.1.1 (http://www.R-project.org/). Treatment contrasts were used after modelling to determine significant differences between factor levels (Crawley 2005). The levels of significance were adjusted for multiple comparisons with the step-up false discovery rate method (Benjamini and Hochberg 1995).

Figures associated with macroinvertebrates were constructed with only those factors of interest (tree species and leaf species) that were significant in the minimal adequate model. Macroinvertebrate communities are likely to change as a result of seasonal variation. Thus time was not considered a main factor in the analyses. Time was only represented in macroinvertebrate graphs when it modified the effect of main factors, that is when it interacted significantly with tree or leaf species.

The proportions of nutrients and lignin that remained in experimental leaves at the time of collection were estimated by dividing the final nutrient or lignin mass in each sample by the mean content in four samples of undecomposed leaves. Net immobilisation (*sensu* Swift et al. (1979), i.e. acquisition of nutrients from external sources into decomposing litter) and net mineralisation of nutrients were considered in terms of the percentage of the initial amount that remained in the sample at the time of collection. Net immobilisation was considered to occur once the percentage of an element surpassed 100% of the initial sample content and net mineralisation to occur when the percentage of an element diminished to less than 80% of the initial sample, considering there to be a 20% loss through leaching, Swift et al. 1979).

Results

Microenvironment conditions and natural macroinvertebrate community under the canopy of different tree species

Independently of temporal variations the abundance of Aranea was highest under the canopy of *O. xalapensis*, Coleoptera larvae were most abundant under *B. ovalis* trees and Pseudoesecorpionidae were very scarce under *Q. laurina* trees (Table 1, Fig. 2a). The abundance of Diptera larvae did not change significantly with time (Table 1) but was always larger under *B. ovalis*, intermediate under *O. xalapensis* and smaller under *Q. laurina* trees. There were no differences between tree species in macroinvertebrate abundances in the soil or diversity measures in the litter or soil community (Table 1).

There were no differences in the soil microenvironment among tree species (Table 1). During the early rainy season (June–July), soil temperature and water content as well as the standing crop of litter were relatively high and declined thereafter. Soil bulk density was lower in the first part of the experiment than in the second (Table 2). Canopy cover did not change significantly through time or between tree species (data not presented). There was seasonal variation in the abundance of four of the common taxa in the litter and seven in the soil (Tables 1 and 2). The highest taxa abundances in the litter corresponded to the warmest and wettest months when the mass of the standing crop of litter was also high. However, taxa abundances in the soil displayed the opposite trend, being highest in the cool dry season.

Macroinvertebrate communities in experimental decomposition boxes

Regardless of the litter species in the box, more Hemiptera, Formicidae and Diplura invaded decomposition boxes under the canopy of *B. ovalis* and more Pseudoscorpionidae under *O. xalapensis* (Table 1, Fig. 2b). Also, independently of the tree species, six macroinvertebrate taxa preferentially invaded some leaf species (Fig. 3a). Diptera larvae and Hemiptera were most abundant in *O. xalapensis* boxes. *P. chiapensis* boxes had the least abundance of Formicidae and Diplura, while Coleoptera larvae preferentially invaded *P. chiapensis* and *O. xalapensis* above the

Table 1 Results of GLM

	Collection date	Tree species	Leaf species	Tree species × leaf species	Collection date × leaf species
Soil microenvironment					
Soil temperature (°C)	$25.84^{a,***}$	ns^{p}	na	na	na
Vol. soil water content (cm^3 cm^{-3})	$0.20^{a,***}$	ns^{p}	na	na	na
Standing litter mass (g)	$24.26^{a,***}$	ns^{p}	na	na	na
Soil bulk density (g cm^{-3})	$8.94^{a,**}$	ns^{p}	na	na	na
Common macroinvertebrates					
In litter (ind m^{-2})					
Aranea	$528.74^{c,***}$	$415.52^{b,*}$	na	na	na
Coleoptera larvae	$189.43^{c,***}$	$160.49^{b,*}$	na	na	na
Diplopoda	$467.90^{c,***}$	ns^{b}	na	na	na
Diptera larvae	ns^{c}	$177.46^{b,*}$			
Pseudoescorpionida	$112.63^{c,*}$	$93.12^{b,*}$	na	na	na
In soil (ind m^{-2})					
Chilopoda	$293.11^{c,***}$	ns^{b}	na	na	na
Coleoptera	$650.30^{c,***}$	ns^{b}	na	na	na
Coleoptera larvae	$252.26^{c,***}$	ns^{b}	na	na	na
Diplura	$313.29^{c,***}$	ns^{b}	na	na	na
Diptera larvae	$379.42^{c,***}$	ns^{b}	na	na	na
Hemiptera	$1,016.22^{c,***}$	ns^{b}	na	na	na
Pseudoescorpionida	$294.01^{c,***}$	ns^{b}	na	na	na
In experimental boxes (ind box)					
Araneida	$1,357.07^{c,***}$	ns^{d}	ns^{e}	ns^{f}	ns^{g}
Chilopoda	$1,183.52^{c,**}$	ns^{d}	$1,080.98^{e,*}$	ns^{f}	$1,015.39^{g,*}$
Coleoptera	$3,982.00^{c,***}$	ns^{d}	ns^{e}	ns^{f}	ns^{g}
Coleoptera larvae	ns^{c}	ns^{d}	$1,051.95^{e,***}$	ns^{f}	ns^{g}
Diplopoda	ns^{c}	ns^{d}	$2,350.14^{e,***}$	ns^{f}	ns^{g}
Diplura	$2,950.7^{c,***}$	$2,833.5^{d,**}$	$2,529.50^{e,***}$	ns^{f}	ns^{g}
Diptera larvae	$1,486.38^{c,***}$	ns^{d}	$1,271.92^{e,***}$	ns^{f}	ns^{g}
Formicidae	ns^{c}	$10,364.3^{d,***}$	$9,639.60^{e,*}$	ns^{f}	ns^{g}
Hemiptera	ns^{c}	$3,424.8^{d,***}$	$3,217.10^{e,**}$	ns^{f}	ns^{g}
Pseudoescorpionidae	$1,114.03^{c,***}$	$987.98^{d,***}$	ns^{e}	ns^{f}	ns^{g}

Maroinvertebrate diversity in experimental boxes					
Shannon's index (*H'*)	$43.40^{h,***}$	ns^{i}	$4.36^{j,**}$	ns^{k}	$5.38^{l,***}$
Taxa richness	$96.37^{c,***}$	ns^{d}	ns^{e}	ns^{f}	ns^{g}
Experimental litter					
Litter mass (g)^{m}	$1,677.09^{h,***}$	ns^{i}	$21.49^{j,***}$	ns^{k}	$12.11^{l,***}$
N (g)	$67.96^{h,***}$	ns^{i}	$17.20^{j,***}$	ns^{k}	ns^{l}
P (cmol kg^{-1})	ns^{h}	ns^{i}	$106.66^{j,***}$	ns^{k}	$5.88^{l,**}$
Mg (cmol kg^{-1})	$82.92^{h,***}$	ns^{i}	$309.11^{j,***}$	ns^{k}	ns^{l}
Ca (cmol kg^{-1})	$34.20^{h,***}$	ns^{i}	$27.72^{j,***}$	ns^{k}	ns^{l}
Lignin (g)	$456.33^{h,***}$	ns^{i}	$133.13^{j,***}$	$2.32^{k,*}$	$6.11^{l,***}$
Lignin in *O. xalapensis* (g)	$55.07^{n,***}$	$3.11^{o,*}$	na	na	na

The analysis of deviance of the minimal adequate models are presented.

The three way interaction and the interaction collection date × tree species do not appear because they were not significant for any of the variables. *F* and χ^2 values are presented with the correspondent level of significance (*$P<0.05$, **$P<0.01$, ***$P<0.001$). Those variables for which no significant explanatory variables were found are not presented.

ns Non significant factor, *na* factor not applicable to the model

[a] $F_{(1,46)}$

[b] $\chi^2_{(2,44)}$

[c] $\chi^2_{(1,190)}$

[d] $\chi^2_{(2,188)}$

[e] $\chi^2_{(3,185)}$

[f] $\chi^2_{(6,174)}$

[g] $\chi^2_{(3,180)}$

[h] $F_{(1,190)}$

[i] $F_{(2,188)}$

[j] $F_{(3,185)}$

[k] $F_{(6,174)}$

[l] $F_{(3,180)}$

[m] For the litter mass model an additional quadratic factor (CD^2) was included because it significantly improved the fit of the model. $F_{(1,183)}=172.779$ *** for this factor

[n] $F_{(1,45)}$

[o] $F_{(2,43)}$

[p] $F_{(2,44)}$

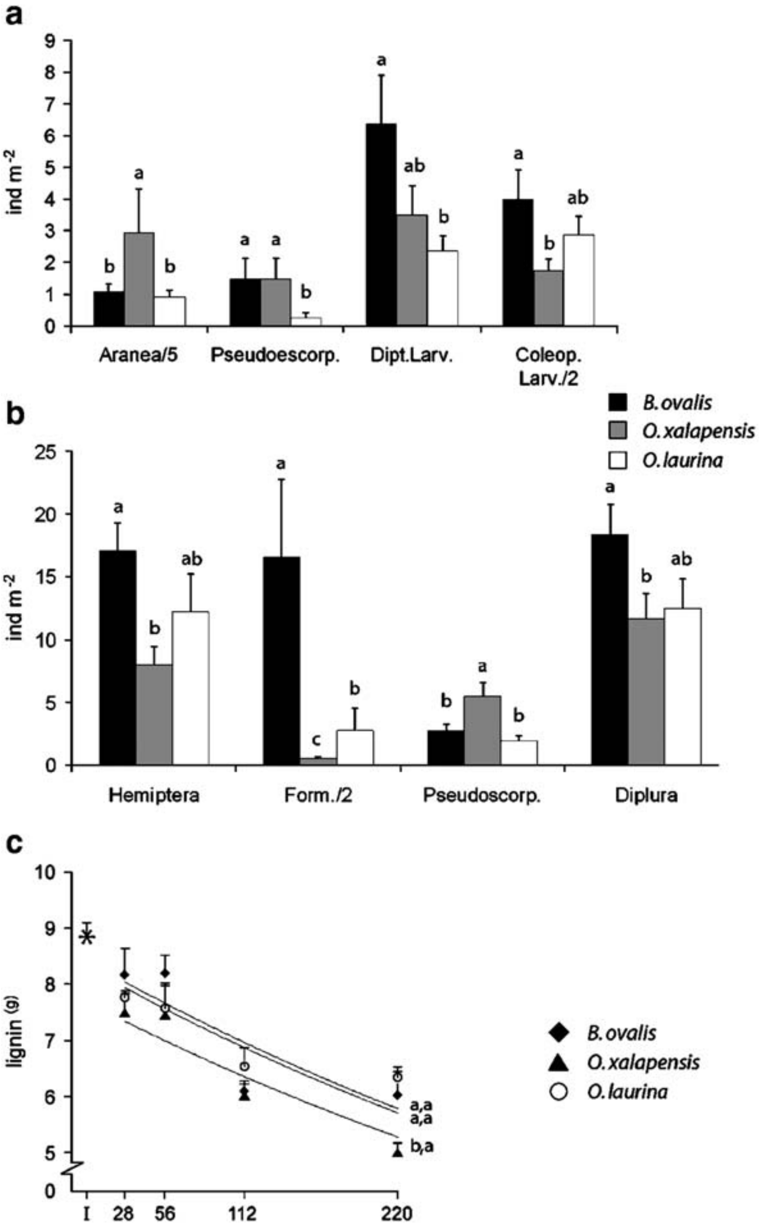

Fig. 2 The effect of tree species on **a** the dominant macroinvertebrate taxa in natural litter, **b** the dominant macroinvertebrate taxa that invaded experimental boxes and **c** the lignin content of decomposing *O. xalapensis* litter. Mean abundance (+SE) are presented. To improve presentation the abundance of Aranea has been divided by five and those of Coleoptera and Formicideae by two. Only those variables that were significantly different between tree species are presented. *Different letters* indicate significant differences according to treatment contrasts that followed GLM. For (**c**) the *first letter* compares the intercepts and the *second letter* the slopes. *Lines* are the predicted values from the GLM model and *I* represents the initial lignin content, this value was not included in the model since litter had not undergone any experimental treatment

other species. Diplopoda were considerably more abundant in decomposition boxes containing *P. chiapensis* than any other species (Fig. 3a).

The community richness and diversity as well as the abundances of most common macroinvertebrate taxa in decomposition boxes increased as the experiment proceeded, particularly in the last collection date (Table 2). However, *H′* increased more rapidly in the boxes containing *P. chiapensis* and *O. xalapensis* leaves (Table 1, Fig. 3b). Chilopoda increased in abundance with time in all boxes except for those containing *P. chiapensis* which had a uniformly high abundance through out the experiment (Fig. 3c).

Mass loss and chemical dynamics in experimental boxes

The species of canopy tree did not affect the leaf mass that remained in the decomposition boxes throughout the experiment (Table 1). During the first half of the

Table 2 Temporal variation in microenvironmental conditions and macroinvertebrate communities during the course of the decomposition experiment

	Days after the start of the experiment			
	28	56	112	220
Soil microenvironment				
Soil temperature (°C)	na	14.60 (0.40)	13.34 (0.36)	12.89 (1.12)
Vol. soil water content ($cm^3\ cm^{-3}$)	0.34 (0.07)	0.18 (0.03)	0.18 (0.03)	0.07 (0.06)
Standing litter mass (g)	81.81 (22.57)	69.98 (17.57)	55.45 (15.01)	50.26 (12.98)
Soil bulk density ($g\ cm^{-3}$)	0.08 (0.01)	0.10 (0.04)	0.13 (0.01)	0.11 (0.01)
Common Macroinvertebrates				
In litter ($ind\ m^{-2}$)				
Aranea	20.83 (8.67)	5.17 (0.80)	4.17 (0.80)	3.00 (1.14)
Coleoptera larvae	6.50 (1.44)	10.00 (2.10)	3.50 (0.89)	3.00 (0.67)
Diplopoda	26.17 (6.92)	10.83 (2.55)	7.67 (2.21)	2.50 (1.79)
Pseudoescorpionida	2.67 (0.99)	1.00 (0.39)	0.33 (0.33)	0.33 (0.22)
In soil ($ind\ m^{-2}$)				
Chilopoda	14.83 (1.11)	19.17 (2.59)	30.00 (5.43)	49.17 (6.31)
Coleoptera	23.17 (3.92)	34.50 (6.93)	61.67 (9.09)	90.83 (11.06)
Coleoptera larvae	8.67 (1.44)	18.33 (2.71)	29.83 (2.90)	25.83 (2.60)
Diplura	14.83 (3.67)	11.33 (1.36)	14.00 (2.37)	31.83 (4.22)
Diptera larvae	3.67 (1.15)	9.17 (1.09)	31.50 (5.06)	48.17 (5.69)
Hemiptera	0.83 (0.46)	3.17 (0.87)	13.83 (5.51)	42.33 (15.62)
Pseudoescorpionida	2.33 (0.85)	3.33 (0.67)	8.00 (2.86)	17.83 (4.01)
In experimental boxes (ind box)				
Aranea	4.42 (0.68)	6.67 (0.93)	7.42 (1.18)	9.67 (1.31)
Chilopoda	3.17 (0.61)	3.83 (0.84)	2.25 (0.50)	6.00 (0.83)
Coleoptera	27.42 (3.66)	13.08 (1.60)	26.33 (2.48)	74.33 (7.25)
Diplura	8.42 (1.84)	8.42 (1.78)	13.67 (1.67)	26.17 (3.74)
Diptera larvae	2.00 (0.65)	3.67 (1.01)	2.25 (0.53)	9.08 (1.39)
Pseudoescorpionidae	0.75 (0.26)	1.92 (0.38)	3.33 (0.66)	7.58 (1.35)
Maroinvertebrate diversity in experimental boxes				
Shannon's index (*H′*)	2.05 (0.04)	2.16 (0.04)	2.25 (0.03)	2.43 (0.03)
Taxa richness	1.12 (0.05)	0.97 (0.08)	1.18 (0.06)	1.54 (0.06)

Mean and standard error (in brackets) are presented. Only those variables for which collection time was significant (independently or interactively) in the GLM are presented (see Table 1).

na Not available

experiment *P. chiapensis* needles lost mass more rapidly than other species of leaves and *B. ovalis* leaves had the most mass remaining after 112 days. However, by the last collection date, there were no differences among leaf species (Fig. 4a).

During the first 28 days, *O. xalapensis* leaves lost more lignin under *O. xalapensis* trees than under the other tree species (reflected in the significantly different model intercepts in Fig. 2c). During the rest of the experiment the rate of lignin loss was equivalent between tree species (insignificantly different model slopes in Fig. 2c). Therefore, *O. xalapensis* leaves under *O. xalapensis* trees had lost at least 11% more lignin than under any other tree by the end of the experiment.

Most of the differences in chemical composition between undecomposed leaf species (see initial points in graphs in Fig. 4b–f) prevailed throughout the experiment. Noticeably, *O. xalapensis* leaves always had higher contents of calcium and magnesium and a lower content of lignin than the rest of the species (Fig. 4c,d,e). The content of phosphorus was highest and that of magnesium lowest in *P. chiapensis* (Fig. 4e,g). *B. ovalis* sustained the highest content of

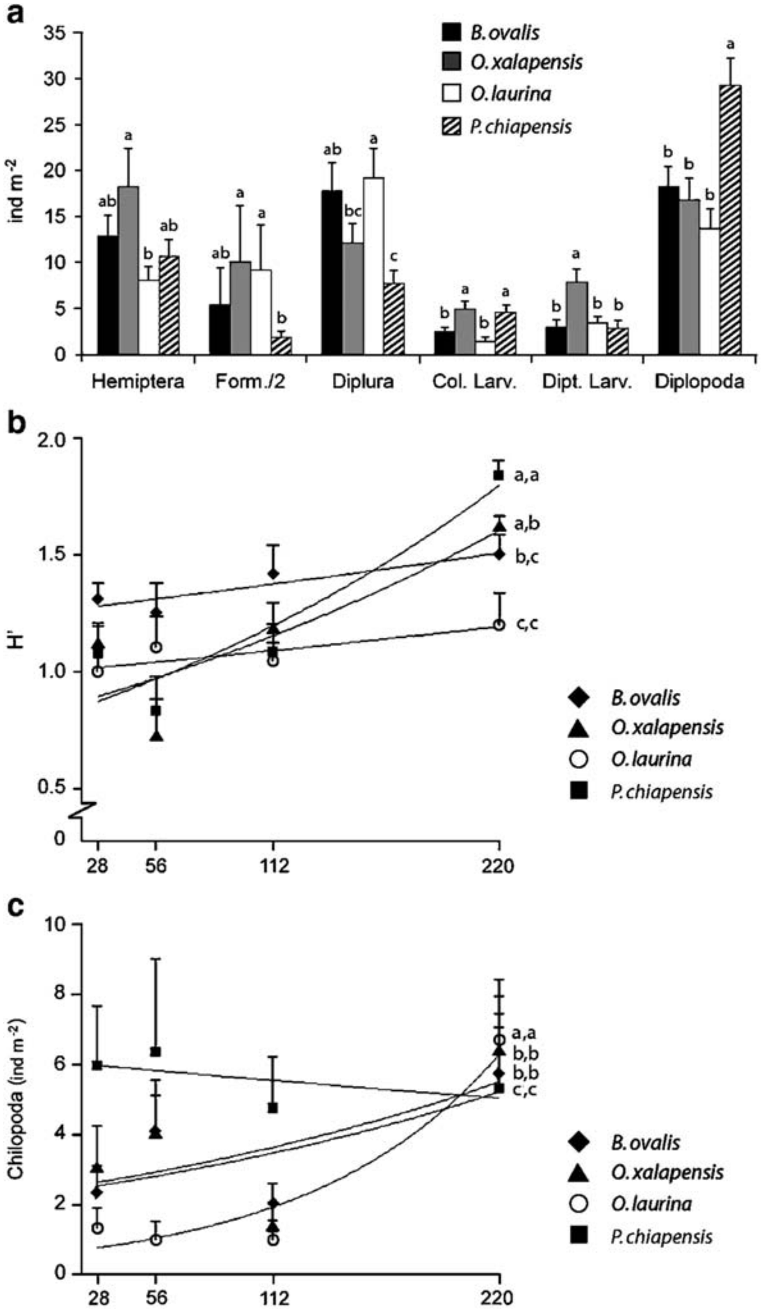

Fig. 3 The effect of leaf species on the macroinvertebrate community that invaded experimental boxes. Mean + SE are presented. **a** The abundance of those dominant macroinvertebrate taxa that were significantly different between leaf species independently of collection date, **b** Shannon's *H′* and **c** Chilopoda. In (**a**) the abundance of Formicidae has been divided by two to improve presentation. Different letters indicate significant differences according to treatment contrasts. In (**b**) and (**c**) the *first letter* compares the intercepts and the *second letter* the slopes and the *lines* are predicted values of GLM. Values per leaf species through time are included when the interaction between collection date and leaf species was significant

lignin throughout the experiment. However, leaf species differed in the pattern of nutrient release and lignin loss during decomposition. Overall, nutrient mineralisation was consistent with the general observation that nutrients are lost sooner from litter when they are in higher concentration (Stohlgren 1988). For example, in net terms, by the end of the experiment about 9% and 11% of the nitrogen had been mineralised in the litter of *P. chiapensis* and *Q. laurina* sp. However, in *B. ovalis* and *O. xalapensis* litter, nitrogen was immobilised for most of the experiment (Fig. 4e). Magnesium and phosphorus were mineralised more rapidly from *O. xalapensis* leaves than from any other leaf species (Fig. 4d,f) and no net phosphorus mineralization was recorded in *Q. laurina* leaves by the end of the experiment (Fig. 4f).

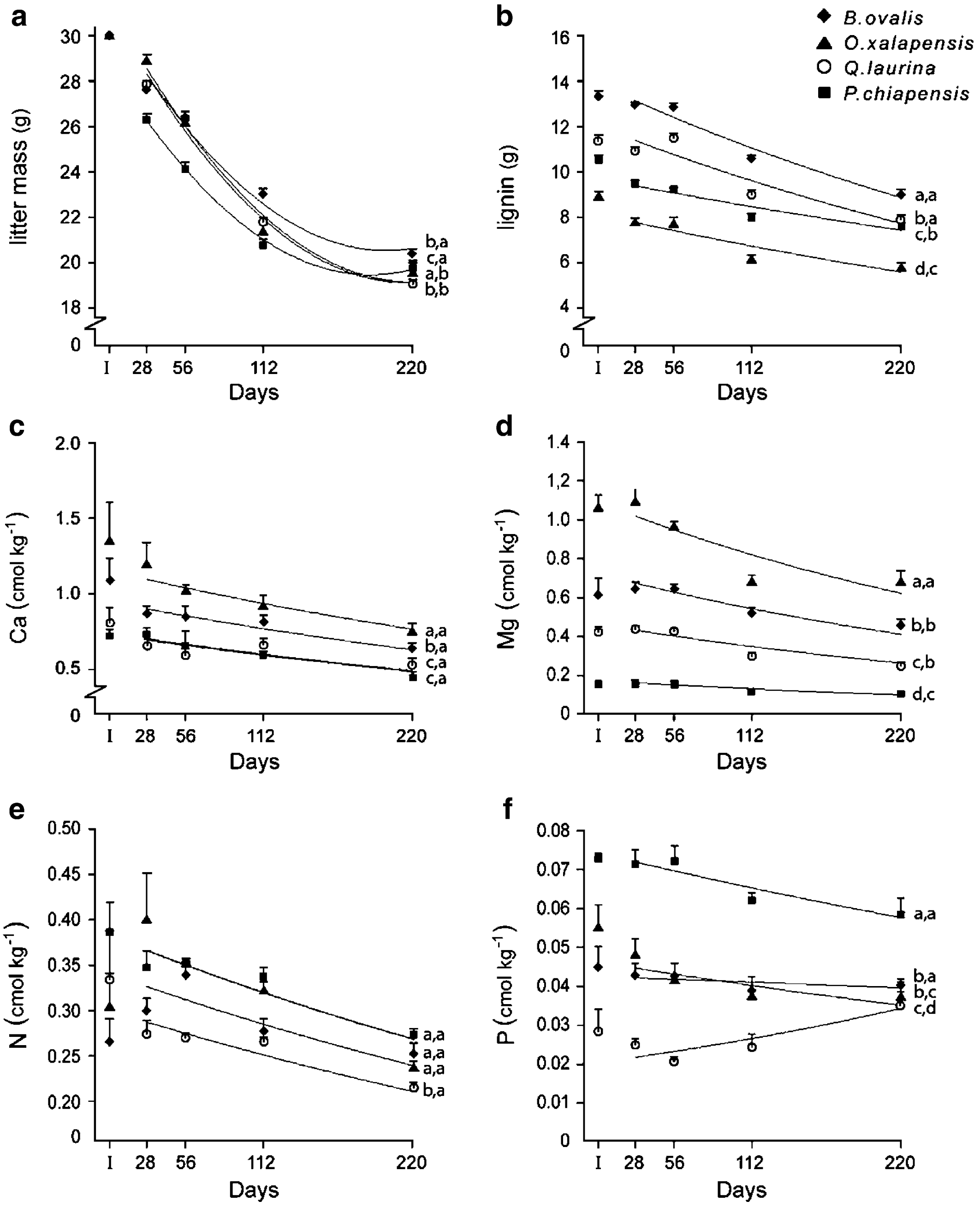

Fig. 4 The effect of leaf species on the dynamics of (**a**) litter mass, (**b**) lignin and (**c**–**f**) nutrient contents in experimental leaf litter. Mean + SE and GLM predicted values are presented. *I* represents the initial conditions, this value was not included in the model since litter had not undergone any experimental treatment. *Different letters* indicate significant differences according to treatment contrasts that followed GLM. The *first letter* compares the intercepts and the *second letter* the slopes

Discussion

It has recently been suggested that hotspots of biological activity in the soil are distributed in patches at the plot scale as a result of the interaction between macroinvertebrate activity and plants. However, this has seldom been investigated (Lavelle et al. 2006). The results of the experiment presented in this paper show that trees can indeed promote a functional domain under their canopy. It is demonstrated that the species of tree can determine the litter macroinvertebrate community and decomposition process occurring in the area under the influence of individual trees. Despite the fact that no differences in soil microenvironment conditions or litter availability were detected under different tree species, significant differences were found in the abundances of Aranea, Pseudoescorpionidae, Diptera larvae and Coleoptera larvae in the natural litter. This implies that the effect that the species of tree has on the community may be more related to the characteristics of their litter. This is supported by the fact that the tree species effect was only found in the litter community and not in the top soil. Further, it is also consistent with the finding that the aggregated patterns of macroinvertebrate taxa were more frequent in the litter community than in the top soil (Negrete-Yankelevich et al. 2006) and with the reported strong association between macroinvertebrate community and litter identity (Warren and Zou 2002).

Spatial patterns in soil biota have been suggested to be dynamic rather than static over time (Ettema and Wardle 2002), and their abundance to fluctuate more than biotic and abiotic factors (Görres et al. 1998). In contrast, we found that for all four taxa whose abundance in the litter differed between tree species, this difference was independent of time. It is possible that this permanent association was related to some chemical or structural characteristics of the leaves of these species. The four macroinvertebrate taxa differed in the tree species under which they were most abundant, suggesting that the high diversity sustained in old TMCF (Negrete-Yankelevich et al. 2006) may be a result of the patchy litter layer produced by a diverse tree community combined with differential preferences of taxa for particular environments. Abundance of Diptera and Coleoptera larvae was highest under *B. ovalis*, which had leaves with the highest lignin concentration and the slower decomposition and nutrient mineralisation. Structural properties of litter are known to be important determinants of invertebrate communities, even when nutritional qualities of litter are low (Anderson 1975).

Aranea and Pseudoscorpionidae, both predator taxa, were highly abundant under *O. xalapensis* and least abundant under *Q. laurina*. This may be an indication of a bottom-up control of the food-web (Scheu and Schaffer 1998). *O. xalapensis* had the lowest lignin content and released cations most rapidly, which may have been an indication of higher microbial activity (Wardle 1992). Predator macroinvertebrates may have been exploiting mesofauna grazers feeding on the micro-organisms that are known to increase rapidly in abundance with increasing nutritious litter availability (Halaj and Wise 2002).

Although we did not directly study the most important component of the decomposer community (microorganisms), indirect evidence from decomposition results suggests that a specialised decomposer community has developed under the canopy of *O. xalapensis* trees. This community is capable of breaking down more lignin from *O. xalapensis* litter during the initial phase of decomposition. It is possible that the sustained dominance of *O. xalapensis* leaf species under its trees influences the decomposer community composition and when that same leaf species is introduced experimentally the combination of decomposers that most efficiently breaks down lignin is readily available. Wardle et al. (2002) have suggested such a mechanism of plant selection of different decomposer communities associated with feedback. This hypothesis is also supported by the findings of Coûteaux et al. (1991) in a microcosm experiment. Chestnut litter with low nitrogen concentration favoured the development of organisms that were capable of breaking down resistant compounds in late stages of decomposition. In contrast, Ayres et al. (2006) in another laboratory experiment found that the litter of three temperate species did not loose mass faster in the presence of indigenous micro and meso-soil biota. However, in this last experiment the rate of release of particular substances from decomposing litter was not tested.

A key question is the extent to which the character of the resident macroinvertebrate community under each tree species constrains the composition of the macroinvertebrate assemblage that invades experimental litter. If the tree species effect on the macroinvertebrate community is related to nutrient quality and leaf structure of the litter, then one would expect to see the pattern of influence by tree species in natural litter replicated in the pattern of influence by leaf species in experimental boxes. Consistently, Coleoptera and Diptera larvae abundances were determined by tree species in the litter and by leaf species in boxes. However, the pattern of influence was not identical in both situations. While both larvae were most abundant in the litter of *B. ovalis*, they were most abundant in boxes containing *O. xalapensis.*

This and other discrepancies (highlighted below) between the abundances in taxa observed in natural litter and in the litter boxes suggest that there must be other factors apart from litter quality that are determining the community composition in boxes and natural litter. Possibly the presence of these larvae in natural communities is also influenced by the chemical and physical environments associated with litter resources that have decomposed for more than 1 year (Warren and Zou 2002) or there is a differential response (such as differential invasion ability) between species included within Coleoptera and Diptera.

The abundances of two predatory taxa in the natural litter (Aranea and Pseudoescorpionidae) were determined by canopy tree species, but they were not significantly different between leaf species in boxes. If the abundance of these taxa is determined by other characteristics of the tree species that are not associated with the quality or structure of leaf species (such as the availability of woody material), then one would expect that the tree species effect should remain evident inside boxes, independently of the leaf species being decomposed. This was only the case for Pseudoescorpionidae, the numbers of which were significantly determined by tree species, both in the natural litter and in the boxes. In both cases pseudoscorpions were least abundant under *Q. laurina* trees. This result is consistent with other studies that have found that pseudoscorpions remain unaffected by the addition of different qualities of organic matter resources to the forest floor (Salamon et al. 2006).

It is noticeable that Hemiptera, Formicidae and Diplura were determined by tree species in experimental boxes but not in the natural litter. These taxa were most abundant in boxes placed under *B. ovalis* and least abundant in boxes under *O. xalapensis*. The leaves of these two species were the ones with the highest and lowest lignin content respectively. Possibly, Hemiptera, Formicidae and Diplura were more likely to forage for food in decomposition boxes under *B. ovalis* because the leaf litter available naturally was more recalcitrant than the one available under *O. xalapensis*. However, these taxa did not avoid the *B. ovalis* litter in the litter boxes. In fact there was a greater abundance of Diplura in *B. ovalis* litter than in *O. xalapensis* litter, while there were no differences between *B. ovalis* and *O. xalapensis* litter for Hemiptera and Formicidae. Therefore the influence of *B. ovalis* trees on these taxa may be determined not only by the quality of senescent leaves but also by other factors such as the physical and chemical resource environments created by litter decomposition after the first year (Warren and Zou 2002).

Nutrient limitation has been associated with bottom-up control of food-web complexity (Halaj and Wise 2002). If this is the case for these P-deficient forests, then one would expect that boxes containing *P. chiapensis* (with higher concentration of P) would be invaded by a diverse and abundant macroinvertebrate community. By the end of the experiment *P. chiapensis* boxes had the highest diversity of taxa; moreover the abundance of a purely detrivorous group (Diplopoda) and that of a purely predatory group (Chilopoda) were highest in *P. chiapensis* for most of the experiment. This result is consistent with the suggestion that the widespread colonisation of *P. chiapensis* after TMCF disturbance has a substantial effect on the composition and spatial structure of the decomposition process and soil biota (Negrete-Yankelevich et al. 2007b).

The richness and diversity of macroinvertebrates, as well as abundances of individual taxa in experimental boxes increased as the experiment proceeded. As litter decomposed, the microorganism community would have developed and the primary consumers could have migrated in search of food, followed by predators (as shown for microarthropods by Santos et al. (1981) and mites by Hansen and Coleman (1998)). However, the temporal variation in abundance of taxa inside the boxes corresponds with that followed by the soil community (and not the litter) outside. Possibly the macroinvertebrate community migrated seasonally into the soil and decomposition boxes seeking a more protected environment as conditions became harsher on the surface. The first explanation is more likely for the richness and diversity of taxa and for Aranea abundance, because they increased with time in decomposition boxes, but not in the top soil.

The diversity of taxa in experimental boxes seems to have become associated with the quality of litter only by the time this was most advanced in decomposition. Diversity inside decomposition boxes increased most in *O. xalapensis* and *P. chiapensis* by the last collection date. These two leaf species were the ones that had the least lignin content for most of the experiment. However, other factors must have operated at the beginning of the experiment because *B. ovalis* litter started out with a higher H', although it had the highest lignin content. Possibly the different physical properties of undecomposed leaf species provide different qualities of habitat or permeability to initial invasion for certain taxa.

Evidence suggests that for most individual taxa the response to leaf species is associated with a characteristic of the experimental litter that persisted during the whole experiment. From all seven dominant taxa that differed significantly between leaf species, only for Chilopoda did this effect disappear as decomposition proceeded. It is noteworthy that different taxa preferentially invaded different leaf species in boxes. This suggests that there is not a single leaf species that is the best resource for the whole macroinvertebrate community, but rather that different assemblages of organisms are associated with the decomposition of different leaf species. This evidence together with the fact that macroinvertebrate taxa differed from each other in the tree species under which they were most abundant in the natural litter, is consistent with the suggestion by Negrete-Yankelevich et al. (2006) that the patchiness of litter created by a diverse tree community in old TMCF promotes patchiness in the soil biota which in turn sustain a high overall community diversity, possibly by partitioning resources.

To our understanding, this is the first time that the effect of tree species on the decomposition process and macroinvertebrate community has been tested experimentally and simultaneously for many taxa. Overall results support the hypothesis that the hotspots of biological activity in the soil are distributed in patches at the plot scale as a result of the interaction between soil biota and plants (Lavelle et al. 2006). It has been demonstrated that the species of tree can determine the decomposition process and the litter macroinvertebrate community (even at a higher taxa level) occurring in the area under the influence of individual trees. An important mechanism by which this influence occurs appears to be the production of different qualities of litter and not the microenvironment in the soil. However, the influence seems to be determined not only by the quality of senescent leaves but by other factors such as the physical and chemical resource environments created by decomposition after the first year. For *O. xalapensis* there is evidence that the decomposer community is able to optimise the break down of lignin from the litter produced by the same species of tree.

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