CHAPTER 6.

THE INFLUENCE OF SINGLE-TREES ON SPATIAL PATTERNS IN THE MACROINVERTEBRATE COMMUNITY OF A LATE SUCCESSIONAL FOREST

Introduction

At some scale, all ecological phenomena occur in a spatially explicit (as opposed to random) manner (Carlile *et al.*, 1989). The scale at which spatial pattern is evident depends in its turn upon the scale at which the driving forces, or processes responsible for generating the pattern, are operating (Legendre & Legendre, 1998). In Chapter 4 it was shown that when macroinvertebrate abundances in Tarantulas were studied at a 5-metre grain interval (sampling scale), only in the 100-year-old forest was a spatially explicit pattern consistently detected. This chapter explores the local influence of single-trees of different species as the driving force of this spatial structuring in the soil macroinvertebrate community.

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. In a mixed forest context the single-tree influence can be the result of three phenomena related to differences between neighbouring trees of different ages, shapes or species. First, below-ground different plants create distinct soil physicochemical environments in the rhizosphere by absorbing nutrients and producing metabolic resources and molecular signals for nearby organisms (Griffiths *et al.*, 1992; Moore *et al.*, 2003; Phillips *et al.*, 2003). Second, neighbouring tree canopies can generate patches of contrasting litter qualities and quantities (Boettcher & Kalisz, 1990; Hirabuki, 1991). Third, different canopy and root structures can promote particular microenvironmental conditions as a result of variation in light penetration, through fall, stem flow and evapotranspiration (Whelan & Anderson, 1996; Schume *et al.*, 2003; Radersma & Ong, 2004). The interaction of these mechanisms, by which a tree can generate a zone of influence in the soil around its trunk, have been shown to result in contrasting soil properties across boundaries of areas associated with individual conifers in single-species stands (Zinke, 1962; Hokkanen *et al.*, 1995; Kuuluvainen & Linkosalo, 1998).

The influence of individual trees on soil biogeochemistry has scarcely been studied in mixed forests (Turner & Franz, 1985; Boettcher & Kalisz, 1990; Finzi *et al.*, 1998; Dijkstra, 2003) and only in temperate areas. Boettcher & Kalisz (1990) for example, found that even in mixed species forests on steep slopes, where the canopies of different tree species overlap and litter mixing is more likely, cation availability and mineralisable N concentration differed between the areas under different tree species. This is consistent with the findings in mixed-species forest in northwestern Connecticut where different tree-species accumulated different amounts of litter and the soils under their canopies differed in organic matter content and Ca and N mineralisation rates (Finzi *et al.*, 1998; Dijkstra, 2003).

Even if the effect of single trees on soil processes has been scarcely studied, the mechanisms by which particular plant species create distinct chemical environments in the soil, which result in a bottom-up control of the decomposer food-web, have been demonstrated in a variety of field, laboratory and greenhouse settings (see for example Wardle, 1992; Bradgett *et al.*, 1999; Warren & Zou, 2002 and Wardle *et al.*, 2003). These mechanisms involve both below- and above-ground processes.

Below-ground, the roots of different plant species may release diverse sources of labile-C and produce different quantities of litter that promote distinct micro-organism community assemblages and patterns of nutrient cycling (Bradley & Fyles, 1995; Grayston *et al.*, 1998; Saetre, 1998; Kourtev *et al.*, 2002). Plants may also demonstrate differing capability for nutrient uptake, which may induce changes in the community composition of microorganisms (Kaye & Hart, 1997). Above-ground, the quality of leaf litter associated with plant species is also a determinant of microbe community composition in both the litter itself and the soil below (Swift *et al.*, 1979; Switzer & Shelton, 1979; Conn & Dighton, 2000; Satti *et al.*, 2003). Different combinations of microbes either in the soil or litter can exert bottom-up controls of 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 (Coûteaux *et al.*, 1991; Maraun *et al.*, 2003; Wardle *et al.*, 2003).

Microclimatic differences generated in the zone of influence of different plant species result from differences in vegetation thickness, the abundance and physical structure of litter and the structure of root network. These differences can also directly control the survival of organisms at all levels of the decomposer food-web (Swift *et al.*, 1979; Lavelle *et al.*, 1993; Decaëns *et al.*, 1998).

The influences that single plants have on the soil environment were they are rooted can be expected to be particularly pronounced under trees, given their relatively long life spans (Zinke, 1962; Boettcher & Kalisz, 1990; Phillips & Marion, 2004). The long-term interaction between a tree and the soil under its influence could also provide the sufficient time for the development of a distinct decomposition food-web associated with the species-specific set of conditions. There are some examples in the literature that have shown an association between the tree's identity and the soil community composition at different levels of the decomposer food-web. Distinct fungal community structures have been found to be associated with the dominance of coniferous *vs* deciduous trees in southern Quebec (Widden, 1985). In northern Germany some species of oribatid mites were found to be more common under *Fagus sylvatica* and others under *Picea abies*-dominated stands (Migge *et al.*, 1998). Different macroinvertebrate communities were found to have developed under the influence of different species of trees in southern Congo (Mboukou-Kimbatsa *et al.*, 1998), in central Amazonia (Vohland & Schroth, 1999) and in Puerto Rico (Warren & Zou, 2002).

This chapter explores whether single trees in a late-successional forest have developed distinct biogeochemical cycles and macroinvertebrate communities in the nearby soil as a result of species-specific characteristics. Results in previous chapters suggest that after 100 years of succession a complex relationship develops between the diversity and spatial structuring of litter resources and the macroinvertebrate community in the litter and soil. The 100-year-old forest had the highest diversity of tree genera, litter components and macroinvertebrate taxa (Chapter 3). The most common macroinvertebrate taxa displayed aggregated distributions more frequently in the later stages of succession and their centres of aggregation often corresponded

to the distribution of litter and nutrients in the soil (Chapter 4). Although some individual macroinvertebrate taxa displayed aggregated distributions in the 100-year-old forest, no areas of low diversity were found, suggesting that different taxa concentrate in different areas. Furthermore, during the experimental analysis of litter decomposition, the leaves of a common late-successional tree species mineralised more nutrients and attracted a more diverse macroinvertebrate community compared with the litter of a pioneer tree, even though the latter decomposed more rapidly (Chapter 5). All of this evidence suggests that later in succession, not only do highly diverse communities develop below- and above-ground, but also that there is an explicit spatial framework in which they interact. The key question is whether the spatial framework is associated with a soil mosaic created by the influence of a highly diverse tree species assemblage.

To answer this question a decomposition experiment was performed in the 100-year-old forest of the Tarantulas chronosequence. The areas under the canopies of *Quercus* sp., *Oreopanax xalapensis* and *Beilschmedia ovalis* trees were used as experimental units to determine if:

- microenvironmental conditions and macroinvertebrate communities are different under the canopies of contrasting species of trees

- decomposition rate and chemical evolution of decomposing leaves differ under the canopy of contrasting species of trees, independently of the quality of the litter being decomposed

- leaves of a given tree species ('foliar species') decompose and release nutrients at different rates under the influence of different canopies

- the macroinvertebrate community associated with a canopy tree species is exclusively related to the litter provided by the tree or its characteristics prevail even if the decomposing litter belongs to a different species.

Methods

The experiment presented in this chapter was carried out under the canopy of 12 experimental trees in the 100-year-old forest of the Tarantulas chronosequence (figure 2.6). Freshly fallen leaves collected from the forest floor were used in this experiment, being very careful to collect only those leaves that were most complete and unaffected by herbivory. The leaves were dried in a herbarium drier until they reached constant mass. Leaves were stored in paper bags in the laboratory at room temperature until processing.

The area under twelve trees belonging to three species (four *Beilschmiedia ovalis,* four *Oreopanax xalapensis* and four *Quercus laurina*) were used as experimental areas (figure 2.6). On 21-22 May 2001 four sets of litter boxes were buried 1.5 m away from the base of each tree trunk, facing north, south east and west under the litter layer. Each set consisted of four litter boxes containing each one of four species of leaves (*Pinus chiapensis, Beilschmiedia ovalis, Oreopanax xalapensis and Quercus laurina*). 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).

The day the experiment was set, two monoliths were extracted from the ground under each experimental tree (1 m away from the base of the trunk in a randomly selected direction). Every time a set of experimental boxes was collected, another two monoliths were extracted (one meter away on each side of the location of the experimental boxes, figure 2.6). Every time monoliths were extracted microenvironmental conditions were also measured. In the collection after 28 days soil temperature could not be measured as a result of a technical failure.

Details on monolith extraction, microenvironmental measurements, decomposition boxes construction, extraction and processing, macroinvertebrate sorting and identification and chemical analysis of experimental litter can be found in Chapter 2.

Statistical Analysis

Microenvironmental conditions and macroinvertebrate community under the canopy of different tree species

(a) Microenvironmental conditions, litter mass and soil bulk density under experimental trees

The effect of tree species (three levels), tree individual (nested within tree species, 12 levels) and collection date (four levels) on microenvironmental conditions, litter mass and soil bulk density (data pooled for the two monoliths) was tested with 3-way ANOVAs.

(b) Soil and litter macroinvertebrate communities under experimental trees

Three-way ANOVAs were used to test the effect of tree species (three levels), tree individual (nested within tree species, 12 levels) and collection date (four levels) on the diversity indices and the abundance of the most common macroinvertebrate taxa in the soil and litter under experimental trees.

(c) Relationship between macroinvertebrate community composition and environmental conditions

CCAs and Variance Partitioning were performed in three steps:

(1) General ordinations (followed by Variance Partitioning) of the macroinvertebrate communities in the soil and litter with respect to tree species (three dummy variables), collection date (four dummy variables), microenvironmental conditions (including litter mass and soil bulk density). These analysis were each run once including temperature and excluding the collection after 28 days and a second time excluding temperature and including the collection after 28 days. Because soil temperature turned out to be an important explanatory variable, the analyses described beyond this point included soil temperature and excluded the collection after 28 days.

(2) Seasonal effect. Ordinations of the litter and soil macroinvertebrate communities with respect to collection date and microenvironmental conditions, excluding the effect of tree species (three dummy variables as covariates)

(3) Permanent tree species effect. Ordinations of the litter and soil macroinvertebrate communities with respect to tree species excluding the effect of season (collection date and microenvironmental variables as covariates)

Details of the CCA and Variance Partitioning procedures can be found in Chapter 2.

Macroinvertebrate communities in experimental decomposition boxes placed under different tree species

(a) Diversity indices and abundance of most common taxa

For details of the analysis of diversity indices and abundance of most common taxa in experimental decomposition boxes see Chapter 2.

(b) Mass loss and chemical evolution in decomposition boxes

For details of the analyses of mass loss and chemical evolution during decomposition of experimental leaves in decomposition boxes see Chapter 2.

(c) Relationship between macroinvertebrate community composition in decomposition boxes, microenvironmental conditions and experimental treatments

CCAs and Variance Partitioning were performed in four steps:

(1) General ordination (followed by Variance Partitioning) of the macroinvertebrate communities in decomposition boxes with respect to tree species (three dummy variables), collection date (four dummy variables), foliar species (four dummy variables), microenvironmental conditions and nutrient, RF and ASF concentrations in remaining sample. These analysis

were each run once including temperature and excluding the collection after 28 days and a second time excluding temperature and including the collection after 28 days. Because soil temperature turned out to be an important explanatory variable, the analyses described beyond this point included soil temperature and excluded the collection after 28 days. When Variance Partitioning was performed, the foliar species in the box on its own did not explain a significant proportion of the variation in the invading community composition and therefore it was ignored as a factor in subsequent analyses.

(2) Season and chemical evolution effect. Ordination of the macroinvertebrate communities in decomposition boxes with respect to collection date and nutrient RF and ASF concentrations, excluding the effect of tree species (three dummy variables as covariates).

(3) Season and microenvironment effect. Ordination of the macroinvertebrate communities in decomposition boxes with respect to collection date and microenvironmental conditions, excluding the effect of tree species (three dummy variables as covariates).

(4) Permanent tree species effect. Ordination of the macroinvertebrate communities in decomposition boxes with respect to tree species excluding the effect of season (three dummy variables as covariates).

Details of the CCA and Variance Partitioning procedures can be found in Chapter 2.

In this chapter the Monte-Carlo randomisation tests are presented along with all CCAs. These randomisations were performed considering each of the experimental boxes as independent observations. However, placing the boxes in groups of four within each experimental tree (*O. xalapensis, B. ovalis, Quercus sp.* and *P. chiapensis*) introduces a block effect (individual tree) that is not considered in the randomisation test. Despite this limitation, the Monte-Carlo tests were a useful

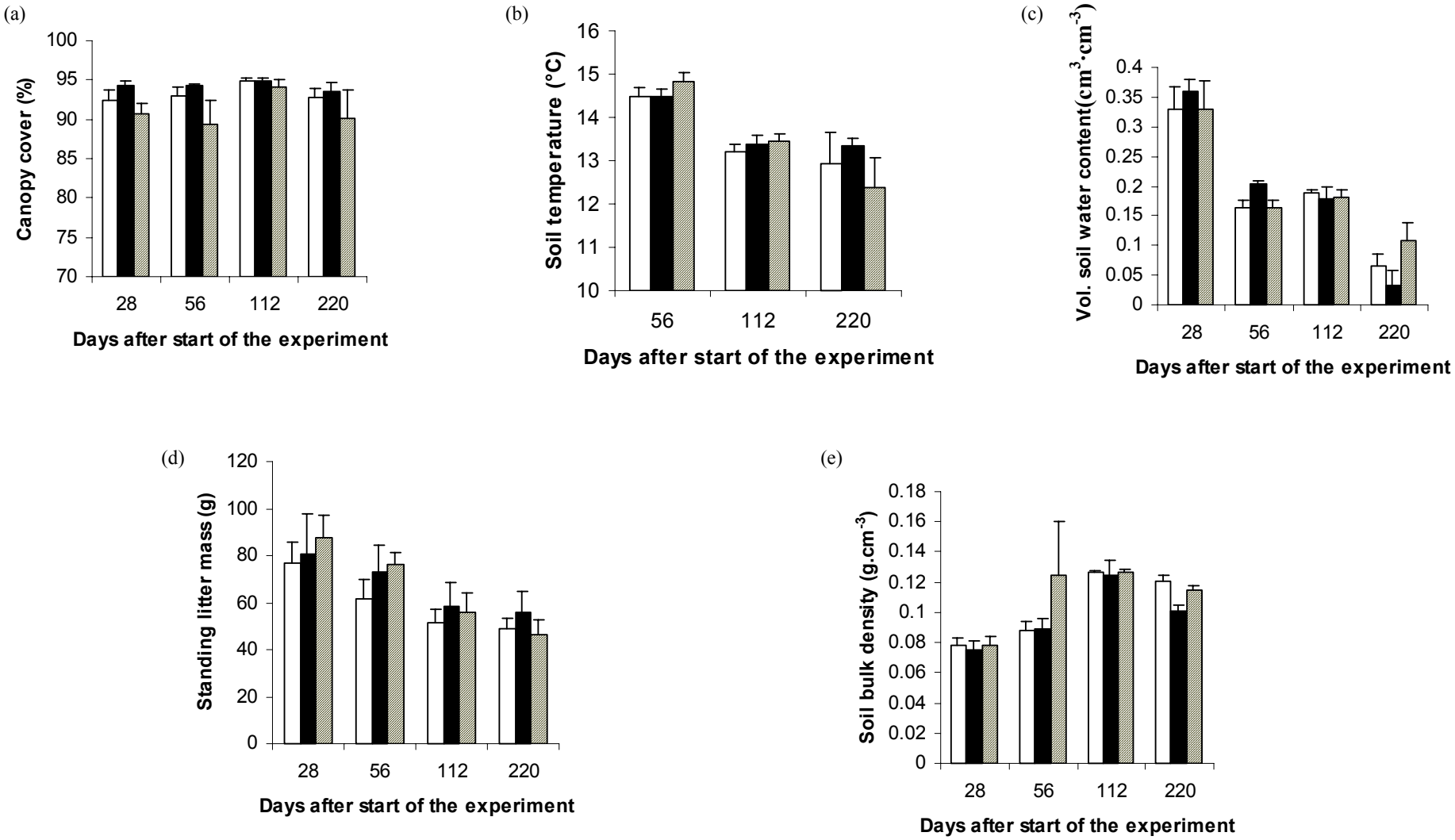


Figure 6.1 (a) Canopy cover, (b) soil temperature, (c) volumetric soil water content, (d) Standing litter mass per monolith and (e) Soil bulk density under the canopy of experimental trees measured 28, 56, 112 and 220 days after the start of the decomposition experiment. White bars represent *Quercus* sp trees, black bars *Beilschmedia ovalis* trees and grey bars *Oreopanax xalapensis* trees. Values presented are mean + standard error. Sample size (n) is 4 per tree species in each sampling date. Soil temperature is not available for the first sampling date.

preliminary way of testing the robustness of the patterns shown by the CCAs for spurious effects. Therefore randomisation tests should be interpreted conservatively bearing in mind that for the effect of tree species, individual boxes in each group are pseudo-replicates and only 4 real replicates exist per tree species per collection time.

Results

Microenvironmental conditions and macroinvertebrate community under the canopy of different tree species

Microenvironmental conditions

During the course of the experiment, the extent of canopy cover recorded under the crown of different tree species was not significantly different. However, there was a significant difference in canopy cover between collection dates regardless of the species of tree ($F=5.64$, d.f.=3, $P<0.01$)[1]. Canopy cover was higher in the collection after 112 days (figure 6.1a). In contrast for soil temperature ($F=4.30$, d.f.=4, $P<0.01$) and volumetric soil water content ($F=4.06$, d.f.=6, $P=0.001$) there was a significant interaction between collection date and tree species (figure 6.1b-c).

For all three species of trees, soil temperature was higher at the first collection date than at the third and fourth, but for *O. xalapensis* it diminished even further between the third and the fourth collections (figure 6.1b). Volumetric soil water content was highest at the first collection date, intermediate at the second and third, and lowest at the fourth. However, for *O. xalapensis* the drop in soil water content between the third and fourth collections was smaller than for the other species of trees (figure 6.1c).

The mass of standing litter per monolith was higher at the first collection date, intermediate at the second and lowest at the third and fourth ($F=14.92$, d.f.=3, $P<0.001$; figure 6.1d). Soil bulk density was lower during the first half of the experiment than in the second half (10.96, d.f.=3, $P<0.001$; figure 6.1e).

Macroinvertebrate community

(a) Number of macroinvertebrate taxa, equitability and Shannon's Diversity Index

The number of taxa, equitability and Shannon's index of diversity differed significantly between collection times in the litter ($F=11.54$, d.f.=4, $P<0.001$; $F=6.18$, d.f.=4, $P<0.001$ and $F=6.18$, d.f.=4, $P<0.001$) and soil ($F=25.66$, d.f.=4, $P<0.001$; $F=9.60$, d.f.=4, $P<0.001$ and $F=9.60$, d.f.=4, $P<0.001$) extracted under experimental trees. However, there was no significant effect of the tree species on these variables, except for the number of macroinvertebrate taxa in the soil where there was a significant interaction between collection time and tree species ($F=2.79$, d.f.=8, $P<0.05$).

In the litter, the number, equitability and Shannon's diversity index of macroinvertebrate taxa reached their maximum mean value in the samples collected 28 and 56 days after the start of the experiment (figure 6.2a-c). The lowest mean number of taxa was recorded at the last two collection dates, while the lowest equitability and Shannon's diversity indices were recorded only at the last collection date (figure 6.2a-c). In the soil, the number of taxa, equitability and Shannon's index of diversity increased steadily as the experiment proceeded, with the lowest values recorded at the first collection date. The highest values were recorded at the end of the experiment, except for the number of taxa under *O. xalapensis* that reached its maximum value in the third collection time (figure 6.2d-f).

Both in the litter and the soil there were significant differences in the number of macroinvertebrate taxa between the individual experimental trees that were used as replicas of the different tree species ($F=5.14$, d.f.=9, $P<0.001$ and $F=4.26$, d.f.=9, $P<0.001$).

[1] ANOVA tables including the error degrees of freedom for all F ratios, are given in Appendix CH6.

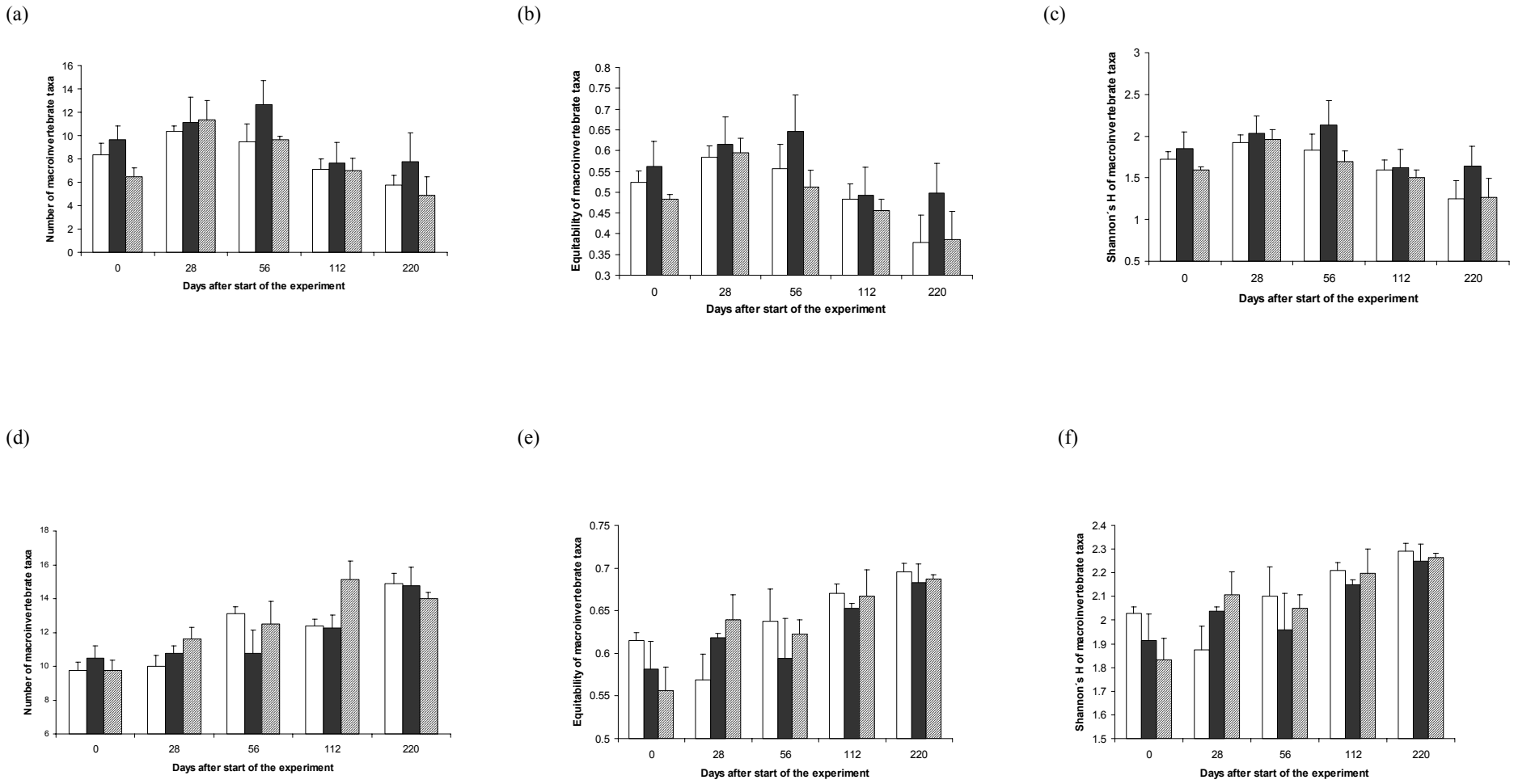


Figure 6.2 Number of taxa, equitability and Shannon's index of diversity in (a-c) litter and (d-e) soil under the canopy of experimental trees, measured 0, 28, 56, 112 and 220 days after the start of the decomposition experiment. White bars represent *Quercus* sp. trees, black bars *Beilschmedia ovalis* trees and grey bars *Oreopanax xalapensis* trees. Values presented are mean + standard error. Sample size (n) is four per tree species at each sampling date. Monoliths collected from each tree on the same collection date where pooled.

	Tree species (Ts)		Collection time (Ct)		Ts × Ct		
Macroinvertebrate taxon or larval group	**F-ratio (d.f.=2,36)**	**P-value**	**F-ratio (d.f.=3,36)**	**P-value**	**F-ratio (d.f.=6,36)**	**P-value**	**Rando-misation test**
Chilopoda	2.78	0.07	1.63	0.18	0.70	0.69	y
Diplopoda	3.08	0.06	4.77	<0.001	0.64	0.74	y
Pseudoescorpionida	1.96	0.15	3.45	0.02	0.54	0.82	y
Acari	1.30	0.28	4.03	0.01	0.32	0.95	y
Aranea	2.86	0.07	5.22	<0.001	4.39	<0.001	y
Coleoptera	0.10	0.90	3.19	0.02	0.28	0.97	y
Homoptera	0.66	0.52	1.20	0.32	0.77	0.63	y
Hemiptera	1.01	0.37	2.74	0.04	0.59	0.78	y
Formicidae	0.97	0.39	1.34	0.27	1.54	0.17	y
Diplura	4.37	0.02	1.05	0.39	0.69	0.70	y
Collembola	2.75	0.07	4.85	<0.001	0.70	0.69	y
Isopoda	1.89	0.16	0.83	0.51	0.30	0.96	y
Enchytraeidae	2.87	0.07	2.54	0.05	1.04	0.42	y
Coleoptera larvae	2.98	0.06	7.23	<0.0001	2.13	0.05	y
Diptera larvae	4.55	0.02	1.13	0.35	0.59	0.78	y
Lepidoptera larvae	0.31	0.74	1.09	0.37	1.85	0.09	y
Other pupae and larvae	2.98	0.06	7.23	<0.0001	2.13	0.05	y

Table 6.1. Summary of two-way analyses of variance comparing the macroinvertebrate abundance per taxon in the litter under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*) and collection time (28, 56, 112 and 210 days after placement). The number of taxa in the two monoliths per tree extracted in each collection date were pooled. The final column indicates whether a randomisation test was performed to determine the P-value (performed in case of failure to meet the assumptions of homogeneity of variance and normality that permit the use of standard F distribution curves). Taxa with a mean abundance greater than 0.5 per sample are included. Bonferroni adjusted significance level for multiple testing is P≤0.001.

(b) Abundance of the most common macroinvertebrate taxa

Seventeen macroinvertebrate groups were considered common because they reached a minimum mean abundance of 0.5 per monolith either in the soil or litter during the course of the experiment (tables 6.1 and 6.2; figure 6.3). Tree species alone (and not collection time) had a significant effect on the abundance of two of these taxa in the litter and not in the soil (comparison with P<0.05). The abundance of Diplura was always highest under the canopy of *B. ovalis*, followed by *Quercus* sp. and lowest under *O. xalapensis*. Diptera larvae were most abundant under the canopy of *B. ovalis*, followed by *O. xalapensis* and least abundant under *Quercus* sp. (tables 6.1 and 6.2; figure 6.3).

For six of the common taxa in the litter and nine in the soil, only collection time (and not tree species) had a significant effect (tables 6.1 and 6.2; figure 6.3) on their abundance. Frequently, the abundance of litter taxa peaked 28 or 56 days after the start of the experiment. This was the case for Diplopoda, Hemiptera, Collembola, Oligochatea and Pseudoescorpionida. However, the peak abundance of Acari in the litter was recorded after 220 days and of Coleoptera after 112 days. In the soil, the abundance of many taxa peaked in the monoliths collected at the end of the experiment. This was the case for Chilopoda, Homoptera, Diplura, Pseudoescorpionida and Diptera larvae. As an exception, the abundance of Enchytraeidae was highest after 56 days, while that of Coleoptera larvae was recorded 112 days after the start of the experiment (tables 6.1 and 6.2; figure 6.3).

	Tree species (Ts)		**Collection time (Ct)**		**Ts × Ct**		
Macroinvertebrate taxon or larval group	**F-ratio (d.f.=2,36)**	**P-value**	**F-ratio (d.f.=3,36)**	**P-value**	**F-ratio (d.f.=6,36)**	**P-value**	**Rando-misation test**
Chilopoda	2.86	0.07	14.55	<0.0001	0.71	0.68	y
Diplopoda	1.99	0.15	0.94	0.45	0.40	0.91	y
Pseudoescorpionida	1.38	0.26	8.39	<0.0001	0.75	0.65	y
Acari	0.79	0.46	34.24	<0.0001	4.39	0.001	y
Aranea	2.48	0.09	0.60	0.66	0.88	0.54	y
Coleoptera	1.23	0.30	19.92	<0.0001	3.02	0.01	y
Homoptera	0.54	0.59	6.13	0.001	0.72	0.67	y
Hemiptera	0.85	0.43	1.17	0.34	0.89	0.54	y
Formicidae	0.47	0.63	1.88	0.13	1.15	0.35	y
Diplura	0.44	0.65	9.29	<0.0001	1.54	0.17	y
Collembola	0.91	0.41	7.42	<0.0001	2.37	0.03	y
Isopoda	0.56	0.58	1.10	0.37	0.83	0.58	y
Enchytraeidae	1.29	0.29	2.75	0.04	0.84	0.58	y
Coleoptera larvae	1.34	0.27	19.98	<0.0001	1.38	0.23	y
Diptera larvae	1.15	0.33	30.98	<0.0001	0.83	0.58	y
Lepidoptera larvae	2.14	0.13	1.11	0.36	0.75	0.65	y
Other pupae and larvae	0.96	0.39	0.35	0.84	0.82	0.59	y

Table 6.2. Summary of two-way analyses of variance comparing the macroinvertebrate abundance per taxon in the soil under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*) and collection time (28, 56, 112 and 210 days after placement). The number of taxa in the two monoliths per tree extracted in each collection date were pooled. The final column indicates whether a randomisation test was performed to determine the P-value (performed in case of failure to meet the assumptions of homogeneity of variance and normality that permit the use of standard F distribution curves). Taxa with a mean abundance greater than 0.5 per sample are included. Bonferroni adjusted significance level for multiple testing is P≤0.001.

Tree species and collection time had a significantly interactive effect on the abundance of three common taxa in the litter and three in the soil (tables 6.1 and 6.2). In the litter this interaction was a result of the abundance of taxa being highest in a particular collection time under the canopy of *O. xalapensis*. Aranea were most abundant under this species of tree after 28 days, while Lepidoptera larvae and other larvae and pupae were most abundant 56 days after the start of the experiment. For Acari, Coleoptera and Collembola in the soil there was a general trend of increasing abundance with collection time. However, significant differences were recorded in the abundance of these taxa between tree species at particular collection dates. In the soil extracted after 56 days there was a significantly higher abundance of Acari under *Quercus* sp. trees, while in the soil extracted after 220 days this taxon was most abundant under *B. ovalis*. At the start of the experiment, Coleoptera were most abundant under *B. ovalis,* while after 112 days they were most abundant under *O. xalapensis*. In the case of the abundance of Collembola, there was no significant effect of collection time under *O. xalapensis* while under *Quercus* sp. and *B. ovalis* the lowest abundance was recorded after 112 days and the highest 220 days after the experiment had started.

Neither collection time nor tree species had a significant effect on the abundance of five common taxa in the litter (Chilopoda, Homoptera, Formicidae, Isopoda and Lepidoptera larvae) and seven taxa in the soil (Hemiptera, Formicidae, Isopoda, Lepidoptera larvae and other larvae and pupae (tables 6.1 and 6.2; figure 6.3).

Relationship between macroinvertebrate community composition and environmental conditions

A canonical correspondence analysis (CCA) of the macroinvertebrate community found in the soil and litter under experimental trees (table 6.3) showed a number of associations between community composition and the combination of environmental variables, tree species and collection time. In the litter the variables tested explained 56.9% of the total variance (or 43.7% when the collection after 28 days was included and the soil temperature was excluded from the analysis). In the soil, explanatory variables accounted for 36.9% of the variance of macroinvertebrate taxa (or 34.3% if

temperature was excluded and the first collection included). Owing to the significant proportion of variation in macroinvertebrate taxa explained by soil temperature, the analysis described beyond this point were all carried out excluding samples collected after 28 days and including soil temperature.

When the variance was partitioned among sets of variables (table 6.3), microenvironmental conditions accounted for the highest amount of explained variation (51.3% in the litter and 26.9% in the soil), followed by tree species in the litter (21.7%) and collection time in the soil (19.9%). The variables that explained the least variation were collection date in the litter (20.9%) and tree species (8.4%) for the soil. The tree species alone did not have a statistically significant effect on the composition of the soil community.

When the variance due to tree species was extracted as a covariate and collection time and environmental variables were included as explanatory variables in a CCA, 38.1% of the variance in litter macroinvertebrate taxa was explained (eigenvalues: unconstrained 1.258, canonical 0.506; figure 6.4). Fifty six days after the start of the experiment soil temperature and standing litter mass demonstrated the highest and soil bulk density the lowest values recorded during the experiment. In these conditions, the litter community under experimental trees had a number of characteristic components such as Orthoptera, Formicidae, Diplura Hemiptera and other larvae and pupae. After 112 days, soil temperature and standing litter mass had decreased and soil bulk density increased from the values recorded at 56 days. At this collection time, the abundance of Gasteropoda and Homoptera increased. At the final collection time, after 220 days, environmental conditions had not changed substantially compared to the previous collection except for a further reduction in standing litter mass. At this final collection date Chilopoda, Acari, and Hymenoptera became common in the litter community. Taxa such as Diplopoda, Pseudoescorpionida, Opiliones and diptera and lepidoptera larvae, were characteristic of the last two collections (112 and 220 days).

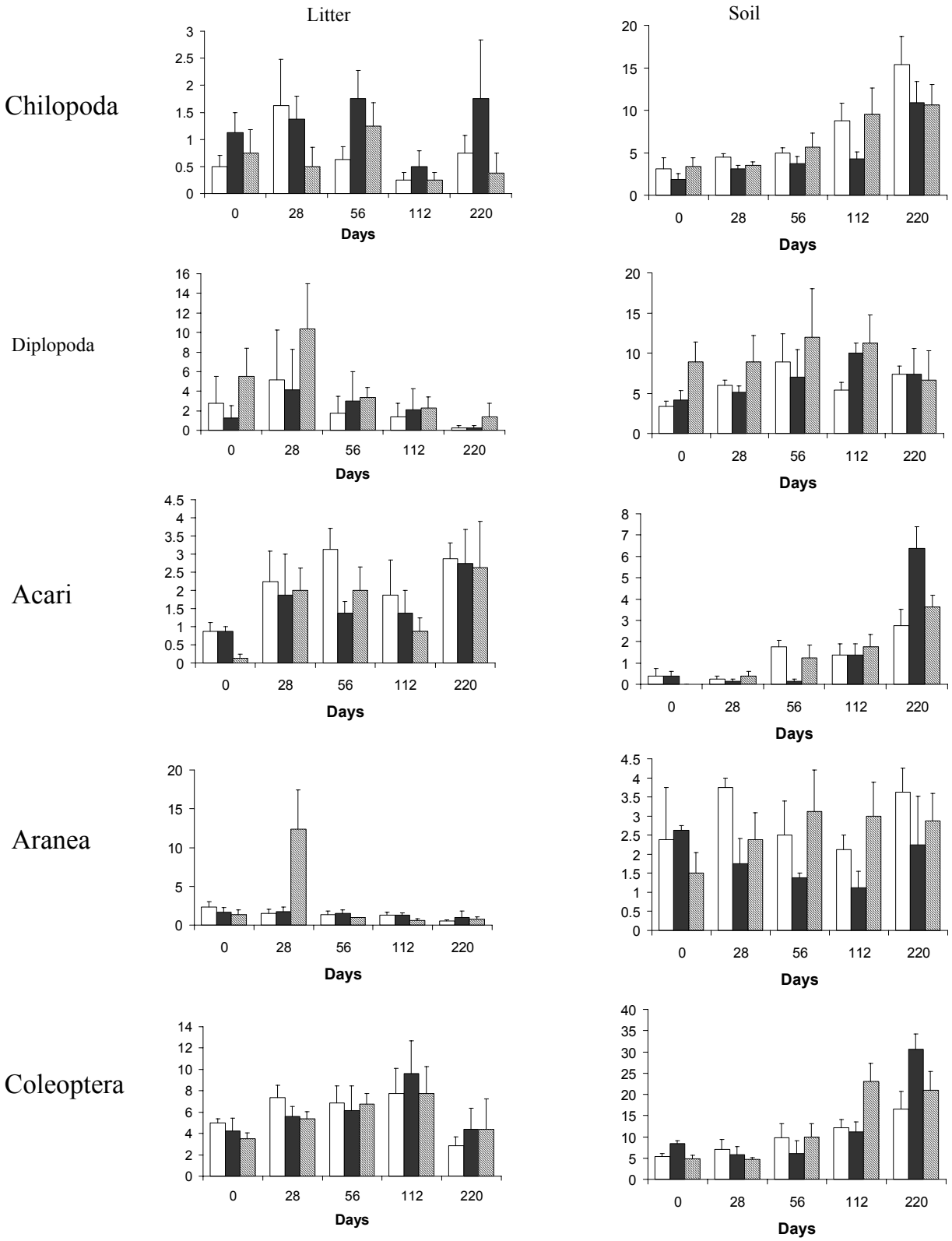


Figure 6.3 Abundance of macroinvertebrate taxa and larval group in the litter and soil under the canopy of experimental trees, measured 0, 28, 56, 112 and 220 days after the start of the decomposition experiment. White bars represent *Quercus* sp.trees, black bars *Beilschmedia ovalis* trees and grey bars *Oreopanax xalapensis* trees. Values presented are mean + standard error. Sample size (n) is four per tree species in each sampling date. The two monoliths collected from each tree on the same collection date where averaged.

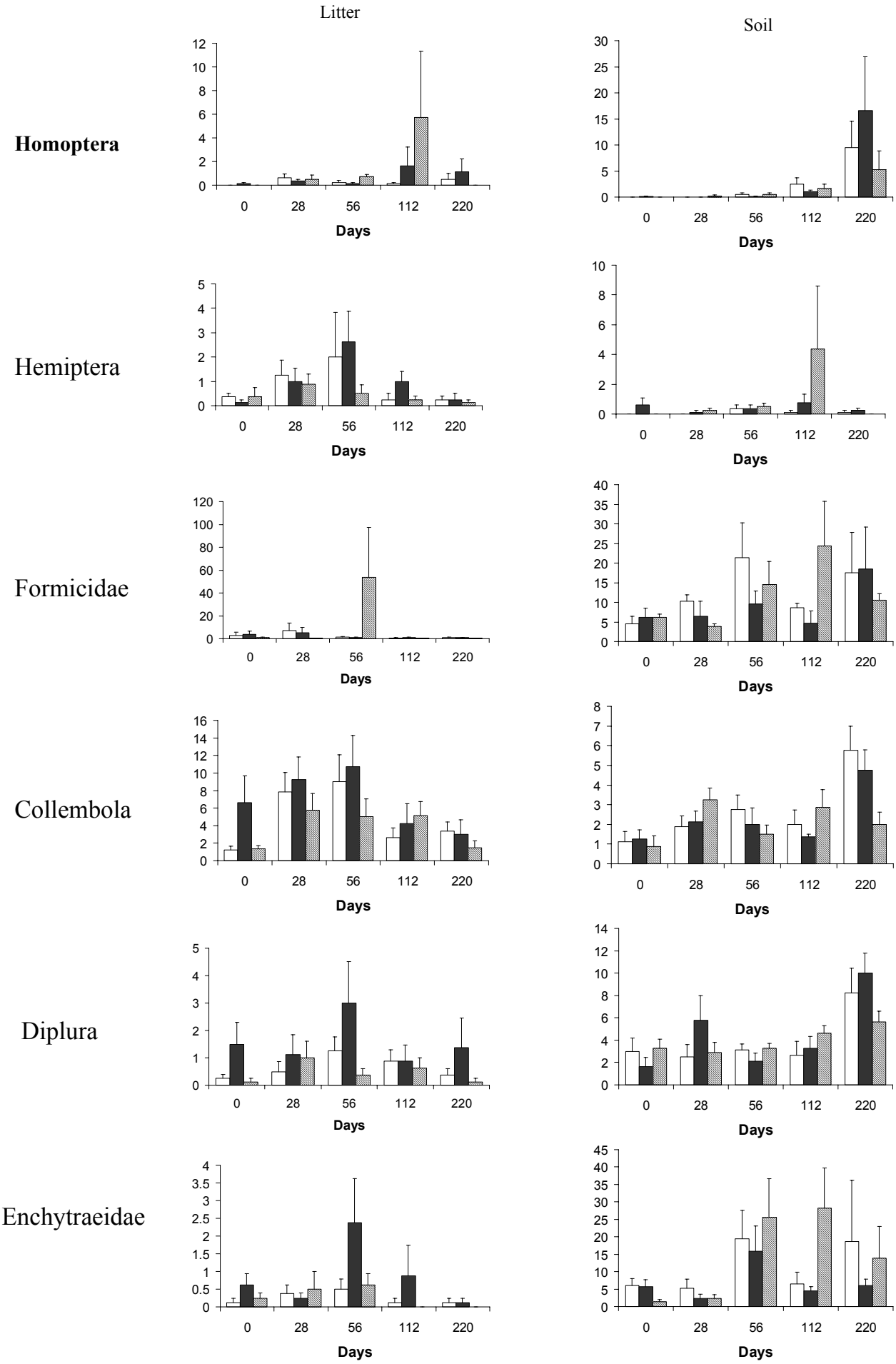


Figure 6.3 continuation...

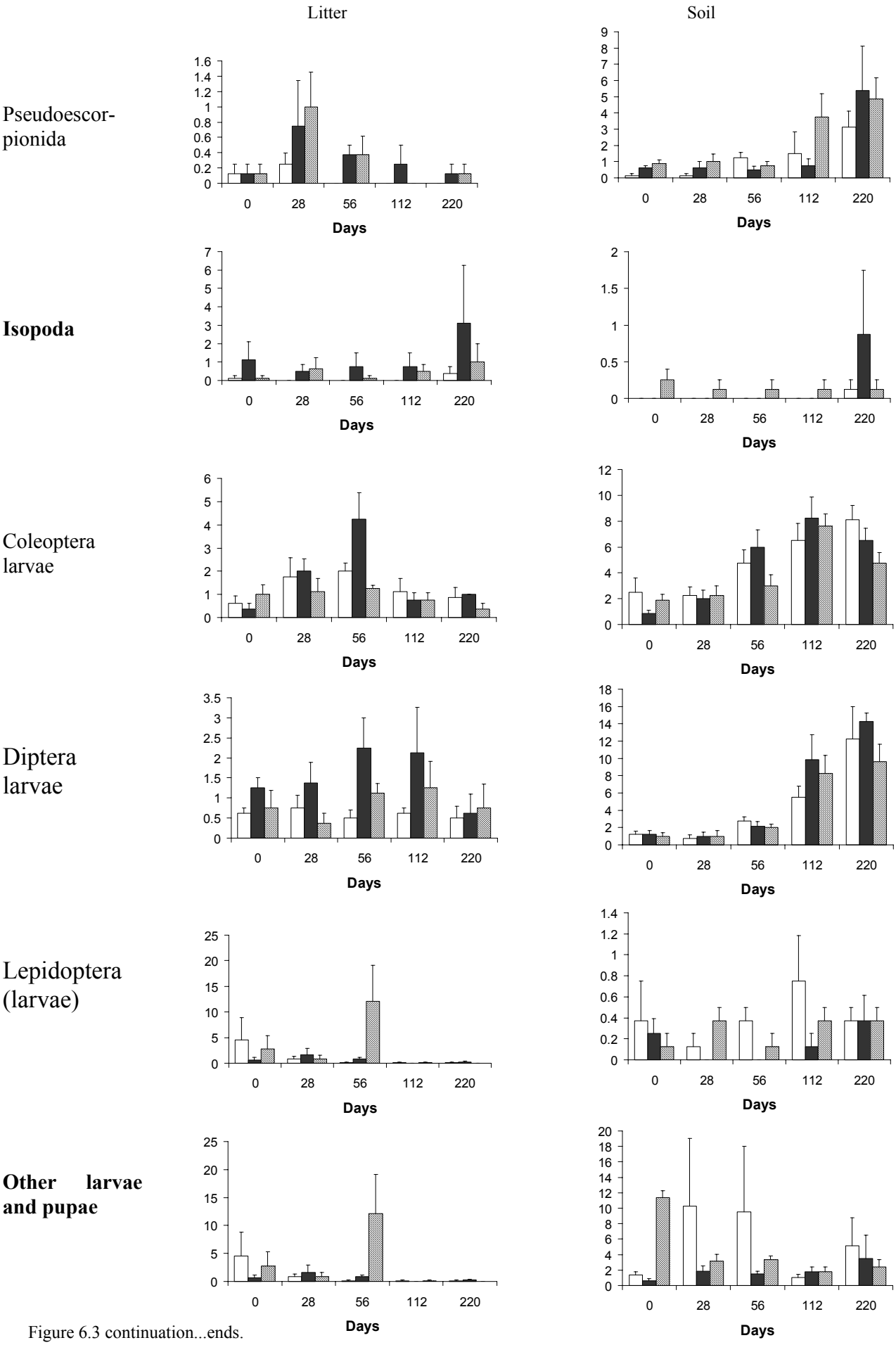


Figure 6.3 continuation...ends.

Groups of explanatory variables included in CCA	Extracted inertia	% of taxa variance explained (all axes)	Significance of Monte-Carlo test
Litter	Total:1.606		
Tree species	0.348	21.7	*
Collection date	0.335	20.9	*
microenvironment	0.836	51.3	*
All variables	0.972	56.9	*
Soil	Total: 0.611		
Tree species	0.051	8.4	n.s.
Collection date	0.122	19.9	*
Microenvironment	0.169	26.9	*
All variables	0.262	36.8	*

Table 6.3. Partitioning of the total inertia of monolith macroinvertebrate taxa in CCA amongst different groups of explanatory variables. Includes all experimental boxes. Analyses of litter and soil community presented separately. Notice that the CCAs were run independently from each other and therefore the sum of the extracted inertia per group of variables does not correspond to the extracted inertia by a single run including all variables. * denotes $P<0.05$ and n.s. denotes $P>0.05$ in Monte-Carlo significance tests.

The effect that the species of tree had on the composition of the litter community independently of the time of collection ('permanent tree species effect') was explored through a CCA of the macroinvertebrate data, introducing tree species as explanatory variables and collection time as a covariate (figure 6.5). The permanent tree species effect accounted for 21.0% of the variance in litter community composition under experimental trees (eigenvalues: unconstrained 1.411, canonical 0.296). The litter collected under *O. xalapensis* trees was characterised by the presence of Formicidae, other larvae and pupae, Homoptera and Hymenoptera (to a lesser extent), while the communities under *B. ovalis* had Enchytraeidae, Pseudoescorpionida, Isopoda, diptera larvae and Chilopoda as characteristic members. The communities under *Quercus* sp. were less distinct (as indicated by the position of the species centroid in the CCA biplot in figure 6.5), however, Orthoperta, Gasteropoda, Opiliones and Acari were frequent members. There was an important similarity in the communites found under *Quercus* sp. and *B. ovalis* trees. Taxa that characterised communities under both species of tree included Hemiptera, Aranea, Collembola and Coleoptera.

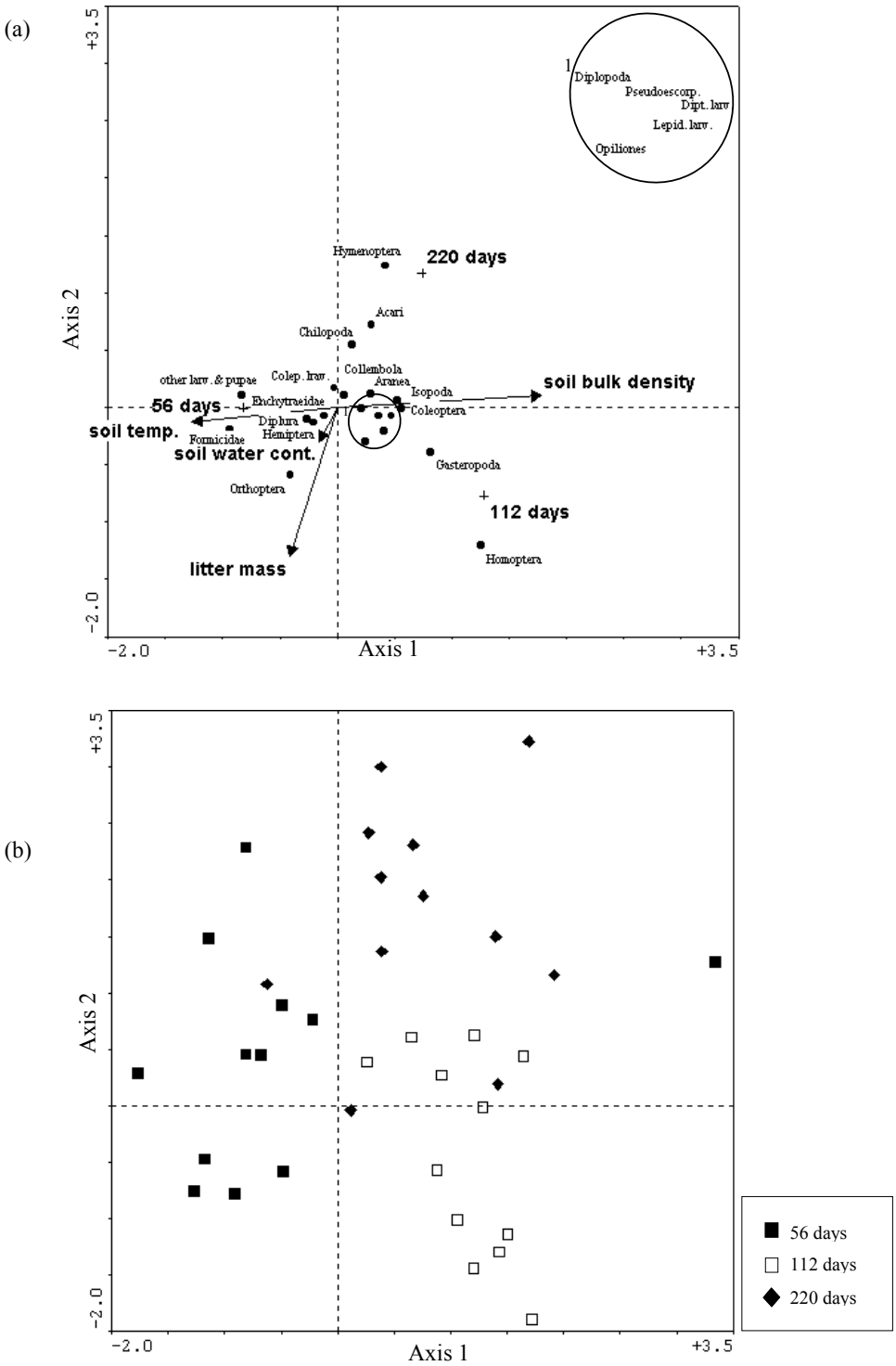


Figure 6.4. Relationship between the variation in microenvironment and litter community composition. Ordination diagrams based on canonical correspondance analyses of community composition in the litter collected under experimental trees. Community composition is ordinated with respect to collection time (dummy variables) and microenvironmental conditions. The species of trees has been introduced as dummy covariables. The first two axes account for 29.1% of variation, Monte-Carlo permutations significance test $p<0.005$ (taxa with fewer than five individuals in the experiment are excluded). (a) Biplot of taxa-explanatory variables and (b) sample scatterplots symbol coded by collection date. For clarity, inset in (a) provides labels for the taxa points within the ellipse denoted 1.

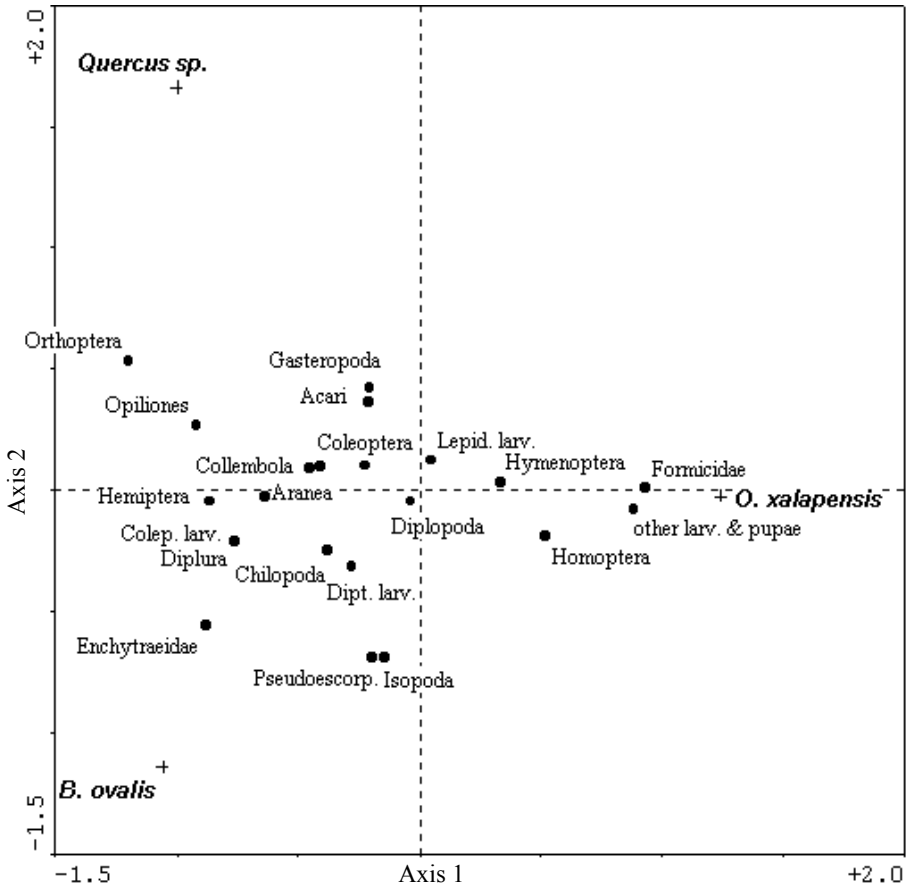


Figure 6.5 Relationship between tree species and litter community composition. Biplot of taxa-explanatory variables based on canonical correspondance analyses of community composition in the litter collected under experimental trees. Community composition is ordinated with respect to the species of tree. Collection time has been introduced as dummy covariables. The first two axes account for 21% of variation, Monte-Carlo permutations significance test $p<0.005$ (taxa with fewer than five individuals in the experiment were excluded). Note that sample scores are not plotted because all explanatory variables are dummy and sample scores are identical within treatments.

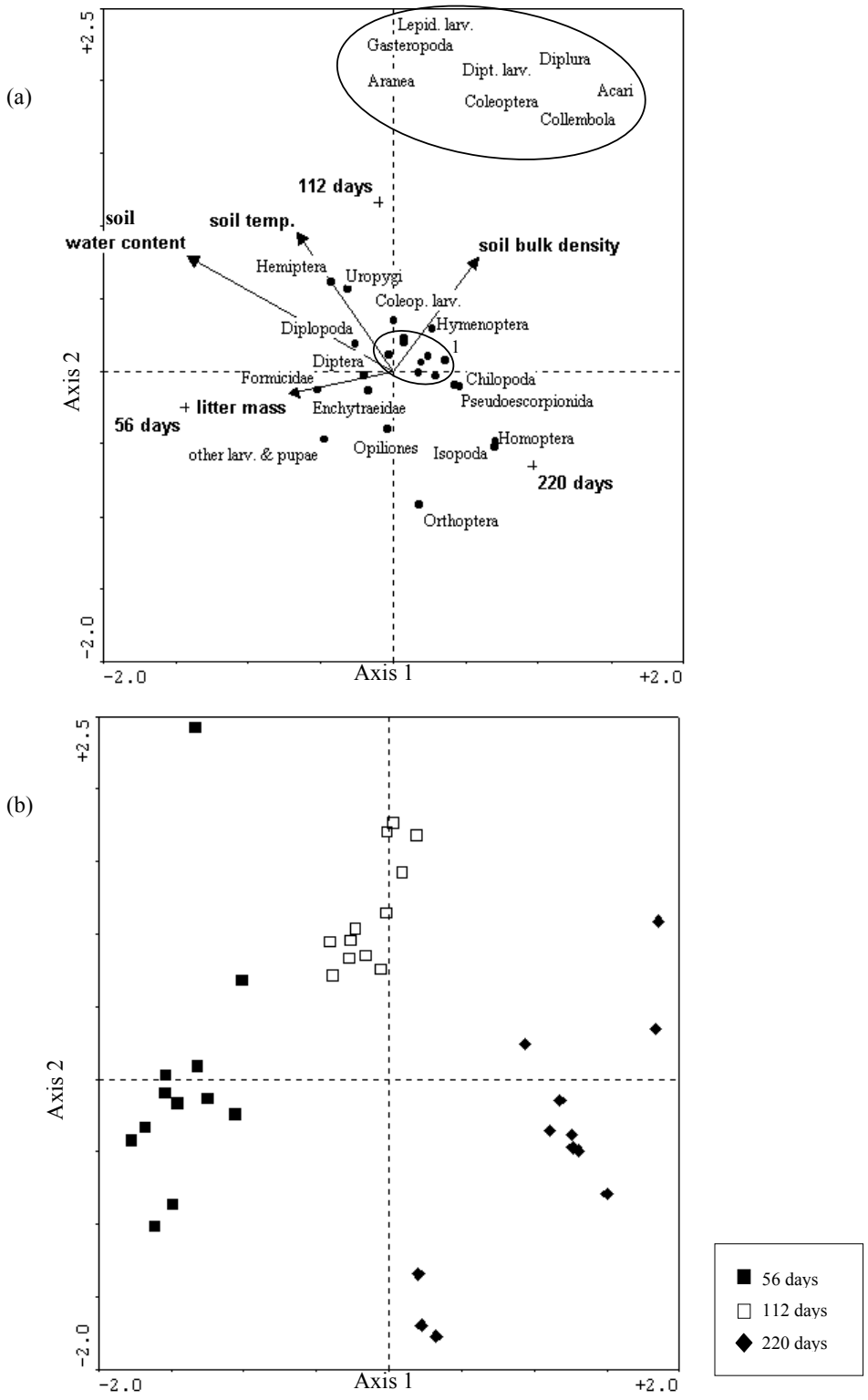


Figure 6.6. Relationship between the variation in microenvironment and soil community composition. Ordination diagrams based on canonical correspondance analyses of community composition in the soil collected under experimental trees. Community composition is ordinated with respect to collection time (dummy variables) and microenvironmental conditions. The first two axes account for 23.8 % of variation, Monte-Carlo permutations significance test $p<0.005$ (taxa with fewer than five individuals in the experiment were excluded). (a) Biplot of taxa-explanatory variables and (b) sample scatterplots symbol coded by collection date. For clarity, inset in (a) provides labels for the taxa points within the ellipse denoted 1.

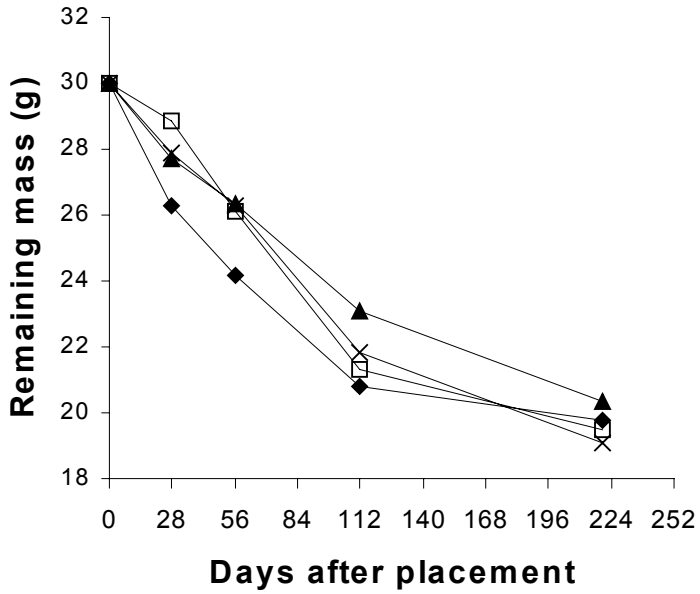
Nearly 31% of the variance in macroinvertebrate taxa was explained in a CCA of the community in the soil under experimental trees with respect to collection time and microenvironmental conditions together, groups of variables that were significant in the variance partitioning process (eigenvalues: unconstrained 0.611, canonical 0.200; table 6.4; figure 6.6). 56 days after the start of the experiment, standing litter mass, volumetric soil water content and soil temperature reached the highest values and soil bulk density its lowest. At this collection time, taxa such as Formicidae, Enchytraeidae and other larvae and pupae were characteristic of the soil community. After 112 days, when standing litter, volumetric soil water content and temperature had decreased, but soil bulk density had increased compared to the values after recorded after 56 days, Hemiptera, Uropygi and Coleoptera larvae became more common in the soil community. After 220 days when volumetric soil water content and litter mass reached a minimum, Orthoptera, Isopoda, Homoptera, Pseudoescorpionida and Chilopoda characterised the soil community.

Mass loss and chemical evolution during decomposition of Quercus sp., Beilschmedia ovalis, Oreopanax xalapensis and *Pinus chiapensis under the canopy of experimental trees.*

Mass loss

Tree species did not have a significant effect on the leaf mass remaining in the decomposition boxes throughout the experiment. However, there was a significant interaction between the effects of collection time and foliar species ($F=6.18$, $d.f=6.18$, $P<0.001$; figure 6.7). At the first two collection times (28 and 56 days after the start of the experiment) only the boxes containing *P. chiapensis* needles had less mass remaining than those containing the leaves of other species of leaves. However, after 112 days both the boxes containing *P. chiapensis* and *O. xalapensis* leaves, had less mass remaining than the boxes containing *Quercus* sp. or *B. ovalis* leaves. *B. ovalis* had the most mass remaining at this collection date. By the last collection date, there were no differences among foliar species with respect to the mass remaining in boxes with different species of leaves (figure 6.7b).

(a)



(b)

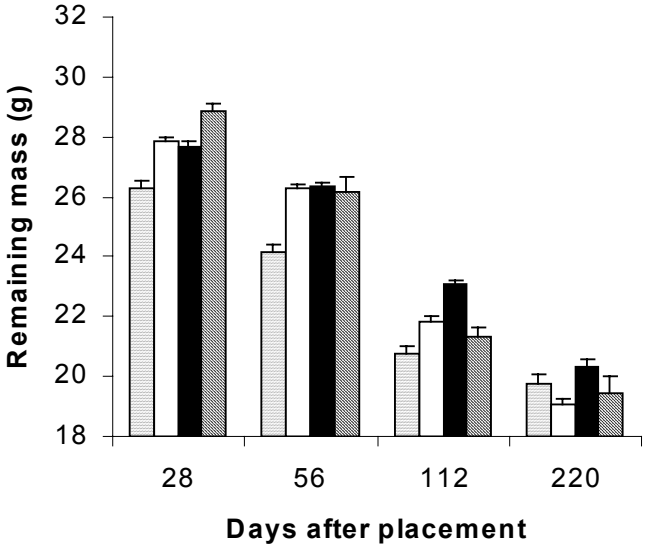


Figure 6.7 Mass loss through time in experimental decomposition boxes containing different species of leaves. (a) Mean values per foliar species are coded by the following symbols: × *Quercus* sp., ▲ *Beilschmedia ovalis*, □ *Oreopanax xalapensis* and ♦ *Pinus chiapensis*. Exponential decay constants (*k*) are 0.81 for *Quercus sp.*, 0.70 for *B. ovalis,* 0.80 for *O. xalapensis* and 0.83 for *P.chiapensis* leaves. (b) Light grey bars represent *P. chiapensis*, white bars represent *Quercus sp.*, black bars *Beilschmedia ovalis* and dark grey bars *Oreopanax xalapensis* leaves; values presented are mean + standard error. Sample size (n) is 12 per collection date per foliar species, except for the collection after 28 days where n= 11 for *O. xalapensis*. Values for boxes with the same species of leaves under different tree species were pooled.

***Beilschmedia ovalis* litter**																			
Forest age	**Days**	**C**		N		**P**		**Na**		**K**		**Ca**		**Mg**		**ASF**		**RF**	
Initial	0	15.89 g	56.15%	0.25 g	0.88%	0.04 cmol	1.50 $cmol.kg^{-1}$	0.01 cmol	0.40 $cmol.kg^{-1}$	0.13 cmol	4.79 $cmol.kg^{-1}$	1.02 cmol	36.06 $cmol.kg^{-1}$	0.57 cmol	20.40 $cmol.kg^{-1}$	0.98 g	3.46%	19.23 g	67.95%
		%of I.	%	%of I.	%	%of I.	cmol. Kg^{-1}	%of I.	cmol. Kg^{-1}	%of I.	cmol. Kg^{-1}	%of I.	cmol. Kg^{-1}	%of I.	cmol. Kg^{-1}	%of I.	%	%of I.	%
Under *B. ovalis*	28	99.86	56.24	126.63	1.13	109.61	1.65	43.85	0.18	66.94	3.22	67.50	24.42	98.06	20.07	108.92	3.78	97.52	66.47
	56	92.34	56.34	111.89	1.08	83.33	1.36	49.73	0.22	43.96	2.29	85.25	33.41	103.28	22.90	120.09	4.52	95.84	70.78
	112	80.72	56.14	100.77	1.11	86.68	1.62	33.78	0.17	26.22	1.56	65.72	29.36	66.17	16.72	96.41	4.14	76.85	64.68
	220	69.76	56.20	85.82	1.10	86.22	1.86	33.92	0.19	33.52	2.31	59.84	30.96	70.95	20.76	85.30	4.24	65.67	64.03
O. xalapensis	28	96.36	56.20	107.01	0.99	96.95	1.52	67.47	0.28	59.67	2.97	90.75	33.99	111.27	23.58	102.15	3.67	96.38	68.03
	56	93.74	56.25	136.50	1.30	84.83	1.36	61.80	0.26	63.63	3.26	73.95	28.50	107.16	23.36	130.42	4.83	93.73	68.07
	112	82.16	56.00	104.95	1.13	75.34	1.38	58.02	0.28	51.36	2.99	84.13	36.83	98.03	24.28	80.30	3.38	80.37	66.30
	220	73.74	55.76	83.13	1.00	93.37	1.89	63.46	0.34	41.66	2.69	55.53	26.97	79.82	21.93	93.07	4.34	68.39	62.59
Quercus spp.	28	97.81	56.32	102.91	0.94	81.09	1.25	52.51	0.22	224.16	11.03	80.19	29.65	103.23	21.59	99.24	3.52	97.08	67.65
	56	93.80	56.32	128.48	1.22	111.33	1.79	51.48	0.22	52.14	2.67	74.26	28.64	108.59	23.69	129.19	4.78	94.91	68.97
	112	81.82	56.11	102.26	1.11	92.60	1.70	30.77	0.15	37.37	2.19	72.03	31.73	81.88	20.40	83.17	3.52	78.90	65.49
	220	71.43	56.01	107.18	1.33	85.55	1.80	45.15	0.25	46.86	3.14	59.00	29.72	74.16	21.13	87.64	4.24	66.84	63.43
***Oreopanax xalapensis* litter**																			
Initial	0	15.53 g	55.32%	0.32 g	1.00%	0.06 cmol	1.83 $cmol.kg^{-1}$	0.38 cmol	0.49 $cmol.kg^{-1}$	1.41 cmol	11.97 $cmol.kg^{-1}$	1.11 cmol	44.55 $cmol.kg^{-1}$	1.11 cmol	35.05 $cmol.kg^{-1}$	0.72 g	2.28%	15.51 g	48.93%
		%of I.	%	%of I.	%	%of I.	cmol. Kg^{-1}	%of I.	cmol. Kg^{-1}	%of I.	cmol. Kg^{-1}	%of I.	cmol. Kg^{-1}	%of I.	cmol. Kg^{-1}	%of I.	%	%of I.	%
Under *B. ovalis*	28	93.75	55.44	154.14	1.66	79.54	1.56	46.09	0.25	54.15	6.93	61.21	29.15	92.03	34.48	111.87	2.73	93.23	48.77
	56	85.32	55.67	117.29	1.40	69.19	1.49	57.30	0.34	32.76	4.63	75.26	39.55	93.33	38.59	120.64	3.25	92.12	53.17
	112	68.17	55.52	104.76	1.56	63.71	1.72	43.80	0.32	12.10	2.13	71.93	47.18	68.03	35.11	99.09	3.33	70.32	50.66
	220	60.46	55.38	82.44	1.38	70.92	2.15	33.66	0.28	10.59	2.10	52.29	38.58	64.06	37.18	100.10	3.78	68.47	55.48
O. xalapensis	28	90.19	55.30	113.70	1.27	105.18	2.13	182.99	1.01	59.56	7.91	300.91	148.61	121.66	47.27	113.48	2.87	86.54	46.94
	56	81.48	55.71	101.57	1.27	73.32	1.66	90.19	0.56	44.45	6.58	69.12	38.06	91.74	39.75	123.09	3.47	84.42	51.06
	112	67.82	55.25	107.08	1.59	77.98	2.10	48.16	0.35	22.28	3.93	69.00	45.27	72.84	37.60	101.05	3.39	69.61	50.17
	220	61.56	55.21	77.12	1.26	68.72	2.04	50.68	0.41	17.80	3.45	62.72	45.30	69.74	39.63	99.57	3.68	59.73	47.38
Quercus spp.	28	90.37	55.57	135.64	1.52	76.48	1.56	89.65	0.50	48.86	6.50	89.72	44.43	93.35	36.37	110.78	2.81	89.21	48.52
	56	81.97	55.45	123.27	1.52	85.83	1.92	97.17	0.59	61.07	8.94	84.24	45.89	93.55	40.10	197.89	5.52	85.82	51.35
	112	66.20	55.55	116.23	1.78	70.51	1.96	28.09	0.21	11.71	2.13	68.05	45.99	57.86	30.76	85.84	2.97	73.86	54.82
	220	62.27	55.41	85.59	1.39	71.75	2.11	52.11	0.42	14.68	2.83	53.68	38.47	64.93	36.61	82.65	3.03	72.43	57.02

Table 6.5 Mean concentration and remaining absolute amount of nutrients, RF and ASF in experimental leaves at the time of recovery. Treatments consisted of experimental tree species (*Beilschmedia ovalis*, *Oreopanax xalapensis* and *Quercus spp*.), collection time (28, 56, 112 and 210 days after placement) and foliar species contained in the box (*B. ovalis*, *O. xalapensis*,

*Quercus spp.*and *Pinus chiapensis*). The remaining amount of nutrients is expressed in terms of percentage of the initial absolute quantity in original 30g litter sample (%of I.), except for the initial value, where it is expressed in grams or centimoles. Continues in the next page.

***Pinus chiapensis* litter**																			
Forest age	**Days**	**C**		**N**		**P**		**Na**		**K**		**Ca**		**Mg**		**ASF**		**RF**	
Initial	0	16.94 g	56.76%	0.38 g	1.29%	0.07 cmol	2.43 $cmol.kg^{-1}$	0.01 cmol	0.32 $cmol.kg^{-1}$	0.11 cmol	3.73 $cmol.kg^{-1}$	0.72% cmol	24.10 $cmol.kg^{-1}$	0.16 cmol	5.25 $cmol.kg^{-1}$	0.90 g	3.04%	16.86 g	56.47%
		%of I.	**%**	**%of I.**	**%**	**%of I.**	**cmol. Kg^{-1}**	**%of I.**	**cmol. Kg^{-1}**	**%of I.**	**cmol. Kg^{-1}**	**%of I.**	**cmol. Kg^{-1}**	**%of I.**	**cmol. Kg^{-1}**	**%of I.**	**%**	**%of I.**	**%**
Under *B. ovalis*	28	88.47	56.50	93.47	1.35	104.48	2.86	101.73	0.36	59.64	3.49	104.06	28.10	94.28	6.59	144.20	4.96	85.44	44.84
	56	81.09	56.69	90.67	1.44	97.42	2.92	66.40	0.26	32.53	2.74	83.86	30.89	78.66	6.09	90.86	5.40	74.91	59.42
	112	71.10	56.77	80.51	1.46	88.99	3.05	79.38	0.35	32.13	1.71	63.97	28.42	66.39	5.81	107.63	3.88	69.78	59.50
	220	66.26	56.68	71.83	1.39	87.69	3.22	97.62	0.47	64.80	1.81	100.93	23.23	99.50	5.25	98.11	4.93	89.68	59.39
O. xalapensis	28	87.79	56.68	86.76	1.27	101.16	2.80	120.71	0.44	48.29	2.75	118.90	27.66	90.44	5.94	121.53	3.39	84.85	57.60
	56	80.39	56.73	92.09	1.47	101.56	3.07	96.37	0.38	32.62	2.24	85.74	35.63	68.78	5.90	92.79	4.59	76.33	59.57
	112	70.18	56.78	94.48	1.73	84.21	2.92	58.19	0.26	28.18	1.74	58.61	29.45	62.83	5.15	113.80	4.02	69.34	61.43
	220	65.21	56.68	65.06	1.28	76.45	2.85	51.84	0.25	305.35	1.61	95.70	21.63	102.95	5.05	116.11	5.29	89.12	59.97
Quercus spp.	28	87.52	56.71	89.79	1.32	87.92	2.44	102.23	0.37	71.83	13.02	47.47	26.33	116.10	6.17	109.98	4.03	86.00	57.45
	56	80.81	56.44	90.65	1.44	98.67	2.96	74.33	0.29	37.31	3.30	78.28	14.08	66.71	7.50	81.99	4.11	70.81	59.76
	112	67.47	56.63	85.27	1.62	82.94	2.99	38.54	0.18	33.94	2.06	62.99	27.90	74.50	5.18	92.80	3.68	72.25	59.13
	220	67.00	56.68	74.95	1.44	77.61	2.82	75.80	0.36	59.64	1.89	104.06	22.62	94.28	5.83	144.20	4.20	85.44	60.81
Quercus spp litter																			
Initial	**0**	**16.01 g**	**56.80%**	**0.31 g**	**1.10%**	**0.03 cmol**	**0.95%**	**0.01 cmol**	**0.24%**	**0.04 cmol**	**1.28%**	**0.75 cmol**	**26.60%**	**0.40 cmol**	**14.18%**	**1.02 g**	**3.63%**	**16.80 g**	**59.61%**
		%of I.	**%**	**%of I.**	**%**	**%of I.**	**cmol. Kg^{-1}**	**%of I.**	**cmol. Kg^{-1}**	**%of I.**	**cmol. Kg^{-1}**	**%of I.**	**cmol. Kg^{-1}**	**%of I.**	**cmol. Kg^{-1}**	**%of I.**	**%**	**%of I.**	**%**
Under *B. ovalis*	28	98.37	56.79	92.94	1.04	84.78	0.82	34.18	0.08	393.20	5.13	69.04	18.67	102.31	14.75	141.65	5.23	97.38	59.00
	56	91.98	56.41	76.05	0.91	68.46	0.70	49.91	0.13	90.25	1.25	71.50	20.54	101.94	15.61	125.26	4.91	97.43	62.70
	112	77.48	56.76	80.40	1.15	74.02	0.91	58.28	0.18	80.46	1.33	85.14	29.21	70.18	12.84	82.25	3.85	76.01	58.43
	220	66.35	56.58	61.92	1.03	144.14	2.06	51.45	0.18	106.13	2.05	63.91	25.52	60.50	12.88	82.71	4.51	67.78	60.65
O. xalapensis	28	99.01	56.82	85.59	0.96	101.81	0.98	37.70	0.09	115.09	1.49	82.31	22.12	97.48	13.97	107.23	3.93	98.13	59.09
	56	94.19	56.82	84.54	0.99	71.62	0.72	76.71	0.19	72.72	0.99	76.35	21.56	95.94	14.45	135.18	5.21	100.07	63.34
	112	77.94	56.73	77.24	1.09	76.90	0.94	48.67	0.15	81.17	1.34	92.67	31.59	74.00	13.45	68.07	3.17	80.87	61.76
	220	68.43	56.54	66.98	1.08	138.28	1.91	83.73	0.29	97.54	1.82	69.17	26.77	61.83	12.76	96.45	5.10	66.38	57.57
Quercus spp.	28	99.40	56.84	70.42	0.78	77.55	0.74	63.74	0.15	116.10	1.50	96.95	25.96	109.08	15.57	152.54	5.58	96.24	57.75
	56	92.91	56.91	82.74	0.99	82.35	0.84	79.68	0.21	66.37	0.92	78.89	22.63	106.24	16.25	130.81	5.12	100.21	64.41
	112	76.80	56.69	79.32	1.14	105.90	1.31	38.03	0.12	96.18	1.60	71.68	24.78	68.30	12.59	103.30	4.88	77.11	59.73
	220	67.39	56.62	59.70	0.98	76.34	1.07	56.28	0.20	96.33	1.83	63.69	25.06	52.22	10.95	96.69	5.19	67.86	59.83

Table 6.5 Continuation.

The differences in decomposition rates between species of leaves were reflected in the difference of exponential decay constants *k* (figure 6.7a). However, similarly to the pattern found in the decomposition experiment presented in Chapter 5, asymptotes for all four species appear to be well beyond zero (figure 6.7a), showing that the litter is formed by two components, one that decays exponentially in the first year of decomposition and a second that is resistant to decay in this initial phase.

Chemical evolution

As it was discussed in Chapter 3, in this study the proportions found for ASF and RF fibre fractions in the abscised leaves of four tree species (*Pinus chiapensis*, *Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*) do not appear to correspond to the conventional fractions found by most authors using the same extraction technique (Van Soest, 1994). This discrepancy was discussed in detail in Chapter 3, therefore the reader is referred to p.102 and table CH3.19 in Appendix CH3 for details. Here it should be sufficient to say that it is evident that the range of ASF values in this study is considerably lower and that of RF considerably higher than the concentrations reported in the literature. Therefore ASF and RF have only been interpreted as representing fibrous fractions of the litter that are relatively more and less labile.

Sixty two percent of the variance in the nutrient, ASF and RF concentration variables was accounted for by three principal components (from here on termed foliar quality components; table 6.4). The first foliar quality component (PCA1) accounted for 33.7% of the total variance and was mostly determined by the contrasting variation in carbon and RF in one direction and calcium and magnesium in the other (see factor loadings in table 6.4). The second component (PCA2) extracted 17.3% of the total variance and represented mainly the variation in phosphorus and nitrogen in one direction and calcium in the other. The third component (PCA3) accounted for 10.9% of the variance and was mainly determined by the variation in ASF, sodium and magnesium in one direction and the variation in nitrogen in the other.

	Factor loading		
Variable	**Axis 1**	**Axis 2**	**Axis 3**
Total Carbon	**-0.81**	**-0.27**	-0.20
Total Nitrogen	0.36	**-0.67**	**0.38**
P	0.20	**-0.87**	-0.16
MG^{++}	**0.64**	-0.20	**-0.37**
NA^{+}	0.45	0.06	**-0.54**
K^{+}	0.58	0.04	-0.29
CA^{++}	**0.81**	**0.44**	0.06
ASF	-0.43	-0.08	**-0.47**
RF	**-0.64**	0.18	-0.20
Eigenvalues	3.03	1.55	0.98
% of Variance extracted	33.7	17.3	10.9

Table 6.4. Principal Component Analysis of the nutrients, RF and ASF concentrations in the leaves remaining in experimental boxes at the time of recovery. Boxes from all treatments included. Tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), collection time (0, 28, 56, 112 and 210 days after placement) and species of leaf contained in the box (*Quercus* sp., *Beilschmedia ovalis, Oreopanax xalapensis* and *Pinus chiapensis*) were the experimental treatments. The four highest absolute values of factor loadings are highlighted in bold.

There were significant differences between foliar species in the concentration of nutrients, RF and ASF at the start of the experiment (see Chapter 3, figure 3.6). These initial differences were reflected in differences between the mean values of PCA1 ($F=0.07$, d.f.=3, $P<0.0001$) and PCA2 ($F=0.08$, d.f.=3, $P<0.0001$) at the start of the experiment and prevailed throughout the experiment (figure 6.8a-b). During the experiment the mean value of PCA1 was higher for *Oreopanax xalapensis* than for the other foliar species ($F=2.98$, d.f.=9, $P<0.01$; figure 6.8a and 6.9). This implies that *O. xalapensis* leaves always had higher concentrations of calcium and magnesium and lower concentrations of total carbon and RF than the other foliar species. The mean value of PCA2 was lower for *Pinus chiapensis* than for the other foliar species ($F=2.07$, d.f.=9, $P<0.05$; figure 6.8a-b). This reflects the fact that the concentration of phosphorus and total nitrogen was significantly higher and calcium lower in *P. chiapensis* than in the other species (see Chapter 3, figure 3.6).

At the start of the experiment, there was no significant difference between foliar species in the mean value of PCA3. However, when the boxes retrieved throughout the experiment were considered a small but significant interactive effect between foliar species and tree species was recorded ($F=2.53$, d.f.=6, $P<0.05$; figure 6.8b). *O. xalapensis* displayed a significantly higher PCA3 mean value than the other species, particularly when placed under *B. ovalis* and *Quercus* sp. This reflects the fact that

O. xalapensis developed the highest concentrations of nitrogen through the experiment (table 6.5).

The species of tree under which the experiment was carried out had a significant interactive effect with foliar species on the value of PCA1 ($F=2.49$, d.f.=6, $P<0.05$; figure 6.9). This interaction was a result of significant differences between *O. xalapensis* leaves decomposing under different tree species. Decomposition boxes containing *O. xalapensis* leaves that decomposed under the canopies of *O. xalapensis* trees recorded the highest value of PCA1, those under the canopies of *Quercus* sp. trees demonstrating intermediate values and those decomposing under *B. ovalis* trees recording the lowest values. In consequence those *O. xalapensis* leaves that decomposed under the canopy of *O. xalapensis* trees had the higher concentrations of magnesium and calcium and lower concentrations of RF and total carbon compared to those under other canopy tree species. Conversely, *O. xalapensis* leaves decomposing under the canopy of *B. ovalis* had the lowest concentrations of magnesium and calcium and the highest concentrations of RF and total carbon.

Collection time and foliar species had a significant interactive effect on PCA1 ($F=2.98$, d.f.=9, $P<0.01$) and PCA2 ($F=2.07$, d.f.=9, $P<0.05$; figure 6.10 a-b). In the case of PCA1 this interaction was because collection date only had a significant effect on the boxes containing *Quercus* sp. leaves and no significant effect on other species. For *Quercus* sp., PCA1 reached its lowest value after 56 days of decomposition, and its highest value at the end of the experiment (figure 6.10a). In consequence, during the first 56 days of decomposition of *Quercus* sp. leaves, the concentrations of carbon and RF increased while the concentrations of calcium and magnesium decreased. After 56 days, the converse pattern was recorded. The concentrations of carbon and RF decreased and the concentrations of calcium and magnesium increased. The interactive effect of foliar species and collection time on PCA2 was a consequence of the effect of collection time on *Quercus* sp. and *B. ovalis* leaves, but not on *O. xalapensis* or *P. chiapensis* leaves (figure 6.10 b). In *Quercus* sp. and *B. ovalis* leaves, the values of PCA2 decreased with the progression

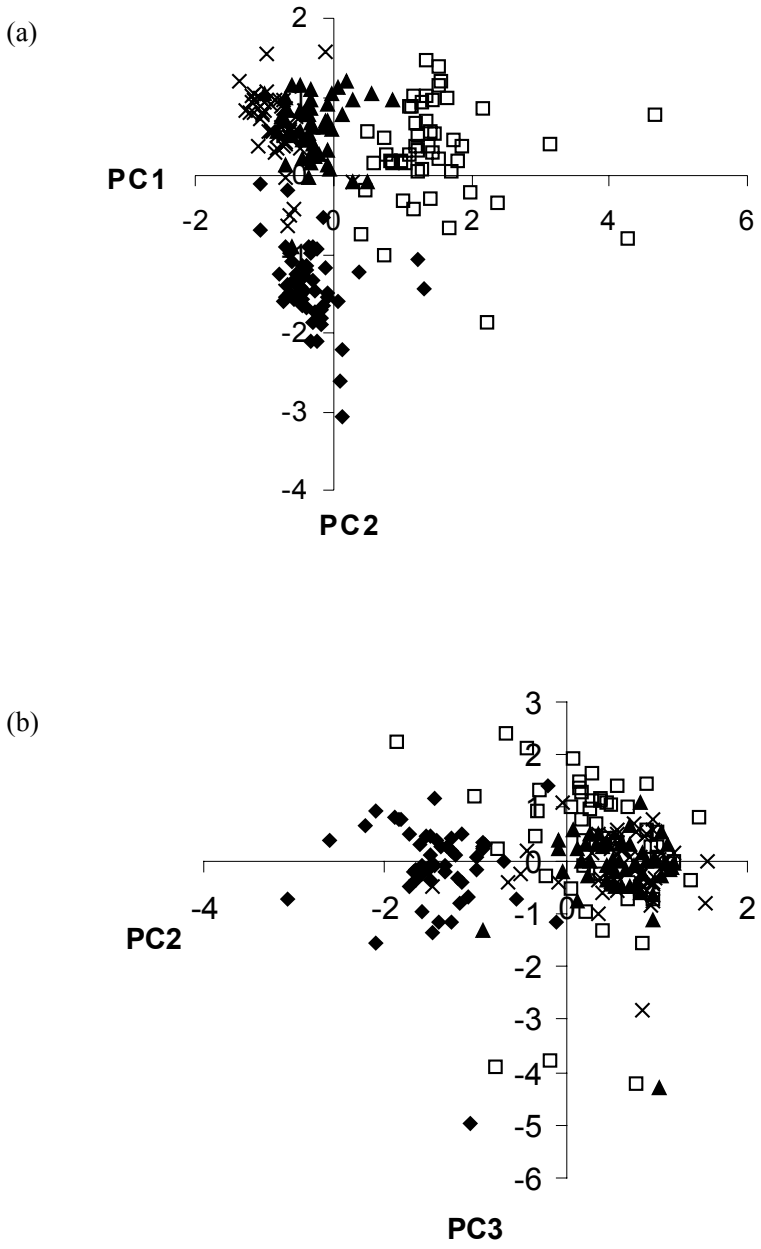


Figure 6.8 Ordination diagrams based on principal component analyses of nutrients, ASF and RF concentrations in decomposition boxes at the time of collection. Variables included in the components were Carbon (%), Nitrogen (%), P (cmol.kg^{-1}), Mg^{++}(cmol.kg^{-1}), Na^{+}(cmol.kg^{-1}), K^{+}(cmol.kg^{-1}) and Ca^{++}(cmol.kg^{-1}). Sample scores plotted for (a) principal component one (PCA1) against PCA2 and (b) PCA2 against PCA3. Foliar species are coded with the following symbols: × *Quercus sp*., ▲*Beilschmedia ovalis*, □ *Oreopanax xalapensis* and ♦*Pinus chiapensis*.

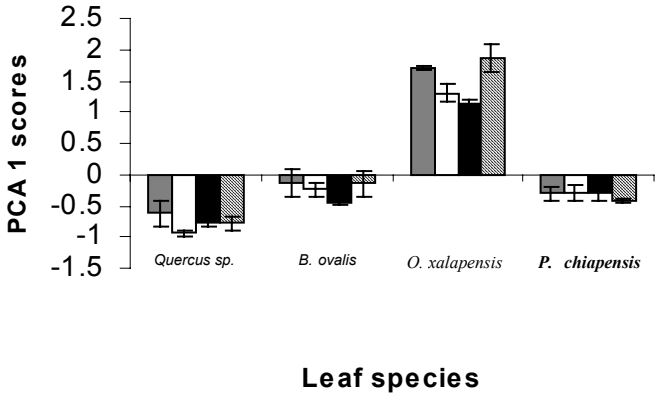


Figure 6.9 Graphs illustrating interactive effect between experimental tree species and decomposing foliar species on the first principal component formed by nutrients, ASF and RF concentration variables in decomposition boxes. Variables included in the PCA were Carbon (%), Nitrogen (%), P (cmol.kg^{-1}), Mg^{++}(cmol.kg^{-1}), Na^{+}(cmol.kg^{-1}), K^{+}(cmol.kg^{-1}) and Ca^{++}(cmol.kg^{-1}). The species of experimental tree and initial conditions are colour coded as follows: dark grey bars represent the chemical conditions of leaves before the experiment, white bars represent boxes places under the canopy of *Quercus* sp., black bars under *Beilschmedia ovalis* and light grey bars under *Oreopanax xalapensis* trees; values presented are mean ± standard error. Sample size (n) for the starting conditions is 3 per foliar species except for *P. chiapensis* where n=4; Sample size (n) is 16 per leaf species - tree species combination, except for the *O. xalapensis* boxes placed under *B. ovalis* were n=15. Values for boxes collected in different dates are pooled.

of the experiment and therefore the concentration of calcium decreased and the concentrations of nitrogen and phosphorus increased.

Collection time had a significant main effect on the values of PCA3 ($F=6.51$, d.f.=3, $P<0.01$) and did not interact with foliar species (figure 6.10c). The value of PCA3 was significantly higher in the boxes retrieved after 112 days than at the other collection dates. At this collection time, litter in experimental boxes tended to have high concentration of phosphorus and low of potassium, ASF and sodium.

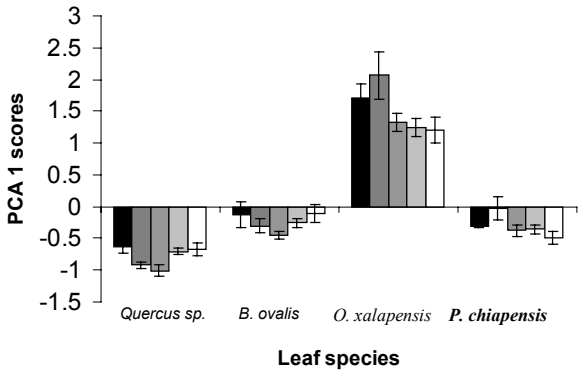
Table 6.5 presents a summary of the evolution of nutrient content in experimental leaves during the decomposition experiment. For the sake of clarity only mean values

of nutrient concentration and percentage of initial content are presented. The standard deviations associated with the nutrient concentrations are presented in a separate table in Appendix CH6 (table CH6.29). As in the experiment presented in Chapter 5, the dispersion around the treatment means of these measurements was thought to be the result of three factors: (1) unaccounted differences between the local environments where the boxes were placed, (2) changes in the chemistry of the litter during the handling period and (3) errors associated with the measurements performed during the laboratory analyses.

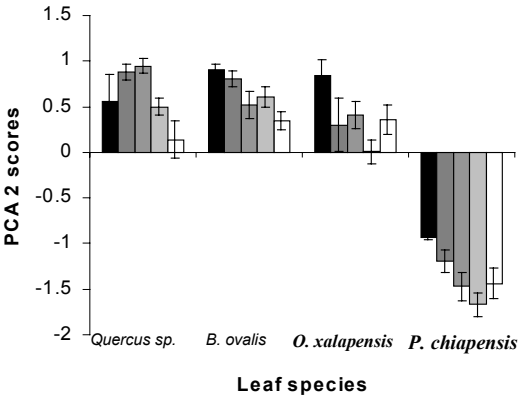
The percentage of initial nutrient mass that remained at the time of collection was estimated by dividing the final nutrient mass in each sample by the mean nutrient content in four samples of undecomposed leaves. Therefore the error associated with the measurement of initial nutrient content was not considered in this estimate. This assumption was considered to be reasonable since the variation around the mean initial concentrations was moderate for most nutrients (see also figure 3.6 in Chapter 3). The percentages of initial concentration presented in table 6.5 and described below are intended to explore in what stages of the experiment mineralisation and immobilisation were most likely to have occurred. Values in table 6.5 should not be considered as precise comparisons, but rough estimates of initial *vs*. final nutrient content. The statistical tests on the effect of experimental treatments on the chemical quality of experimental litter were discussed previously in this section.

By the end of the experiment, in the litter of *P. chiapensis* and *Quercus* sp. nitrogen had been mineralised (more than 80% of the initial amount had been lost), independently of the tree where decomposition happened. In *B. ovalis* and *O. xalapensis* litter, for most of the experiment nitrogen was immobilised (more than 100% of initial amount was present) and when the last boxes were retrieved net mineralisation had not occurred (table 6.5). Conversely, calcium and magnesium were in general released more rapidly from *B. ovalis* and *O. xalapensis* litter than from *P. chiapensis* and *Quercus* sp. litter. In particular, in *P. chiapensis* boxes no net release beyond 6% of these elements happened by the end of the experiment (table 6.5). Phosphorous was mineralised more rapidly from *O. xalapensis* leaves than from

(a)



(b)



(c)

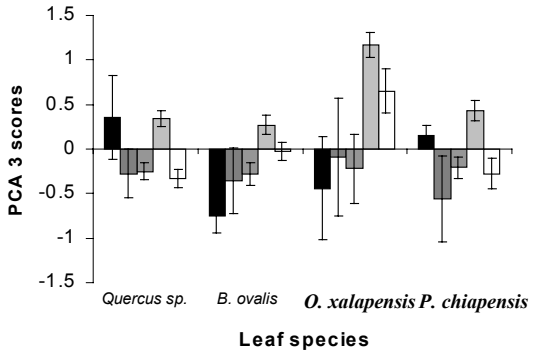


Figure 6.10 Graphs illustrating the effects of foliar species and collection date on the first three principal components ((a)PCA1, (b)PCA2 and (c)PCA3) formed by nutrients, ASF and RF concentration variables in decomposition boxes. Variables included in the PCA were Carbon (%), Nitrogen (%), P ($cmol.kg^{-1}$), $Mg^{++}(cmol.kg^{-1})$, $Na^{+}(cmol.kg^{-1})$, $K^{+}(cmol.kg^{-1})$ and $Ca^{++}(cmol.kg^{-1})$. Values presented are means ± standard error. Collection dates are colour coded in a gradient from black to white (starting conditions, 28, 56, 112 and 220 days after the start of the experiment). Sample size (n) for the starting conditions is 3 per foliar species except for *P. chiapensis* where n=4; for the rest of collection dates n=12 except for *O. xalapensis* boxes collected after 28 days where n=11.

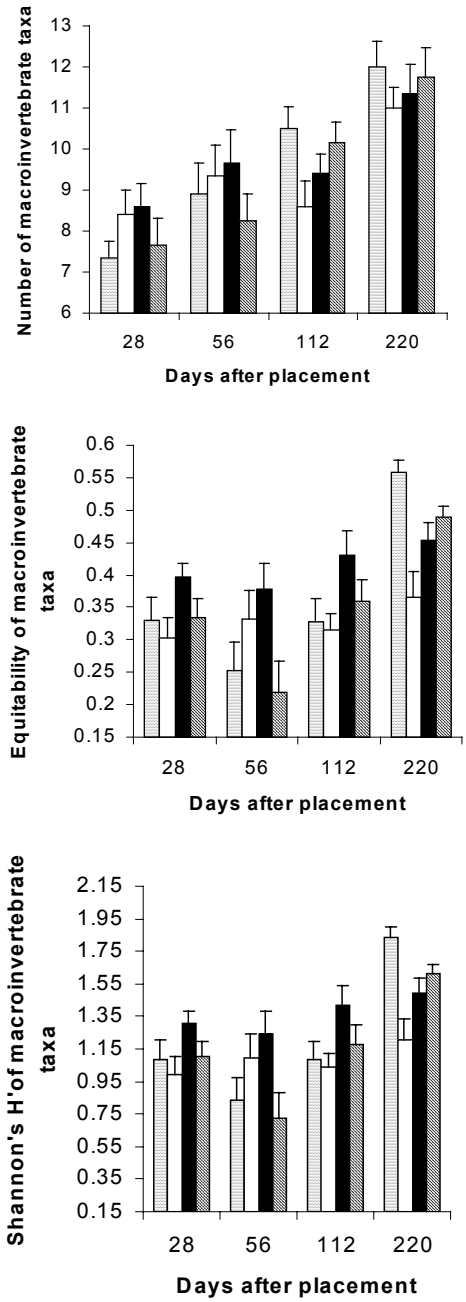


Figure 6.11 (a) Number of taxa, (b) equitability and (c) Shannon's index of diversity in experimental decomposition boxes containing different species of leaves and collected 28, 56, 112 and 220 days after the start of the experiment. Light grey bars represent *Pinus chiapensis* boxes, white bars *Quercus* sp., black bars *Beilschmedia ovalis* and dark grey bars *Oreopanax xalapensis* boxes. Values presented are mean + standard error. Sample size (n) is 12 per leaf species at each sampling date. Decomposition boxes containing the same foliar species collected under different experimental tree species where pooled.

any other foliar species. However, *O. xalapensis* was the only species of tree where *O. xalapensis* litter still had *c.* 100% of this nutrient after 28 days (table 6.5). By the last collection date, the highest amount of N released from *O. xalapensis* litter had happened under *O. xalapensis* trees and the most P released from *Quercus* sp. litter had occurred under *Quercus* sp. trees (table 6.5).

Macroinvertebrate communities in experimental decomposition boxes placed under different tree species

Number of macroinvertebrate taxa, equitability and Shannon's Diversity Index

The number of macroinvertebrate taxa in decomposition boxes increased as the experiment proceeded ($F=23.75$, d.f.=3, $P<0.001$; figure 6.11a). The boxes retrieved at the last two collection dates contained more taxa than those collected at the first two. The foliar species being decomposed or the species of the canopy tree did not have a significant effect on the number of macroinvertebrate taxa found in decomposition boxes (figure 6.11 a).

The collection time and the foliar species being decomposed had a significant interactive effect on the equitability and the Shannon's index of diversity of macroinvertebrate taxa ($F=3.77$, d.f.=9, $P=0.001$ for both variables). At the last collection time a higher mean equitability and diversity index were recorded for all foliar species pooled together. At the collection after 56 days, boxes containing *B. ovalis* leaves displayed the highest equitability and diversity and the boxes containing *O. xalapensis* leaves had the lowest mean values for these variables (figure 6.11 b-c). At the last collection date, boxes containing *P. chiapensis* had higher equitability and diversity than other foliar species collected at the same time (figure 6.11 b-c).

Abundance of common macroinvertebrate taxa

Sixteen macroinvertebrate taxa were considered common because they reached a minimum mean abundance of 0.5 per decomposition box over the course of the experiment (table 6.6). The species of tree under which the boxes were placed had a significant main effect on four of these common taxa. Chilopoda were most abundant

	Tree species (Ts)		Collection time (Ct)		LEAF SPECIES (LS)		TS × CT		TS × LS		Ct × Ls		TS × CT × LS		
Taxa	**F-ratio**	**P-value**	**F-ratio**	**P-value**	**F-ratio**	**P-value**	**F-ratio**	**P-value**	**F-ratio**	**P-value**	**F-ratio**	**P-value**	**F-ratio**	**P-value**	**R. T.**
Chilopoda	3.93	**0.02**	5.77	**0.0009**	3.76	**0.01**	1.34	0.24	1.36	0.24	1.00	0.44	1.43	0.13	y
Diplopoda	2.48	0.09	15.50	**<0.0001**	9.39	**<0.0001**	1.62	0.14	0.29	0.94	1.41	0.19	0.46	0.97	y
Pseudoescor-pionidae	8.61	**0.0003**	16.50	**<0.0001**	0.21	0.89	5.00	**<0.0001**	0.53	0.78	0.50	0.87	0.79	0.70	y
Acari	0.12	0.89	36.13	**<0.0001**	2.12	0.10	1.05	0.40	0.86	0.53	0.77	0.65	0.65	0.85	y
Aranea	0.26	0.77	4.38	0.01	1.36	0.26	0.88	0.51	0.60	0.73	1.79	0.07	1.13	0.33	y
Coleoptera	0.95	0.39	38.84	**<0.0001**	2.09	0.10	2.07	0.06	0.73	0.63	1.22	0.29	0.51	0.95	y
Homoptera	1.15	0.32	5.02	0.002	1.20	0.31	1.18	0.32	0.64	0.70	1.24	0.28	0.69	0.82	y
Hemiptera	3.86	**0.02**	4.69	0.003	2.39	0.07	1.05	0.39	0.36	0.90	0.45	0.91	0.70	0.80	y
Hymenoptera (other than Formicidae)	2.24	0.11	24.83	**<0.0001**	2.70	**0.05**	1.06	0.39	0.89	0.51	1.94	**0.05**	1.18	0.29	y
Formicidae	5.96	**0.003**	1.45	0.23	0.85	0.47	1.78	0.11	0.87	0.52	1.59	0.12	1.30	0.19	y
Diplura	0.01	0.99	3.49	**0.02**	0.67	0.57	0.69	0.66	1.38	0.22	1.77	0.08	0.76	0.74	y
Collembola	1.90	0.15	4.11	**0.01**	2.28	0.08	1.36	0.23	0.63	0.71	3.13	0.00	0.58	0.91	y
Enchytreida	2.47	0.09	1.58	0.20	0.80	0.50	0.95	0.46	0.64	0.70	1.47	0.16	0.71	0.79	y
Coleoptera larvae	4.29	**0.02**	2.99	**0.03**	7.28	**0.0001**	1.61	0.15	1.06	0.39	1.26	0.26	0.97	0.49	y
Diptera larvae	2.43	0.09	13.90	**0.008**	7.36	**0.0001**	2.63	**0.02**	0.33	0.92	0.79	0.63	1.26	0.23	y
Other pupae and larvae	4.59	0.01	1.23	0.30	0.67	0.57	1.70	0.13	0.93	0.48	1.86	0.06	1.57	0.08	y

Table 6.6. Summary of two-way analyses of variance comparing the macroinvertebrate abundance per taxon in the litter under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*) and collection time (28, 56, 112 and 210 days after placement). The number of taxa in the two monoliths per tree extracted in each collection date were pooled. The final column indicates whether a randomisation test was performed to determine the P-value (performed in case of failure to meet the assumptions of homogeneity of variance and normality that permit the use of standard F distribution curves). Taxa with a mean abundance greater than 0.5 per sample are included. Comparison wise P-values ≤0.05 are highlighted. Bonferroni adjustment for multiple testing is P≤0.0002.

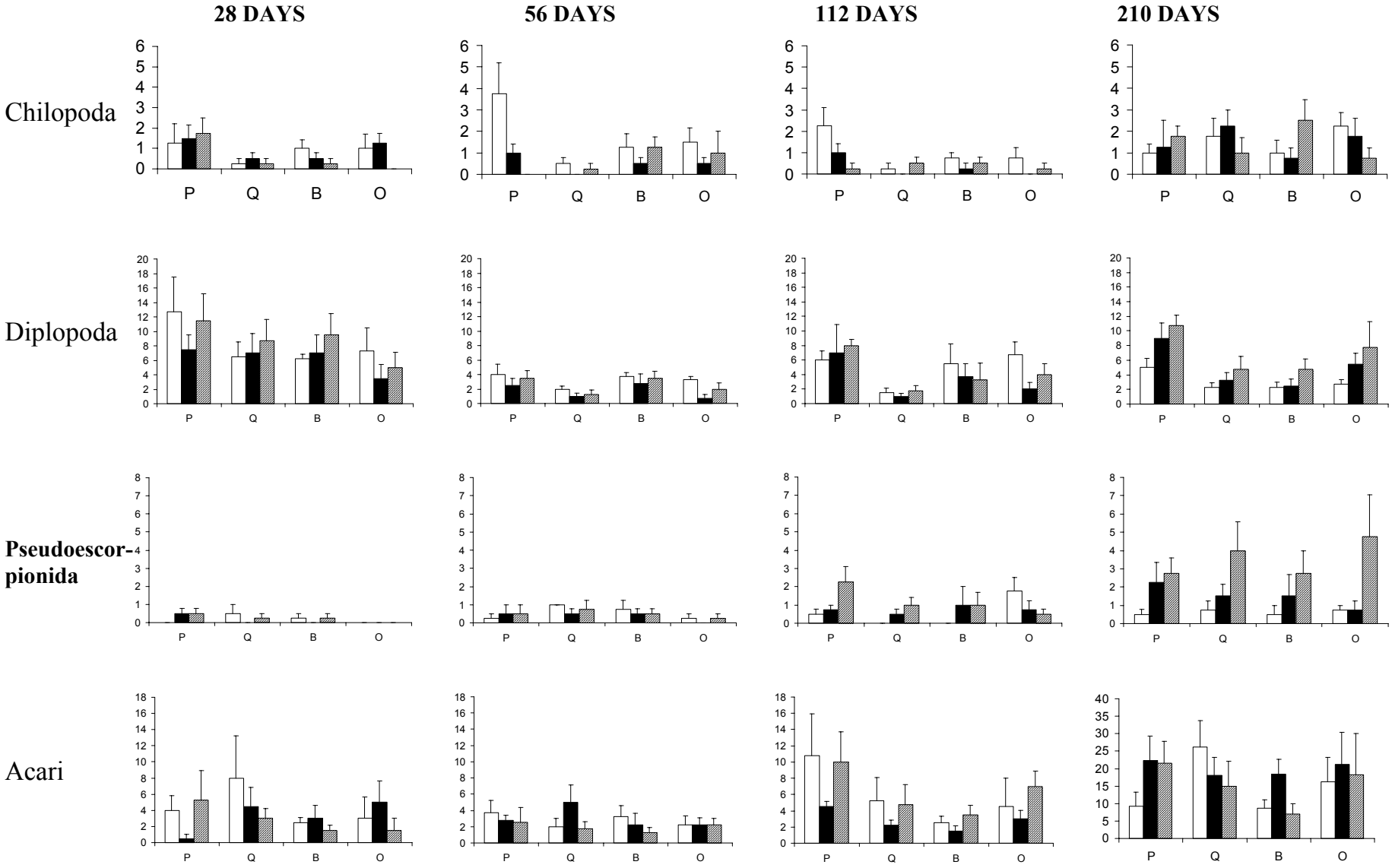


Figure 6.12 Macroinvertebrate abundance per taxon and larval group in decomposition boxes under the canopy of experimental trees. Treatments consisted of leaf species(*Pinus chiapensis* (P), *Quercus* sp. (Q), *Beilschmiedia ovalis* (B) and *Oreopanax xalapensis* (O)), collection time(28, 56, 112 and 220 days after the start of the decomposition experiment) and species of experimental tree (white bars represent *Quercus* sp., black bars *Beilschmedia ovalis* and grey bars *Oreopanax xalapensis*). Values presented are means + standard error. Sample size (n) is four per combination of treatments. Note changes in scale in the y-axis that have been made to accommodate substantial differences in taxa abundance.

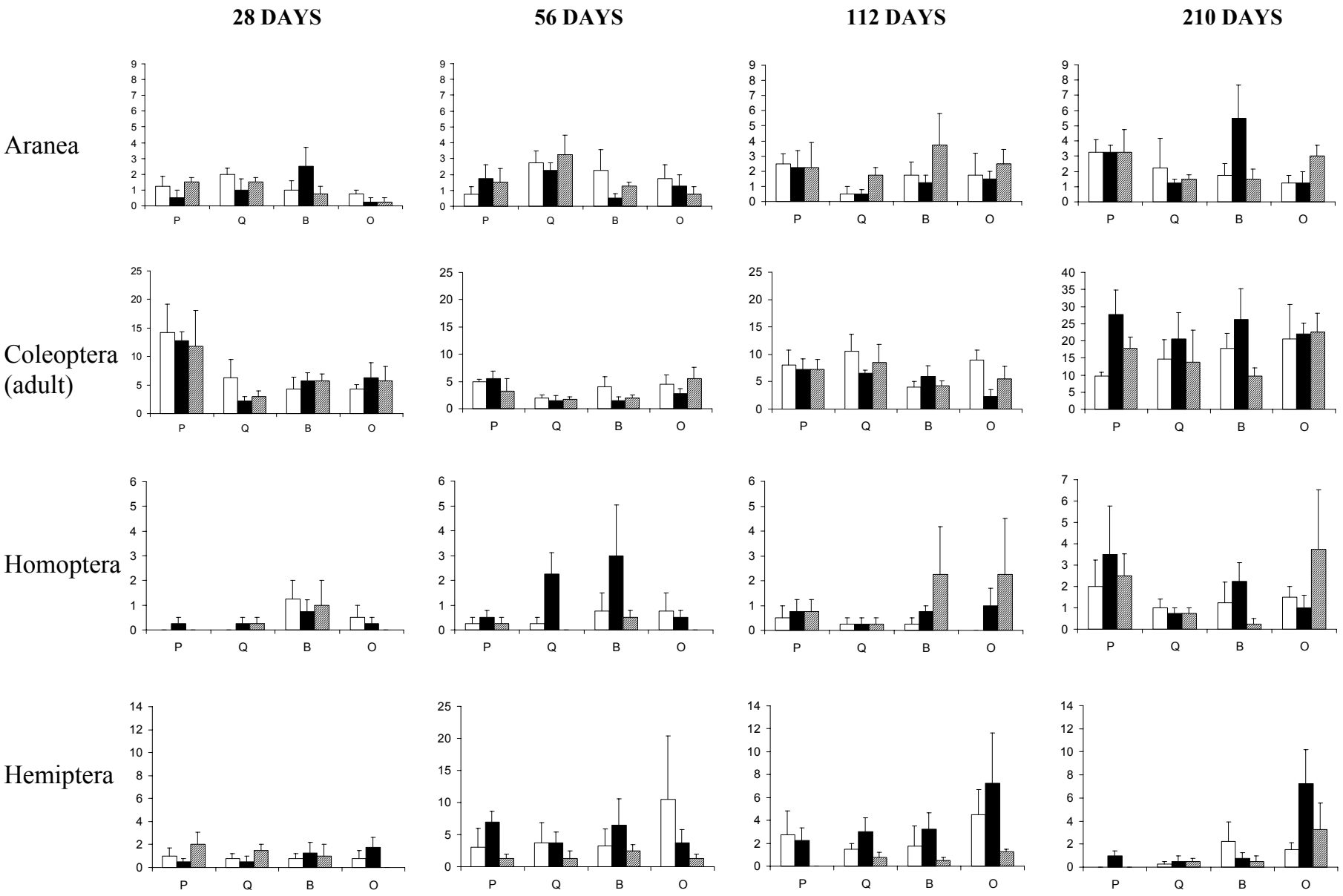


Figure 6.12 continuation...

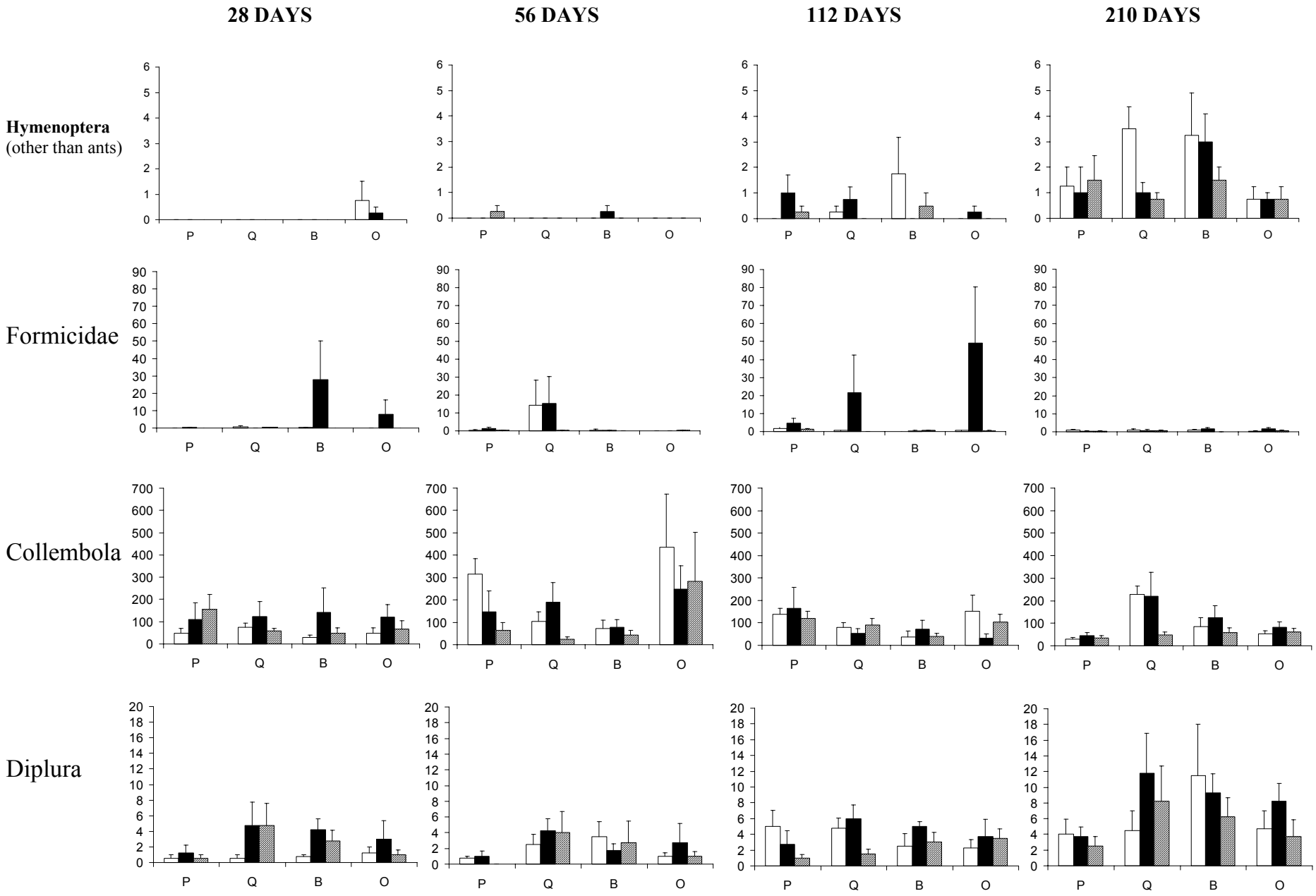


Figure 6.12 continuation...

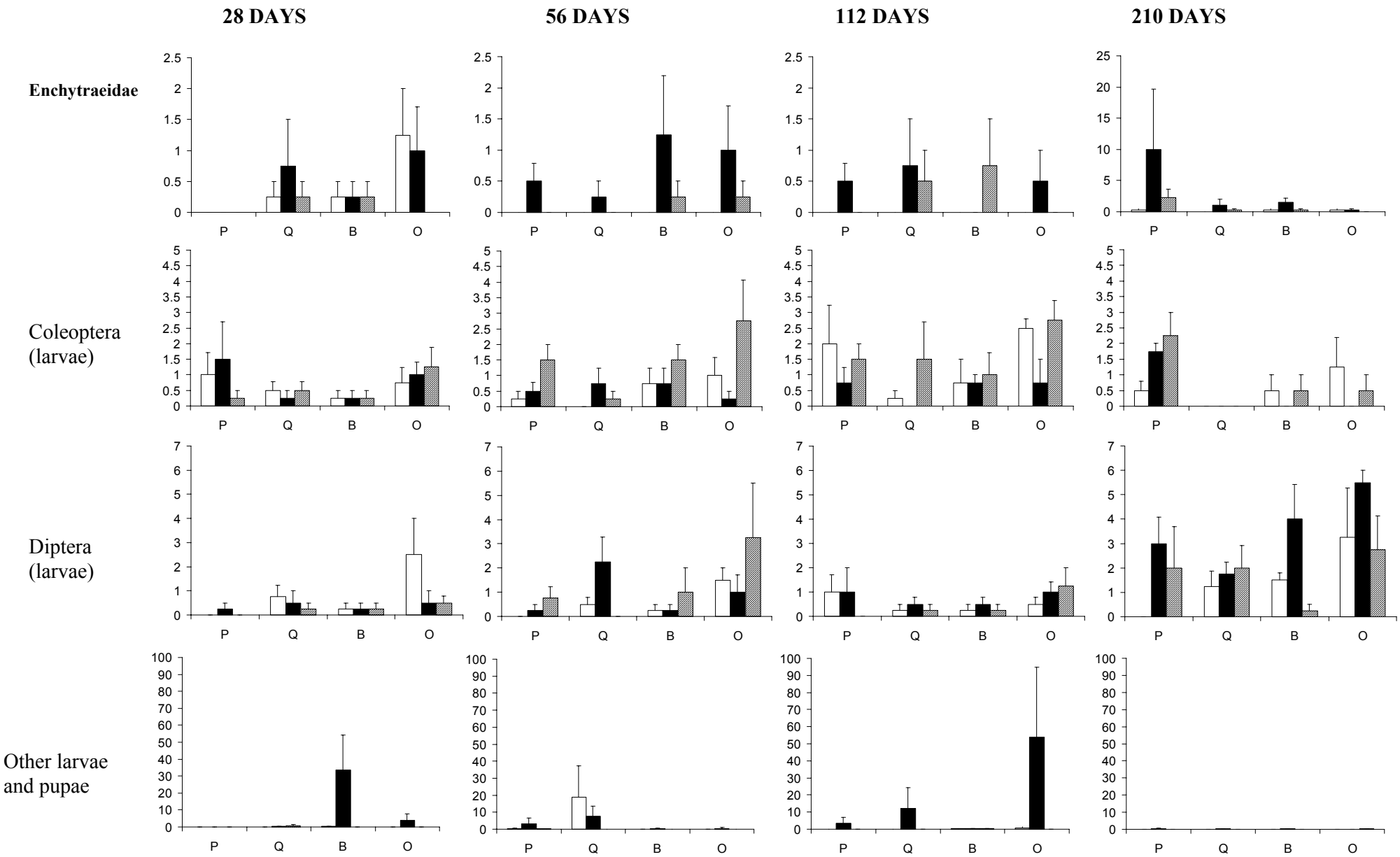


Figure 6.12 continuation...ends.

under the canopy of *Quercus* sp., Formicidae and Hemiptera under *B. ovalis* and Lepidoptera larvae under *O. xalapensis* (figure 6.12).

The collection time had a significant main effect on the abundance of eight common macroinvertebrate taxa in the decomposition boxes (table 6.6). In most cases (Chilopoda, Acari, Aranea, Coleoptera, Homoptera and Diplura) there was an increase in abundance as the experiment proceeded, particularly at the last collection time. However, Diplopoda were most abundant in boxes recovered after 28 days, then had the lowest abundance after 56 days, values subsequently increasing at the last two collection times. Hemiptera displayed the opposite pattern, being least abundant after 28 days, peaking in abundance after 56 days, then declining thereafter (figure 6.12).

The foliar species being decomposed in the box had a significant main effect on three macroinvertebrate taxa (table 6.6). Independently of other treatments, boxes containing *P. chiapensis* had the highest abundance of Chilopoda while those containing *Quercus* sp. had the lowest. *P. chiapensis* boxes also had the highest abundance of Diplopoda while *O. xalapensis* the highest abundance of Diptera larvae.

The time of collection and species of tree had an interactive effect on the abundance of two taxa inside decomposition boxes (table 6.6). For both Pseudoescorpionida and Dipera larvae, there were no differences in abundance between boxes placed under different tree species, except for the last collection date, when pseudoscorpions were most abundant in boxes under *O. xalapensis* and Diptera larvae under *B. ovalis* (followed by *O. xalapensis*; figure 6.12).

The time of collection and foliar species being decomposed had a significant interactive effect on two taxa (table 6.6). While the abundance of Hymenoptera (other than Formicidae) increased as the experiment proceeded in boxes containing all four foliar species, the increment in boxes containing *Querscus* sp. and *B. ovalis* was of greater magnitude, particularly by the last collection time (figure 6.12). In the

case of Collembola, significant differences in abundance were only recorded between boxes containing different foliar species in the second and fourth collection times. At the second collection boxes containing *O. xalapensis* leaves had the highest abundance of Collembola, while at the fourth collection the highest abundance of this taxon was recorded in the boxes containing *Quercus* sp. leaves.

The species of tree in the canopy and foliar species had no significant interactive effect on the macroinvertebrate taxa, nor did the interaction of the three experimental treatments (table 6.6). Enchytraeidae was the only taxon that was not significantly affected by any of the experimental treatments.

Relationship between macroinvertebrate community composition, microenvironmental variables and experimental treatments

A CCA of the macroinvertebrate community in decomposition boxes with respect to experimental treatments and microenvironmental conditions (table 6.7) showed numerous associations between community composition and the combination of tree species, leaf species, collection time, microenvironmental conditions and nutrient concentrations in decomposing leaves. The variables tested explained 22.9% of the total variance (or 18.0% when the collection after 28 days was included and the soil temperature excluded from the analysis). As a result of the significant proportion of variation in macroinvertebrate taxa explained by soil temperature, the analyses described beyond this point are all carried out excluding the collection after 28 days and including soil temperature.

Groups of explanatory variables included in CCA	Extracted inertia from a total of 1.429	% of taxa variance explained (all axis)	Significance of Monte-Carlo test
Tree species	0.056	3.9	*
Collection date	0.153	10.7	*
microenvironvent	0.133	9.3	*
Foliar species	0.047	3.3	n.s.
Nutrients	0.192	12.6	*
All variables	0.382	22.9	*

Table 6.7. Partitioning of the total inertia in macroinvertebrate taxa found in decomposition boxes. Inertia was partitioned amongst different groups of explanatory variables. Notice that the CCAs were run independently from each other and therefore the sum of the extracted inertia per group of variables does not correspond to the extracted inertia by a single run including all variables. * denotes $P<0.05$ and n.s. denotes $P>0.05$ in Monte-Carlo significance tests.

When the variance was partitioned among sets of variables (table 6.7), nutrient, RF and ASF concentrations accounted for the highest amount of explained community composition variation (12.6%), followed by collection time (10.7%) and microenvironmental variables (9.3%). The variables that explained the least variation were canopy tree species (3.9%) and foliar species (3.3%). Foliar species alone did not explained a statistically significant proportion of the community composition.

Nearly 18% of the variance in community composition was explained by a CCA including nutrient concentrations and collection times as explanatory variables (eigenvalues: unconstrained 1.373, canonical 0.265). When microenvironmental conditions were included instead of nutrient concentration, 14.2% of the variance in community composition was explained (eigenvalues: unconstrained 1.373, canonical 0.195). In both cases tree species was specified as a covariate. The highest concentrations of potassium and sodium (figure 6.13) and highest soil temperature (figure 6.14) were recorded at the earliest collection time included in the analysis (56 days after the experiment had started). The communities at this stage were characterised by the presence of Orthoptera, Collembola, Diptera and Lepidoptera larvae. By 112 days, RF and phosphorous were at their lowest concentrations in experimental leaves. Potassium and sodium had diminished and calcium, magnesium and nitrogen increased (figure 6.13) compared to values recorded after 56 days. At the same time, volumentric soil water content was relatively high (figure 6.14). At this stage the community had Hemiptera, Formicidae, other larvae and pupae and Coleoptera larvae as characteristic elements. At the last collection time (after 220 days) RF and ASF concentrations were relatively high and sodium and potassium reached their lowest mean concentrations in decomposing leaves (figure 6.13). At this stage, soil water content and soil temperature were relatively low and canopy cover high (figure 6.14). In the boxes collected at this time a number of taxa were abundant in the community. These include Aranea, Chilopoda, Pseudoescorpionida, Opiliones, Hymenoptera, Acari, Coleoptera, Isopoda, Diplopoda, Diplura, Homoptera, Gasteropoda and Diptera larvae.

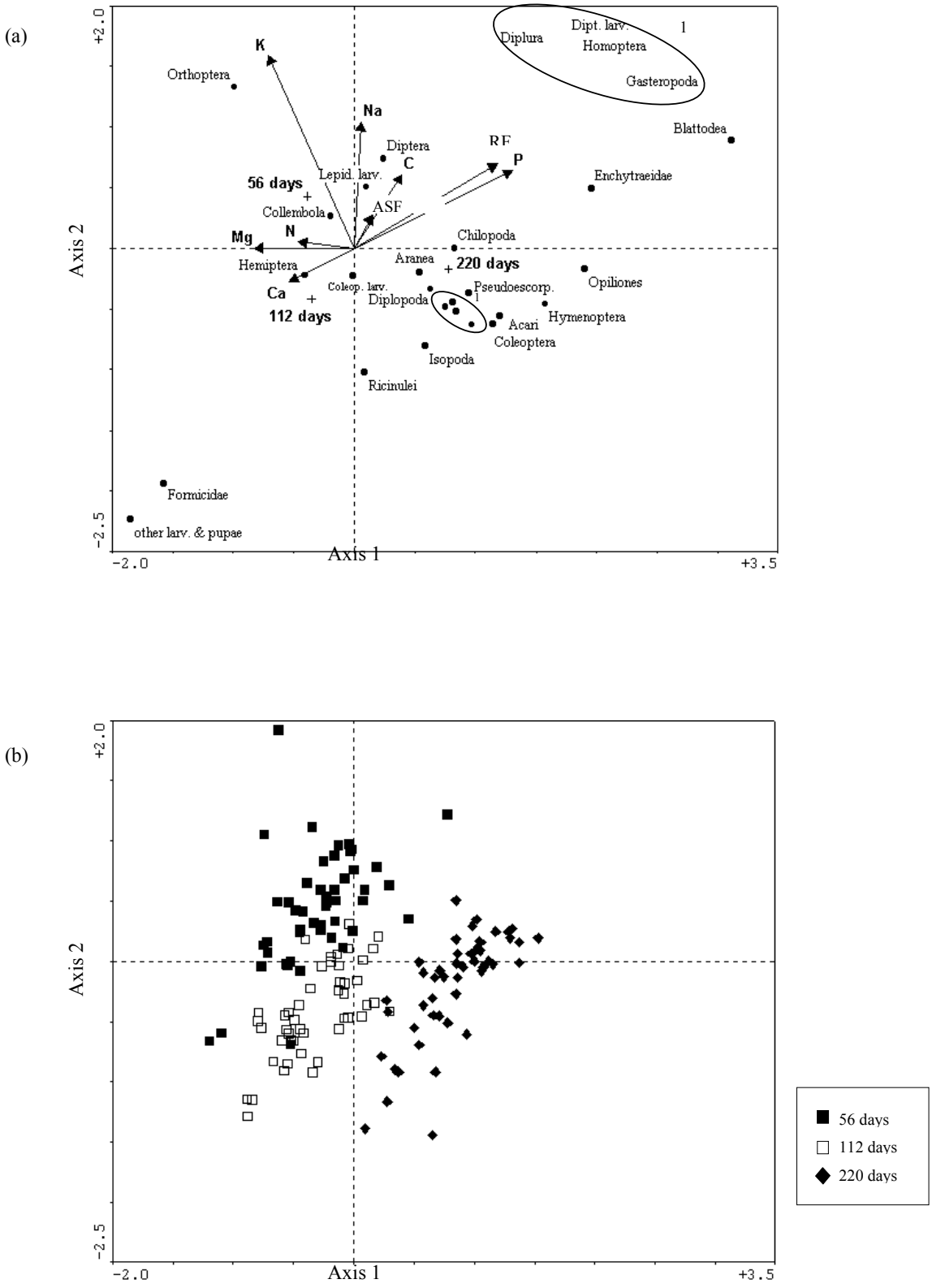


Figure 6.13. Relationship between the variation in nutrient concentrations in decomposing leaves and community composition in experimental boxes. Ordination diagrams based on canonical correspondance analyses of community composition in the decomposition boxes placed under experimental trees. Community composition is ordinated with respect to the number of days in the field (dummy variables) and nutrient, RF and ASF concentrations in the decomposing leaves. The species of trees have been introduced as dummy covariables. The first two axes account for 16.0% of variation, Monte-Carlo permutations significance test $p<0.015$ (taxa with fewer than five individuals in the experiment were excluded). (a) Biplot of taxa-explanatory variables and (b) sample scatterplots symbol coded by collection date. For clarity, inset in (a) provides lables for the taxa points within the ellipse denoted 1.

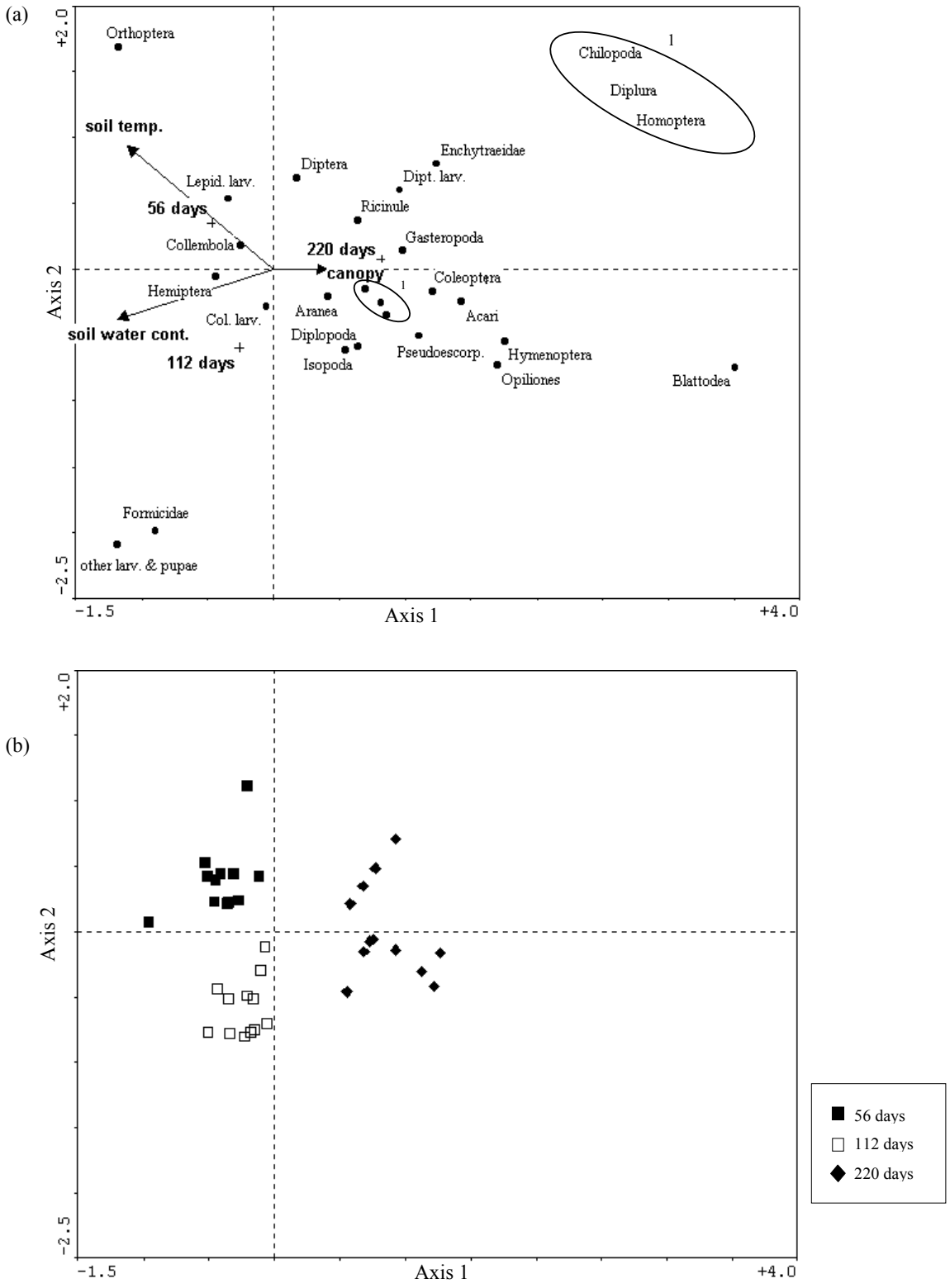


Figure 6.14. Relationship between the variation in microenvironment and community composition within experimental boxes. Ordination diagrams based on canonical correspondance analyses of community composition in the decomposition boxes placed under experimental trees. Community composition is ordinated with respect to number of days in the field (dummy variables) and nutrient, RF and ASF concentrations in the decomposing leaves. The species of trees have been introduced as dummy covariables. The first two axes account for 16.0 % of variation, Monte-Carlo permutations significance test $p<0.015$ (taxa with fewer than five individuals in the experiment were excluded). (a) Biplot of taxa-explanatory variables and (b) sample scatterplots symbol coded by collection date. For clarity, inset in (a) provides lables for the taxa points within the ellipse denoted 1.

The relationship between tree species and community composition was explored through a CCA including tree species as an explanatory variable and collection time as a covariate (eigenvalues: unconstrained 1.157, canonical 0.049). This analysis accounted for 4.2% of the variance in community composition, associated with differences between tree species that did not vary through the experiment (figure 6.15). The boxes placed under the canopy of *O. xalapensis* were characterised by taxa such as Opiliones, Pseudoescorpionida, Lepidoptera larvae, Homoptera, Coleoptera, Diplopoda and Aranea. Those boxes placed under *B. ovalis* had Enchytraeidae, Diptera, Isopoda, Formicidae and other larvae and pupae as distinctive taxa, while Hymenoptera, Ricinulei, Chilopoda, and Gasteropoda were characteristic of the boxes that were placed under *Quercus* sp.

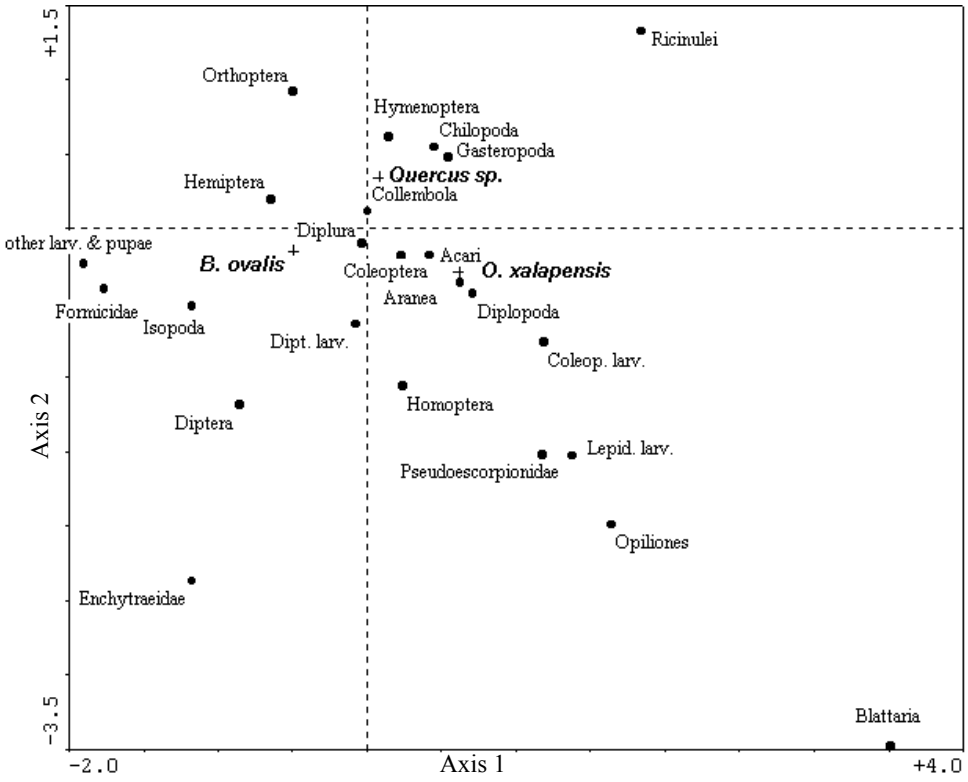


Figure 6.15. Relationship between tree species and community composition in experimental boxes. Biplot of taxa-explanatory variables based on canonical correspondance analyses of community composition in the decomposition boxes placed under experimental trees. Community composition is ordinated with respect to the species of tree. The number of days in the field have been introduced as a dummy covariable. The first two axes account for 4.2% of variation, Monte-Carlo permutations significance test $p<0.005$ (taxa with fewer than five individuals in the experiment were excluded). Note that sample scores are not plotted because all explanatory variables are dummy and sample scores are identical within treatments.

Discussion

Seasonal changes in microenvironment and the macroinvertebrate community

Independently of the species of tree, seasonal variation was detected both in soil microenvironmental conditions and the composition of the macroinvertebrate communities. During the first two months of the experiment (June-July), which corresponded with the rainy season, soil temperature and water content, as well as the standing crop of litter were relatively high. By October, at the start of the dry season, these variables had declined, reaching their lowest value in January (last collection date). As expected, in the litter the highest number, equitability and diversity of macroinvertebrate taxa corresponded with the warmest and wettest months. However, the soil community displayed the opposite trend. The diversity indices increased as the microenvironment became cooler and dryer. A possible explanation for this is that the macroinvertebrate community migrates seasonally into the soil as environmental conditions become harsher on the surface. In the canonical ordinations microenvironmental conditions were consistently the most important set of variables for explaining community composition in both soil and litter. Furthermore, presumably as a result of the higher exposure, in the litter microenvironment accounted for a higher percentage of the variance (*c.* 51% *vs.* 27%) than in the soil. Because in these forests the higher temperatures and humidities coincide with the season when the mass of standing crop of litter is also high, it is not possible to determine whether changes in macroinvertebrate communities were caused by the greater availability of litter or the milder climatic conditions.

It was somewhat surprising that there were no significant differences between tree species in the peaks of abundance of the standing crop of litter. Williams-Linera & Toledo (1996) found that in a similar (but lower altitude) forest in Veracruz, trees with a tropical biogeographic affinities abscised their leaves between March and April, and Holarctic species from September through March. However, of the three Holarctic species that they tested, *Quercus* sp. displayed peak litterfall (March) closer to the time when tropical species dropped their leaves. The fact that *Quercus*

spp. may have an early leaf shedding peak compared to other Holactic genera, can explain the fact that at the first collection date (June) all experimental trees displayed a peak value of standing litter and no significant differences were found between species.

As expected, the abundance of most macroinvertebrate taxa followed the seasonal pattern described above. In the litter the highest abundances were recorded in the relatively warm and wet months while in the soil they occurred in the drier and cooler months. However, Acari and Coleoptera constituted an exception because they were most abundant in the litter during the relatively cool-dry months. Presumably, at least some species within these two taxa are more resistant to harsher environments. Therefore they may increase in abundance and be capable of exploiting the habitat vacated by the general migration to the soil in dryer months.

The tree-species effect on macroinvertebrate communities

Canopy cover was the only environmental variable for which tree species did not have a significant interaction with season. The canopy cover for all species was *c*.3% higher in October. This small difference in canopy cover did not translate into particularly lower soil temperature and humidity in the soil in the same month. The seasonal trend in environmental variables prevailed over differences between tree species. However, small differences in the effect of seasonal patterns under different tree species were detected. In January (the cool dry period) soil temperature was even lower and soil water content slightly higher under *O. xalapensis* trees. Despite the moderate magnitude of the differences in soil microenvironmental conditions detected under different tree species, significant differences were found in the macroinvertebrate community. This implies that the effect that the species of tree has on the community may be more related to factors other than the environmental conditions created by the canopy. Furthermore, the tree species effect was stronger in the litter community than it was in the soil.

When the variance in the community compositon was partitioned among explanatory variables, tree species accounted for *c.* 22% in the litter while in the soil this factor

was not significant. Therefore the strongest effect of single trees on the macroinvertebrate community was presumably related to litter characteristics rather than the environment created in the soil. This is consistent with the finding that the aggregated patterns of macroinvertebrate taxa were most frequent in the litter community (Chapter 4) and with other studies that have found a strong association of community composition and litter identity (Mboukou-Kimbatsa *et al.*, 1998; Migge *et al.*, 1998; Vohland & Schroth, 1999; Warren & Zou, 2002). Particularly relevant is the study by Vohland & Schroth (1999). They found in a mixed tree-crop plantation in humid tropical Amazonia that the abundance and diversity of macroinvertebrates was positively correlated with differences in the standing crop of litter produced by different tree-crop species. The macroinvertebrate community composition was characterised by a mosaic of species distribution and diversity dictated by the distribution of planted tree-species. Furthermore, Sulkava & Huhta (1998) found in a microcosm experiment that patches of litter from different tree species developed different macroinvertebrate communities, but these differences in community composition were not evident in the humus immediately underneath.

Only for the abundance of two taxa was the influence of tree species independent of season. Diplurans and Diptera larvae were always most abundant under the canopy of *B. ovalis* in the litter. It is possible that this permanent association was related to some characteristic of the leaves of this species, either chemical or structural. For other taxa the influence of the tree species interacted with seasonal variation. In terms of the litter community, the canopy of *O. xalapensis* seemed to be the only tree species that had an interactive effect with season. Within the wet-warm season, three taxa (Aranea, Coleoptera larvae and Lepidoptera larvae) had an outstandingly high peak of abundance in the litter under the canopy of this species. Lepidoptera larvae and the larvae of many members of Coleoptera are phytophagous (Brusca, 2003) and may be feeding directly on recently fallen leaves. These peaks of abundance could be a response to the litter of this species having lower RF and carbon contents (herbivore deterrents) when recently fallen (Chapter 3, figure 3.6). Members of Aranea are predators (Brusca, 2003) and may be exploiting the increase in population of these phytophagous larvae.

In contrast to the litter, the interaction between tree species and season in the soil was not associated with a particular tree species. Instead, within the general trend of increasing abundance during the cool-dry season, the abundance of some taxa was relatively high under particular tree species at different times. For example after 56 days Acari were most abundant under *Quercus* sp. while after 220 days they were most abundant under *B. ovalis*. With the available data it is only possible to speculate that this may be a response to differences in the point during decomposition at which different foliar species release most nutrients (see below). In other words the unsynchronised timing of nutrient release could exert indirect control over the population of Acari through pulses of bottom-up controls of the food-web.

Because seasonal litterfall produces cohorts of litter, and the litter of different tree species release nutrients to the environment at different stages of decomposition (see below), the nutrients and leachates filtering to the soil may differ in timing between tree species. Therefore the cycles of microbial populations in the soil could also be unsynchronised between tree species. Kourtev *et al.* (2002) found for example that Japanese barberry (*Berberis thunbergii*), Japanese stilt grass (*Microstegium vimineum*) and blueberry (*Vaccinium* spp.) developed distinct microorganism community structures in the rhizosphere and even in bulk soil beneath the root mass. They suggested that the movement of soluble organic compounds, leachates from decaying litter or exudates from the rhizosphere could explain this vertical effect beyond the area of influence of the plant. The unsynchronised peaks in abundance of Acari under the two species of trees recorded here may be a response to the fluctuations in the microbial community; for example populations of fungi, as a high proportion of mite families are fungal feeders (Seastedt, 1984) that follow peaks in availability of nutrients. A link between peaks in Acari abundance and more advanced stages of decomposition in litter have been observed previously by Anderson (1975) and Hansen & Coleman (1998).

The tree-species effect on decomposition

The species of tree under which decomposition boxes were placed had no effect on the rate of decomposition. Foliar species had characteristic patterns of mass loss and these were not altered by the tree species under which they decomposed. The litter of all species appears to have a component that decomposes exponentially in the first year and a component that remains resistant to decay. These results are consistent with the suggestion made for other high altitude cloud forests (Bruijnzeel & Veneklaas, 1998) and in Chapter 5 that decomposition rate is primarily constrained by the environmental conditions created by frequent fog. Different soil chemical or biological conditions do not appear to significantly alter the trend of mass loss. These hypotheses, will not be further examined here as they have already been discussed in detail in Chapter 5.

Even if the initial concentration of nitrogen was not statistically different between foliar species (see Chapter 3, figure 3.6), differences between mean concentrations of this nutrient between foliar species were the only univariate predictor of the decomposition rate. This is in accordance with several decomposition studies that found initial nitrogen concentration to be a good indicator of decomposability (McClaugherty *et al.*, 1985; Mentemeyer & Berg, 1986; Stohlgren, 1988; Taylor *et al.*, 1989).

In terms of nutrient evolution in decomposing litter, the foliar species identity prevailed again as a driving factor over the tree species. In general by the end of the experiment, in the litter from Holarctic species (*P. chiapensis* and *Quercus* sp.) nitrogen had been mineralised, while in the litter from tropical species (*B. ovalis* and *O. xalapensis*) the nitrogen had generally been immobilised. The opposite trend occurred with Ca and Mg that were lost relatively slowly from Holarctic species. In particular in *P. chiapensis* the concentration of N remained high and the one of Ca remained low throughout the experiment. These results are consistent with the general observation that nutrients are lost sooner from litter when they are in higher concentration (McClaugherty *et al.*, 1985; Berg, 1986; Mentemeyer & Berg, 1986; Stohlgren, 1988). The fact that net nitrogen mineralisation was recorded in the litter

from Holarctic species suggests that the failure to find significantly higher initial concentrations of N in these foliar species was an artefact of the small sample size.

The changes in litter quality as decomposition proceeded were different between foliar species. Nutrient concentrations in *O. xalapensis* and *P. chiapensis* were more constant through time than they were in *Quercus* sp. and *B. ovalis.* This was indicated by the fact that collection date did not have a significant effect on the foliar quality components of *O. xalapensis* and *P. chiapensis* and thus the litter quality was constant through decomposition for these foliar species. In *Quercus* sp. litter the release of carbon and break down of RF was particularly slow during the first 56 days and increased in rate thereafter. As carbon mineralisation rate increased, the quality of the litter increased because the concentrations of nitrogen, calcium and magnesium also increased and therefore their mineralisation was triggered (after the second collection date for Mg and the third for N and Ca). The concentration of P in this foliar species also increased, as carbon was mineralised, but probably not enough because immobilisation rather than mineralisation followed. In *B. ovalis* the quality of the litter also increased as decomposition proceeded. Both N and P increased in concentration with decomposition until the end of the experiment. In this foliar species none of these nutrients had reached a mineralisation phase by the end of the experiment.

Even if the foliar species identity was the most important determinant of the evolution of nutrients during decomposition, some important differences were found between litter from the same species decomposing under different canopies. The trend followed by N in *O. xalapensis* litter deserves special attention in this regard. The initial concentration of N in this foliar species was low and under all experimental trees it passed through a fast immobilisation phase during the first 28 days (so much so that *O. xalapensis* developed the highest values of PCA3). However, the acquisition of N from external sources under *Quercus* sp. and *B. ovalis* was substantially higher than under *O. xalapensis*. Furthermore, *O. xalapensis* litter that was set to decompose under trees of the same species sustained a relatively

lower concentration of RF and a higher concentration of magnesium and calcium compared to *O. xalapensis* litter set to decompose under other species of trees.

These results suggest that under the canopy of *O. xalapensis* trees, a specialised decomposer community has developed. This community is capable of breaking down more RF from *O. xalapensis* litter, minimising the immobilisation of nitrogen and therefore releasing more nutrients to the environment. It could be suggested that the decomposer community and the nutrient environment under *O. xalapensis* are in general more beneficial for nutrient release than those under other species. This is not likely because other foliar species did not have a faster release of nutrients or loss of RF under *O. xalapensis* and therefore the most likely conclusion is a certain degree of coupling between litter and decomposer community composition under *O. xalapensis*. Similar evidence of tree-decomposer community coupling was found under *Quercus* sp. trees. The only place where *Quercus* sp. litter had not immobilised P by the end of the experiment was under trees of its own species. It is possible that the sustained dominance of a particular foliar species under each tree influences the decomposer community composition and when that same foliar species is introduced experimentally the combination of decomposers that most efficiently liberate nutrients is readily available. Wardle (2002) has suggested the possibility of such a mechanism of plant selection of different decomposer communities associated with a feedback mechanism. This hypothesis is also supported by the findings by 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 summary, the results suggest that the foliar species identity is the prime determinant of decomposition rate and nutrient release to the environment. It is possible that the production of a specific quality of litter is the most important mechanism by which a tree influences the decomposer food-web that develops under its canopy. However, only for *O. xalapensis* and *Quercus* sp. was evidence found for a feedback between the decomposer community and the tree species, in that the

decomposer community has become particularly suitable to optimise the release of nutrients from the litter produced by the same species of tree.

The macroinvertebrate community that invaded decomposing litter

The next question is whether the different patterns in nutrient release from different foliar species are coupled with a distinct evolution of the macroinvertebrate community composition inside decomposition boxes. Also, a key question is the extent to which seasonal patterns and the character of the resident macroinvertebrate community under each tree species constrain the composition of the macroinvertebrate assemblage that invades litter of each foliar species.

When the variance in the community composition was partitioned amongst explanatory variables the most important drivers were revealed. Chemical composition of the litter was the prime determinant of community composition, followed by collection date and microenvironmental variables. Tree species accounted for only *c*.4% of the explainable variance and foliar species did not account for a significant amount of the variation. This hierarchy of drivers was also confirmed in terms of diversity indices and the abundance of most individual taxa. The number, equitability and Shannon's H' of macroinvertebrate taxa as well as individual abundances in experimental boxes increased as the experiment proceeded. As the litter inside decomposition boxes started to decompose, the microorganism community will have developed and the primary consumers could have migrated in search for food, followed by predators. This progression could explain the increase in number, individual abundance and diversity of taxa that accompanied the decomposition process.

The ordination of the macroinvertebrate community with respect to the chemical composition of experimental leaves is consistent with this hypothesis. The macroinvertebrate community associated with the final collection date was the most distinct and diverse (figure 6.13). At this collection date, the chemical composition of the leaves indicates that considerable microbial activity had developed. Ca, Mg and N had declined in concentration and RF and carbon concentration reached their

highest values. At this stage, P was also at its highest concentration because this nutrient was limiting and often not mineralised (see above). This result is consistent with the widely reported increase in number and diversity of mites found in litterbags as decomposition of forest litter proceeds (Anderson, 1975; Hansen & Coleman, 1998).

Seasonal changes could also explain the observed increase in diversity indices and taxa abundances through time, because the course of decomposition coincided with the change from the wet-warm to the cool-dry season. The variation in abundance and diversity of taxa inside the boxes corresponds to that followed by the soil (and not the litter) community outside. The protected environment inside the boxes could explain the resemblance with the soil community in terms of seasonal patterns of variation. Because the boxes had to be disguised, half of their height was buried in the surface soil, so that the top opening was levelled with the top litter surface. It is possible that macroinvertebrates from the litter migrated into decomposition boxes (as they would migrate to the soil) because the semi-closed and semi-buried boxes provided a protected environment during the dry-cool season.

In the ordination of the macroinvertebrate community with respect to leaf chemistry (figure 6.13), the foliar concentration of K and Na appeared as important driving factors of community composition. This is surprising because Na and K are highly mobile elements and microbial activities are not required for their release (Seastedt, 1984). It is possible that the decrease in concentration of these elements covaried with degree of decomposition because they are easily lost with time through leaching. Therefore the macroinvertebrate community composition may not be driven by the concentration of these elements but by the course of the decomposition process that was occuring as they were lost through leaching.

In summary, most of the explainable variation in the macroinvertebrate community found in decomposition boxes was accounted for by the chemical evolution of the decomposing litter and the seasonal patterns that happened as decomposition proceeded. Only a very small (yet significant) portion of the variation was related

exclusively to the species of tree under which boxes decomposed (*c.*4%). Most surprising was that the identity of the litter being decomposed did not account for a significant portion of the variation in the community composition. This may be an indication that the litter quality is not as significant a determinant of the composition of the macroinvertebrate community as is its state of decomposition.

So far, evidence from macroinvertebrate communities in monoliths point towards tree species having a stronger effect on the litter community than in the soil. Because no seasonal differences in peaks of abundance in the standing crop of litter were found, I suggested that this difference could be related to unsynchronised release of nutrients from the litter produced by different trees. However, when different foliar species were set to decompose in experimental boxes, most of the taxa seemed to be driven by the time litter was most advanced in decomposition regardless of the foliar species. With this apparently contradictory evidence, the only remaining possibility is that indeed the macroinvertebrate community composition is influenced by differences in chemical characteristics of the litter produced by different trees, but this only becomes evident at some stage of decomposition beyond the first year of decomposition.

This hypothesis is consistent with the study by Warren & Zou (2002) who found a significant correlation between the abundance of Diplopoda and other macroinvertebrate taxa pooled together and differences in the quantity and quality of standing semi-decomposed litter (Oe horizon) between plantations of different tree species in Costa Rica. However, similar to the results presented here, most abundances of taxa were not associated with the quality of freshly fallen leaves. These results are consistent with the hypothesis that macroinvertebrate abundances respond to factors associated with late stages of decomposing litter. It is also possible that macroinvertebrate taxa abundances are associated with the microbial community developed in advanced stages of decomposition.

In the study by Warren & Zou (2002) Diplopoda was the only group whose biomass was correlated with quality in the recently fallen litter (Oi horizon). Biomass was

positively correlated with the N concentration and negatively with the C/N ratio. In the experiment presented here Diplopoda was one of the few taxa whose abundance was significantly affected by the foliar species in decomposition boxes. They were more abundant in boxes containing *O. xalapensis* leaves. It is possible that in both studies, because members of this taxon were feeding directly on litter, their abundance was higher in more palatable litter. In this study *O. xalapensis* leaves, must have been the most palatable, because they had the lowest concentration of carbon and RF (see Chapter 3, figure 3.6).

In Chapter 4 it was found that the most abundant macroinvertebrate taxa had significantly aggregated distributions in the sampling grid of the 100-year-old forest. Because the data presented in Chapter 4 were obtained within one month, they do not capture any seasonal variation in taxa abundances. Therefore, the aggregation detected in the macroinvertebrate taxa distribution could have resulted from the combination of two factors. First, a response to the distribution of litter microbial activity was high (probably the litter that had been produced several months earlier), second, a response to soil and chemical characteristics associated with different tree species. Although the second of these factors was the one that explained the least variation in experimental boxes, it accounted for *c.* 22% of the variation in the natural litter macroinvertebrate communities under experimental trees. The "tree species effect" is the only one that can explain the fact that different litter taxa were aggregated in different areas of the grid. It may well be that when sampling is not carried out through time (as in Chapter 4) or it is not associated with a single litter cohort (as in the litter under experimental trees) this factor accounts for a higher percentage of the variation. Even if compared to the seasonal variation, the "permanent tree-species effect" is relatively small, it may be not negligible in determining the spatial distribution of macroinvertebrate taxa at any one point in time and where litter is made up of several cohorts. Spatial patterns of soil biota have been previously suggested to be dynamic rather than static over time (Ettema & Wardle, 2002), and their abundance to have higher fluctuations than do underlying patterns of abiotic and biotic resources (Görres *et al.*, 1998).

Conclusion

1. Although seasonal changes accounted for more variation in the macroinvertebrate community through time, some support was found for the idea that spatially explicit patterns in geochemical characteristics and macroinvertebrate communities in the 100-year-old forest of Tarantulas are driven by the influence of single trees.

2. Only moderate differences were found between the soil microenvironmental conditions under different species of trees and the chemical characteristics of the foliar species determined the decomposition rate and chemical evolution of decomposing leaves. It is possible that the production of a specific quality of litter is the most important mechanism by which a tree influences the decomposer food-web that develops under its canopy. However, for *O. xalapensis* and *Quercus* sp. evidence was found for a feedback between the decomposer community and the tree species, in that the decomposer community has become particularly suitable for the release of nutrients from the litter produced by that species of tree.

3. There were some detectable differences in the composition of macroinvertebrates communities that inhabit the litter under different species of tree, but these are less evident in the surface soil than in the litter. Results of the decomposition experiment did not support the hypothesis that these differences in macroinvertebrate community can be explained by differences in litter quality and decomposition trends between the litter of different tree species. It is suggested that differences in litter decomposability and nutrient release that occur beyond the first year of decomposition may account for these differences.

Chapter 7.
General discussion

The research carried out in this thesis has demonstrated that studying remote ecosystems that are threatened by human activities calls for a different approach to conservation research. Because the background information is often scarce and the accessibility difficult, trade-offs in terms of precision and replication need to be considered from the very beginning. Further, as happened in this case, unexpected events can further constrain the body of data that is finally obtained. I suggest that this situation is not exceptional, but very common in conservation research aimed at the most threatened ecosystems. To overcome this problem research should be focused on those processes that are thought to be essential for the survival of the system or that are most threatened by human activities.

I hypothesised that the biogeochemical cycle relating the above-ground vegetation with the soil decomposer food-web would be one of the most disturbed processes after selective logging of TMCF and concentrated the research there. The hierarchical and multidimensional concept of Biodiversity (figure 1.1) proposed by Noss (1991) was used to ensure that surrogate variables were chosen at a relevant level of organisation and across its three dimensions: compositional, structural and functional. What follows is a discussion of how efficient this structured approach to research was at (1) identifying elements in the system that are particularly vulnerable to disturbance and (2) delivering useful information for decision-making in the conservation of the TMCF in Oaxaca.

Did the surrogate variables selected across the three dimension of biodiversity, deliver valuable information on the impact of selective logging and the process of secondary succession? In terms of compositional changes above-ground, as expected from previous studies (Quintana-Ascencio & González-Espinosa, 1993; Blanco-Macias, 2001; Galindo-Jaimes *et al.*, 2002), the basal area dominance by different tree genera clearly distinguished all of the successional stages of the Tarantulas chronosequence. The evolution of the tree community through succession was

characterised by the diminishing dominance by pine and oak, together with the increasing area covered by a diverse group of genera of tropical origin. Evidence from other studies in Chiapas and in the Laguna chronosequence (Blanco-Macias, 2001; Ramírez-Marcial *et al.*, 2001), suggest that the prolonged dominance of pine alone, is an indication of a continuous low intensity impact through the extraction of firewood.

It was hypothesised that the tree genera dominating the canopy would not only be a good above-ground surrogate because of the distinct communities found at different times after disturbance. More importantly, it was predicted that the changes in tree dominance would translate into equally discriminating patterns in the soil microenvironmental conditions, litter fall and quantity and quality of litter standing crop. Some detectable changes in soil microenviroment that occur through succession may be associated with changes in the canopy structure. However, the most conspicuous variation associated with the changes in tree community was related to the organic matter provided to the soil subsystem.

This study presents evidence that the increase in tree genus diversity through succession is accompanied by changes in the soil microenvironment. Even though the canopy cover had recovered to pristine levels, after 15 years of succession soil temperature had not recovered fully from the increase caused by disturbance. As there is no information available about tree dominance in pristine forests of El Rincón, it is possible that the three dimensional complexity of pristine canopies (including epiphyte cover) may not have recovered after 100 years of succession, and as a consequence the fog retention capacity and soil protection from solar radiation, are still different from pristine conditions. In future conservation research in the Mexican TMCF, emphasis should be given to determine the relationship between the three dimensional complexity of the canopy (partly associated with the diversity of the tree community) and fog retention capacity. Further, the daily and seasonal variability in soil microenvironmental conditions may be more sensitive than the mean values to differences in canopy structure and therefore the effect of secondary succession on soil microenvironment may have been underestimated.

As predicted, the changes in canopy dominance were clearly translated into substantial modifications of the quantity and quality of the standing crop of litter. Of particular importance was the presence of pine and oak. Even if they did not always dominate the basal area of the forest, their litter conspicuously dominated all successional stages. Further, in mid-succession (45 and 75-year-old forests), when these two genera were most dominant, the forests appeared to be accumulating undecomposed litter on the floor. Evidence from decomposition experiments suggest that this accumulation of litter is not a result of slow decomposition rate but a product of higher litter fall from these two genera. Unfortunately, the continuous disappearance of litter traps in the field, made it impossible to corroborate this.

As predicted, the successional changes in tree compositional diversity above-ground are not only coupled with differences in the availability of litter, but are also closely associated with changes in the nutrient content in the soil. Nutrients seem to be more available in early succession and progressively locked-up in undecomposed organic matter and vegetation through succession. There is no information available for the nutrient status of pristine forests in Oaxaca. However, according to the literature, mature TMCF around the world are characterised by low nutrient availability (Vitousek, 1984; Bruijnzeel & Veneklaas, 1998). If this is the case for the pristine forest in Oaxaca, the evidence in this study suggests that undisturbed succession is returning the forest to its efficient nutrient cycling. This efficient nutrient cycling seems to be associated with the increasing dominance of late successional trees of tropical origin, that appear to produce less litter than pine or oak. Of particular relevance seems to be the cycling of P, which is particularly scarce in the Oaxacan forest soils. This nutrient was noticeably scarce in the litter of late successional species and more abundant in pine. This study did not measure the changes in available forms of this element, but it is probable that logging residues release this element to the soil, and it returns to be trapped in vegetation through succession. Future research should focus on the role that pine plays in the cycling of P, because the persistence of late successional tropical trees in these forests may not only depend on the availability of light but also be associated with their ability to compete

in phosphorus-poor soils. Continuous disturbance through selective logging of oak may promote the release of this element to the soil and facilitate pine persistence.

In terms of compositional diversity below-ground, higher macroinvertebrate taxa were generally good surrogates for the impact of logging and for secondary succession. However, their most conspicuous response to disturbance seems to be delayed in the soil community (but not in the litter). The soil community composition and diversity two months after disturbance was distinguishable from, but similar to the one in late succession. It drifted furthest from its pristine composition after 15 years of succession. An exception to this was the Collembola, which responded quickly to disturbance with a substantial increase in abundance. The other extreme was represented by the earthworms, which were almost exclusive to the pristine forests. These two taxa could in combination be a valuable target for more detailed conservation research. In particular the native worm *Ramiellona willsoni*, which appears to be the only earthworm present in these forests, seems to be specially vulnerable because it does not return to secondary forests even 100 years after disturbance. Further research on this species should focus on whether its absence from secondary succession is a result of its slow recolonisation ability or a product of an extreme sensitivity to differences in environmental or resource conditions between secondary and primary forest. The sensitivity to the diversity of litter resources and to the soil temperature are good candidate explanations, that could be easily tested in controlled laboratory conditions.

One of the most important findings is that even if the soil macroinvertebrate community in the 100-year-old forest was more similar to the pristine community than the community in any other successional stage, it was still substantially different. This means that 100 years of succession are not enough for the macroinvertebrate community to recover its original composition, even in terms of higher taxa.

The number of taxa in the soil was a good univariate indicator of secondary succession below ground in all three chronosequences. Further, in the soil mid

successional community, composition could be distinguished from early and late assemblages. In contrast, the litter community seemed to be less indicative of successional changes and more sensitive to variation in physical environmental conditions.

In terms of the structural dimension of biodiversity, it was predicted that the decrease in number of tree genera following logging disturbance would diminish the spatial heterogeneity in the soil at the within-plot scale. These changes were expected to be detected by surrogate variables such as the degrees of aggregation in soil microenvironmental variables, litter components and macroinvertebrate taxa. The homogenisation in the soil was expected to reverse as the tree community became more diverse through succession. These predictions were true for the degree of aggregation in litter resources and macroinvertebrate taxa, but not for the majority of nutrients in the soil (except total P) or microenvironmental conditions.

Pine and oak seem to be playing, again, important roles in driving the soil spatial patterns. Pine litter was found to be relatively scarce in Mg and Ca and oak litter in P. Accordingly, patches of *Quercus* litter in late succession and of *Pinus* litter in early succession appear to coincide with the areas of P and Mg-Ca deficit in the soil respectively. Particularly noticeable is the evidence that links oak litter with a P deficit in the soil. As oak's domination of the canopy diminished with succession, its litter became more aggregated and the patchiness of P increased. Further, it was found that in the 100-year-old forest, the decomposer organisms resident under oak canopies were able to decompose oak leaves incorporating less P from external sources than were the decomposers under the canopies of other tree genera. In this late successional stage, where the dominance of oak has diminished considerably and the remaining trees from this genus are presumably old, there has been a long time to develop a zone of influence in the soil around individual oaks. This zone of influence might have promoted a decomposer food-web specialised in a more efficient decomposition of phosphorus poor oak leaves. Similar evidence of a degree of specialisation was found under *Oreopanax* trees, where local leaves were decomposed immobilising less nitrogen than under other tree genera. This evidence

suggests that, at least in late succession, above-ground and below-ground biodiversities can be closely interdependent in their compositional, structural and functional dimensions.

The decomposition rate did not turn out to be a good surrogate for the impact of logging on the functional dimension of biodiversity. It was found that in all successional stages decomposition rate was sustained at equivalent rates for two standard experimental leaves of contrasting qualities. Mass loss appears to be too coarse an indicator of the decomposition process. More fine detail surrogates, such as release of P, N and Ca from decomposing litter, better reflected successional changes in biogeochemical cycling. The consequence of this finding is that the decomposer food-web in the different successional stages is probably not very specialised only to degrade litter of a certain quality. Therefore there is no evidence that disturbance affects the ability of the ecosystem to perform decomposition in terms of mass loss. However, more research is needed to assess the impact on nutrient mineralisation efficiency. If logging disturbance affected in any way the capability of the decomposer food-web to continue its decomposition function, this ability has fully recovered after 15 years of succession.

Ideally the study of the functional dimension of biodiversity requires more than measuring a particular process (for example decomposition rate or nutrient cycling). It should also involve distinguishing between the interaction that different groups of organisms have with the process, which includes identifying functional groups (such as trophic guilds) and their frequency of occurrence (Martinez, 1996). A functional group is formed by those organisms that share common biogeochemical attributes with respect to a particular ecosystem process (Naeem, 1998).

By deciding that higher macroinvertebrate taxa were going to be used as remote surrogates for soil organisms (with the intention to cover a greater range of organisms across the food-web) the possibility of identifying functional groups in the system was largely sacrificed. This is because the species included within many higher taxa, such as Collembola for example, perform several functions with respect

to decomposition. Some may be fungivorous, others predators, and yet others detritivorous (Verhoef & Brussaard, 1990; Addison *et al.*, 2003; Chauvat *et al.*, 2003). However, some taxa such as Diplopoda (detritivores) and Aranea (predators), do consist largely of a single functional group. This is why it has been suggested that there is probably some relationship between functional group richness of an area and its higher taxon richness (Gaston, 1994).

The results of this study could be used as the first step into further investigation of logging disturbance on functional diversity in the soil. Once it is known which higher taxa are most sensitive to disturbance, specific research into functional groupings could be directed towards them. Collembola seem a good candidate group, because their taxonomy and feeding guilds are relatively well defined (Chauvat *et al.*, 2003) and they were shown in this study to be sensitive to disturbance and secondary succession. Functional diversity can be measured by determining which and how many functional groups are represented in an ecological system. First, a typology of functional groups should be developed based on a variety of interactions with an ecological process (such as decomposition). Membership of functional by species groups is evaluated by characterising the interactions with a process both qualitatively (which prey were consumed) and quantitatively (how much was consumed). Standard statistical procedures can be used to quantify the similarity and difference between entities according to qualified and quantified functions (Martinez, 1996).

Hierarchical controls and nested scales of variation have been incorporated in ecological theory in different contexts (O'Neill *et al.*, 1986; Kotliar & Weins, 1990; Ehrenfeld *et al.*, 1997; Ettema & Wardle, 2002), and have been pointed out to be central in the Biodiversity concept (Noss, 1990; Gaston, 1996). Hierarchical controls and nested scales also emerged as possible explanations throughout this thesis. For example, it was suggested that larger scale climatic controls constrained decomposition process and macroinvertebrate populations overriding the effect of other potential smaller scale controls such as tree community composition and diversity. This dominance of the climatic control was probably happening at larger

temporal and spatial scales than the one selected for the study. The temporal variation was clearly observed in Chapter 6 where most of the variation of the macroinvertebrate taxa in natural populations and inside experimental boxes was explained by seasonal patterns that need to be studied with appropriate replication at a yearly scale. Climate could also be exerting control over soil organisms and decomposition at a larger spatial scale. For example the large variability in Macroinvertebrate data found between chronosequences could be explained by climatic differences. This means that in a mosaic landscape created by a patchy pattern of disturbance, climatic controls may interact with disturbance at larger spatial scales to determine biogeochemical processes. Some evidence that supports nested spatial controls of litter and nutrients was found in Chapter 4 where two different nested scales of autocorrelation were often detected in variograms. The smaller scale (5-24 m) was modelled by an exponential element in the equation and could be explained by the influence of vegetation heterogeneity. The larger scale (more than 24m) was described by a secondary power equation integrated in the model and must be controlled by factors operating at larger scales such as soil type or climate.

The project was not designed to test for the impact of logging on the biogeochemical processes at various scales or levels of organisation. Only one scale and one level of organisation were selected. This was because changes in the tree community composition (organismal level of organisation) caused by disturbance at a plot-size scale were expected to have consequences for the soil biogeochemistry at equivalent scale and level of organisation. The evidence shows that this is an over simplification of the system. It has been pointed out before that even if environmental properties are thought to be functionally linked, the spatial scales at which they vary can be very different (Ehrenfeld *et al.*, 1997). As suggested by Noss (1990) a more comprehensive evaluation of the impact of logging would not only include surrogates across the three dimensions of biodiversity, but would also incorporate indicators at different levels of organisation which usually operate at nested spatial scales.

In conclusion results from this study should be useful for decision-making in the conservation of the TMCF in Oaxaca. Low intensity selective logging compromises the compositional and spatial components of biodiversity above- and below-ground and full recovery may take more than 100 years. In the absence of further information, conservation measures should pay particular attention to the native worm *Ramiellona willsoni* that seems not to be able to re-establish in secondary forest. The complex spatial structures developed in old forests may be essential for the maintenance of a fully functional and diverse soil system. Therefore, the homogenisation of the canopy is likely to be a threat to the conservation of these forests and all efforts should be put in place to control sustained disturbance, even if it is of low intensity. Finally, this study has succeeded in directing future research towards vulnerable taxa and processes that may be crucial to sustain the diverse, slow growing and nutrient poor character of the TMCF in Mexico.

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APPENDIX CH3

Source of variation	Degrees of freedom effect	Mean Square effect	Degrees of freedom error	Mean Square error	F-ratio	P-value	Randomisation test
ANOVA comparing							
Site	3	765.31	24	55.43	13.806	<0.0001	y
two-way ANOVA comparing Tarantulas, Tarbis and Laguna chronosequences							
Chronose-quence	2	0.954	6	33.61	0.028	0.973	y
Forest age	3	17.01	6	33.61	0.506	0.692	y
ANCOVA of mean per successional stage. Includes Tarantulas, Tarbis and Laguna chronosequences as well as Pris, PrisII, Tar0 and Tar00 (Date as covariant)							
Forest age	5	91.83	9	2.85	32.25	<0.0001	n

Table CH3.1. Analyses of variance comparing canopy cover in the different study sites. For the ANOVA and two-way ANOVA within site point measurements were used as replicates, for the ANCOVA the mean of within site point measurements was used as a single replicate. The last column indicates whether a randomisation test was performed to determine the P-value (done in case of failure to meet the assumptions of homogeneity of variance and normality that permit the use of standard F distribution curves)

Source of variation	Degrees of freedom effect	Mean Square effect	Degrees of freedom error	Mean Square error	F-ratio	P-value	Randomisation test
ANOVA comparing Pris, PrisII, Tar0 and Tar00							
Site	3	128.38	24	2.80	45.91	<0.0001	y
two-way ANOVA comparing Tarantulas and Tarbis chronosequences							
Chronose-Quence	1	75.52	3	0.417	181.10	0.009	y
Forest age	3	9.99	3	0.417	23.96	0.013	y
ANCOVA of mean per successional stage. Includes Tarantulas and Tarbis chronosequences as well as Pris, PrisII, Tar0 and Tar00 (Date as covariant)							
Forest age	5	12.64	5	0.655	19.31	0.003	y

Table CH3.2. Analyses of variance comparing soil temperature in the different study sites. For the ANOVA and two-way ANOVA within site point measurements were used as replicates, for the ANCOVA the mean of within site measurements was used as a single replicate. The last column indicates whether a randomisation test was performed to determine the P-value (done in case of failure to meet the assumptions of homogeneity of variance and normality that permit the use of standard F distribution curves)

Source of variation	Degrees of freedom effect	Mean Square effect	Degrees of freedom error	Mean Square error	F-ratio	P-value	Randomisation test
ANOVA comparing Pris, PrisII, Tar0 and Tar00							
Site	3	0.011	24	0.002	6.706	0.002	y
two-way ANOVA comparing Tarantulas, Tarbis and Laguna chronosequences							
Chronose-Quence	2	0.332	6	0.024	13.833	0.006	y
Forest age	3	0.008	6	0.024	0.333	0.802	y
ANCOVA of mean per successional stage. Includes Tarantulas, Tarbis and Laguna chronosequences as well as Pris, PrisII, Tar0 and Tar00 (Date as covariant)							
Forest age	5	0.0006	9	0.003	0.207	0.95	n

Table CH3.3. Analyses of variance comparing volumetric soil water content in the different study sites. For the ANOVA and two-way ANOVA within site point measurements were used as replicates, for the ANCOVA the mean of within site measurements was used as a single replicate. The last column indicates whether a randomisation test was performed to determine the P-value (done in case of failure to meet the assumptions of homogeneity of variance and normality that permit the use of standard F distribution curves)

Source of variation	Degrees of freedom effect	Mean Square effect	Degrees of freedom error	Mean Square error	F-ratio	P-value	Randomisation test
Repeated measures ANOVA (Forest age $\times$ *Collection period*)							
Forest age	3	0.968	23	0.4699	2.059	0.134	n
Col. date	5	5.535	115	0.111	49.900	<0.0001	n
Age × col	15	0.478	115	0.111	4.311	<0.0001	n
ANOVA collection period 7/12/01-24/1/02 alone without the 45 years old forest							
Forest age	3	0.110	22	0.111	0.993	0.415	n

Table CH3.4. Analyses of variance comparing the volume of litter·day^{-1}·trap^{-1} found in each of the four successional stages of the Tarantulas chronosequence. For the repeated measures ANOVA collection occasion was used as the repetition factor with six levels. For the collection period 7/12/01-24/1/02 a separate one-way analysis of variance was performed without considering the 45-year-old forest. This was due to the fact that only one litter trap was left intact for that successional stage in that period.

Source of variation	Degrees of freedom effect	Mean Square effect	Degrees of freedom error	Mean Square error	F-ratio	P-value	Randomisation test
ANOVA comparing Pris, PrisII, Tar0 and Tar00							
Site	3	1022.81	24	872.16	1.17	0.341	n
two-way ANOVA comparing Tarantulas, Tarbis and Laguna chronosequences							
Chronose-quence	2	268.35	6	1228.06	0.22	0.810	y
Forest age	3	4801.65	6	1228.06	3.909	0.073	y
ANCOVA of mean per successional stage. Includes Tarantulas, Tarbis and Laguna chronosequences as well as Pris, PrisII, Tar0 and Tar00 (Collection date as covariant)							
Forest age	5	441.07	9	166.89	2.64	0.097	n

Table CH3.5 Analyses of variance comparing volume of standing litter in the different study sites. For the ANOVA and two-way ANOVA within site point measurements were used as replicates, for the ANCOVA the mean of within site measurements was used as a single replicate. The last column indicates whether a randomisation test was performed to determine the P-value (done in case of failure to meet the assumptions of homogeneity of variance and normality that permit the use of standard F distribution curves)

MANOVA					
Effect	**Wilks' λ**	**Rao's R**	**Degrees of freedom 1**	**Degrees of freedom 2**	**P-value**
Forest age	0.205	22.088	18	529	0.001

ANOVAs of individual variables						
Individual variable	**Degrees of freedom effect**	**Mean Square effect**	**Degrees of freedom error**	**Mean Square error**	**F-ratio**	**P-value**
Unidentifiable	3	6522.14	192	472.74	13.80	<0.0001
Lauracea	3	23.13	192	0.57	40.32	<0.0001
Pinus spp.	3	4177.12	192	160.61	26.01	<0.0001
Quercus spp.	3	4353.64	192	84.86	51.30	<0.0001
other species	3	1179.87	192	76.89	15.35	<0.0001
w & r	3	568.36	192	359.75	1.58	0.20

Table CH3.6. One-way multivariate analysis of variance of the litter components in the Tarantulas chronosequence (forest ages: 15, 45, 75 and 100 years). It includes mass per sample (g) of the following categories: unidentifiable material, Lauracea, *Pinus* spp., *Quercus* spp., other species and woody and reproductive material (w & r). Bonferroni adjusted significance level for multiple testing is P≤0.008.

MANOVA					
Effect	**Wilks' λ**	**Rao's R**	**Degrees of freedom 1**	**Degrees of freedom 2**	**P-value**
Foliar species	0.0001	43.901	27	3	0.005

ANOVAs of individual variables						
Individual variable	**Degrees of freedom effect**	**Mean Square effect**	**Degrees of freedom error**	**Mean Square error**	**F-ratio**	**P-value**
Carbon	3	1.52	9	0.02	68.39	<0.0001
Nitrogen	3	0.10	9	0.07	1.39	0.31
Phosphorus	3	1.33	9	0.08	17.49	<0.0001
Sodium	3	0.04	9	0.01	2.80	0.10
Potassium	3	64.21	9	4.09	15.72	<0.0001
Calcium	3	286.37	9	80.22	3.57	0.06
Magnesium	3	527.60	9	10.77	49.01	<0.0001
ASF	3	1.09	9	0.38	2.86	0.10
RF	3	186.93	9	2.62	71.33	<0.0001

Table CH3.7. One-way multivariate analysis of variance of nutrient and fibre concentration in the senescent leaves of *Beilschmedia ovalis*, *Pinus chiapensis*, *Quercus* spp. and *Oreopanax xalapensis*. It includes Carbon (%), Nitrogen (%), P (cmol.kg^{-1}), Mg^{++}(cmol.kg^{-1}), Na^{+} (cmol.kg^{-1}), K^{+}(cmol.kg^{-1}), Ca^{++}(cmol.kg^{-1}), percent of fibre acid soluble fraction(ASF) and percent of fibre residual fraction (RF). Sample size is three except for *P. chiapensis* where it is four. Bonferroni adjusted significance level for multiple testing is P≤0.006.

MANOVA					
Effect	**Wilks' λ**	**Rao's R**	**Degrees of freedom 1**	**Degrees of freedom 2**	**P-value**
Forest age	0.1403	5.125	21	109	<0.0001

ANOVAs of individual variables						
Individual variable	**Degrees of freedom effect**	**Mean Square effect**	**Degrees of freedom error**	**Mean Square error**	**F-ratio**	**P-value**
Carbon	3	3024.72	192	67.41	44.87	<0.0001
Nitrogen	3	0.73	44	0.18	4.08	0.01
Phosphorus	3	0.57	192	0.21	2.69	0.05
Sodium	3	7.86	192	0.16	49.75	<0.0001
Potassium	3	7.17	192	0.27	26.84	<0.0001
Calcium	3	302.65	192	10.40	29.09	<0.0001
Magnesium	3	65.43	192	2.97	22.02	<0.0001

Table CH3.8. One-way multivariate analysis of variance of the nutrient concentration in the first 5 cm of soil of the Tarantulas chronosequence (forest ages: 15, 45, 75 and 100 years). It includes Carbon (%), Nitrogen (%), P ($cmol.kg^{-1}$), Mg^{++}($cmol.kg^{-1}$), Na^{+} ($cmol.kg^{-1}$), K^{+}($cmol.kg^{-1}$) and Ca^{++} ($cmol.kg^{-1}$). Bonferroni adjusted significance level for multiple testing is $P \leq 0.007$.

Source of variation	**Degrees of freedom effect**	**Mean Square effect**	**Degrees of freedom error**	**Mean Square error**	**F-ratio**	**P-value**	**Randomisation test**
ANOVA comparing Pris, PrisII, Tar0 and Tar00							
Site	3	44.13	24	10.26	4.30	0.015	n
two-way ANOVA comparing Tarantulas, Tarbis and Laguna chronosequences							
Chronose-quence	3	13.09	6	22.86	0.572	0.572	y
Forest age	2	118.60	6	22.86	5.19	0.049	y
ANCOVA of mean per successional stage. Includes Tarantulas, Tarbis and Laguna chronosequences as well as Pris, PrisII, Tar0 and Tar00 (Collection date as covariant)							
Forest age	5	3.83	9	1.52	2.52	0.109	n

Table CH3.9. Analyses of variance comparing the number of macroinvertebrate taxa per sample found in the litter of the different study sites. For the ANOVA and two-way ANOVA within site point measurements were used as replicates, for the ANCOVA the mean of within site measurements was used as a single replicate. The last column indicates whether a randomisation test was performed to determine the P-value (done in case of failure to meet the assumptions of homogeneity of variance and normality that permit the use of standard F distribution curves)

Source of variation	Degrees of freedom effect	Mean Square effect	Degrees of freedom error	Mean Square error	F-ratio	P-value	Randomisation test
ANOVA comparing Pris, PrisII, Tar0 and Tar00							
Site	3	0.094	24	0.191	4.948	0.008	y
two-way ANOVA comparing Tarantulas, Tarbis and Laguna chronosequences							
Chronose-quence	3	0.015	6	0.078	0.192	0.898	y
Forest age	2	0.316	6	0.078	4.051	0.077	y
ANCOVA of mean per successional stage. Includes Tarantulas, Tarbis and Laguna chronosequences as well as Pris, PrisII, Tar0 and Tar00 (Collection date as covariant)							
Forest age	5	0.010	9	0.004	2.52	0.108	n

Table CH3.10. Analyses of variance comparing the equitablility index of macroinvertebrate taxa per sample found in the litter of the different study sites. For the ANOVA and two-way ANOVA within site point measurements were used as replicates, for the ANCOVA the mean of within site measurements was used as a single replicate. The last column indicates whether a randomisation test was performed to determine the P-value (done in case of failure to meet the assumptions of homogeneity of variance and normality that permit the use of standard F distribution curves)

Source of variation	Degrees of freedom effect	Mean Square effect	Degrees of freedom error	Mean Square error	F-ratio	P-value	Randomisation test
ANOVA comparing Pris, PrisII, Tar0 and Tar00							
Site	3	0.928	24	0.187	4.95	0.008	y
two-way ANOVA comparing Tarantulas, Tarbis and Laguna chronosequences							
Chronose-quence	3	0.157	6	0.788	0.199	0.893	y
Forest age	2	2.466	6	0.788	3.13	0.117	y
ANCOVA of mean per successional stage. Includes Tarantulas, Tarbis and Laguna chronosequences as well as Pris, PrisII, Tar0 and Tar00 (Date as covariant)							
Forest age	5	0.96	9	0.039	2.44	0.116	n

Table CH3.11. Analyses of variance comparing the Shannon Diversity index of macroinvertebrate taxa per sample found in the litter of the different study sites. For the ANOVA and two-way ANOVA within site point measurements were used as replicates, for the ANCOVA the mean of within site measurements was used as a single replicate. The last column indicates whether a randomisation test was performed to determine the P-value (done in case of failure to meet the assumptions of homogeneity of variance and normality that permit the use of standard F distribution curves)

Source of variation	Degrees of freedom effect	Mean Square effect	Degrees of freedom error	Mean Square error	F-ratio	P-value	Randomisation test
ANOVA comparing Pris, PrisII, Tar0 and Tar00							
Site	3	2.036	24	5.631	0.362	0.781	n
two-way ANOVA comparing Tarantulas, Tarbis and Laguna chronosequences							
Chronose-quence	3	64.799	6	8.48	7.64	0.018	n
Forest age	2	127.950	6	8.48	15.08	0.004	n
ANCOVA of mean per successional stage. Includes Tarantulas, Tarbis and Laguna chronosequences as well as Pris, PrisII, Tar0 and Tar00 (Date as covariant)							
Forest age	5	4.50	9	1.30	3.47	0.050	n

Table CH3.12. Analyses of variance comparing the number of macroinvertebrate taxa per sample found in the soil of the different study sites. For the ANOVA and two-way ANOVA within site point measurements were used as replicates, for the ANCOVA the mean of within site measurements was used as a single replicate. The last column indicates whether a randomisation test was performed to determine the P-value (done in case of failure to meet the assumptions of homogeneity of variance and normality that permit the use of standard F distribution curves)

Source of variation	Degrees of freedom effect	Mean Square effect	Degrees of freedom error	Mean Square error	F-ratio	P-value	Randomisation test
ANOVA comparing Pris, PrisII, Tar0 and Tar00							
Site	3	0.003	24	0.013	0.254	0.875	n
two-way ANOVA comparing Tarantulas, Tarbis and Laguna chronosequences							
Chronose-quence	3	0.024	6	0.032	0.75	0.561	y
Forest age	2	0.101	6	0.032	3.15	0.116	y
ANCOVA of mean per successional stage. Includes Tarantulas, Tarbis and Laguna chronosequences as well as Pris, PrisII, Tar0 and Tar00 (Date as covariant)							
Forest age	5	0.002	9	0.002	0.725	0.621	n

Table CH3.13. Analyses of variance comparing the equitablility index of macroinvertebrate taxa per sample found in the soil of the different study sites. For the ANOVA and two-way ANOVA within site point measurements were used as replicates, for the ANCOVA the mean of within site measurements was used as a single replicate. The last column indicates whether a randomisation test was performed to determine the P-value (done in case of failure to meet the assumptions of homogeneity of variance and normality that permit the use of standard F distribution curves)

Source of variation	Degrees of freedom effect	Mean Square effect	Degrees of freedom error	Mean Square error	F-ratio	P-value	Randomisation test
ANOVA comparing Pris, PrisII, Tar0 and Tar00							
Site	3	0.037	24	0.144	0.254	0.857	n
two-way ANOVA comparing Tarantulas, Tarbis and Laguna chronosequences							
Chronose-quence	3	0.260	6	0.352	0.738	0.567	y
Forest age	2	1.100	6	0.352	3.125	<0.118	y
ANCOVA of mean per successional stage. Includes Tarantulas, Tarbis and Laguna chronosequences as well as Pris, PrisII, Tar0 and Tar00 (Date as covariant)							
Forest age	5	0.017	9	0.023	0.726	0.623	n

Table CH3.14. Analyses of variance comparing the Shannon diversity index of macroinvertebrate taxa per sample found in the soil of the different study sites. For the ANOVA and two-way ANOVA within site point measurements were used as replicates, for the ANCOVA the mean of within site measurements was used as a single replicate. The last column indicates whether a randomisation test was performed to determine the P-value (done in case of failure to meet the assumptions of homogeneity of variance and normality that permit the use of standard F distribution curves

	Axes				**Total inertia**
	1	2	3	4	
Eigenvalues	.139	.074	.060	.046	2.810
Taxa-environment correlations	.584	.642	.568	.581	
Cumulative percentage variance					
Taxa data	5.0	7.6	9.7	11.4	
taxa-environment relation	29.3	45.0	57.6	67.4	
Sum of all unconstrained eigenvalues					2.810
Sum of all canonical eigenvalues					0.474
P-value in Monte-Carlo test	0.015				<0.005

Table CH 3.15. Canonical Correspondance Analysis of litter macroinvertebrate community composition in Tarantulas chronosequence, with respect to successional stage (four dummy variables), soil microclimate (soil temperature (°C), volumetric soil water content ($cm^3.cm^{-3}$) and canopy cover (%)), litter composition (weight of *Pinus* leaves, Lauracea leaves, *Quercus* leaves, other leaves, unidentifiable material and woody and reproductive material) and soil nutrient content (Carbon (%), Nitrogen (%), P (ppm), Mg^{++}(ppm), Na^{+}(ppm), K^{+}(ppm) and Ca^{++}(ppm)). Two 15-year-old forest and one 100-year-old forest samples were excluded due to their extreme values.

	Axes				Total inertia
	1	2	3	4	
Eigenvalues	0.116	0.078	0.071	0.046	2.326
Taxa-environment correlations	0.595	0.614	0.620	0.531	
Cumulative percentage variance					
Taxa data	5.0	8.3	11.4	13.3	
taxa-environment relation	26.5	44.2	60.2	70.7	
Sum of all unconstrained eigenvalues					2.326
Sum of all canonical eigenvalues					0.439
P-value in Monte-Carlo test	<0.005				<0.005

Table CH3.16. Canonical Correspondance Analysis of soil macroinvertebrate community composition in Tarantulas chronosequence, with respect to successional stage (four dummy variables), soil microclimate (soil temperature (°C), volumetric soil water content ($cm^3.cm^{-3}$) and canopy cover (%)), litter composition (weight of *Pinus* leaves, Lauracea leaves, *Quercus* leaves, other leaves, unidentifiable material and woody and reproductive material) and soil nutrient content (Carbon (%), Nitrogen (%), P (ppm), Mg^{++} (ppm), Na^{+} (ppm), K^{+} (ppm) and Ca^{++} (ppm)). One 45-year-old forest sample was excluded due to its extreme values.

	Axes				Total inertia
	1	2	3	4	
INCLUDING SOIL TEMPERATURE AND EXCLUDING LAGUNA CHRONOSEQUENCE					
Eigenvalues	0.157	0.136	0.059	0.039	1.864
Taxa-environment correlations	0.842	0.827	0.635	0.670	
Cumulative percentage variance					
Taxa data	8.4	15.7	18.9	21.0	
taxa-environment relation	32.3	60.5	72.7	80.7	
Sum of all unconstrained eigenvalues					1.864
Sum of all canonical eigenvalues					.485
P-value in Monte-Carlo test	<0.005				<0.005
INCLUDING LAGUNA CHRONOSEQUENCE AND EXCLUDING SOIL TEMPERATURE					
Eigenvalues	.245	0.117	0.096	0.041	2.264
Taxa-environment correlations	0.695	0.793	0.655	0.612	
Cumulative percentage variance					
Taxa data	10.8	16.0	20.3	22.1	
taxa-environment relation	44.0	65.0	82.3	89.6	
Sum of all unconstrained eigenvalues					2.264
Sum of all canonical eigenvalues					0.558
P-value in Monte-Carlo test	<0.005				<0.005

Table CH3.17. Canonical Correspondance Analysis of litter macroinvertebrate community composition with respect to successional stage (dummy variables), soil microclimate (soil temperature, volumetric soil water content and canopy cover), litter mass and soil bulk density variables. Includes Tarantulas (seven random subsamples), Laguna (unless stated) and Tarbis chronosequences plus recently logged sites (Tar0 and Tar00) and pristine sites (Pris and PrisII).

	Axes				Total inertia
	1	2	3	4	
INCLUDING SOIL TEMPERATURE AND EXCLUDING LAGUNA CHRONOSEQUENCE					
Eigenvalues	0.128	0.075	0.033	0.031	1.831
Taxa-environment correlations	0.710	0.610	0.570	0.524	
Cumulative percentage variance					
Taxa data	7.0	11.1	12.9	14.6	
taxa-environment relation	37.3	59.3	69.0	78.2	
Sum of all unconstrained eigenvalues					1.831
Sum of all canonical eigenvalues					0.342
P-value in Monte-Carlo test	<0.005				<0.005
INCLUDING LAGUNA CHRONOSEQUENCE AND EXCLUDING SOIL TEMPERATURE					
Eigenvalues	0.119	0.068	0.031	0.020	1.987
Taxa-environment correlations	0.643	0.572	0.535	0.455	
Cumulative percentage variance					
Taxa data	6.0	9.4	10.9	12.0	
taxa-environment relation	41.0	64.4	74.9	81.8	
Sum of all unconstrained eigenvalues					1.987
Sum of all canonical eigenvalues					0.290
P-value in Monte-Carlo test	<0.005				<0.005

Table CH3.18. Canonical Correspondance Analysis of soil macroinvertebrate community composition with respect to successional stage (dummy variables), soil microclimate (soil temperature, volumetric soil water content and canopy cover), litter mass and soil bulk density variables. Includes Tarantulas (seven random subsamples), Laguna (unless stated) and Tarbis chronosequences plus recently logged sites (Tar0 and Tar00) and pristine sites (Pris and PrisII).

Species	RF (%)	ASF (%)	provinence	Reference
Genus *Pinus*				
Pinus chiapensis	**56.5**	**3.0**	**TMCF Oaxaca, Mexico**	**This thesis**
Pinus rigida	22.4	23.9	Appalachian Mountains, USA.	White *et al.*, 1988
Pinus sylvestris	18.1-31.7	24.0-27.0	Devon, UK	Sanger *et al.* 1998
Other conifers				
Araucaria araucana	19.3	---	NW Patagonia, Argenitna	Satti *et al.*, 2003
Austrocedrus chilensis	18.7	---	NW Patagonia, Argenitna	Satti *et al.*, 2003
Fitzroya cupressoides	35.3	---	NW Patagonia, Argenitna	Satti *et al.*, 2003
Picea abies (fresh)	20.8	---	Central Sweden	Berg and Tamm, 1991
Genus *Quercus*				
***Quercus* sp.**	**59.6**	**3.6**	**TMCF Oaxaca, Mexico**	**This thesis**
Quercus suber	9.0	42.1	South Spain	Gallardo and Merino, 1993
Quercus canarensis	10.5	37.9	South Spain	Gallardo and Merino, 1993
Quercus pyrenaica	9.0	43.1	South Spain	Gallardo and Merino, 1993
Quercus prinus	23.6	---	Appalachian Mountains, USA.	Blair, 1988
Quercus robur	26.3-40.2	20.6-25.6	Devon, UK	Sariyildiz and Anderson, 2003
Other broadleaves				
Beilschmedia ovalis	**68.0**	**3.5**	**TMCF Oaxaca, Mexico**	**This thesis**
Oreopanax xalapensis	**48.9**	**2.3**	**TMCF Oaxaca, Mexico**	**This thesis**
Lomatia hirsuta	23.9	---	NW Patagonia, Argenitna	Satti *et al.*, 2003
Maytenus boaria	13.2	---	NW Patagonia, Argenitna	Satti *et al.*, 2003
Nothofagus dombeyi	16.0	---	NW Patagonia, Argenitna	Satti *et al.*, 2003
Nothofagus antarctica	17.5	---	NW Patagonia, Argenitna	Satti *et al.*, 2003
Nothofagus nervosa	20.7	---	NW Patagonia, Argenitna	Satti *et al.*, 2003
Nothofagus obliqua	19.2	---	NW Patagonia, Argenitna	Satti *et al.*, 2003
Nothofagus pumilio	11.9	---	NW Patagonia, Argenitna	Satti *et al.*, 2003
Nothofagus spp.	30.8	19.9	Across New Zeland	Wardle *et al.*, 2002
Metrosideros polymorpha	13.0-32.0	30.0-50.0	tmcf Hawaii, USA	Vitousek *et al.*, 1994
Fagus grandifolia	24.1	---	New Hampshire, USA	Melillo *et al.*, 1982
Fagus sylvatica	36.9-45.0	27.1-31.8	Devon, UK	Sariyildiz and Anderson, 2003
Liriodendron tulipifera	15.1	26.9	Appalachian Mountains, USA.	White *et al.*, 1988
Kalmia latifolia	19.1	18.9	Appalachian Mountains, USA.	White *et al.*, 1988
Cornus florida	4.6	---	Appalachian Mountains, USA.	Blair, 1988
Acer rubrum	9.6	---	Appalachian Mountains, USA.	Blair, 1988
Acer Saccharum	10.1	---	New Hampshire, USA	Melillo *et al.*, 1982
Prunus pensylvanica	19.3	---	New Hampshire, USA	Melillo *et al.*, 1982
Betula papyrifera	14.5	---	New Hampshire, USA	Melillo *et al.*, 1982
Fraxinus americana	12.2	---	New Hampshire, USA	Melillo *et al.*, 1982
Fraxinus angustifolia	5.1	29.5	South Spain	Gallardo and Merino, 1993
Salix atrocinerea	6.9	22.4	South Spain	Gallardo and Merino, 1993
Grevillia robusta (fresh)	22.0	---	Semi-arid Kenya	Kwabiah *et al.*, 2003
Sesbania sesban (fresh)	6.0-14.0	---	Semi-arid Kenya	Kwabiah *et al.*, 2003
Azadirachta indica (fresh)	8.0	---	Semi-arid Kenya	Kwabiah *et al.*, 2003
Calliandra calothyrsus (fresh)	13.0	---	Semi-arid Kenya	Kwabiah *et al.*, 2003
Leucaena leucocephala (fresh)	15.0	---	Semi-arid Kenya	Kwabiah *et al.*, 2003
Gliricidia sepium (fresh)	17.0	---	Semi-arid Kenya	Kwabiah *et al.*, 2003

Table CH3.19. Mean proportion of acid soluble fraction (ASF) and remaining fraction (RF) of fibre in leaf litter from four tree species in this study (in bold) and in the litter and fresh leaves of several conifers and woody broadleaves reported in other studies. All studies used the extraction technique described by Van Soest (1994).

15-year-old forest

Pinus | Total carbon | Total phosphorus

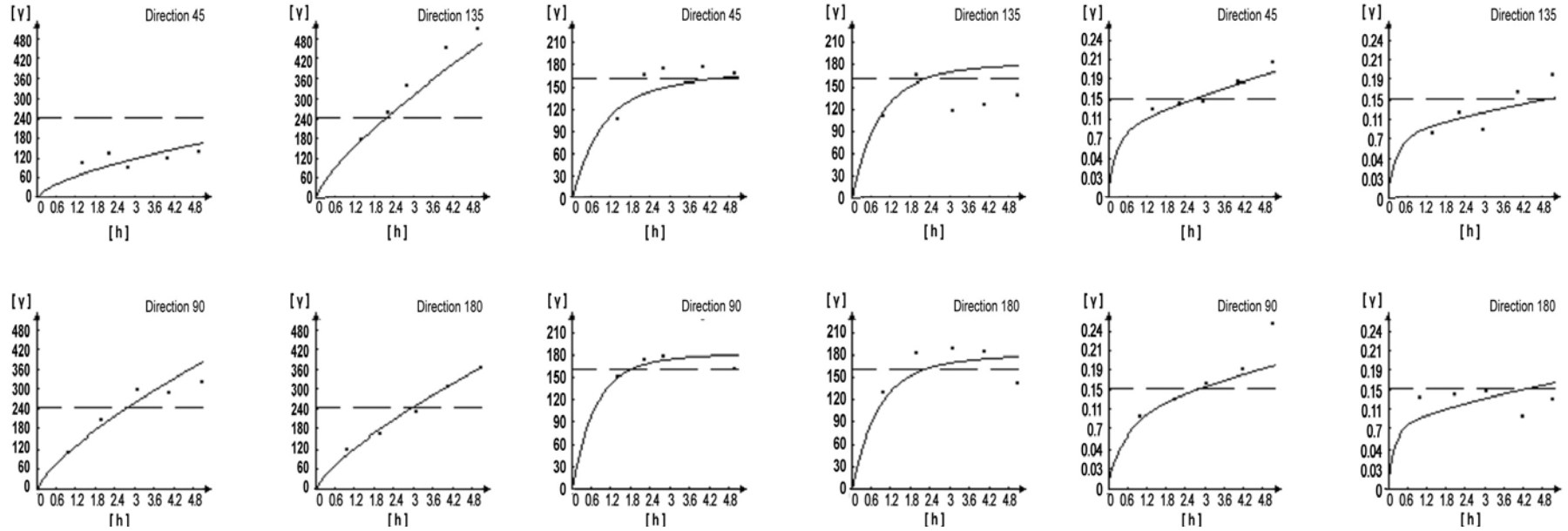


Figure CH4.1 Experimental and model variograms of litter components and soil chemistry variables that had an autocorrelated phase in the 15-year-old forest. Experimental variograms in the direction of maximum and minimum anisotropy, plus their perpendicular directions are presented. One lag is equivalent to 5 m (for nested model equations and goodness of fit see table 4.3)

15-year-old forest

Sodium-Na^{+} Calcium-Ca^{++} Magnesium-Mg^{++}

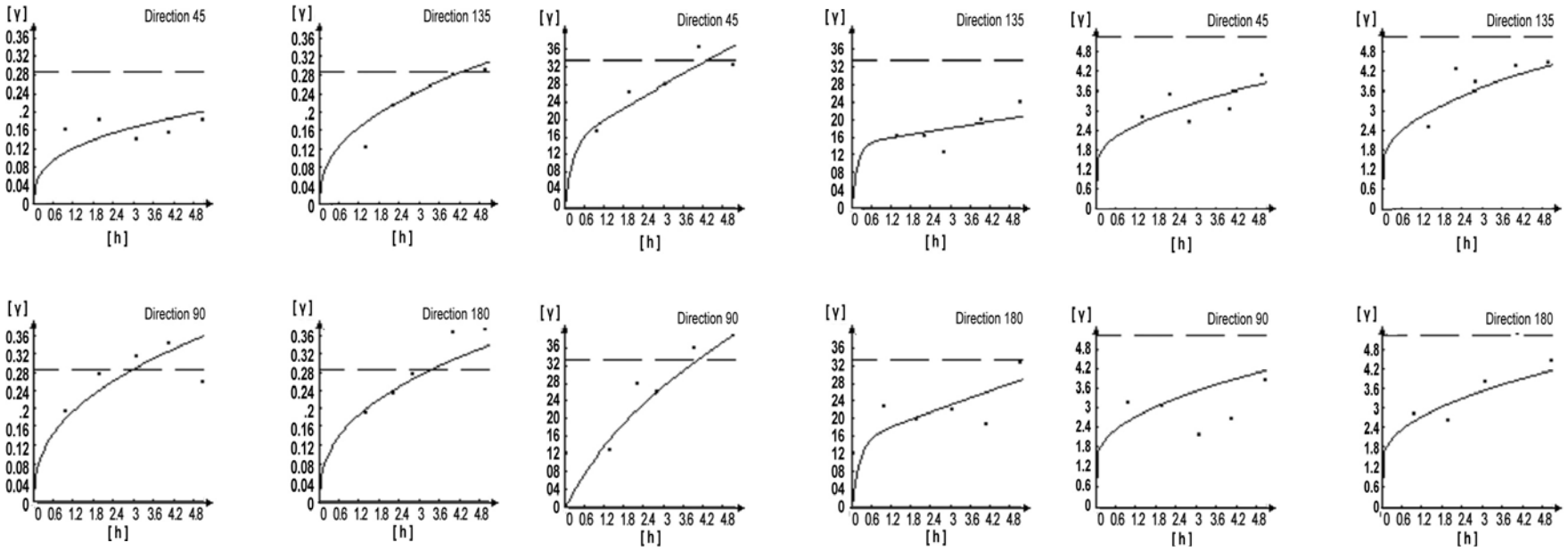


Figure CH4.1. continuation...ends.

45-year-old forest

Quercus Ln (*Pinus*) Ln (other species)

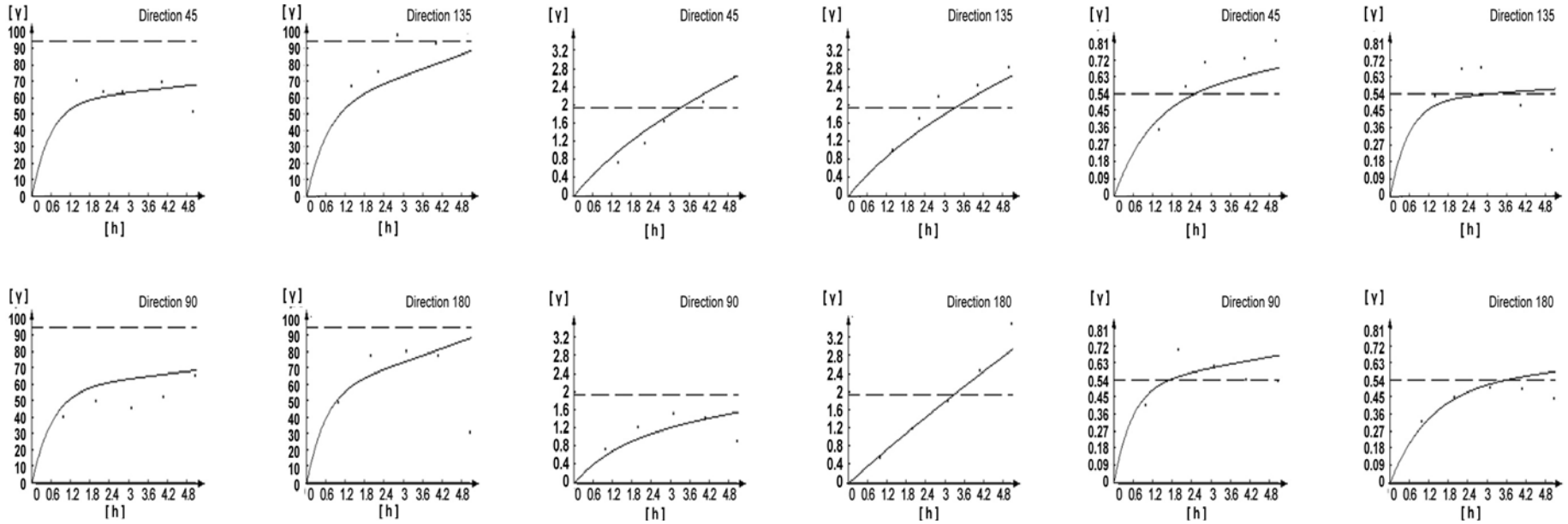


Figure CH4.2 Experimental and model variograms of litter components and soil chemistry variables that had an autocorrelated phase in the 45-year-old forest. Experimental variograms in the direction of maximum and minimum anisotropy, plus their perpendicular directions are presented. One lag is equivalent to 5 m (for nested model equations and goodness of fit see table 4.3)

45-year-old forest

Woody and reproductive

Total phosphorus

Ln (sodium- Na^{+})

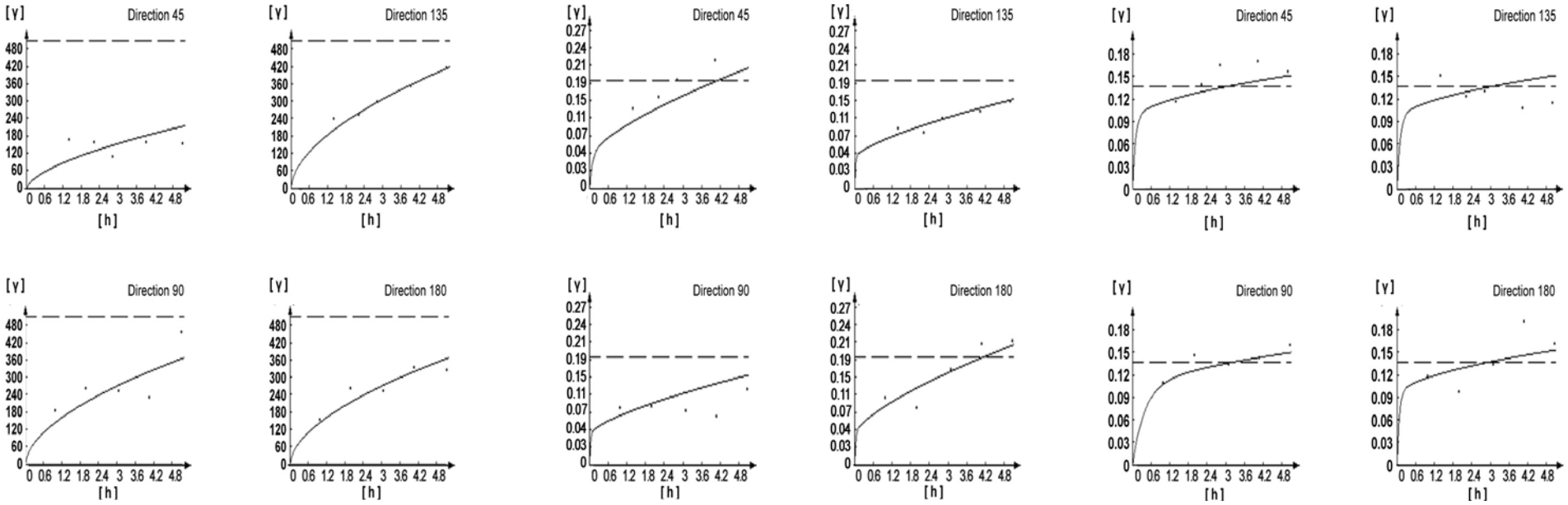


Figure CH4.2 continuation....

45-year-old forest

Ln (magnesium-Mg^{++})

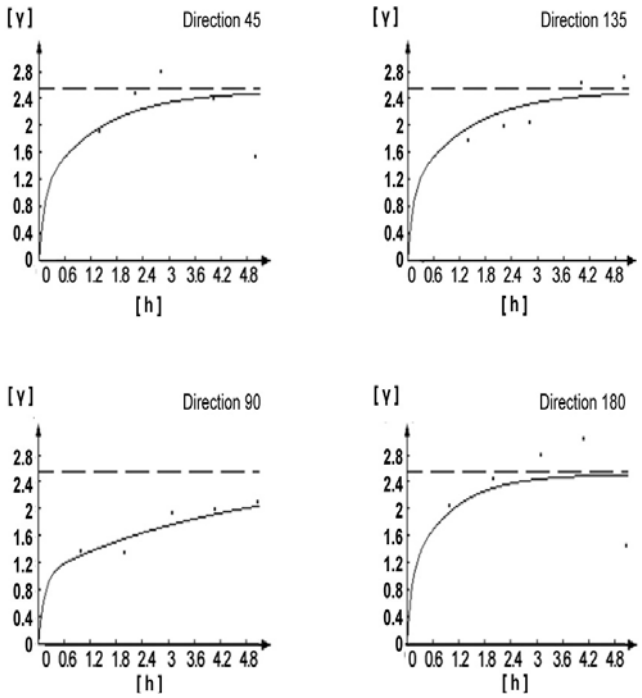


Figure CH4.2 continuation...ends.

75-year-old forest

Ln (unidentifiable material) | *Quercus* | Ln (*Pinus*)

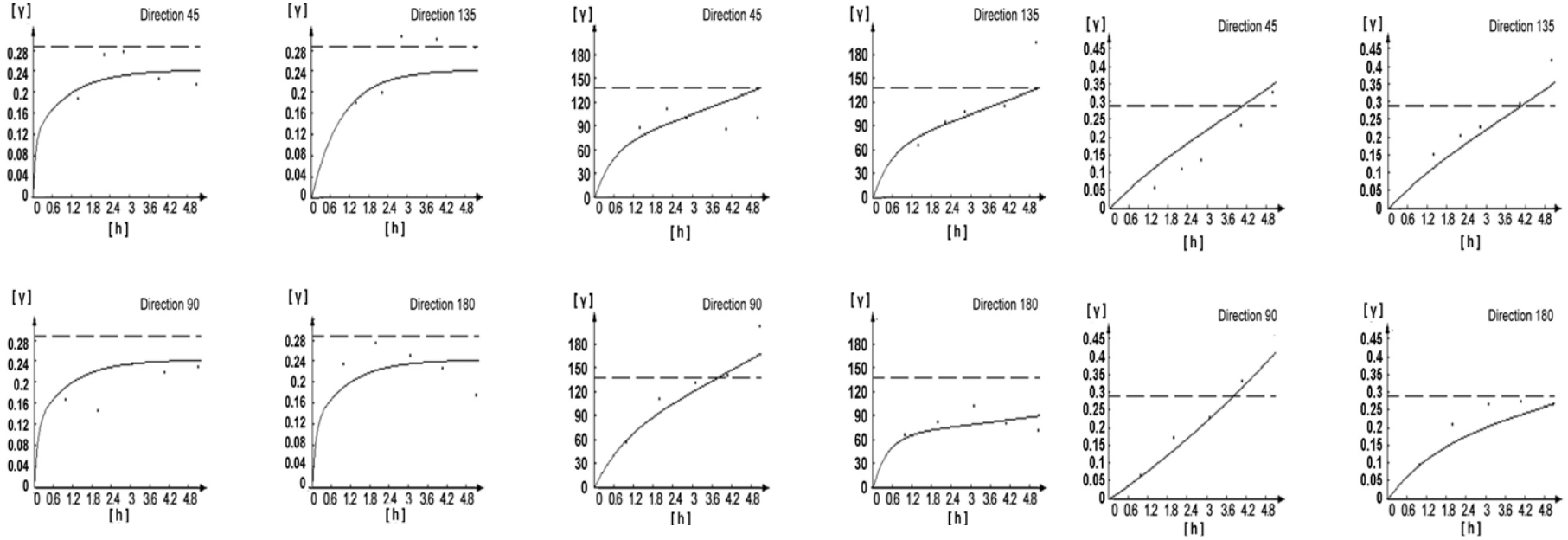
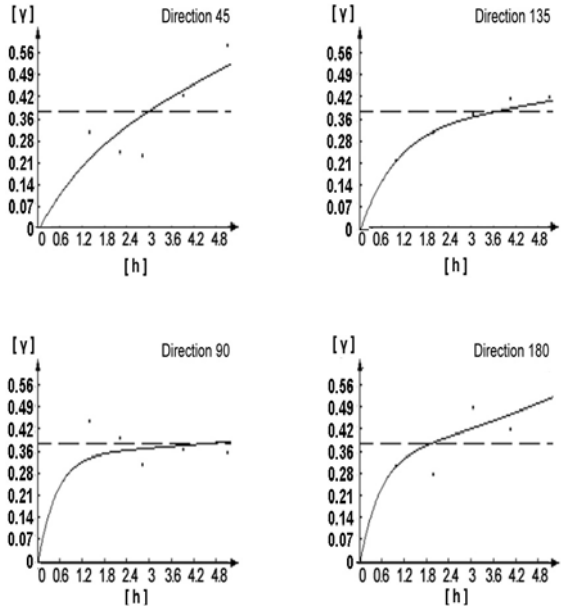


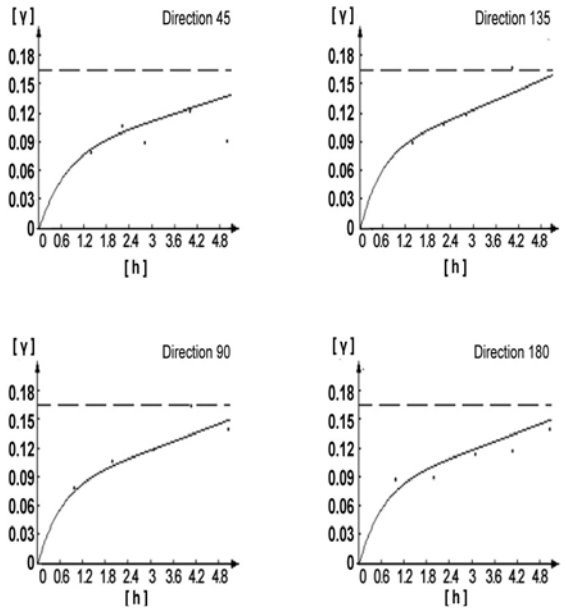
Figure CH4.3 Experimental and model variograms of litter components and soil chemistry variables that had an autocorrelated phase in the 75-year-old forest. Experimental variograms in the direction of maximum and minimum anisotropy, plus their perpendicular directions are presented. One lag is equivalent to 5 m (for nested model equations and goodness of fit see table 4.3)

75-year-old forest

Ln (other species)



Ln (potassium-K^{+})



Ln (calcium- Ca^{+})

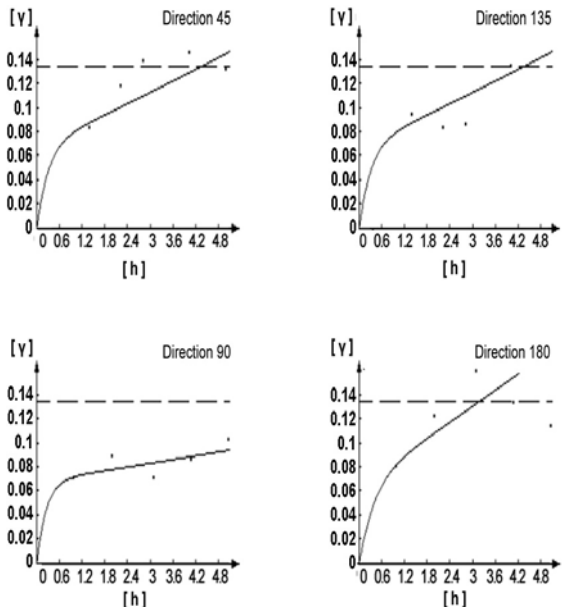


Figure CH4.3 continuation...ends.

100-year-old forest

Ln (total litter mass) | Ln (unidentifiable material) | Ln (*Quercus*)

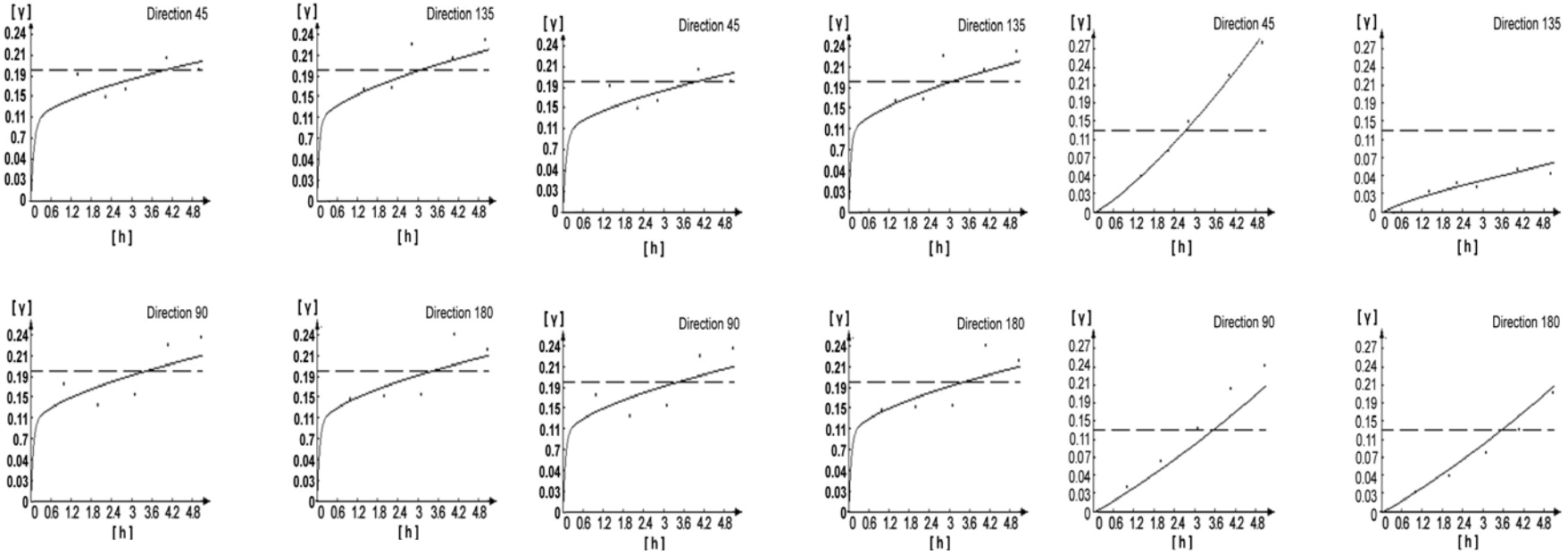


Figure CH4.4 Experimental and model variograms of litter components, soil chemistry variables and Shannon's index of diversity which had an autocorrelated phase in the 100-year-old forest. Experimental variograms in the direction of maximum and minimum anisotropy, plus their perpendicular directions are presented. One lag is equivalent to 5 m (for nested model equations and goodness of fit see table 4.3)

100-year-old forest

Ln (Lauraceae)

Ln (woody and reproductive material)

Ln (total phosphorus)

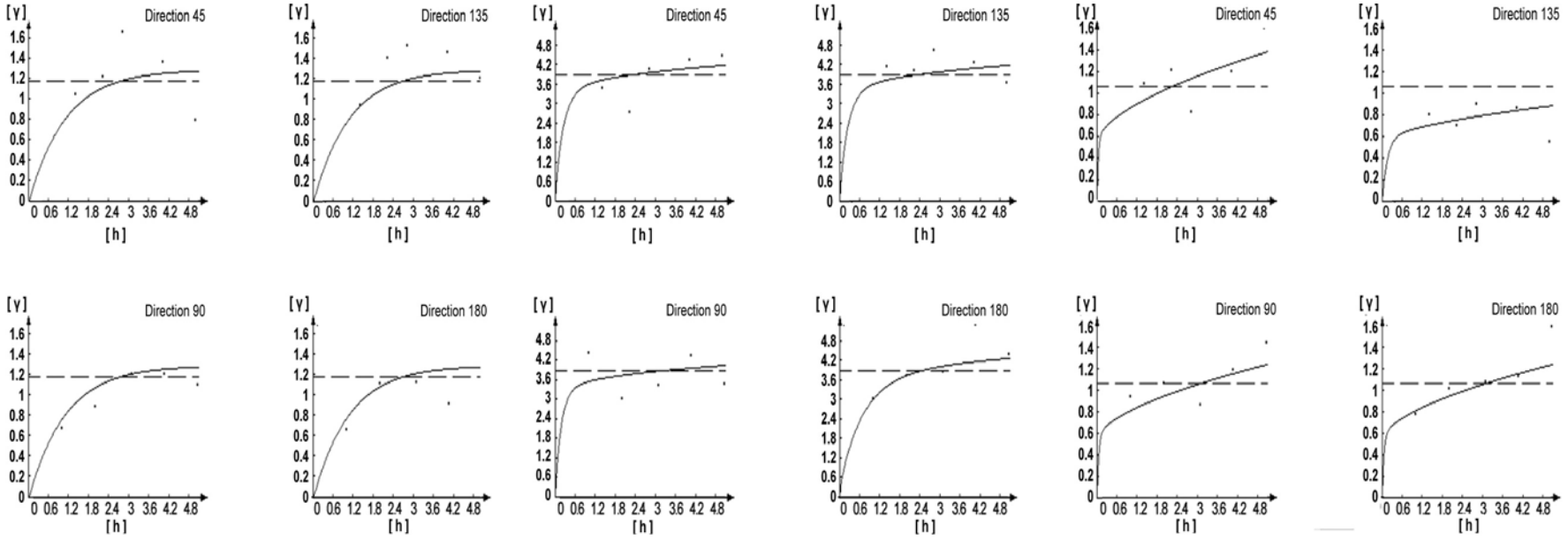


Figure CH4.4 continuation....

100-year-old forest

Ln (sodium- Na^{+}) Ln (calcium- Ca^{++}) Ln (magnesium- Mg^{++})

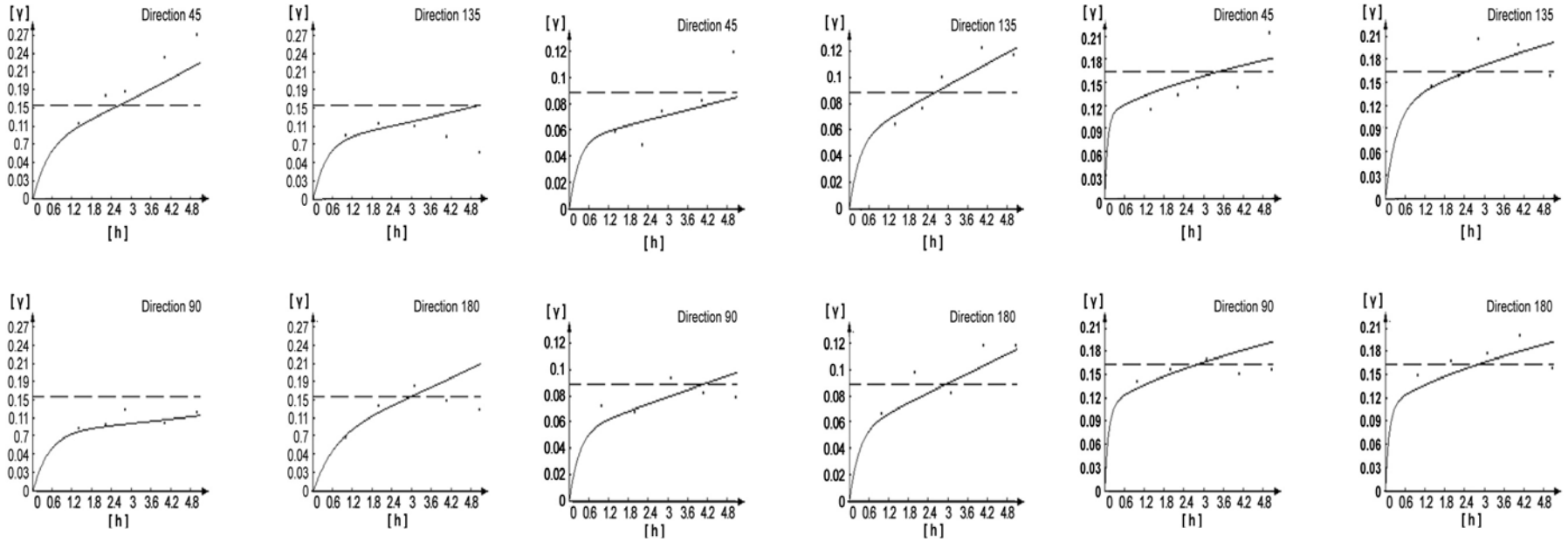
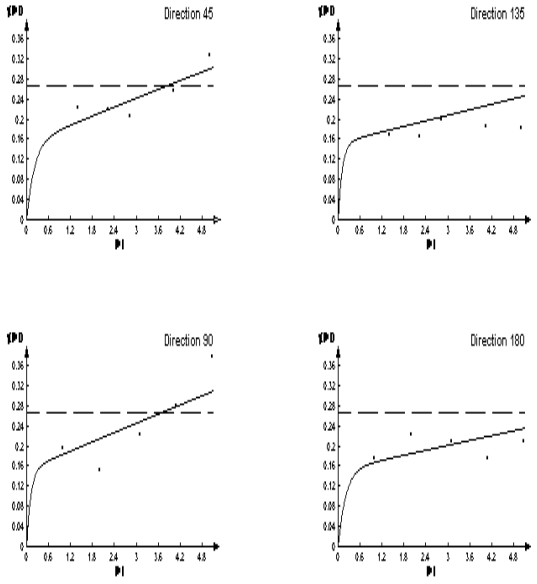


Figure CH4.4 continuation...

100-year-old forest

Litter Shannon's H'



Soil Shannon's H'

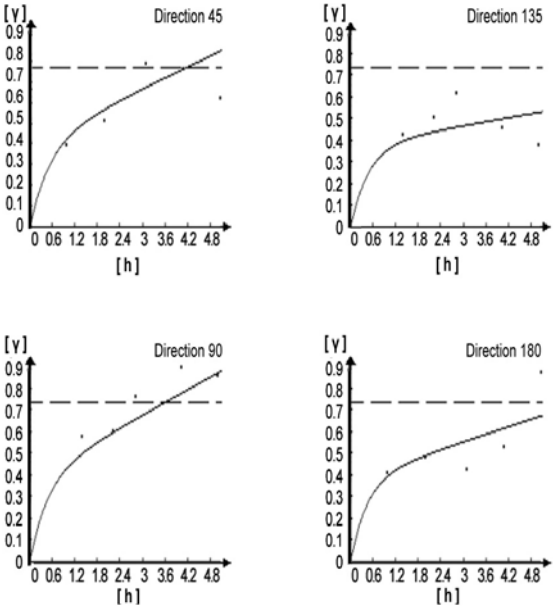


Figure CH4.4 continuation...ends.

APPENDIX CH 5.

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Collection time (Ct)	3	1072.23	357.41	441.20	<0.0001
Forest age (Fa)	3	0.85	0.28	0.35	0.790
Fa × Ct	9	7.26	0.81	-	-
Leaf species (Ls)	1	22.51	22.51	22.07	<0.0001
Fa × Ls	3	1.12	0.37	0.36	0.779
Ct × Ls	3	12.26	4.09	4.01	0.010
Error	102	104.37	1.02		
Total	124				

Table CH5.1 Analysis of variance of leaf dry mass remaining in experimental decomposition boxes at the time of collection. Treatments consisted of forest age (15, 45, 75 and 100 years old), collection time (28, 56, 112 and 210 days after placement) and species of leaf contained in the box (*Persea americana* and *Pinus chiapensis*).

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Collection time (Ct)	3	9.49	3.16	39.5	<0.0001
Forest age (Fa)	3	0.41	0.14	1.75	0.226
Fa × Ct	9	0.72	0.08	-	-
Leaf species (Ls)	1	95.43	95.43	954.3	<0.0001
Fa × Ls	3	1.66	0.55	5.50	0.002
Ct × Ls	3	4.03	1.34	13.4	<0.0001
Error	102	10.77	0.10		
Total	124				

Table CH5.2 Analysis of variance comparing the sample scores in the first axis extracted from the principal component analysis of nutrients, cellulose and lignin concentrations in decomposition boxes. Treatments consisted of forest age (15, 45, 75 and 100 years old), collection time (28, 56, 112 and 210 days after placement) and species of leaf contained in the box (*Persea americana* and *Pinus chiapensis*).

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Collection time (Ct)	3	76.71	25.57	37.05	<0.0001
Forest age (Fa)	3	1.12	0.37	0.53	0.673
Fa × Ct	9	6.17	0.69	-	-
Leaf species (Ls)	1	10.79	10.79	41.5	<0.0001
Fa × Ls	3	0.60	0.20	0.77	0.513
Ct × Ls	3	4.27	1.42	5.46	0.002
Error	102	24.73	0.26		
Total	124				

Table CH5.3 Analysis of variance comparing the sample scores in the second axis extracted from the principal component analysis of nutrients, cellulose and lignin concentrations in decomposition boxes. Treatments consisted of forest age (15, 45, 75 and 100 years old), collection time (28, 56, 112 and 210 days after placement) and species of leaf contained in the box (*Persea americana* and *Pinus chiapensis*).

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Collection time (Ct)	3	55.01	18.34	12.92	0.001
Forest age (Fa)	3	1.91	0.64	0.45	0.723
Fa × Ct	9	12.76	1.42	-	-
Leaf species (Ls)	1	0.01	0.01	0.02	0.888
Fa × Ls	3	0.18	0.06	0.13	0.942
Ct × Ls	3	6.77	2.26	4.91	0.003
Error	102	46.33	0.46		
Total	124				

Table CH5.4 Analysis of variance comparing the sample scores in the third axis extracted from the principal component analysis of nutrients, cellulose and lignin concentrations in decomposition boxes. Treatments consisted of forest age (15, 45, 75 and 100 years old), collection time (28, 56, 112 and 210 days after placement) and species of leaf contained in the box (*Persea americana* and *Pinus chiapensis*).

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Collection time (Ct)	3	149.39	49.80	7.48	0.008
Forest age (Fa)	3	12.12	4.04	0.61	0.625
Fa × Ct	9	59.95	6.66	-	-
Leaf species (Ls)	1	88.31	88.31	18.59	<0.0001
Fa × Ls	3	2.93	0.98	0.21	0.889
Ct × Ls	3	4.50	1.50	0.32	0.811
Error	102	472.26	4.75		
Total	124				

Table CH5.5 Analysis of variance comparing the number of macroinvertebrate taxa extracted from experimental decomposition boxes. Treatments consisted of forest age (15, 45, 75 and 100 years old), collection time (28, 56, 112 and 210 days after placement) and species of leaf contained in the box (*Persea americana* and *Pinus chiapensis*).

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Collection time (Ct)	3	0.67	0.22	3.14	0.080
Forest age (Fa)	3	0.26	0.09	1.29	0.336
Fa × Ct	9	0.60	0.07	-	-
Leaf species (Ls)	1	0.18	0.18	9.00	0.003
Fa × Ls	3	0.04	0.01	0.50	0.683
Ct × Ls	3	0.08	0.03	1.50	0.219
Error	102	2.07	0.02		
Total	124				

Table CH5.6 Analysis of variance comparing the equitability index of macroinvertebrate taxa extracted from experimental decomposition boxes. Treatments consisted of forest age (15, 45, 75 and 100 years old), collection time (28, 56, 112 and 210 days after placement) and species of leaf contained in the box (*Persea americana* and *Pinus chiapensis*).

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Collection time (Ct)	3	7.30	2.43	3.33	0.070
Forest age (Fa)	3	2.78	0.93	1.27	0.342
Fa × Ct	9	6.56	0.73	-	-
Leaf species (Ls)	1	1.91	1.91	9.55	0.003
Fa × Ls	3	0.48	0.16	0.80	0.497
Ct × Ls	3	0.90	0.30	1.50	0.219
Error	102	22.52	0.20		
Total	124				

Table CH5.7 Analysis of variance comparing Shannon diversity index of macroinvertebrate taxa extracted from experimental decomposition boxes. Treatments consisted of forest age (15, 45, 75 and 100 years old), collection time (28, 56, 112 and 210 days after placement) and species of leaf contained in the box (*Persea americana* and *Pinus chiapensis*).

	Axes				**Total inertia**
	1	2	3	4	
Eigenvalues	0.217	0.108	0.071	0.024	1.952
Taxa-environment correlations	0.691	0.61	0.445	0.561	
Cumulative percentage variance					
Taxa data	11.1	16.6	20.3	21.5	
taxa-environment relation	45	67.4	82.1	87.1	
Sum of all unconstrained eigenvalues					1.952
Sum of all canonical eigenvalues					0.482
P-value in Monte Carlo test	0.045				<0.005

Table CH5.8 Canonical Correspondance Aanalysis of macroinvertebrate community composition in experimental decomposition boxes at the time of collection. Community composition was ordinated with respect to successional stage (four dummy variables: 15-, 45-, 757 and 100-year-old forests), collection date (four dummy variables: after 28, 56, 112 and 220 days), species of leaf being decomposed (two dummy variables: *Pinus chipaensis* and *Persea americana*) and soil nutrient concetration (Carbon (%), Nitrogen (%), P (cmol.kg^{-1}), Mg^{++}(cmol.kg^{-1}), Na^{+}(cmol.kg-1), K^{+}(cmol.kg^{-1}), Ca^{++}(cmol.kg^{-1}) Lignin (%) and Cellulose (%)). Uropigi, Ricinulei, Blattaria and Thysanura were excluded from the analysis because fewer than five specimens of each taxon were recovered in the whole experiment.

	Axes				Total inertia
	1	2	3	4	
100-YEAR-OLD FOREST					
Eigenvalues	0.224	0.079	0.031	0.023	0.832
Taxa-environment correlations	0.858	0.848	0.768	0.658	
Cumulative percentage variance					
Taxa data	27.0	36.5	40.3	43.1	
taxa-environment relation	54.6	74	81.6	87.3	
Sum of all unconstrained eigenvalues					0.832
Sum of all canonical eigenvalues					0.411
P-value in Monte Carlo test	0.01				0.05
75-YEAR-OLD FOREST					
Eigenvalues	0.187	0.112	0.068	0.044	0.928
Taxa-environment correlations	0.819	0.817	0.704	0.781	
Cumulative percentage variance					
Taxa data	20.1	32.1	39.5	44.3	
taxa-environment relation	38.9	62.1	76.4	85.6	
Sum of all unconstrained eigenvalues					0.928
Sum of all canonical eigenvalues					0.48
P-value in Monte Carlo test	0.12				0.06
45-YEAR-OLD FOREST					
Eigenvalues	0.441	0.18	0.044	0.031	1.204
Taxa-environment correlations	0.839	0.847	0.804	0.9	
Cumulative percentage variance					
Taxa data	36.6	51.6	55.3	57.8	
taxa-environment relation	59.2	83.4	89.3	93.4	
Sum of all unconstrained eigenvalues					1.204
Sum of all canonical eigenvalues					0.745
P-value in Monte Carlo test	0.165				0.04
15-YEAR-OLD FOREST					
Eigenvalues	0.498	0.265	0.094	0.071	1.791
Taxa-environment correlations	0.908	0.893	0.691	0.846	
Cumulative percentage variance					
Taxa data	27.8	42.6	47.8	51.8	
taxa-environment relation	47.3	72.5	81.4	88.2	
Sum of all unconstrained eigenvalues					1.791
Sum of all canonical eigenvalues					1.052
P-value in Monte Carlo test	0.02				<0.005

Table CH5.9 Canonical Correspondance Aanalyses of macroinvertebrate community composition in experimental decomposition boxes at the time of collection. The community composition in samples from each successional stage was ordinated separately with respect to collection date (four dummy variables: after 28, 56, 112 and 220 days), species of leaf being decomposed (two dummy variables: *Pinus chipaensis* and *Persea americana*) and nutrient concentration in leaves (Carbon (%), Nitrogen (%), P (cmol.kg-1), Mg^{++}(cmol.kg-1), Na^{+} (cmol.kg-1), K^{+}(cmol.kg-1), Ca^{++}(cmol.kg-1), Lignin (%) and Cellulose (%)). Uropigi, Ricinulei, Blattaria and Thysanura were excluded from the analysis because fewer than five specimens of each taxon were recovered in the whole experiment.

	Axes				Total inertia
	1	2	3	4	
FIRST COLLECTION DATE: 28 DAYS					
Eigenvalues	0.212	0.13	0.056	0.041	1.156
Taxa-environment correlations	0.771	0.785	0.757	0.774	
Cumulative percentage variance					
Taxa data	18.3	29.5	34.4	38	
taxa-environment relation	41	66.1	77	85	
Sum of all unconstrained eigenvalues					1.156
Sum of all canonical eigenvalues					0.517
P-value in Monte Carlo test	0.35				0.30
SECOND COLLECTION DATE: 56 DAYS					
Eigenvalues	0.455	0.329	0.114	0.062	1.794
Taxa-environment correlations	0.864	0.743	0.877	0.698	
Cumulative percentage variance					
Taxa data	25.3	43.7	50.1	53.5	
taxa-environment relation	44.4	76.7	87.8	93.9	
Sum of all unconstrained eigenvalues					1.794
Sum of all canonical eigenvalues					1.023
P-value in Monte Carlo test	0.36				0.15
THIRD COLLECTION DATE: 112 DAYS					
Eigenvalues	0.21	0.059	0.034	0.024	0.698
Taxa-environment correlations	0.887	0.868	0.764	0.813	
Cumulative percentage variance					
Taxa data	30	38.5	43.4	46.9	
taxa-environment relation	55.2	70.8	79.8	86.1	
Sum of all unconstrained eigenvalues					0.698
Sum of all canonical eigenvalues					0.38
P-value in Monte Carlo test	<0.005				<0.005
FOURTH COLLECTION DATE: 220 DAYS					
Eigenvalues	0.299	0.105	0.08	0.04	1.149
Taxa-environment correlations	0.914	0.681	0.788	0.612	
Cumulative percentage variance					
Taxa data	26	35.2	42.2	45.7	
taxa-environment relation	49.5	67	80.3	87	
Sum of all unconstrained eigenvalues					1.149
Sum of all canonical eigenvalues					0.604
P-value in Monte Carlo test	0.005				0.01

Table CH5.10 Canonical Correspondance Aanalyses of macroinvertebrate community composition in experimental decomposition boxes at the time of collection. The communities of experimental boxes recovered in each collection date are ordinated with respect to successional stage (four dummy variables: 15, 45, 75 and 100 year-old) and nutrient content in leaves (Carbon (%), Nitrogen (%), P ($cmol.kg^{-1}$), Mg^{++}($cmol.kg^{-1}$), Na^{+}($cmol.kg^{-1}$), K^{+}($cmol.kg^{-1}$) and Ca^{++}($cmol.kg^{-1}$)). Uropigi, Ricinulei, Blattaria and Thysanura were excluded from the analysis because less than 5 specimens of each taxon were recovered in the whole experiment.

Persea americana																		
	Days	**C (%)**		**N (%)**		**P (cmol.Kg^{-1})**		**Na (cmol.Kg^{-1})**		**K (cmol.Kg^{-1})**		**Ca (cmol.Kg^{-1})**		**Mg (cmol.Kg^{-1})**		**ASF (%)**		**RF (%)**	
Forest age		**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Initial	0	53.33	0.50	1.56	0.08	2.61	0.43	0.55	0.05	24.8	3.94	91.15	7.72	33.78	5.13	2.51	0.62	42.97	2.78
15-year-old	28	53.72	0.76	1.70	0.37	3.61	0.30	0.47	0.14	19.78	3.05	57.91	14.68	31.77	2.96	3.93	1.22	62.04	3.47
	56	53.32	0.99	1.62	0.19	1.72	0.24	0.43	0.08	18.57	3.19	46.99	10.79	38.79	4.78	3.78	1.42	63.07	5.01
	112	54.60	0.28	1.82	0.06	2.53	0.91	0.37	0.14	6.79	4.15	38.73	18.71	34.87	4.72	4.71	1.43	77.35	7.84
	220	53.62	0.97	1.60	0.39	3.35	0.67	0.44	0.15	3.12	1.91	40.22	10.48	32.37	11.05	4.93	2.88	71.36	7.76
45-year-old	28	54.03	0.38	1.50	0.16	1.99	0.27	0.41	0.08	19.04	0.99	55.51	5.10	32.86	2.11	3.80	0.52	61.05	2.46
	56	53.52	0.56	1.71	0.23	2.56	0.48	0.59	0.11	21.94	3.50	62.84	14.65	38.77	1.91	3.26	0.68	63.26	2.16
	112	53.90	0.34	2.01	0.24	2.67	0.39	0.35	0.07	8.54	5.55	50.90	4.95	35.61	6.13	4.84	0.59	83.49	0.36
	220	53.50	0.92	1.76	0.11	4.21	0.19	0.29	0.15	4.50	1.70	46.66	10.24	39.41	6.01	3.93	0.29	67.69	3.02
75-year-old	28	52.93	0.54	1.64	0.08	2.20	0.24	0.71	0.39	20.14	7.99	77.29	5.51	34.16	8.20	4.64	4.38	54.64	5.12
	56	52.17	0.25	1.60	0.19	2.03	0.14	0.33	0.12	17.24	3.89	62.43	7.87	42.10	4.80	3.49	1.39	59.62	1.38
	112	54.10	0.31	2.15	0.15	2.52	0.29	0.29	0.09	3.75	1.58	49.82	6.17	30.79	5.56	5.27	1.18	82.43	2.14
	220	53.62	0.75	1.76	0.31	4.27	0.33	0.42	0.14	4.61	2.38	47.24	13.38	34.55	9.28	3.88	0.07	67.55	7.88
100-year-old	28	53.70	0.76	1.56	0.26	2.17	0.13	0.61	0.13	17.55	1.84	58.63	8.86	36.88	1.57	2.92	1.55	62.54	4.59
	56	52.95	1.02	2.01	0.15	1.78	0.66	0.29	0.06	12.78	7.00	46.42	9.19	30.69	3.45	4.61	0.93	62.47	3.62
	112	54.34	0.53	1.74	0.11	2.54	0.39	0.22	0.06	2.29	0.70	44.40	7.80	30.25	3.33	7.12	4.39	69.12	1.72
	220	55.43	0.69	1.60	0.48	4.43	0.36	0.28	0.07	2.42	1.09	50.41	1.07	30.17	7.99	4.08	0.74	68.23	1.05

Table CH5.11 Mean and standard deviation of nutrients, sodium, RF and ASF concentrations in experimental leaves at the time of recovery and in undecomposed leaves (initial). Treatments consisted of forest age (15, 45, 75 and 100 years old), collection time (28, 56, 112 and 210 days after placement) and species of leaf contained in the box (*Persea americana* and *Pinus chiapensis*). Continues in the next page.

Pinus chiapensis																		
	Days	**C (%)**		**N (%)**		**P (cmol.Kg^{-1})**		**Na (cmol.Kg^{-1})**		**K (cmol.Kg^{-1})**		**Ca (cmol.Kg^{-1})**		**Mg (cmol.Kg^{-1})**		**ASF (%)**		**RF (%)**	
Forest age		**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Initial	0	56.24	0.57	1.26	0.21	1.97	0.10	0.31	0.05	10.84	0.60	25.93	31.31	7.86	0.44	1.93	0.98	48.32	2.66
15-year-old	28	55.97	0.07	1.30	0.16	1.73	0.26	0.58	0.06	10.76	1.22	16.15	1.26	8.17	1.46	2.59	0.77	67.26	3.06
	56	55.51	0.97	1.40	0.07	1.78	0.29	0.54	0.29	10.14	1.26	16.06	1.34	9.27	1.49	3.08	0.67	67.22	0.91
	112	56.33	0.56	1.53	0.23	3.68	0.46	0.49	0.16	5.82	4.31	19.77	14.29	10.39	2.94	4.07	0.58	77.20	7.00
	220	55.96	0.45	1.54	0.21	3.34	1.03	0.51	0.21	9.00	10.47	12.62	3.23	7.89	2.44	4.48	1.03	70.53	7.64
45-year-old	28	56.22	0.31	1.39	0.11	1.72	0.26	0.43	0.05	10.76	1.16	16.60	1.07	7.74	1.43	2.92	1.39	68.16	2.64
	56	56.12	0.44	1.43	0.05	1.91	0.42	0.48	0.12	9.24	3.34	19.73	6.88	8.12	2.16	3.56	0.87	68.05	1.81
	112	56.02	0.72	1.93	0.31	2.93	0.91	0.35	0.07	5.31	0.50	12.94	0.80	9.37	0.62	3.32	0.41	79.70	0.23
	220	56.37	0.45	1.53	0.24	4.58	0.68	0.41	0.17	2.81	0.82	14.35	1.60	9.20	1.40	2.91	1.07	62.60	4.74
75-year-old	28	56.24	0.45	1.26	0.07	1.84	0.35	0.37	0.08	10.96	1.39	15.89	1.73	7.10	1.15	2.75	0.84	66.11	3.11
	56	56.25	0.37	1.47	0.05	1.70	0.28	0.50	0.12	8.49	1.91	14.32	1.66	8.15	1.62	2.89	0.92	67.85	1.07
	112	56.47	0.17	2.01	0.22	2.94	1.23	0.36	0.09	4.78	1.04	19.81	1.93	9.56	0.52	2.74	1.10	70.07	0.58
	220	56.56	0.33	1.49	0.13	4.20	0.14	0.48	0.22	2.44	0.23	12.26	1.20	9.58	1.17	3.81	0.47	65.64	4.00
100-year-old	28	55.98	0.50	1.37	0.12	2.20	0.24	0.48	0.10	11.04	1.64	17.72	4.40	8.40	1.28	3.27	0.84	64.49	2.15
	56	56.03	0.23	1.61	0.10	1.70	0.25	0.33	0.12	9.99	0.66	15.07	1.45	8.78	1.35	3.97	0.88	64.48	2.14
	112	56.08	0.32	1.37	0.34	2.18	0.62	0.27	0.12	3.62	1.24	13.32	2.32	8.46	2.29	4.19	1.51	66.26	3.25
	220	56.25	0.35	1.68	0.18	4.58	0.38	0.45	0.09	4.62	3.17	12.88	0.88	9.29	0.96	4.34	0.59	63.91	4.28

Table CH5.11 Continuation.

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Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	170.44	85.22	2.22	0.164
Individual tree [Tree species]	9	344.89	38.32	6.80	<0.001
Collection time (Ct)	3	95.31	31.77	5.64	0.002
Ts × Ct	6	40.83	6.80	1.21	0.312
Error	75	422.50	5.63		
Total	95				

Table CH6.1. Three-way analysis of variance comparing canopy cover measured under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species) and collection time (28, 56, 112 and 210 days after placement).

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	0.57	0.29	0.16	0.856
Individual tree [Tree species]	9	16.29	1.81	7.61	<0.001
Collection time (Ct)	2	37.34	18.67	78.53	<0.001
Ts × Ct	4	4.09	1.02	4.30	0.004
Error	54	12.84	0.24		
Total	71				

Table CH6.2. Three-way analysis of variance comparing soil temperature measured under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*) , individual tree (nested within tree species) and collection time (56, 112 and 210 days after placement).

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	0.001	0.001	0.090	0.913
Individual tree [Tree species]	9	0.060	0.007	4.670	<0.001
Collection time (Ct)	3	0.891	0.297	207.940	<0.001
Ts × Ct	6	0.035	0.006	4.060	0.001
Error	75	0.107	0.001		
Total	95				

Table CH6.3. Three-way analysis of variance comparing volumetric soil water content measured under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species) and collection time (28, 56, 112 and 210 days after placement).

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	914.70	457.40	0.28	0.764
Individual tree [Tree species]	9	14826.60	1647.40	4.96	<0.001
Collection time (Ct)	3	14856.50	4952.20	14.92	<0.001
Ts × Ct	6	919.40	153.20	0.46	0.835
Error	74	24566.90	332.00		
Total	94				

Table CH6.4. Three-way analysis of variance comparing mean litter mass per monolith measured under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species) and collection time (28, 56, 112 and 210 days after placement). The litter masses from the two monoliths extracted in each collection date were pooled.

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	0.003	0.002	1.590	0.256
Individual tree [Tree species]	9	0.009	0.001	1.030	0.421
Collection time (Ct)	3	0.030	0.010	10.960	<0.001
Ts × Ct	6	0.005	0.001	0.960	0.458
Error	74	0.068	0.001		
Total	94				

Table CH6.5. Three-way analysis of variance comparing soil bulk density measured under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species) and collection time (28, 56, 112 and 210 days after placement). The bulk densities of soil in the two monoliths extracted in each collection date were pooled.

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	39.76	19.88	0.84	0.461
Individual tree [Tree species]	9	211.93	23.55	5.14	<0.001
Collection time (Ct)	4	211.56	52.89	11.54	<0.001
Ts × Ct	8	25.49	3.19	0.70	0.693
Error	36	164.95	4.58		
Total	59				

Table CH6.6. Three-way analysis of variance comparing number of macroinvertebrate taxa in the litter under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species) and collection time (0, 28, 56, 112 and 210 days after placement). The number of taxa in the two monoliths per tree extracted in each collection date were pooled.

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	0.06	0.03	1.65	0.245
Individual tree [Tree species]	9	0.17	0.02	1.92	0.080
Collection time (Ct)	4	0.25	0.06	6.18	0.001
Ts × Ct	8	0.03	0.00	0.34	0.943
Error	36	0.36	0.01		
Total	59				

Table CH6.7. Three-way analysis of variance comparing equitability of macroinvertebrate taxa in the litter under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species) and collection time (0, 28, 56, 112 and 210 days after placement). The number of taxa in the two monoliths per tree extracted in each collection date were pooled.

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	0.68	0.34	1.65	0.245
Individual tree [Tree species]	9	1.87	0.21	1.92	0.080
Collection time (Ct)	4	2.67	0.67	6.18	0.001
Ts × Ct	8	0.30	0.04	0.34	0.943
Error	36	3.89	0.11		
Total	59				

Table CH6.8. Three-way analysis of variance comparing Shannon's H of macroinvertebrate taxa in the litter under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species) and collection time (0, 28, 56, 112 and 210 days after placement). The number of taxa in the two monoliths per tree extracted in each collection date were pooled.

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	6.81	3.40	0.51	0.617
Individual tree [Tree species]	9	60.04	6.67	4.26	0.001
Collection time (Ct)	4	160.78	40.19	25.66	<0.001
Ts × Ct	8	35.03	4.38	2.79	0.016
Error	36	56.40	1.57		
Total	59				

Table CH6.9. Three-way analysis of variance comparing number of macroinvertebrate taxa in the soil under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species) and collection time (0, 28, 56, 112 and 210 days after placement). The number of taxa in the two monoliths per tree extracted in each collection date were pooled.

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	0.001	0.001	0.220	0.809
Individual tree [Tree species]	9	0.031	0.003	1.520	0.178
Collection time (Ct)	4	0.086	0.022	9.600	<0.001
Ts × Ct	8	0.021	0.003	1.170	0.344
Error	36	0.081	0.002		
Total	59				

Table CH6.10. Three-way analysis of variance comparing equitability of macroinvertebrate taxa in the soil under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species) and collection time (0, 28, 56, 112 and 210 days after placement). The number of taxa in the two monoliths per tree extracted in each collection date were pooled.

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	0.02	0.01	0.22	0.809
Individual tree [Tree species]	9	0.33	0.04	1.52	0.178
Collection time (Ct)	4	0.93	0.23	9.60	<0.001
Ts × Ct	8	0.23	0.03	1.17	0.344
Error	36	0.88	0.02		
Total	59				

Table CH6.11. Three-way analysis of variance comparing Shannon's H' of macroinvertebrate taxa in the soil under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species) and collection time (0, 28, 56, 112 and 210 days after placement). The number of taxa in the two monoliths per tree extracted in each collection date were pooled.

	Axes				Total inertia
	1	2	3	4	
EXCLUDING COLLECTION AFTER 28 DAYS AND INCLUDING SOIL TEMPERATURE					
Eigenvalues	0.613	0.138	0.091	0.072	1.606
Taxa-environment correlations	0.951	0.81	0.876	0.754	
Cumulative percentage variance					
Taxa data	38.1	46.8	52.4	56.9	
taxa-environment relation	63	77.3	86.6	94	
Sum of all unconstrained eigenvalues					1.606
Sum of all canonical eigenvalues					0.972
P-value in Monte Carlo test		<0.005			<0.005
EXCLUDING SOIL TEMPERATURE AND INCLUDING COLLECTION AFTER 28 DAYS					
	Axes				**Total inertia**
	1	2	3	4	
Eigenvalues	0.426	0.149	0.095	0.068	1.69
Taxa-environment correlations	0.85	0.809	0.746	0.754	
Cumulative percentage variance					
Taxa data	25.2	34.1	39.7	43.7	
taxa-environment relation	51.4	69.4	80.9	89.1	
Sum of all unconstrained eigenvalues					1.69
Sum of all canonical eigenvalues					0.829
P-value in Monte Carlo test		<0.005			<0.005

Table CH6.12. Canonical Correspondance Analyses of macroinvertebrate community composition in the litter collected under experimental trees. Community composition was ordinated with respect to tree species (three dummy variables: *Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), collection date (four dummy variables: after 28 (unless stated), 56, 112 and 220 days), soil temperature (°C; unless stated), volumetric soil water content ($g.g^{-1}$), canopy cover (%), litter mass per monolith (g) and soil bulk density ($g.cm^{-3}$). Diptera, Blattodea and Thysanura were excluded from the analysis because fewer than five specimens of each taxon were recovered in the whole experiment).

	Axes				Total inertia
	1	2	3	4	
EXCLUDING COLLECTION AFTER 28 DAYS AND INCLUDING SOIL TEMPERATURE					
Eigenvalues	0.127	0.045	0.032	0.021	0.611
Taxa-environment correlations	0.876	0.646	0.646	0.627	
Cumulative percentage variance					
Taxa data	20.8	28.1	33.4	36.8	
taxa-environment relation	48.6	65.7	78	86	
Sum of all unconstrained eigenvalues					0.611
Sum of all canonical eigenvalues					0.262
P-value in Monte Carlo test	<0.005				<0.005

	Axes				Total inertia
	1	2	3	4	
EXCLUDING SOIL TEMPERATURE AND INCLUDING COLLECTION AFTER 28 DAYS					
Eigenvalues	0.116	0.081	0.04	0.027	0.768
Taxa-environment correlations	0.861	0.822	0.598	0.601	
Cumulative percentage variance					
Taxa data	15	25.6	30.8	34.3	
taxa-environment relation	38.4	65.4	78.7	87.6	
Sum of all unconstrained eigenvalues					0.768
Sum of all canonical eigenvalues					0.301
P-value in Monte Carlo test	<0.005				<0.005

Table CH6.13. Canonical Correspondance Analyses of macroinvertebrate community composition in the soil collected under experimental trees. Community composition was ordinated with respect to tree species (three dummy variables: *Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), collection date (four dummy variables: after 28 (unless stated), 56, 112 and 220 days), soil temperature (°C; unless stated), volumetric soil water content($g.g^{-1}$), canopy cover (%), litter mass per monolith (g) and soil bulk density ($g.cm^{-3}$). Ricinulei, Blattodea and Thysanura were excluded from the analysis because fewer than five specimens of each taxon were recovered in the whole experiment).

	Axes		Total inertia
	1	2	
Eigenvalues	0.258	0.037	1.606
Taxa-environment correlations	0.71	0.549	
Cumulative percentage variance			
Taxa data	18.3	21	
taxa-environment relation	87.4	100	
Sum of all unconstrained eigenvalues			1.411
Sum of all canonical eigenvalues			0.296
P-value in Monte Carlo test	<0.005		<0.005

Table CH6.14. Litter community inertia explained by permanent differences between tree species. Canonical Correspondance Aanalyses of macroinvertebrate community composition in the litter collected under experimental trees. Community composition was ordinated with respect to tree species (three dummy variables: *Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*). Collection time (after 56, 112 and 220 days) was introduced as a covariable. Diptera, Blattodea and Thysanura were excluded from the analysis because fewer than five specimens of each taxon were recovered in the whole experiment).

	Axes				Total inertia
	1	2	3	4	
Eigenvalues	0.264	0.102	0.086	0.028	1.606
Taxa-environment correlations	0.787	0.795	0.828	0.597	
Cumulative percentage variance					
Taxa data	21	29.1	35.9	38.1	
taxa-environment relation	52.1	72.4	89.3	94.7	
Sum of all unconstrained eigenvalues					1.258
Sum of all canonical eigenvalues					0.506
P-value in Monte Carlo test	<0.005				<0.005

Table CH6.15. Litter community inertia explained by microenvironmental variation. Canonical Correspondance Aanalyses of macroinvertebrate community composition in the litter collected under experimental trees. Community composition was ordinated with respect to collection time (three dummy variables: after 56, 112 and 220 days), soil temperature (°C), volumentric soil water content($g.g^{-1}$), canopy cover (%), litter mass per monolith (g) and soil bulk density ($g.cm^{-3}$), tree species (three dummy variables: *Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*) was introduced as a covariable. Diptera, Blattodea and Thysanura were excluded from the analysis because fewer than five specimens of each taxon were recovered in the whole experiment).

	Axes				Total inertia
	1	2	3	4	
Eigenvalues	0.107	0.038	0.028	0.015	0.611
Taxa-environment correlations	0.818	0.6	0.603	0.734	
Cumulative percentage variance					
Taxa data	17.5	23.8	28.4	30.9	
taxa-environment relation	53.6	72.8	87	94.6	
Sum of all unconstrained eigenvalues					0.611
Sum of all canonical eigenvalues					0.2
P-value in Monte Carlo test	<0.005				<0.005

Table CH6.16. Soil community inertia explained by microenvironmental variation. Canonical Correspondance Aanalyses of macroinvertebrate community composition in the soil collected under experimental trees. Community composition was ordinated with respect to collection time (three dummy variables: after 56, 112 and 220 days) and microenvironmental conditions (soil temperature (°C), volumentric soil water content($g.g^{-1}$), canopy cover (%), litter mass per monolith (g) and soil bulk density ($g.cm^{-3}$)). Ricinulei, Blattodea and Thysanura were excluded from the analysis because fewer than five specimens of each taxon were recovered in the whole experiment).

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	0.49	0.24	0.30	0.751
Individual tree [Tree pecies] (It [Ts])	9	7.38	0.82	0.74	0.671
Leaf species (Ls)	3	65.78	21.93	25.39	<0.001
Ts × Ls	6	3.22	0.54	0.62	0.711
Ls× It [Ts]	27	23.31	0.86	0.91	0.597
Collection time (Ct)	3	1870.18	623.39	520.50	<0.001
Ts × Ct	6	4.94	0.82	0.69	0.661
Ct × It [Ts]	27	32.36	1.20	1.26	0.212
Ct × Ls	9	52.82	5.87	6.18	<0.001
Ts ×Ct × Ls	18	7.74	0.43	0.45	0.970
Error	80	75.98	0.95		
Total	190				

Table CH6.17. Four-way analysis of variance comparing foliar mass remaining in decomposition boxes at the time of collection. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species), collection time (28, 56, 112 and 210 days after placement) and foliar species (*Quercus* sp., *Beilschmedia ovalis, Oreopanax xalapensis* and *Pinus chiapensis*). The final column indicates whether a randomisation test was performed to determine the P-value (performed in case of failure to meet the assumptions of homogeneity of variance and normality that permit the use of standard F distribution curves).

Effect of foliar species on scores of axis	Degrees of freedom effect	Mean Square effect	Degrees of freedom error	Mean Square error	F-ratio	P-value	Rando-misation test
PCA1	3	3.40	9	0.07	49.40	<0.0001	y
PCA2	3	2.74	9	0.08	33.13	<0.0001	y
PCA3	3	0.82	9	0.41	1.99	0.186	y

Table CH6.18. One-way analyses of variance comparing the sample scores in the first three axes extracted from the principal component analysis of nutrients, cellulose and lignin concentrations in different species of undecomposed leaves. Leaves of the following species were compared: *Quercus* sp., *Beilschmedia ovalis, Oreopanax xalapensis* and *Pinus chiapensis*. The final column indicates whether a randomisation test was performed to determine the P-value (performed in case of failure to meet the assumptions of homogeneity of variance and normality that permit the use of standard F distribution curves).

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	1.80	0.90	3.40	0.080
Individual tree [Tree pecies] (It [Ts])	9	2.39	0.27	0.77	0.644
Leaf species (Ls)	3	135.45	45.15	160.03	<0.001
Ts × Ls	6	4.22	0.70	2.49	0.047
Ls× It [Ts]	27	7.62	0.28	1.44	0.109
Collection time (Ct)	3	2.54	0.85	3.29	0.036
Ts × Ct	6	0.84	0.14	0.54	0.773
Ct × It [Ts]	27	6.96	0.26	1.31	0.176
Ct × Ls	9	5.27	0.59	2.98	0.004
Ts ×Ct × Ls	18	4.51	0.25	1.28	0.226
Error	80	15.70	0.20		
Total	190				

Table CH6.19. Four-way analysis of variance comparing the sample scores in the first axis extracted from the principal component analysis of nutrients, cellulose and lignin concentrations in decomposition boxes. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species), collection time (28, 56, 112 and 210 days after placement) and foliar species (*Quercus* sp., *Beilschmedia ovalis, Oreopanax xalapensis* and *Pinus chiapensis*).

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	0.08	0.04	0.31	0.742
Individual tree [Tree pecies] (It [Ts])	9	1.14	0.13	0.37	0.932
Leaf species (Ls)	3	137.78	45.93	135.85	<0.001
Ts × Ls	6	1.35	0.22	0.67	0.678
Ls× It [Ts]	27	9.13	0.34	1.28	0.201
Collection time (Ct)	3	4.41	1.47	5.49	0.004
Ts × Ct	6	2.88	0.48	1.79	0.138
Ct × It [Ts]	27	7.23	0.27	1.01	0.467
Ct × Ls	9	4.93	0.55	2.07	0.042
Ts ×Ct × Ls	18	2.63	0.15	0.55	0.923
Error	80	21.20	0.27		
Total	190				

Table CH6.20. Four-way analysis of variance comparing the sample scores in the second axis extracted from the principal component analysis of nutrients, cellulose and lignin concentrations in decomposition boxes. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species), collection time (28, 56, 112 and 210 days after placement) and foliar species (*Quercus* sp., *Beilschmedia ovalis, Oreopanax xalapensis* and *Pinus chiapensis*).

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	1.83	0.92	0.90	0.439
Individual tree [Tree pecies] (It [Ts])	9	9.15	1.02	1.23	0.366
Leaf species (Ls)	3	15.60	5.20	9.88	<0.001
Ts × Ls	6	7.98	1.33	2.53	0.045
Ls× It [Ts]	27	14.19	0.53	0.67	0.877
Collection time (Ct)	3	21.12	7.04	6.51	0.002
Ts × Ct	6	5.05	0.84	0.78	0.594
Ct × It [Ts]	27	29.22	1.08	1.39	0.134
Ct × Ls	9	5.79	0.64	0.82	0.597
Ts ×Ct × Ls	18	21.64	1.20	1.54	0.098
Error	80	62.49	0.78		
Total	190				

Table CH6.21. Four-way analysis of variance comparing the sample scores in the third axis extracted from the principal component analysis of nutrients, cellulose and lignin concentrations in decomposition boxes. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species), collection time (28, 56, 112 and 210 days after placement) and foliar species (*Quercus* sp., *Beilschmedia ovalis, Oreopanax xalapensis* and *Pinus chiapensis*).

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	23.79	11.90	2.19	0.168
Individual tree [Tree pecies] (It [Ts])	9	48.89	5.43	0.91	0.536
Leaf species (Ls)	3	5.47	1.83	0.31	0.814
Ts × Ls	6	22.54	3.76	0.65	0.691
Ls× It [Ts]	27	156.42	5.79	1.36	0.149
Collection time (Ct)	3	314.81	104.94	23.75	<0.001
Ts × Ct	6	16.33	2.72	0.62	0.716
Ct × It [Ts]	27	119.30	4.42	1.03	0.437
Ct × Ls	9	54.01	6.00	1.40	0.200
Ts ×Ct × Ls	18	103.67	5.76	1.35	0.182
Error	81	346.14	4.27		
Total	191				

Table CH6.22. Four-way analysis of variance comparing number of macroinvertebrate taxa in decomposition boxes under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species), collection time (28, 56, 112 and 210 days after placement) and foliar species (*Quercus* sp., *Beilschmedia ovalis, Oreopanax xalapensis* and *Pinus chiapensis*.

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	0.01	0.01	0.28	0.765
Individual tree [Tree pecies] (It [Ts])	9	0.22	0.02	1.18	0.362
Leaf species (Ls)	3	0.19	0.06	5.92	0.003
Ts × Ls	6	0.08	0.01	1.27	0.303
Ls× It [Ts]	27	0.29	0.01	0.96	0.535
Collection time (Ct)	3	0.76	0.25	11.94	<0.001
Ts × Ct	6	0.14	0.02	1.14	0.368
Ct × It [Ts]	27	0.57	0.02	1.88	0.016
Ct × Ls	9	0.38	0.04	3.77	0.001
Ts ×Ct × Ls	18	0.21	0.01	1.06	0.411
Error	81	0.91	0.01		
Total	191				

Table CH6.23. Four-way analysis of variance comparing equitability of macroinvertebrate taxa in decomposition boxes under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species), collection time (28, 56, 112 and 210 days after placement) and foliar species (*Quercus* sp., *Beilschmedia ovalis, Oreopanax xalapensis* and *Pinus chiapensis*.

Source of variation	Degrees of freedom effect	Sum of Squares	Mean Square effect	F-ratio	P-value
Tree species (Ts)	2	0.15	0.07	0.28	0.765
Individual tree [Tree pecies] (It [Ts])	9	2.38	0.26	1.18	0.362
Leaf species (Ls)	3	2.08	0.69	5.92	0.003
Ts × Ls	6	0.89	0.15	1.27	0.303
Ls× It [Ts]	27	3.16	0.12	0.96	0.535
Collection time (Ct)	3	8.22	2.74	11.94	<0.001
Ts × Ct	6	1.57	0.26	1.14	0.368
Ct × It [Ts]	27	6.20	0.23	1.88	0.016
Ct × Ls	9	4.15	0.46	3.77	0.001
Ts ×Ct × Ls	18	2.32	0.13	1.06	0.411
Error	81	9.91	0.12		
Total	191				

Table CH6.24. Four-way analysis of variance comparing Shannon's H' of macroinvertebrate taxa in decomposition boxes under experimental trees. Treatments consisted of tree species (*Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), individual tree (nested within tree species), collection time (28, 56, 112 and 210 days after placement) and foliar species (*Quercus* sp., *Beilschmedia ovalis, Oreopanax xalapensis* and *Pinus chiapensis*.

	Axes				Total inertia
	1	2	3	4	
EXCLUDING COLLECTION AFTER 28 DAYS AND INCLUDING SOIL TEMPERATURE					
Eigenvalues	0.181	0.106	0.022	0.018	1.429
Taxa-environment correlations	0.668	0.502	0.588	0.551	
Cumulative percentage variance					
Taxa data	12.6	20.1	21.6	22.9	
taxa-environment relation	47.3	75.1	80.9	85.5	
Sum of all unconstrained eigenvalues					1.429
Sum of all canonical eigenvalues					0.382
P-value in Monte Carlo test	0.025				0.015

	Axes				Total inertia
EXCLUDING SOIL TEMPERATURE AND INCLUDING COLLECTION AFTER 28 DAYS	1	2	3	4	
Eigenvalues	0.133	0.071	0.025	0.013	1.34
Taxa-environment correlations	0.631	0.447	0.555	0.475	
Cumulative percentage variance					
Taxa data	9.9	15.2	17.0	18	
taxa-environment relation	47.5	72.8	81.6	86.3	
Sum of all unconstrained eigenvalues					1.34
Sum of all canonical eigenvalues					0.28
P-value in Monte Carlo test	0.025				0.010

Table CH6.25. Canonical Correspondance Analyses of macroinvertebrate community composition in litter boxes decomposing under experimental trees. Community composition was ordinated with respect to tree species (three dummy variables: *Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), collection date (four dummy variables: after 28 (unless stated), 56, 112 and 220 days), foliar species being decomposed (four dummy variables: *Pinus chiapensis*, *Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*), nutrient concentration in leaves (Carbon (%), Nitrogen (%), P ($cmol.kg^{-1}$), Mg^{++}($cmol.kg^{-1}$), Na^{+} ($cmol.kg^{-1}$), K^{+}($cmol.kg^{-1}$), Ca^{++}($cmol.kg^{-1}$), Lignin (%) and Cellulose (%)) and microenvironmental conditions (soil temperature (°C; unless stated), volumetric soil water content ($cm^3 \cdot cm^{-3}$) and canopy cover (%). Dermaptear were excluded from the analysis because only one specimens was recorded in the whole experiment.

	Axes				Total inertia
	1	2	3	4	
Eigenvalues	0.142	0.078	0.017	0.01	1.429
Taxa-environment correlations	0.658	0.417	0.516	0.382	
Cumulative percentage variance					
Taxa data	10.3	16	17.2	17.9	
taxa-environment relation	53.5	83	89.2	93	
Sum of all unconstrained eigenvalues					1.373
Sum of all canonical eigenvalues					0.265
P-value in Monte Carlo test	0.02				0.015

Table CH6.26. Box community inertia explained by variation in chemical composition in the leaves through time. Canonical Correspondance Analyses of macroinvertebrate community composition in decomposition boxes placed under experimental trees. Community composition was ordinated with respect to collection time (after 56, 112 and 220 days) and nutrient concentrations in leaves (Carbon (%), Nitrogen (%), P ($cmol.kg^{-1}$), Mg^{++}($cmol.kg^{-1}$), Na^{+} ($cmol.kg^{-1}$), K^{+}($cmol.kg^{-1}$), Ca^{++}($cmol.kg^{-1}$), Lignin (%) and Cellulose (%)). Tree species (three dummy variables: *Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*) was introduced as a covariable.

	Axes				Total inertia
	1	2	3	4	
Eigenvalues	0.131	0.046	0.011	0.008	1.429
Taxa-environment correlations	0.719	0.304	0.416	0.353	
Cumulative percentage variance					
Taxa data	9.5	12.9	13.7	14.2	
taxa-environment relation	65.7	88.9	94.3	98.1	
Sum of all unconstrained eigenvalues					1.373
Sum of all canonical eigenvalues					0.199
P-value in Monte Carlo test	0.01				0.005

Table CH6.27. Box community inertia explained by microenvironmental variation through time. Canonical Correspondance Analyses of macroinvertebrate community composition in decomposition boxes placed under experimental trees. Community composition was ordinated with respect to collection time (after 56, 112 and 220 days) and microenvironmental conditions (soil temperature (°C), volumetric soil water content ($cm^3.cm^{-3}$) and canopy cover (%)). Tree species (three dummy variables: *Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*) was introduced as a covariable.

	Axes		Total inertia
	1	2	
Eigenvalues	0.041	0.008	1.429
Taxa-environment correlations	0.337	0.264	
Cumulative percentage variance			
Taxa data	3.6	4.2	
taxa-environment relation	84.2	100	
Sum of all unconstrained eigenvalues			1.157
Sum of all canonical eigenvalues			0.049
P-value in Monte Carlo test	<0.01		<0.005

Table CH6.28. Box community inertia explained by permanent differences between tree species. Canonical Correspondance Aanalyses of macroinvertebrate community composition in decomposition boxes placed under experimental trees. Community composition was ordinated with respect to Tree species (three dummy variables: *Quercus* sp., *Beilschmedia ovalis* and *Oreopanax xalapensis*). Collection time (after 56, 112 and 220 days) and nutrient concentrations in leaves (Carbon (%), Nitrogen (%), P ($cmol.kg^{-1}$), Mg^{++}($cmol.kg^{-1}$), Na^{+} ($cmol.kg^{-1}$), K^{+}($cmol.kg^{-1}$), Ca^{++}($cmol.kg^{-1}$), Lignin (%) and Cellulose (%)) were introduced as a covariables.

***Beilschmedia ovalis* litter**																			
	Days	**C (%)**		**N (%)**		**P (cmol.Kg^{-1})**		**Na (cmol.Kg^{-1})**		**K (cmol.Kg^{-1})**		**Ca (cmol.Kg^{-1})**		**Mg (cmol.Kg^{-1})**		**ASF (%)**		**RF (%)**	
		Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Initial	0	56.15	0.15	0.88	0.14	1.50	0.30	0.40	0.12	4.79	3.39	36.06	8.72	20.40	5.18	3.46	0.64	67.95	1.28
Under *B. ovalis*	28	56.24	0.25	1.13	0.18	1.65	0.30	0.18	0.05	3.22	0.72	24.42	4.40	20.07	3.95	3.78	0.81	66.47	1.38
	56	56.34	0.13	1.08	0.15	1.36	0.06	0.22	0.03	2.29	1.18	33.41	16.59	22.90	0.74	4.52	0.56	70.78	1.65
	112	56.14	0.21	1.11	0.26	1.62	0.97	0.17	0.09	1.56	0.44	29.36	10.63	16.72	7.69	4.14	0.56	64.68	1.34
	220	56.20	0.20	1.10	0.13	1.86	0.23	0.19	0.06	2.31	0.26	30.96	4.37	20.76	1.68	4.24	0.24	64.03	2.75
O. xalapensis	28	56.20	0.09	0.99	0.10	1.52	0.11	0.28	0.07	2.97	0.13	33.99	2.17	23.58	3.19	3.67	0.68	68.03	1.91
	56	56.25	0.23	1.30	0.15	1.36	0.11	0.26	0.06	3.26	0.84	28.50	3.44	23.36	1.45	4.83	0.51	68.07	2.27
	112	56.00	0.26	1.13	0.24	1.38	0.12	0.28	0.13	2.99	0.94	36.83	4.55	24.28	3.64	3.38	0.60	66.30	1.12
	220	55.76	0.68	1.00	0.08	1.89	0.24	0.34	0.12	2.69	1.21	26.97	2.74	21.93	4.39	4.34	0.89	62.59	5.63
Quercus spp.	28	56.32	0.18	0.94	0.12	1.25	0.45	0.22	0.11	11.03	16.61	29.65	11.26	21.59	8.00	3.52	0.23	67.65	1.47
	56	56.32	0.20	1.22	0.16	1.79	0.80	0.22	0.05	2.67	0.86	28.64	4.64	23.69	1.81	4.78	1.57	68.97	4.09
	112	56.11	0.23	1.11	0.15	1.70	0.28	0.15	0.03	2.19	0.15	31.73	2.86	20.40	1.27	3.52	0.31	65.49	0.84
	220	56.01	0.33	1.33	0.27	1.80	0.19	0.25	0.03	3.14	1.72	29.72	7.08	21.13	4.92	4.24	0.34	63.43	3.56
***Oreopanax xalapensis* litter**																			
Initial	0	55.32	0.23	1.00	0.21	1.83	0.36	0.49	0.16	11.97	2.56	44.55	15.44	35.05	4.36	2.28	0.11	48.93	2.29
Under *B. ovalis*	28	55.44	0.08	1.66	0.63	1.56	0.23	0.25	0.02	6.93	1.95	29.15	7.11	34.48	4.02	2.73	0.43	48.77	4.03
	56	55.67	0.33	1.40	0.28	1.49	0.23	0.34	0.14	4.63	3.36	39.55	7.77	38.59	4.34	3.25	0.46	53.17	2.89
	112	55.52	0.15	1.56	0.11	1.72	0.10	0.32	0.11	2.13	0.58	47.18	10.87	35.11	5.10	3.33	0.29	50.66	1.83
	220	55.38	0.25	1.38	0.12	2.15	0.40	0.28	0.05	2.10	0.44	38.58	4.18	37.18	2.78	3.78	0.78	55.48	2.85
O. xalapensis	28	55.30	0.42	1.27	0.16	2.13	0.68	1.01	0.95	7.91	4.78	148.61	186.10	47.27	15.60	2.87	0.62	46.94	2.14
	56	55.71	0.21	1.27	0.16	1.66	0.33	0.56	0.18	6.58	2.13	38.06	6.12	39.75	1.25	3.47	0.70	51.06	5.49
	112	55.25	0.36	1.59	0.25	2.10	0.42	0.35	0.08	3.93	3.20	45.27	16.08	37.60	3.86	3.39	1.25	50.17	1.80
	220	55.21	0.40	1.26	0.07	2.04	0.57	0.41	0.30	3.45	3.86	45.30	18.69	39.63	16.40	3.68	0.88	47.38	4.00
Quercus spp.	28	55.57	0.20	1.52	0.97	1.56	0.29	0.50	0.10	6.50	2.09	44.43	6.22	36.37	5.77	2.81	0.22	48.52	1.07
	56	55.45	0.28	1.52	0.22	1.92	0.22	0.59	0.25	8.94	3.09	45.89	6.82	40.10	4.79	5.52	5.70	51.35	3.76
	112	55.55	0.33	1.78	0.18	1.96	0.31	0.21	0.06	2.13	0.43	45.99	19.94	30.76	7.98	2.97	0.69	54.82	2.87
	220	55.41	0.40	1.39	0.35	2.11	0.45	0.42	0.13	2.83	2.02	38.47	6.99	36.61	6.71	3.03	1.65	57.02	6.09

Table CH6.29 Mean and standard deviation of nutrients, RF and ASF concentrations in experimental leaves at the time of recovery and in undecomposed leaves (initial). Treatments consisted of experimental tree species (*Beilschmedia ovalis*, *Oreopanax xalapensis* and *Quercus spp*.), collection time (28, 56, 112 and 210 days after placement) and foliar species contained in the box (*B. ovalis*, *O. xalapensis*, *Quercus spp*.and *Pinus chiapensis*). Continues in the next page.

***Pinus chiapensis* litter**																			
	Days	**C (%)**		**N (%)**		**P (cmol.Kg^{-1})**		**Na (cmol.Kg^{-1})**		**K (cmol.Kg^{-1})**		**Ca (cmol.Kg^{-1})**		**Mg (cmol.Kg^{-1})**		**ASF (%)**		**RF (%)**	
		Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Initial	0	56.76	0.05	1.29	0.01	2.43	0.07	0.32	0.03	3.73	0.37	24.10	2.37	5.25	0.27	3.04	0.49	56.47	1.01
Under *B. ovalis*	28	56.50	0.09	1.35	0.16	2.86	0.19	0.36	0.03	3.49	0.46	28.10	2.43	6.59	0.98	4.96	2.19	44.84	22.08
	56	56.69	0.14	1.44	0.09	2.92	0.21	0.26	0.04	2.74	0.90	30.89	7.87	6.09	1.24	5.40	0.83	59.42	1.30
	112	56.77	0.10	1.46	0.17	3.05	0.20	0.35	0.12	1.71	0.09	28.42	4.97	5.81	1.37	3.88	0.28	59.50	1.09
	220	56.68	0.17	1.39	0.07	3.22	0.09	0.47	0.25	1.81	0.35	23.23	5.07	5.25	1.71	4.93	1.03	59.39	1.38
O. xalapensis	28	56.68	0.17	1.27	0.42	2.80	0.21	0.44	0.19	2.75	0.24	27.66	5.56	5.94	1.15	3.39	0.88	57.60	0.66
	56	56.73	0.08	1.47	0.13	3.07	1.13	0.38	0.10	2.24	0.92	35.63	19.10	5.90	1.22	4.59	0.31	59.57	0.89
	112	56.78	0.18	1.73	0.32	2.92	0.41	0.26	0.08	1.74	0.12	29.45	5.89	5.15	1.82	4.02	0.45	61.43	1.95
	220	56.68	0.14	1.28	0.16	2.85	1.10	0.25	0.13	1.61	0.38	21.63	4.20	5.05	2.01	5.29	0.75	59.97	0.85
Quercus spp.	28	56.71	0.16	1.32	0.10	2.44	0.85	0.37	0.23	13.02	20.74	26.33	10.14	6.17	2.07	4.03	1.96	57.45	1.04
	56	56.44	0.51	1.44	0.05	2.96	0.08	0.29	0.11	3.30	1.32	14.08	10.35	7.50	0.75	4.11	0.46	59.76	2.55
	112	56.63	0.05	1.62	0.11	2.99	0.46	0.18	0.07	2.06	0.25	27.90	1.84	5.18	0.71	3.68	0.64	59.13	0.53
	220	56.68	0.21	1.44	0.26	2.82	0.81	0.36	0.06	1.89	0.82	22.62	8.46	5.83	2.57	4.20	0.83	60.81	1.59
Quercus spp litter																			
Initial	0	56.80	0.15	1.10	0.51	0.95	0.34	0.24	0.14	1.28	0.39	26.60	6.17	14.18	1.58	3.63	0.97	59.61	1.85
Under *B. ovalis*	28	56.79	0.07	1.04	0.07	0.82	0.11	0.08	0.05	5.13	7.33	18.67	3.23	14.75	3.10	5.23	1.46	59.00	0.96
	56	56.41	1.10	0.91	0.06	0.70	0.07	0.13	0.08	1.25	0.68	20.54	1.56	15.61	1.59	4.91	0.74	62.70	1.78
	112	56.76	0.25	1.15	0.08	0.91	0.07	0.18	0.04	1.33	0.26	29.21	4.19	12.84	1.73	3.85	0.19	58.43	1.26
	220	56.58	0.06	1.03	0.04	2.06	0.99	0.18	0.04	2.05	0.15	25.52	2.26	12.88	0.59	4.51	0.72	60.65	1.98
O. xalapensis	28	56.82	0.22	0.96	0.04	0.98	0.32	0.09	0.05	1.49	0.15	22.12	4.00	13.97	0.99	3.93	0.89	59.09	1.59
	56	56.82	0.28	0.99	0.07	0.72	0.04	0.19	0.10	0.99	0.43	21.56	1.89	14.45	1.02	5.21	0.12	63.34	2.08
	112	56.73	0.05	1.09	0.09	0.94	0.07	0.15	0.05	1.34	0.36	31.59	2.22	13.45	2.65	3.17	0.41	61.76	2.16
	220	56.54	0.30	1.08	0.06	1.91	1.27	0.29	0.13	1.82	0.41	26.77	10.39	12.76	3.83	5.10	0.62	57.57	6.79
Quercus spp.	28	56.84	0.07	0.78	0.22	0.74	0.04	0.15	0.06	1.50	0.43	25.96	1.99	15.57	1.04	5.58	0.68	57.75	0.51
	56	56.91	0.21	0.99	0.03	0.84	0.10	0.21	0.15	0.92	0.39	22.63	5.85	16.25	1.27	5.12	0.74	64.41	2.44
	112	56.69	0.09	1.14	0.06	1.31	0.78	0.12	0.04	1.60	0.13	24.78	2.05	12.59	1.63	4.88	0.88	59.73	2.52
	220	56.62	0.12	0.98	0.20	1.07	0.17	0.20	0.03	1.83	0.16	25.06	3.31	10.95	0.98	5.19	0.81	59.83	2.77

Table CH6.29 Continuation.