

Integrating soil macroinvertebrate diversity,
litter decomposition and secondary
succession in a tropical montane cloud forest
in Mexico

by

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ABSTRACT

This research considers human impacts on three components of biodiversity (composition, spatial structure and function). Given the relict character and unusual biogeochemical balance of tropical montane cloud forests in Mexico, logging poses a pressing threat to their survival. Specifically, this thesis explores the effect of selective logging and above-ground secondary succession on the biogeochemical cycling and soil macroinvertebrate community in a cloud forest in Oaxaca, Mexico. The research investigates: (1) whether the above-ground chain of successional changes in tree dominance, litterfall, litter diversity and soil microenvironmental conditions are coupled with a below-ground succession of soil nutrient availability and macroinvertebrate communities, (2) the role of spatial structuring of environmental conditions and litter resources as determinants of the nutrient availability and macroinvertebrate taxa abundance, (3) the implications of successional changes for decomposition and (4) whether the local influence of single trees explains the spatial structure of macroinvertebrate communities in late successional forests.

The work was carried out in three chronosequences (*c.* 15, 45, 75 and 100 year-old stages) of high altitude (1500–2000 m) tropical montane cloud forest, two recently logged sites and two pristine sites. The macroinvertebrates in the litter and mineral soil were hand sorted from monoliths. Parametric statistics and canonical correspondence analysis were used to determine mean successional trends, and Spatial Analysis by Distance Indices and geostatistical methods were used in combination to determine spatial patterns. Two decomposition experiments were performed to explore the relationship between decomposition rate, litter quality and macroinvertebrate community higher taxa composition in different successional stages and under the canopy of different tree species. The research showed that:

1. The macroinvertebrate community composition in both recently logged sites and pristine forests were distinct compared to secondary successional stages. A decrease in soil temperature and nutrient availability but increase in litter diversity and soil organic matter recorded through succession were accompanied by an increase in the number of macroinvertebrate taxa in the soil. For example, Collembola were most abundant in recently logged sites and earthworms (Megascolecidae) were almost exclusively found in the pristine forests
2. The oldest secondary forest (100-year-old) showed the highest frequency of aggregation in the abundance of individual macroinvertebrate taxa, and the highest and most uniform value of Shannon's diversity. This suggests that high levels of diversity in litter resources and soil chemistry in late succession are associated with complex spatial structuring of highly diverse macroinvertebrate communities.
3. The leaves of a late successional species (*Persea americana*) decomposed at a slightly slower rate than an early successional species (*Pinus chiapensis*) in all successional stages, yet the number and Shannon's diversity of macroinvertebrate taxa that invaded decomposing *P. americana* leaves was consistently higher. The preference of macroinvertebrate taxa for the late-successional leaves was ultimately explained by differences in leaf quality during decomposition. *P. americana* leaves had higher concentrations of cations throughout decomposition and their concentration of lignin and nitrogen became higher.
4. In the 100-year-old forest, the effect of seasonal variation on soil microenvironmental conditions and litter availability was different under the canopy of different tree species. Furthermore, the chemical evolution of the same leaf type (e.g. *Oreopanax xalapensis*) was different when decomposing under different canopies. The highly diverse and spatially complex macroinvertebrate community found in late succession (and experimental litter) was largely explained by the interactive effects of seasonal variation, tree species, litter quality and availability of the decomposing leaf type.

These results provide the first analysis of the relationship between soil biodiversity and the tight biogeochemical cycling in this relict ecosystem type. Overall the results indicate that mature cloud

forests sustain a diverse and spatially heterogeneous macroinvertebrate community. The compositional and spatial components of soil biodiversity are compromised by logging and full recovery may take more than 100 years.

DECLARATION

This thesis has been composed by myself and the work it describes has been carried out by myself except where specific reference is made to other individuals.

Simoneta Negrete-Yankelevich

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CHAPTER 1

INTRODUCTION

The conservation problem

In past geological times Tropical Montane Cloud Forests (TMCF) covered extensive areas in Mexico, but now survive as relict communities distributed in the form of vegetation islands with a total area covering only 0.87% of the Mexican territory (17,400 km²). Around 60% of the cloud forest that remain are in the state of Oaxaca, which is said to possess the greatest cover of this type of ecosystem (Challenger, 1998). The combination of a long evolutionary history with a geological isolation has resulted in a high number of palaeoendemic species and several others of more recent vicariant origin. In terms of total plant species richness per unit area, the cloud forest is the richest ecosystem in Mexico (Rzedowski, 1996; Challenger, 1998).

Mexican TMCFs are inherently fragile because they are the most northerly forests of this type and their persistence depends on the microclimate that is partly maintained by the forest itself. This is demonstrated by the fact that when these forests are logged and abandoned they do not always follow a succession back to their natural composition but they are substituted by pine forest. This fragility renders TMCF conservation and management a priority issue (Challenger, 1998). At global (as well as national) scale TMCFs are considered to be endangered ecosystems (Bruijnzeel & Proctor, 1995).

As in the rest of the country, transculturation, demographic growth and productive strategies oriented towards market economics are substituting traditional management of forests. The cover of this type of vegetation in Mexico has been reduced by at least 50% of its original cover. In its place secondary vegetation, urban areas, extensive pastures, fruit plantations and above all coffee plantations have been established (Challenger, 1998; Ramírez-Marcial *et al.*, 2001; Velázquez *et al.*, 2003)

Despite its relictual character, fragile nature and conservation threats, the TMCF in Mexico is one of the least studied forest ecosystems in the country, particularly those

at high altitudes (Ramírez-Marcial *et al.*, 2001; Velázquez *et al.*, 2003). Little is known about the impact that accelerated logging disturbance is having on its unique characteristics and on the self-preservation mechanisms that have sustained pockets of forests at a latitude where large-scale climatic conditions are no longer very suitable for its regeneration (Rzedowski, 1996). The Mexican Cloud Forest is an example of a conservation problem that is now very widespread. An extremely diverse ecosystem (at least in terms of plants) is now disappearing at an alarming rate and knowledge about its functioning and richness is so scarce that informed decisions about its management are difficult to take. If we are committed to the task now to obtain detailed knowledge about the diversity and functioning of this endangered ecosystem and investigate thoroughly what are the crucial elements that sustain its resilience to human impact, by the time knowledge is robust enough to make informed decisions, there will probably be little forest left to preserve.

Therefore, the question is what is the optimal research approach that will quickly identify vulnerable processes and key taxa, whose damage is likely to imply a threat to the recovery of the system, so that future research can be focused on those taxa and processes. In general the literature on biological diversity too often seems polarised between enthusiasts and sceptics; one side devoted to selling the idea that every single element of ecosystems is vital and conservation should prevail over any social need, and the other extreme who advocates that only very few elements in a system are essential for the preservation of its functioning (Kunin & Lawton, 1996). If these arguments are to be objectively resolved, ways of measuring human impact at all levels of organisation and spatio-temporal dimensions need to be developed.

The concept of biodiversity as a framework

The term *biodiversity* now almost automatically comes to mind when discussing conservation of threatened ecosystems such as TMCF because it addresses environmental problems holistically, rather than in the traditional and fragmented species-by-species, stress-by-stress fashion (Noss, 1990). Ideally, if we can measure biodiversity in an ecosystem, then we could have a very good idea of the environmental deterioration that human activities cause on ecosystems. The concept

has increasingly become the centre of discussion in political and public arenas. In the Biodiversity Convention, signed in 1992 as a result of the UNCED Conference on the Environment and Development ('The Earth Summit', Heywood *et al.*, 1995), the term biodiversity became an official political concern for 156 nations. The definition of 'Biological diversity' produced as a result of the conference was broad and rather vague (table 1.1), therefore its usefulness in environmental assessment has been very limited.

<p>'Biological diversity refers to the variety and variability among living organisms and the ecological complexes in which they occur. Diversity can be defined as the number of different items and their relative frequency. For biological diversity, these items are organised in many levels, ranging from complete ecosystems to the chemical structures that are the molecular basis of heredity. Thus, the term encompasses different ecosystems, species, genes, and their relative abundance'(OTA, 1987).</p>
<p>'Biodiversity is the variety of the world's organisms, including their genetic diversity and the assemblages they form. It is the blanket term for the natural biological wealth that undergirds human life and well-being. The breadth of the concept reflects the interrelatedness of genes, species and ecosystems' (Reid & Miller, 1989).</p>
<p>“'Biological diversity'” encompasses all species of plants, animals and microorganisms and the ecosystems and ecological processes of which they are parts. It is an umbrella term for the degree of nature's variety, including both the number and frequency of ecosystems, species or genes in a given assemblage' (McNeely <i>et al.</i>, 1990).</p>
<p>'Biodiversity is the genetic, taxonomic and ecosystem variety in living organisms of a given area, environment, ecosystem or the whole planet' (McAllister, 1991).</p>
<p>'Biodiversity is the total variety of life on earth. It includes all genes, species and ecosystems and the ecological processes of which they are part' (ICBP, 1992).</p>
<p>'Biological diversity' means the variability among living organisms from all sources including, inter, alia, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part; this includes diversity within species, between species and ecosystems' (Heywood <i>et al.</i>, 1995).</p>
<p>'Biological diversity (=Biodiversity). Full range of variety and variability within and among living organisms, their associations, and habitat-oriented ecological complexes. Term encompasses ecosystem, species and landscape as well as intraspecific (genetic) levels of diversity' (Fiedler & Jain, 1992).</p>
<p>'[biodiversity] The variety of organisms considered at all levels, from genetic variants belonging to the same species through arrays of species to arrays of genera, families, and communities of organisms within particular habitats and the physical conditions under which they live' (Wilson, 1992).</p>
<p>'...biodiversity –the structural and functional variety of life forms at genetic, population, species, community, and ecosystem levels...' (Sundland <i>et al.</i>, 1992)</p>

Table 1. Definitions of 'biological diversity' and 'biodiversity' (modified from Gaston, 1996)

Despite its imprecise definition, the word biodiversity became very frequently used in the scientific literature soon after its first appearance, reflecting its fundamental importance in ecological science. Biodiversity first appeared in the *Biological Abstracts* database in 1988 with four references (Harper & Hawksworth, 1995), and by the end of October 1999 the number had risen to 1318 per year.

One of the characteristics of biodiversity that has made it very popular is that a meaning of the concept can be grasped intuitively, without the necessity of operational (formal) definition, i.e. it can be regarded as a 'pseudo-cognate' (Peters, 1991). This 'comfortable' intuitive meaning has delayed the search for a true rational definition. Worse, repetition and familiarity have made us so certain of the term that it has become blindly accepted as a concrete property of nature (Peters, 1991).

Definition of biodiversity

The concept *biodiversity* first appeared in the scientific literature as an ecological paradigm that describes the variety of life (Gaston, 1996). Some of the authors that used biological diversity in a more precise sense were Lovejoy, (1980), who defined it as the number of species, and Norse & McManus (1980) who included genetic diversity and species richness. A few years later Norse et al. (1986) considered biological diversity as being comprised of three levels: genetic (within species), species (amongst species) and ecological (community) diversity.

Once a concept is so widely used in scientific and non-scientific environments it is important to determine its exact meaning, particularly if its use in scientific research is desirable. There is no single definition for this term; biodiversity refers to different things in different contexts and often it is used as a rather vague concept in political environments. The fact that there are several meanings associated with the word biodiversity is due, in part, to its rapid development.

The role of science is to develop theories that are able to predict phenomena of the real world. All theories are built around concepts or variables (Peters, 1991). Many definitions of 'biodiversity' have been produced (table 1.1). All highlight the broad

character of the concept: they cover at once all life units and processes. However, these definitions cannot be used in scientific practice, because by attempting to be comprehensive, they fail to be operational. An operational definition is the practical specification of the range of phenomena that a concept or term represents. When scientific theories are formulated, they need to be based on operational terms in order to be applicable to the world around us (Peters, 1991). Many of the definitions of biodiversity currently available (table 1.1) cannot be used in scientific theory because they describe vague relationships (variability, variety or interrelatedness) between components (living organisms, genes, ecosystems or species).

Science always begins with a concept. The presence of vague concepts such as biodiversity may be essential to both operationalisation and the social discourse of science (Peters, 1991). However, successful science goes beyond this primal stage to develop variables and theories. Biodiversity has been associated with different phenomena by different scientists (Noss, 1990). If a concept is to prove scientifically useful, it should be sufficiently operational so that informed users associate the concept with similar phenomena. This degree of operationalization is essential to any assessment of predictive power (Peters, 1991).

Some concepts such as biodiversity could be considered too complex and therefore should be fragmented into smaller components that can be operationally definable. As mentioned before, from very early on, scientists realised that biodiversity is expressed at different dimensions and levels of organisation (at least three) and each level can be subdivided in components (see table 1.2 and figure 1.1 for examples of proposed schemes). In theory, the definition of biodiversity not should only state its dimensions, levels of organisation and components but state precisely how those dimensions, levels and components are related to one another, and only then will biodiversity become an operational concept that is defined in the form of a theory. A great number of elements have been suggested as candidates for components of the definition of biodiversity. However, nobody has yet produced a compound definition of biodiversity that can be practically used in scientific research, and still retain the umbrella character of the definitions shown in table 1.1

The concept of 'biodiversity', like many other concepts in ecology, is surrounded by analogous problems to those described by Peters (1991) for 'stability'. Biodiversity applies to many levels of biological organisation (Noss, 1990) and components within each of those levels. However, its meaning is not universal, it will vary across levels and components. For example, phylogenetic distance has been suggested as a surrogate variable of biodiversity at the organismal level (Harper & Hawksworth, 1995) but cannot be equally included in genetic or ecological diversity. An operational definition of biodiversity must therefore indicate what levels and components are to be considered. The sort of theory that can be developed depends on this choice.

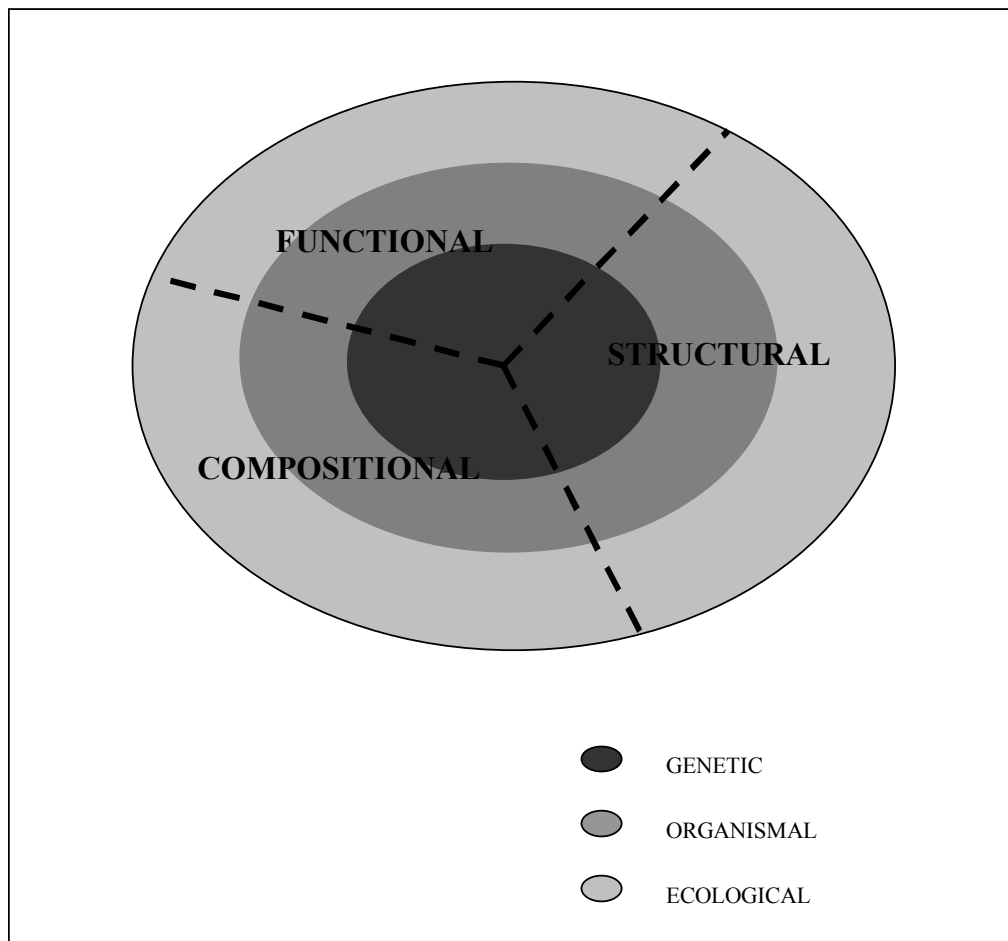


Figure 1.1. Dimensions and levels of biodiversity (modified from Noss, 1990).

Ecological diversity	Genetic diversity	Organismal diversity	Cultural diversity
Biomes	Populations	Kingdoms	Human interactions at all levels
Bioregions	Individuals	Phyla	
Landscapes	Chromosomes	Families	
Ecosystems	Genes	Genera	
Habitats	Nucleotides	Species	
Niche		Subspecies	
Populations		Populations	
		Individuals	

Table 1.2. The levels of organisation and components of biodiversity (modified from Heywood *et al.*, 1995).

In the absence of a clear operational definition, different users of a term may develop independent, even inconsistent, definitions. By this stage a single term carries so many different meanings that one can never be sure which is intended at any one time (Peters, 1991). The word biodiversity is very frequently used in scientific literature and yet is often used vaguely, inconsistently or even wrongly. Clarity can only be achieved if scientists, who use biodiversity in a technical sense at any level, specify what exactly they mean by it and why they are considering that definition. However, this immediate solution proliferates definitions and compounds the problem in the long run (Peters, 1991).

An example of the recurrent problem found in research papers is the use of biodiversity as a synonym of species number or species richness (May, 1995). Species can be counted and the number of species present at a site might seem to be quantitative measures of its biodiversity and allow comparison with other sites. However, if biodiversity means species richness, why do we need both concepts?. Therefore biodiversity must include more elements than the number of species. Species richness ignores other levels of biodiversity such as genetic and ecosystem. Also, it assumes, amongst other things, that all species at a site, within and across systematic groups, contribute equally to its species diversity. A measure of biodiversity (at the species level) of a site ought ideally to consider how different the inhabitants are from each other (phylogenetic distance; Harper and Hawksworth, 1995), the biomass that each species contributes to the living pool of the site and how many of the species found are endemic or rare.

The generation of a global concept that covers all of the dimensions of the diversity of life has not proven useful for its original purpose: to quantify the extent of human damage to fragile ecosystems such as the Mexican TMCF. In this issue the very essence of the human predicament is reflected. The consequences of our actions reverberate in a multidimensional complexity that seems to bridge the capacity of our minds to understand it, understand it in the scientific sense of the word: to be able to model the process so that predictions can be made.

Most scientists performing conservation-related research have left aside the problem of biodiversity's definition by finding ways of avoiding it. Two of the common approaches are: (1) to keep biodiversity as a broad concept, and use other terms such as species richness, gene richness and phylogenetic distance as surrogates that are assumed to reflect the overall biodiversity, and can be included in scientific theory; (2) to define biodiversity deliberately in an artificial and simplistic manner that is still relevant to the needs of the specific case. In the first approach, the concept is addressed in a tangential way, and the research's transcendence relies on the assumption that it is possible to extrapolate findings to a broader scale. In the second alternative, the concept of biodiversity is no longer addressed as a whole; authors select some of its components that are thought to be relevant to a specific problem such as choosing a site for a conservation area.

Avoiding the integrative meaning of biodiversity when performing conservation-related science means to miss the very essence of conservation problems. Environmental impact is a problem only because the effects of environmental stresses will have different consequences at different levels of biological organisation. Effects at one level can be expected to reverberate through other levels often in unpredictable ways (Noss, 1990). As the TMCF in Oaxaca is fragmented, for example, overall species richness in the region may have stayed the same or even increased, yet the integrity of the community may have been compromised with the invasion of light demanding species such as pine (Noss, 1990; Burley & Gauld, 1995) and isolation of genetic populations may be increasing.

Probably the most important outcome of the creation of the concept of biodiversity has been understated. As scientists search for a precise definition of the concept a rich body of theory has developed. Therefore, more useful than the definitions of biodiversity has been the conceptualisation of its dimensions and levels of organisation (Noss, 1990). This provides a conceptual framework that allows us to focus conservation research in the identification of specific, measurable indicators to monitor change and assess human impact at different levels of organisation, within a more feasible timeframe.

Noss (1990) pointed out that one of the crucial characteristics of biodiversity is that it is hierarchical, allowing measuring changes in variables at different levels of organisation (figure 1.1) and obtaining a more comprehensive and multidimensional picture of environmental deterioration. Hierarchy theory suggests that higher levels of organisation incorporate and constrain the behaviour of lower levels (O'Neill *et al.*, 1986). Therefore, global environmental problems such as greenhouse warming and stratospheric ozone depletion impose fundamental constraints on efforts to preserve particular natural areas or endangered species. Hence, the hierarchical nature of biodiversity suggests that environmental deterioration should be measured at multiple levels of organisation and should cover its compositional, structural and functional dimensions.

Whether the impacts of humans on biodiversity can be measured is a different question to whether the impact on its components in different dimensions can be quantified (Gaston, 1996). There is no doubt that biodiversity in the broadest sense of the Rio Convention cannot be measured (Duelli & Orbist, 1998). Many studies are written in such a way as to imply that their findings, although based only on a single variable, concern biodiversity as a whole. However the abstract concept of biodiversity across a range of hierarchical scales, cannot be expressed by a single variable (Gaston, 1996). The complexity is in this sense irreducible, and the search for an all-embracing indicator of human deterioration of biodiversity, however desirable it might seem, will be a fruitless one (Noss, 1990; Gaston, 1996).

Therefore, the choice of indicator variables across the hierarchy of biodiversity will depend fundamentally on the nature of the disturbance.

The hierarchical character of biodiversity therefore provides the theoretical structure to encompass the approach from the top down, focusing efforts on crucial elements. Increasingly detailed measurements can be performed as lower levels of organisation are approached. For example, when attempting to identify biologically significant areas at high risk of impoverishment, it is possible to begin with a coarse-scale inventory of landscape pattern, vegetation, habitat structure and higher taxa distributions. Then intensive research at lower levels of organisation can be focused on critical areas while less intensive monitoring is dedicated to the total landscape under management (Noss, 1990).

The dimensions, levels of organisation and components of biodiversity

Biodiversity can be subdivided in several dimensions (May, 1995) – for example composition, structure, function (Noss, 1990), time and space – that can be studied at different levels of biological organisation – genetic, organismal and ecological. Each of these levels includes several components (table 1.2). A number of schemes have been suggested by which the major features of biodiversity can be distinguished and some sense made of what constitutes the ‘variety of life’ (Gaston, 1996). Whatever the scheme, nested hierarchies (Noss, 1990; Gaston, 1996) and multiple dimensions are emphasised (e.g. table 1.2, figure 1.1).

A conventional division of biodiversity is the one that breaks it down into three levels of biological organisation, genetic, organismic and ecological diversity (Harper & Hawksworth, 1995). Noss (1990) elaborates on this division by pointing out that each of the levels can be studied at the structural, compositional and functional dimensions (figure 1.1). Composition is formed by the identity and variety of elements in the collection; it includes elements such as species lists or allelic richness. Structure refers to the physical organisation or spatial pattern of a system; components such as chromosomal polymorphism and habitat complexity are included in this dimension. Functional involves ecological and evolutionary

processes, it includes elements such as gene flow, nutrient cycling or disturbance. Because the compositional, structural and functional aspects of nature are interdependent, the three dimensions are interconnected.

The patchy pattern of land use that has been occurring in Oaxaca over the last 200 years provides a unique opportunity to study the long-term effects of relatively moderate (yet extensive) disturbance on forest biodiversity at the organismal levels of organisation. As a result of this type of disturbance, within a small area it is possible to find a landscape mosaic of patches of secondary TMCF that have been felled at different times (del Castillo, 1996; Velázquez *et al.*, 2003). Sequences of forest patches of increasing age can be recognised within the same area and used to study the organismic diversity through secondary succession as if it were “frozen in time”. This substitution of time for space is termed chronosequence and allows the study of the trends occurring in a long-term process to be carried out within a human life span.

Organismal diversity refers to diversity expressed at distinct taxonomic hierarchies and generally emphasises the evolutionary origin of biodiversity (May, 1995). Most authors consider species diversity as the most important measure at this level, however higher taxonomic levels can also reflect this diversity. Harper and Hawksworth (1995) favour the term organismal over species diversity because it embraces other taxonomic categories above species. In order to place organismal diversity in a spatial context the terms alpha, beta and gamma diversities were introduced (Whittaker, 1977). Alpha diversity has been defined as the diversity of species (or higher taxa) within local areas. Gamma diversity refers to the regional scale and beta diversity is the ratio of gamma and alpha diversities, which is intended to express community dissimilarity.

The measurability of biodiversity

A measure of biodiversity's deterioration must solve two problems. First, what, ultimately is to be measured? Second, how, realistically, can appropriate data be obtained? (Williams & Humphries, 1996). In general, measures are used to assess a

selected aspect of biodiversity of one or more subsets of objects – a process, a taxon or biota of an area, for example – in comparison either with the entire set (total diversity of the chosen aspect of biodiversity), or with other subsets such as taxa or other areas (Williams & Humphries, 1996). The key point is how to choose the particular aspect of biodiversity that will provide most information about deterioration and how to do it efficiently. Choosing one particular aspect or process to measure is choosing which aspect of biodiversity is hypothesised to hold a key role in the perpetuation of the system or to be most vulnerable to the deterioration by human activities. Consequently, deciding upon which aspect of biodiversity to focus is a deeper problem than, for example, adjudicating among any inherent preferences of taxonomists to count beetle species or of ecologists to study net primary productivity (Gaston, 1996).

What would be then a key aspect of biodiversity that holds an essential role in the subsistence of the Mexican TMCF? The capacity of the canopy to retain a continuous fog cover is largely responsible for the uniqueness of TMCFs in general (Bruijnzeel & Proctor, 1995). The diminished photosynthetic capacity, caused by limited solar radiation, is thought to account for the slow growth, low productivity, poor soils, slow nutrient cycling, and slow decomposition rates in these mountain forests (Vitousek, 1984; Bruijnzeel & Proctor, 1995; Tanner *et al.*, 1998). Mexican TMCF is increasingly being transformed particularly through logging for firewood extraction, which is a moderate type of disturbance that has become continuous pressure directed towards *Quercus* spp. trees (Ramírez-Marcial *et al.*, 2001). As a consequence of the canopy opening the ability of the cloud forest to retain its cloud cover may be reduced. Consequently, the protected environmental conditions in the interior of the forest that are thought to sustain the diverse community change (González-Espinosa *et al.*, 1991; Romero-Nájera, 2000). Also logging produces an above-ground and below-ground flush of nutrient-rich organic matter from residues (Olsson *et al.*, 1996b; Olsson *et al.*, 1996a; Finér *et al.*, 2003). Therefore, soon after disturbance a temporal input of nutrient-rich resources enters the soil system and a less diverse pioneer community, dominated by light-demanding species such as pines and herbaceous species flourish (González-Espinosa *et al.*, 1991; Walker *et al.*,

1996). These pioneers can be expected to produce, under richer soils, more abundant and more nutrient-rich litter that will speed up the decomposition process and maintain high nutrient availability. These new soil and environmental conditions, allow the pioneer species to out-compete the slow-growing, shade-tolerant tropical tree species for a long time (González-Espinosa *et al.*, 1991) and the process is not always fully reversed through succession (Challenger, 1998). Therefore, the relationship between the above-ground tree diversity and the below-ground biogeochemical cycling seems to play an essential role in the maintenance of Mexican TMCF and human activities are seriously threatening its integrity. For this reason I chose to focus the investigation of human impact on the TMCF biodiversity in Oaxaca on the ecosystem biogeochemical processes after logging and through secondary succession.

Once it has been decided where to focus, the next problem is how to measure biodiversity in the most efficient and meaningful way. As mentioned previously, measuring any aspect of biodiversity directly, is still impractical. For example, it is nearly impossible to count all of the species of soil organisms within a temperate suburban garden, let alone a tropical forest. A more realistic approach requires the best quick approximation (Williams & Humphries, 1996). This does not mean that measures based on detailed information about organisms are always irrelevant. On the contrary, they are essential, because they provide the baseline for assessing which rapid and low-cost approximations are most effective (Williams & Humphries, 1996).

In the Oaxacan forest it seems that organic matter decomposition and nutrient cycling are at the centre of the conservation problem. Both the above-ground and the below-ground organismal diversities interact to make the organic matter cycling possible. This is because the species composition, diversity and functioning of terrestrial ecosystems depend on the nutrients supplied by decomposers (Tilman & Downing, 1994), and at the same time the diversity and function of the decomposers system are determined by the characteristics of the above-ground ecosystem (Swift *et al.*, 1979; Wardle, 2002). Even if the task were narrowed by the selection of the

biogeochemical processes, the measurement of biodiversity in both the below- and above-ground subsystems involved is unattainable without the selection of surrogates.

When selecting a surrogate for biodiversity assessment there is an unavoidable compromise between precision and the possibility of extrapolation. More remote surrogates (such as higher taxa) represent a bigger portion of life forms and therefore integrate more of the functional processes that are important for maintaining both ecosystem services and ecosystem viability (Williams & Humphries, 1996), but provide little precision. Conversely, surrogates chosen amongst lower taxa are highly precise but their power of extrapolation to other levels is very limited. Furthermore, while remote surrogates are easier to measure and have lower costs (Williams & Humphries, 1996), proximate surrogates are laborious to identify and require a previous body of knowledge about the system.

Given the scarcity of knowledge about Mexican TMCs, particularly the below-ground subsystem, I have subscribed to the suggestion of Noss (1990) to start to assess the recovery potential of native forests with a holistic approach (distant surrogates), not with a few species as ecological indicators (proximate surrogates). Below-ground, higher taxa of macroinvertebrates were selected as representatives of soil biota because they are relatively easy to identify and have been shown to be good indicators of logging disturbance and subsequent successional stages in several tropical and temperate ecosystems (Okwakol, 1994; Bengtsson *et al.*, 1997; Decaëns *et al.*, 1998; Höfer *et al.*, 2001; Maraun *et al.*, 2003; Pietikäinen *et al.*, 2003). The artificially created group based on human ability to see animals with a minimum body size, it is sensitive to disturbance and succession, partly because the group has members that participate at various levels of the decomposer food-web that performs the organic matter cycling (Swift *et al.*, 1979; Verhoef & Brussaard, 1990; Lussenhop, 1992; Moore *et al.*, 2003).

Above-ground, at least in terms of the tree community, is where more information is available about TMC in Mexico. A few studies have been carried out in Chiapas (González-Espinosa *et al.*, 1991; Quintana-Ascencio & González-Espinosa, 1993;

Romero-Nájera, 2000; Ramírez-Marcial *et al.*, 2001) and Oaxaca (Rzedowski, 1996; Acosta-Castellanos, 1997; Blanco-Macias, 2001) that describe the changes in tree community diversity, composition and structure that happen after disturbance and through secondary succession. Based on the trends described by these studies, it became clear that the relative dominance of tree genera would be a good surrogate for the changes in above-ground organismal diversity triggered by disturbance.

So far I have pointed out that the investigation of human impact on biodiversity is only possible if surrogates are chosen. The hierarchical structure of the biodiversity concept can serve as a framework to select levels of organisation and surrogate variables to concentrate on. In terms of the levels of organisation, I suggested that the patchy form of disturbance in Oaxaca was a good opportunity to study the effect of human activities on TMCF biodiversity at the organismal level. Chronosequences can be defined and biodiversity studied not only after disturbance but also through the recovery process during secondary succession. Once the level of organisation within the biodiversity structure has been selected, the research can concentrate on various surrogate variables within each of the dimensions (functional, compositional and structural), which are thought to be essential for the subsistence of the ecosystem. I proposed that selecting the process of organic matter cycling and accompanying nutrient mineralisation (functional dimension) will permit the research to be focused on a process that appears to be essential for the integrity of this relict ecosystem. I have also suggested that in the absence of detailed background information, tree genera above-ground and higher macroinvertebrate taxa below-ground (compositional dimension) can be used as remote surrogates for the organisms involved in the cycling of organic matter as an ecosystem function. The next step is to choose a relevant surrogate within the structural dimension.

The decomposition of litter and turnover of labile soil organic matter could also be affected by differences between plant species concerning litter quality and timing of litter inputs. In systems with diverse plant phenologies, such as the TMCF, senescence of leaves, stems, and roots at different times for different species might allow for spatial structuring of the decomposition function that determines the overall nutrient turnover (Vitousek & Hooper, 1993). In Mexican TMCF logging

disturbance leads to a decrease in the diversity of trees in the canopy, which is probably accompanied by a decrease in the spatial heterogeneity of the litter resources, and may affect the spatial structuring of soil organisms communities and organic matter cycling. Therefore the level of aggregation of litter resources, macroinvertebrate taxa and nutrients could be good surrogate variables to measure the impact of human activities on the structural dimension of biodiversity.

Rationale and hypotheses

Once surrogate variables had been selected across the dimensions of biodiversity, focusing on organic matter decomposition as a process that is thought to be central for the self preservation mechanisms of the TMCF, this thesis was designed to revolve around two questions: (1) What are the impacts of selective logging on the compositional, structural and functional dimensions of this biodiversity?, and (2) Are those impacts being reversed through the process of secondary succession?

It has been repeatedly suggested that the importance of biodiversity might be in its potential to buffer biogeochemical properties and processes against failure of a single species or group of species to establish or to maintain itself in fluctuating environmental conditions (Vitousek & Hooper, 1993; Tilman & Downing, 1994; Naeem & Li, 1997). This has been called the biological insurance hypothesis for biodiversity (Naeem & Li, 1997), and holds that the more diverse ecosystems are, the more likely functional groups will be to contain some species that can thrive during a given environmental perturbation and thus compensate for other members that are reduced by that disturbance (Tilman & Downing, 1994). These remaining organisms will then make possible the recovery of the ecosystem functions after the disturbance. Clearances of forests for timber represent a major disturbance for above- and below-ground subsystems. The recovery from these disturbances occurs during the process of secondary succession.

According to the biological insurance hypothesis for biodiversity (Naeem & Li, 1997) the soil community found immediately after clearance must consist of a less diverse subset of the community encountered in the standing forest before

disturbance, and the dominant taxa must be different (assuming that no new species have been introduced artificially). The organisms that survive the impact of clearance activities will dominate in the new and radically different conditions. For example, after the input of fresh logging residues, the limiting factor to the decomposer community might not be any more the quality and quantity of the litter and recalcitrant materials found in the forest, but the variability in environmental conditions and the short term character of the resource availability. This might impose restrictions to the subset of organisms that will dominate the community. But what happens to the decomposer community when the process of disturbance is reversed during secondary succession? Does biodiversity progressively recover in the community below-ground?

Above-ground, the abandonment of logged fields triggers a set of changes in a site that leads to a succession of communities characterised by different vegetation types. This sequence of communities represents the recovery from disturbance towards a mature plant community. Plants provide the primary resource for terrestrial decomposer systems and at the same time, the same plants are the primary consumers of mineralised nutrients that are produced at the very end of the decomposition cascade (Swift *et al.*, 1979). Considering this close interdependence between vegetation and the decomposer system, the succession above-ground should be accompanied by equally important changes below-ground (see for example Vitousek *et al.*, 1994; Hughes *et al.*, 1999). The variation in the physicochemical environment and the decomposition resource quality imposed by above-ground succession will presumably have an effect on the organisms of the decomposer community.

Changes above-ground during succession of cloud forest have been studied intensively (González-Espinosa *et al.*, 1991; Quintana-Ascencio & González-Espinosa, 1993; Ramírez-Marcial *et al.*, 2001), however research that has focused on the accompanying and interdependent processes below-ground is scarcer (Waide *et al.*, 1998). Furthermore, little is known of how these two processes are coupled in any ecosystem and how tightly they may follow each other's development (Wardle,

2002). Can we distinguish successional communities below-ground as readily as we can distinguish them above-ground? Do coloniser, middle successional and climax decomposer communities exist?

If we broadly define the decomposer community (following the general definition of community by Begon *et al.* (1996) as the assemblage of organisms that participate in any of the two processes (comminution and catabolism) that lead to decomposition of litter, then the argument can be further developed as follows. The changes in the soil decomposer community that accompany the successional recovery process will depend on the flexibility of the organisms remaining in the cleared land to cope with the new conditions imposed by successional changes and on the ability of other organisms from neighbouring forests to colonise and take over new functions offered by the changing environment. Unless local extinction has happened and no recolonisation is possible, the dominant community members will probably keep changing as succession proceeds. Does the composition of the community return to be characteristic of the primary forest again?

Structure of the thesis

Chapter 3 is devoted to the compositional dimension of biodiversity. It examines the impact of logging on both the composition of the communities above and below-ground subsystems and follows their relationship through secondary succession. To do so, it explores whether changes in the tree community happening above-ground as a result of logging impact and subsequent secondary succession are coupled with below-ground changes in microenvironmental conditions, resource quality and availability, and soil chemistry. It investigates whether these changes in the soil physicochemical environment are also mirrored by the composition and diversity of the macroinvertebrate communities.

It can also be argued that as the complexity of the above-ground community increases with secondary succession the diversity of microenvironments for soil organisms will increase leading to a greater spatial heterogeneity and diversity in the decomposer system. The more complex the chemistry of the resource becomes the

more diverse the enzymatic complexes required to degrade it and the less likely that a single food chain of organisms will be able to perform it (Swift *et al.*, 1979). In other words, it can be hypothesised that later successional stages will provide a greater variety of scenarios that will sustain a more spatially diverse decomposer community.

Chapter 4 investigates the structural dimension of biodiversity. It explores whether given the less diverse tree community developed as a result of the logging disturbance, more spatially homogeneous soil environment and macroinvertebrate communities develop, and whether a more complex spatial structuring of litter resources, nutrient concentration and macroinvertebrate communities develops as the number of dominant species in the canopy increases with succession.

In terms of the function of organic matter cycling, the degree to which litter decomposition rate will reflect successional changes above-ground and below-ground will depend on three characteristics of the members of the soil community; (1) the degree of specialisation to the resource, (2) the adaptability to changes in environmental conditions and (3) the ability to compensate for changes in the community composition itself (pointed out and named as compensatory character by Anderson & Swift, 1983). If a community is very specialised to the resource it consumes, the decomposition rate will experience a major drop if its members are offered a slightly different quality of resource. A community that is less specialised will be able to adapt to a new resource and the decomposition rate will not vary as much.

Chapter 5 investigates the above aspects of the functional dimension of biodiversity. The leaves of an early successional (*Pinus chiapensis*) and of a late successional (*Persea americana*) tree were set to decompose in four successional stages. The evolution of the colonising macroinvertebrate community, decomposition rate, and litter quality were followed for nine months. One could hypothesise that the more advanced in succession a forest is, the better its vegetation will be able to compensate better for abrupt macroclimatic changes, and therefore its local environmental

conditions will be more stable. If that is true then as succession proceeds the decomposer communities involved will be less adapted to environmental change but may be more adapted to heterogeneity in litter quality. Therefore, early successional leaves will be decomposed equally well in late succession as they do in early succession. However, late successional leaves will not decompose at the same rate in early succession, as they do in late succession, because the decomposer community will not be adapted to their quality. Along the same line of reasoning, in late succession the macroinvertebrate community invading both species of leaves should be equally diverse, while in early succession late successional leaves should attract a less diverse community.

Chapter 6 investigates the relationship between the compositional, structural and functional dimensions of biodiversity. It explores whether the diversity of trees in late succession can account for the spatial structuring of soil biogeochemical properties. If different trees in a late successional forest develop distinct biogeochemical cycles and macroinvertebrate communities in the soil around their trunk as a result of species-specific characters, then above-ground and below-ground biodiversities would be closely interdependent in their compositional, structural and functional dimensions.

Finally, Chapter 7 revisits the biodiversity theory in the light of the results presented in previous chapters. The relationship between the compositional, structural and functional dimensions of biodiversity will be analysed in the context of logging disturbance and ecosystem recovery. It will discuss whether the research approach to a complex conservation problem presented in this study has been successful in (1) delivering useful information for decision-making in the conservation of the TMCF in Oaxaca, and (2) directing future research towards those elements in the system that are more vulnerable to disturbance.

CHAPTER 2.

GENERAL METHODS AND SITE DESCRIPTION

Location

The research was carried out in an area known as El Rincón (Villa Alta District), in the Sierra Norte of Oaxaca, Mexico (figure 2.1). The study sites were three secondary chronosequences of Tropical Montane Cloud Forest (Challenger, 1998) named here as Laguna, Tarantulas and Tarbis. Each of these chronosequences is formed by four sites of different successional stage: approximately 15, 45, 75, and 100 years of age. Additionally two pristine forests (Pris and Pris II) and two plots that were logged two months before sampling (Tar 0 and Tar 00) were examined (figure 2.1).

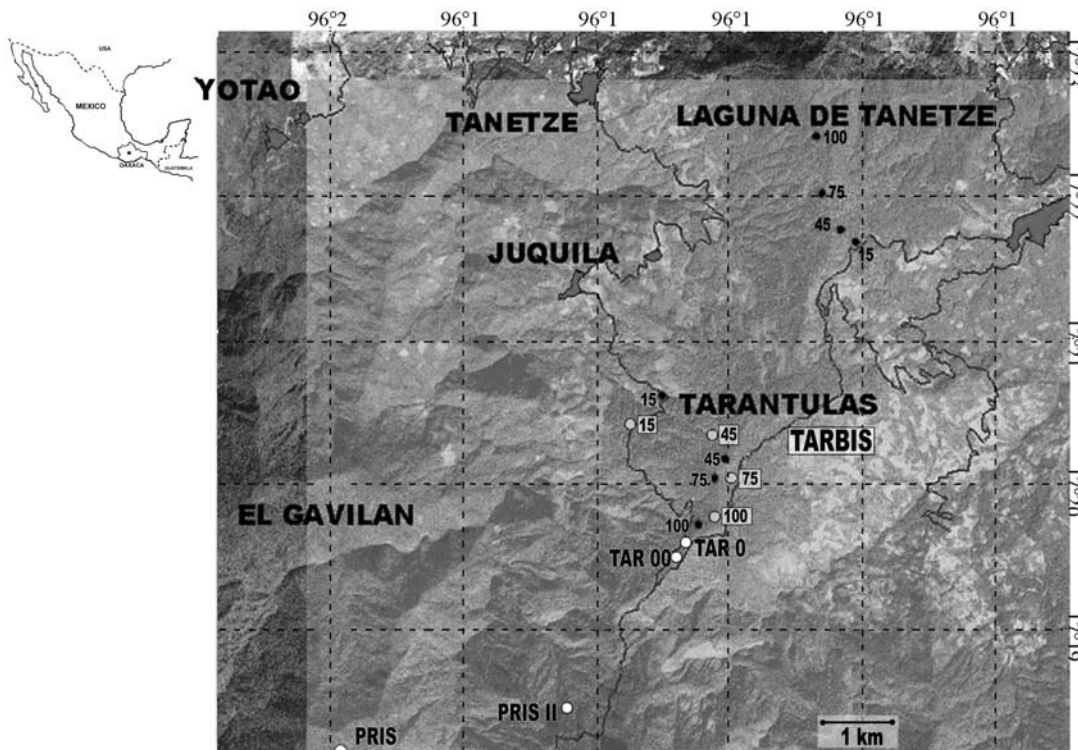


Figure 2.1 Map of Mexico and aerial photograph of El Rincón area showing the location of study sites. The age of the forest stands at each site in years is indicated next to the experimental plots of each chronosequence (Tarantulas, Tarbis and Laguna). The recently logged sites have been marked as Tar 0 and Tar 00 and the pristine sites as Pris and Pris II

All sites are located between the parallels 17°18' and 17°23' N and the meridians 96°15' and 96°21' W. The successional stages within each chronosequence are a

short distance from each other (less than 2000 m) and are situated between the altitudes of 1500 m and 2100 m. General characteristics of each site are described in table 2.1.

Site	Forest age (years)	Orientation	Altitude (m)	Mean slope (%)	Chapters
Tarantulas	15	NW	1700	15	3,4,5
	45	NW	1985	40	3,4,5
	75	NW	1990	24	3,4,5
	100	NW	1975	40	3,4,5,6
Laguna	15	SW	1700	28	3
	45	SE	1800	35	3
	75	NW	1905	13	3
	100	W	1860	15	3
Tarbis	15	SW	1700	15	3
	45	NW	1985	40	3
	75	NW	1990	24	3
	100	NW	1975	40	3
Tar 0	0.2	NW	1975	24	3
Tar 00	0.2	NW	1975	24	3
Pris	Pristine	W	2100	50	3
Pris II	Pristine	W	2233	50	3

Table 2.1 General characteristics of the study sites and the main chapters were they are studied.

Site dating

The age of the forests in each of the studied chronosequences has been identified by del Castillo (1996) based on the age of the oldest *Pinus chiapensis* trees. The disturbance of pristine cloud forests in Mexico leads to the rapid colonisation by pine species due to their heliophilic character (Challenger, 1998). This phenomenon permits a relatively precise determination of the time since the last major disturbance by calculating the age of the oldest pine trees. Del Castillo (1996) dated the chronosequences by coring the oldest *Pinus chiapensis* trees with a Pressel drill, counting the true rings and adding that to the time it takes for *Pinus chiapensis* to reach 1.3 m in height. In order to know how long the trees take to reach that height, del Castillo followed the growth of juvenile trees in permanent *in situ* plots. He

reports that the dates obtained from coring coincide with the information provided by local people about the date of the last timber extraction.

Sierra Norte, Oaxaca still preserves more than 67 percent of its Cloud Forest (Challenger, 1998). However most of the pristine forest that remains is preserved in areas with convoluted topography that are largely inaccessible. For this reason, when selecting the pristine plots, I asked local people to direct us to relatively accessible sites where there is knowledge that the forest has never been logged. The sites that I was recommended to consider had no sign of pine invasion and the tropical components of the forest canopy were taller than in any of the chronosequence sites. This led to the conclusion that they were indeed pristine, or at least had no sign of human intervention over a very long period of time.

Vegetation description

The plant taxonomic nomenclature used in this thesis and the identification of plant specimens were based on the works by Standley and Williams (1976) and Pennington and Sarukhán (1998) and older works cited therein.

The study sites are covered by the characteristic vegetation of the Tropical Montane Cloud Forest (TMCF) type (Challenger, 1998; Blanco-Macias, 2001) also referred to as Bosque mesófilo de Montaña by Rzedowski (1978) and as Montane Rain Forest by Ramírez-Marcial *et al.* (2001). Mexican cloud forest is a very diverse and structurally complex vegetation community. Although it only covers 1% of the territory of Mexico, 10 to 12 percent of the total number of plant species in the country grow in these forests. The high level of species diversity is largely a consequence of two factors. First, as a result of geological shifts, tectonic movement, volcanic processes and changes in climate, the extensive regions of cloud forest that existed in the Pleistocene have now been reduced to a set of relictual vegetation patches. Their isolation and long history (20 to 40 million years) has led to vicariant (allopatric) speciation and high alpha and beta diversity (Rzedowski, 1996; Challenger, 1998). The second reason is that cloud forests are the result of the

combination of the holarctic and neotropical floras that met when North America connected with Central America during the Pleistocene. Trees from holarctic origins usually dominate the highest canopy and a diverse community of evergreen tropical species forms the lower canopy, shrub, epiphyte and herbaceous strata. Many tropical species in Mexican cloud forest are found in latitudes that are situated towards the northern limits of their ranges, reflecting the protective environment found under the high canopy of these forests. Many tropical species are only able to regenerate at this latitude if this canopy is present (Quintana-Ascencio & González-Espinosa, 1993; Galindo-Jaimes *et al.*, 2002). As much as 46% (about 295) of all the plant genera in the mature cloud forest have a neotropical origin. Only about 20 (4%) of the plant genera that are exclusive to cloud forest have a boreal origin, the rest have an Andean provenance (Challenger, 1998).

About 2500 to 3000 species of plants are exclusive to or preferably inhabit Mexican cloud forests. Of these, about 18% are trees, more than 30% are epiphytes (the most diverse group in this ecosystem) and 20% are ferns (these two last groups overlap because many of the ferns are epiphytes) (Rzedowski, 1996).

Bromeliads, orchids and ferns are particularly diverse in cloud forests. There are more epiphytic orchids that are exclusive to cloud forests than to any other ecosystem in Mexico. Ferns in their turn reach higher diversity in cloud forests than in any other terrestrial ecosystem. The most spectacular tree ferns such as *Sphaeropteris horrida* and the endangered species *Cyathea mexicana* are particularly distinctive of these forests (Rzedowski, 1978).

The understory (<3.5 cm in diameter) and canopy vegetation (>3.5 cm in diameter) in the cloud forest of El Rincón area has been characterised by (Blanco-Macias, 2001). She found that this area has probably the highest floristic richness reported to date for Mexican cloud forests (69 families, 128 genera and 209 species of vascular plants in a total of 1.2 ha) and suggests that this might be explained by the particularly high beta diversity developed in a particularly complex local orography. In her study, she found 6 species of plants (*Pinus chiapensis*, *Saurauia serrata*,

Magnolia dealbata, *Cyathea mexicana*, *Marattia weinmannifolia* and *Chamaedorea liebmanni*) that are considered by Mexican legislation (NOM-059-ECOL-1994) to be endangered.

Vegetation succession in El Rincón cloud forest

Blanco-Macias, (2001) studied the ground vegetation in the Tarantulas and Laguna chronosequences. However, the 15-year-old forest that she studied as part of the Laguna chronosequence was different from that studied in this thesis; the site included in her work was cleared before 1999. Additionally, she studied another chronosequence named Yotao (also dated by del Castillo, 1996). In her study Blanco-Macias found that there were considerable differences in the vegetation succession described by the three chronosequences that she studied, however some common patterns arose. For all three chronosequences the density of shrubs and trees diminished with the age of the forest and the complexity of the canopy structure (height variance) increased. The floristic composition of early-successional stages was more similar between chronosequences than it was in late succession (figure 2.2). In general, the number of species in Asteraceae, Brunelliaceae and Pteridaceae was highest in the early succession and the number of species in Arecaceae, Polypodiaceae, Lauraceae and Theaceae was higher in the late succession.

The shift in species canopy dominance through succession described by Blanco-Macias (2001) (table 2.2) followed a similar pattern (in terms of phytogeographic affinity) to the one described in Chiapas by Quintana-Ascencio & González-Espinosa (1993) for pine-oak forest in the Highlands and by Ramirez-Marcial *et al.* (2001) for Tropical Montane Cloud Forest in the North. Holarctic genera, most dominant in early succession, were substituted by Pantropical, Andean-tropical and East Asian-North American genera in late-successional stages. This phenomenon agrees with the suggestion that the highly tropical floristic composition in late-successional cloud forest communities only becomes possible with the microclimate created under the canopy of drought-tolerant and heliophilous holarctic species that colonise recently disturbed sites (Gonzalez-Espinosa, 1991; Quintana-Ascencio & González-Espinosa, 1993; Challenger, 1998; Blanco-Macias, 2001).

	Tarantulas		Laguna		Yotao	
	Tree species	Phyt.Aff.	Tree species	Phyt.Aff.	Tree species	Phyt.Aff.
15-year-old	<i>Gaultheria acuminata</i>	N. Am.-E. Asiatic	<i>Liquidambar macrophylla</i>	Holarctic	<i>Clethra integerrima</i>	N. Am.-E. Asiatic
	<i>Liquidambar macrophylla</i>	Holarctic	<i>Pinus chiapensis</i>	Holarctic	<i>Hedyosmum mexicana</i>	Neotropical-Andean
	<i>Phyllonoma laticuspis</i>	Neotropical-Andean	<i>Quercus sapotifolia</i>	Holarctic	<i>Liquidambar macrophylla</i>	Holarctic
45-year-old	<i>Ilex pringlei</i>	Neotropical-Andean	<i>Bejaria mexicana</i>	Neotropical-Andean	<i>Bejaria mexicana</i>	Neotropical-Andean
	<i>Phyllonoma laticuspis</i>	Neotropical-Andean	<i>Clethra kenoyeri</i>	N. Am.-E. Asiatic	<i>Lyonia squamulosa</i>	N. Am.-E. Asiatic
	<i>Viburnum acutifolium</i>	Holarctic	<i>Phyllonoma laticuspis</i>	Neotropical-Andean	<i>Vaccinium leucanthum</i>	Holarctic
75-year-old	<i>Persea americana</i>	Pantropical	<i>Clethra kenoyeri</i>	N. Am.-E. Asiatic	<i>Ocotea helicterifolia</i>	Pantropical
	<i>Quercus laurina</i>	Holarctic	<i>Phyllonoma laticuspis</i>	Neotropical-Andean	<i>Persea americana</i>	Pantropical
	<i>Ternstroemia hemsleyi</i>	Neotropical-Andean	<i>Rapanea jurgensenii</i>	Neotropical-Andean	<i>Rondeletia liebmannii</i>	Neotropical-Andean
100-year-old	<i>Persea americana</i>	Pantropical	<i>Bejaria mexicana</i>	Neotropical-Andean	<i>Clethra kenoyeri</i>	N. Am.-E. Asiatic
	<i>Quetzalia occidentalis</i>	Pantropical	<i>Ilex pringlei</i>	Neotropical-Andean	<i>Hamelia patens</i>	Neotropical-Andean
	<i>Weinmannia pinnata</i>	Pantropical	<i>Ternstroemia hemsleyi</i>	Neotropical-Andean	<i>Ocotea helicterifolia</i>	Pantropical

Table 2.2 The three most abundant (No. of individuals per hectare) canopy species in each successional stage of El Rincon chronosequences. Dominant tree species taken from Blanco-Macias (2001) and the phylogeographic affinity of their genus extracted from Quintana-Ascencio & González-Espinosa (1993) Rzedowski (1996) and Mabberley (1987).

Cordova & del Castillo (2001) studied the changes in epiphyte cover and community composition in the three chronosequences of El Rincón. They also compared the chronosequences with a pristine site (within the area marked as El Gavilán in figure 2.1).

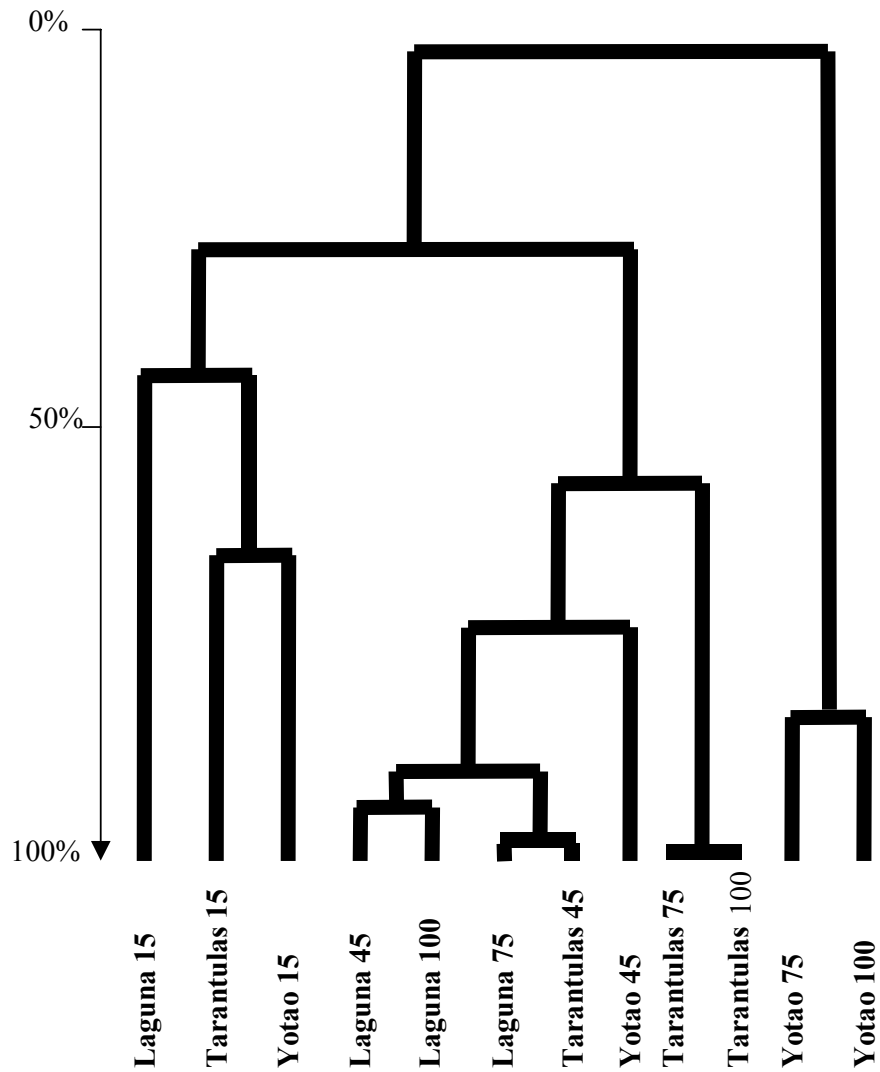


Figure 2.2. Degree of similarity in the vegetation between the successional stages of El Rincón chronosequences. Modified from Blanco-Macias (2001). The diagram represents the results of an analysis of Unweighted Pair Group Method with Arithmetic Mean using the Sørensen Index of Similarity (see p. 34 for values of similarity between groups). It includes all vegetation (dbh > 3.5 cm) in 0.1 ha plots.

They found that young forests have approximately 25% of the total epiphyte cover found in the pristine forest. According to their results, a secondary forest will take more than 100 years to reach the level of epiphyte cover found in a primary forest. Certain groups of epiphytic plants, such as orchids and bromeliads, were only found in late-successional stages. They attribute this positive correlation between epiphyte cover and forest age to the interactions between different types of epiphytes and in other cases to changes in microclimate (particularly air humidity) that occur as succession proceeds.

Characteristics of the soils

The Natural Resources Laboratory in CIIDIR, Oaxaca has studied some of the physiochemical characteristics of the soils in the chronosequences of El Rincón. Tables 2.3 and 2.4 and figure 2.3 summarise the findings of four studies conducted by this research group (Velázquez-Aragón, 2000; Hernández-Pérez, 2001; Bautista-Cruz *et al.*, 2003a; Bautista-Cruz *et al.*, 2003b).

Property	Mean in field and per successional stage				
	Maize	15 yrs	45 yrs	75 yrs	100 yrs
Soil depth (cm)	*	*	85	121	50
pH H ₂ O (1:2)	5.53	4.65	4.42	4.13	4.1
Al _{exch} cmol(+)kg ⁻¹ of soil	*	1.41	2.11	2.13	1.54
CEC _{NH₄OAc} cmol(+)kg ⁻¹ of soil	11.2	10.2	12.5	16.6	18.6
Sand %	63.6	51.04	41.2	49.8	41.72
Silt %	20	30.4	41.2	36.7	40.5
Clay %	16.4	18.6	17.6	13.5	17.8

Table 2.3 Mean physicochemical properties of the soil profile in different successional stages of cloud forest in El Rincón. Modified from Bautista-Cruz *et al.*, (2003b).*= not available; CEC= cation exchange capacity.

Bautista-Cruz *et al.*, (2003b) described the general physiochemical characteristics of the soils in one chronosequence formed by a arable field, a 15-year-old forest and the 45-, 75-, and 100-year-old forests of the chronosequence at Tarantulas (table 2.3). They found that agricultural disturbance had a profound effect on the structural and physiochemical characteristics of the soil. They arrived at the conclusion that the soil under a maize field that was established on an area converted from cloud forest

should be classified as Entisol (*Typic Udorthensis*), whereas the forested successional stages that they studied were all Inceptisols. The soils of 15-year-old Acahual and the 45 year-old forest were Humic Dystrudepts and the 75- and 100-year-old forests were classified as Typic Dystrudepts. Bautista-Cruz *et al.* (2003b) suggest that as succession proceeds the soil becomes more acid (Table 2.3), favouring hydrolysis and desilification of primary and secondary minerals. These processes profoundly change the composition of the soils, increasing loss of minerals such as muscovite and chlorite and enrichment with kaolinite.

Additionally, Velázquez-Aragón (2000) studied the rate of nitrogen mineralisation in incubated soils extracted from three chronosequences. Two of the chronosequences were Tarantulas and Laguna and the third was the chronosequence named Yotao located within El Rincón. His results are summarised in figure 2.3. While mineralised NH_4^+ increased with the age of the forest (GLM: $F=1737.64$, $d.f.=1, 39$, $P<0.0001$), mineralised NO_3^- diminished (GLM: $F=9476.26$, $d.f.=1, 39$, $P<0.0001$). The overall mineralised nitrogen increased with succession (GLM: $F=74.67$, $d.f.=1, 39$, $P<0.0001$). There were also significant differences between the chronosequences for all three types of mineralisation (GLMs: $P<0.05$) but no interaction between mineralisation rate and chronosequence (see differences between chronosequences below).

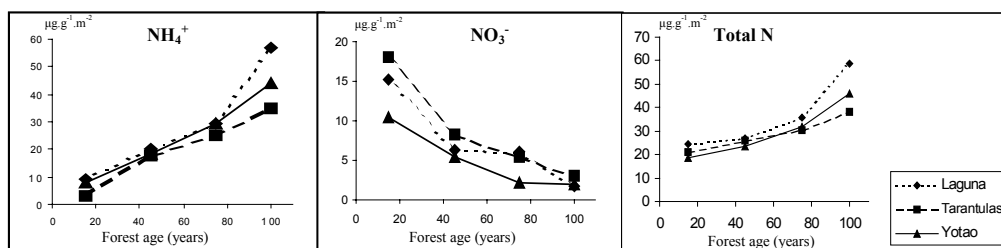


Figure 2.3 Nitrogen mineralised after incubation in soils from different chronosequences: Tarantulas (T), Laguna (L) and Yotao (Y). Data taken from Velázquez-Aragón (2000). While mineralised NH_4^+ concentration increases with the age of the forest, mineralised NO_3^- concentration diminishes. The overall concentration of mineralised nitrogen increased with the age of the forest.

Bautista-Cruz *et al.*, (2003a) described one soil profile in each of the 45-, 75- and 100-year-old forest of the Tarantulas chronosequence. With the information and samples from these profiles, they were able to conduct physical, chemical,

mineralogical and micro-morphological analysis of soils. Table 2.4 summarises their findings for the surface genetic horizons (O and the next A horizon) that include the soil depth that concerns this study. The mineralogical composition of the coarse fraction in the chronosequence was dominated by muscovite and quartz with Albites as accessories. In the fine fraction, kaolinite clay was the main component followed by quartz, biotite, iron oxidate and aluminium. The four profiles studied showed noticeable differences in their genetic horizon structure and depth. The researchers identified four horizons (O, ABh, Bs, and CB) in the 100 year-old forest, six in the 75-year-old forest (O, A1, A2, Bsw, Bsw2 and Bsw3) and three in the 45-year-old forest (O, A and BC). The horizons in each forest summed to a total depth of approximately 85, 121 and 50 cm respectively.

Property	Genetic Horizon O			Next genetic Horizon		
	45 years	75 years	100 years or more	45 years (A)	75 years (A1)	100 years or more (Abh)
Depth (cm)	20	10	15	29	8	15
pH H₂O 1:2	3.95	3.46	3.55	4.34	3.15	3.73
E.A. cmol(+)kg⁻¹ of soil	3.31	5.23	5.56	5.92	14.44	5.52
Al_{exch} cmol(+)kg⁻¹ of soil	1.39	3.02	1.48	4.87	10.99	3.12
ECEC cmol(+)kg⁻¹ of soil	11.46	12.16	9.80	6.33	16.42	5.87
CEC_{NH₄Oac} cmol(+)kg⁻¹ of soil	76.45	73.23	84.50	32.84	49.79	13.78
BSP %	10.65	9.47	5.00	1.25	3.98	2.59
Sand %	23.03	24.89	8.92	21.71	29.91	7.79
Silt %	37.24	38.76	70.84	37.96	38.67	74.77
Clay %	39.73	36.34	20.24	40.33	31.42	17.45
Texture class	clay loam	clay loam	silt loam	clay	clay loam	clay loam
Bulk density g. cm⁻³	*	*	1.24	*	1.02	1.35
Humidity % (gravimetric)	51.85	30.39	31.26	66.62	39.67	25.63
n value	*	*	*	*	0.436	0.212
Wet colour	10YR 4/4	10YR 4/4	10YR 6/8	10YR 3/2	10YR 3/2	10YR 6/6
Dry colour	10YR 5/4	10YR 4/3	10YR 8/8	10YR 4/3	10YR 3/4	10YR 8/4
Porosity %	*	*	53.3	*	61.6	50.2

Table 2.4 Physicochemical properties of the surface genetic horizons (O and the next A horizon) in different successional stages of Cloud Forest in El Rincón. Modified from Bautista-Cruz *et al.*, 2003a.*= not available; E.A.= Exchangeable acidity; Al_{exch}= exchangeable aluminium; ECEC= Effective cation exchange capacity, CEC= cation exchange capacity; BSP= base saturation percentage.

One of the outstanding features of these profiles is that there is a lack of a defined A horizon in the oldest forest. Bautista-Cruz *et al.* (2003a) suggest that this is a product of a very acidic environment. In terms of the biological activity in their profiles they

only found evidence of mesofaunal activity in the 45-year-old profile, where abundant excreta and evidence of fauna-associated changes in the aggregate structure were observed.

Hernández-Pérez (2001) grew seedlings of different tree species in pots containing the soils extracted from different successional stages of the Tarantulas chronosequence. She found that the successional stage of the soil affected the survival of all species tested. Some species of seedlings (*Ilex pringlei* and *Brunellia mexicana*) survived better in the soils from those stages where that species establishes most readily during succession in the field. However, this was not the pattern of responses displayed by all of the species. Hernández-Pérez suggests that soil biogeochemical characteristics in each successional stage interact with microenvironmental conditions such as light availability to determine whether a species of tree is able to establish in a particular successional stage. Furthermore, soil biogeochemical conditions might be more important for the establishment of some species (such as *Ilex pringlei*) than for others (such as *Pinus chiapensis*).

Climate

Cloud forests in Mexico are now restricted to climatic islands in mountainous areas where, as a result of orographic cooling of humid air below the dewpoint, there is continuous fog at the level of the vegetation (Bruijnzeel & Veneklaas, 1998; Challenger, 1998). This characteristic makes the climatic conditions within the cloud forest radically different from its surroundings. As a result cloud forests are more common in windward slopes, in the transition zones between tropical and temperate climates. General information about the regional climatic patterns was obtained from the nearest meteorological station, named Villa Alta, which is approximately 16 km to the east of the studied areas. The climate in Villa Alta has been classified as temperate humid to sub-humid, with a mean precipitation of 1500 to 2000 mm per year, but it can be up to 3000 mm in rainy months (summer) and 40 mm in dry months (winter). The mean annual temperature is 20 to 22 °C, with an absolute maximum of 42 °C and absolute minimum of 4 °C (data provided directly by

Comisión Nacional del Agua). This information should only be interpreted as general guidance given the particularity of the climatic conditions where cloud forest develops. Microclimatic soil conditions in the study sites were measured during every survey and experiment in this thesis in an attempt to provide more direct evidence of the environment experienced by the soil ecosystem in each successional stage.

Site differences between and within the chronosequences in El Rincón

Chronosequences can be considered as models of secondary succession as if they were “frozen in time”. This substitution of time for space allows the study of a long-term process to be carried out within a human life span. Ideally, chronosequences of the same forest type should only differ from each other in location and all successional stages within a chronosequence should be identical except for the age of the forest. In reality even in the best of scenarios the sites chosen to form a chronosequence differ in aspects other than location and age of the forest plots. These differences should be as well known as possible because they may interact or be confounded with the successional process. What follows is a description of differences between study sites in El Rincón that are not purely related to the age of the forest. In the following chapters it will be discussed how these site characteristics may constrain the interpretation of results.

Previous research performed in El Rincón has shown that there are some ecological differences between chronosequences despite the short distance between them and the common type of original vegetation (Blanco-Macias, 2001; Hernández-Pérez, 2001). These differences are probably a product of the interaction between the successional process, site characteristics and anthropogenic influences.

An analysis of Unweighted Pair Group Method with Arithmetic Mean (UPGMA) performed on vegetation presence-absence data (Blanco-Macias, 2001; figure 2.2) showed that the community composition is more similar between chronosequences in early-successional stages than it is in late-successional stages, particularly if the sequences being compared are distant. Overall, Tarantulas and Laguna

chronosequences were the most similar and Yotao (the most distant sequence) the most singular in its species composition, particularly in late-successional stages. The three 15-year-old forests formed a distinct group and the 45-year-old forests were all relatively similar to each other (figure 2.2). The 75- and 100-year-old forests in Laguna were more similar to the group formed by the 45-year-old forests (71.7 to 73.5% Sørensen similarity index) than to the 75- and 100-year-old forests in Tarantulas (53.1 to 66.8% Sørensen similarity index). The Tarantulas 75- and 100-year-old forests had the highest similarity index recorded in the whole study (75.5%).

In terms of the chronosequences studied in this thesis, the number of plant species in 0.1 ha in the Tarantulas chronosequence was always higher (above 30) than in Laguna (below 30), except for the 75-year-old forests where the number was higher in Laguna (above 35) (Blanco-Macias, 2001). The trend in Shannon's diversity index also differed between chronosequences. In Tarantulas it was below 2.4 in the 15-year-old forest and around 2.9 in the other successional stages. In contrast, in Laguna this index was around 2.6 in the 15- and 45-year-old forests, above 2.8 in the 75-year-old and around 2.7 in the 100-year-old plot. The population density of plants for both chronosequences diminished with the age of the forest. However, it was always significantly higher in Tarantulas than in the other chronosequences.

With respect to the soil, the only comparative work between the chronosequences is the nitrogen mineralisation study by Velázquez-Aragón (2000). For all chronosequences the overall mineralised nitrogen concentration and the ammonia fraction increase with the age of the forest. However concentrations were always higher for Laguna than for the other two chronosequences (figure 2.3). The concentration of mineralised nitrate decreased with the age of the forest for all chronosequences, but it was always higher for Tarantulas than for the other two chronosequences (figure 2.3).

Three main factors may be determining the differences in plant community composition and nitrogen mineralisation between chronosequences:

- (1) Cloud forests have been described as having a very high beta diversity, particularly when mature forests are compared (Rzedowski, 1996; Challenger, 1998). The species composition developed after disturbance of a forest patch depends on the availability of seeds from the surrounding forests. If mature forests surrounding two newly open patches diverge in species composition, the community developed through succession in those patches is similarly bound to be different. For this reason a tendency to diverge in species composition with time after disturbance is expected to happen when comparing chronosequences separated by a few kilometres.

- (2) Blanco-Macias (2001) suggests that the floristic differences between Tarantulas and Laguna are partly a result of differences in the geographic location. Tarantulas is in direct contact with the humid northern winds coming from the Gulf of Mexico, while Laguna is under the influence of a rain shadow (figure 2.1). This could result in a higher environmental humidity in Tarantulas.

- (3) Blanco-Macias (2001) found that there were more multi-stem trees in Laguna than in Tarantulas, which she considers a sign of greater disturbance by firewood collection. This disturbance could have caused an overall loss of plant diversity in Laguna.

The differences between chronosequences in El Rincón raise the question of whether they really represent replicates of the same successional process. Despite the differences, all three chronosequences studied here follow the successional process that TMCF undertake after a major anthropogenic disturbance. This successional process has been discussed in previous sections and therefore will not be described here. It should suffice to say that for all sites the major disturbance that started the successional process opened the canopy to an extent that permitted the growth and dominance of light-tolerant woody species. These pioneers replaced for a long time the diverse canopy dominated by species of a tropical origin. And finally, in all three chronosequences the older the successional stage the greater the proportion of tropical species that form the canopy.

There are also differences in altitude, slope and orientation between successional stages in all the chronosequences (table 2.1). The influence of these site characteristics could be confounded with the effect of the successional stage, particularly if they follow similar trends in all chronosequences. The 15-year-old forests of all three chronosequences are located at a lower altitude and the 75-year-old forests at higher altitude than other successional stages. Similarly both of the pristine sites are located at an altitude between 100 and 200 meters higher than the rest of the study sites and on a particularly steep slope.

Chronosequences are the best tool available to study successional trends within the span of a human life. The sites forming each chronosequence in El Rincón are circumscribed within a surprisingly small area, all chronosequences are located within the same catchment and the age of the forests after the last major disturbance has been reliably determined. The pristine forests and recently logged sites are also located very close to the chronosequences. If the differences between chronosequences and between successional stages described above are taken into consideration when interpreting the results of this study, the chronosequences of El Rincón can be considered a unique and appropriate model of the secondary succession undergone by TMCF in Oaxaca after logging disturbance.

Human activity and site history

The northern sierra of Oaxaca is inhabited by Zapoteco people. Generally, the members of each community share a common land, which they work and subsist from. In this area private property is extremely uncommon. The community of Juquila Vijanos owns all of the field sites studied here. They have preserved a considerable section of their land as forests, but poverty and a lack of an alternative income has led them to exert increasing pressure on the forest.

As in many mountainous regions of Mexico, in Sierra Norte, Oaxaca the use of the cloud forests is included within a strategy of *ecological floors*. In this system people

take advantage of the altitudinal shifts in ecosystems and ecotones to distribute the production of different products according to their highest productivity within that gradient (Challenger, 1998). Because of the cool, moist shady conditions under which cloud forest flourishes, most mesophytic regions in Mexico, including the land belonging to the community of Juquila Vijanos, are devoted mainly to coffee plantations. As a consequence of the recent drop in coffee prices in the world market, isolated regions such as Sierra Norte cannot compete because of the high transportation costs involved.

Another complicating factor in the economy of this Oaxacan region is the special protection (protección especial - endémica) status afforded to *Pinus chiapensis* in Mexican legislation (NOM-O59-ECOL-1994). This species has been protected because its populations are diminishing at the national scale, however, it is most common in this particular area of Sierra Norte. The legal protection means that it becomes very difficult and costly to acquire permission for legal timber extraction. The only use of the forest that people are authorised to undertake without having to produce an integrated management plan (Manifiestación de Impacto Ambiental) is the extraction of firewood for domestic use (LGEEPA Art 3, Fracc. XX; Art. 28 Fracc XIII, Reglamento en Materia de Impacto Ambiental Art. 9). This is where the legal control becomes less well defined. As the economic pressure increases, more and more firewood is extracted with a supposed domestic purpose. After talking to local people and scientists that have worked in the area for some years, I developed the impression that the firewood is being traded illegally.

The main target for firewood in the cloud forest is the genus *Quercus* which is converted into small pieces (about 1 m long and 10 cm in diameter) *in situ* (figure 2.4). All of the extraction is done with a hand held chainsaw that runs on gasoline. People attempt to control the felling of each tree with ropes that are pulled by different men on each side of the tree. In reality, with this method there is little control on what the outcome is, and the trees in the best of cases smash at least a few other canopy species during their descent. In other cases, falling trees get tangled in the branches of other trees, never make it to the ground and they simply rot in a

semivertical position. *Quercus* species in old stands of cloud forest grow side by side with a very diverse mixture of canopy species (Blanco-Macias, 2001, see also Chapter 3). This means that the logging process is highly inefficient. Much of forest becomes severely damaged, with great human physical effort and very little benefit is obtained. After the firewood has been extracted sites are generally abandoned completely and secondary succession begins. Some of the sites continue to be impacted by collection of loose branches and twigs for firewood, mainly undertaken by women and children. The extent of this activity is unknown.



Figure 2.4 Photographs showing the cloud forest in Tarantulas (100-year-old) before and after logging. Photographs taken by A. Gove.

Although the steep and cool character of the land covered by cloud forest make it highly inappropriate for cultivation of crops, an increasing portion of the cloud forest in Sierra Norte is being burnt down illegally to be converted into arable land. This is the result of increasing economic pressure in the area. Because cloud forest lies on shallow soils, the first crop rotation renders a reasonably good yield, but subsequent rapid erosion makes the land useless for agriculture very soon after (Challenger, 1998). Although community authorities told me that the sites studied were originally disturbed by firewood extraction, there is no hard evidence to demonstrate this, except for the recently logged sites. Some study plots may have been used for crops at some point before secondary succession occurred. However, I think this is not very

likely for two reasons. First, because the community of Juquila Vijanos is one of the communities that has converted the least land into arable land and second because the pressure to convert forest into arable land was less strong in the past than it is now. Another important issue to consider about the chronosequences is that it is difficult to determine whether the last major disturbance (being dated by coring the pine trees) was performed on a primary forest rather than a secondary forest already recovering from a previous disturbance. This issue is of particular relevance to soil studies because of the long time scale involved in soil accumulation and fertility recovery.

Site selection criteria

The sampling plots within Tarantulas and Laguna chronosequences were selected within the precise areas where the age of the forest had been established by del Castillo (1996), coinciding also with the same area where the vegetation has been surveyed (Blanco-Macias, 2001) and soil profile description has been carried out (Bautista-Cruz *et al.*, 2003a). The criteria for the selection of the pristine plots were that they had the same aspect and were as near as possible to the chronosequences (figure 2.1). The recently logged sites (Tar 0 and Tar 00) were located nearest to the 100 year-old forest in the Tarantulas chronosequence and were logged by local people precisely two months before their sampling. Their exact age is not known or whether they were ever logged, their appearance was similar to the 100-year-old forest and no pine trees were located nearby. For this reason, they were considered as a mature forest that was older than 100 years.

The chronosequence named Tarbis was a second set of sites selected within the Tarantulas area. The selection of a second set of sites in the Tarantulas area was decided after the authorities of Yotao denied me permission to work in the chronosequence that del Castillo had dated within boundaries of their land.

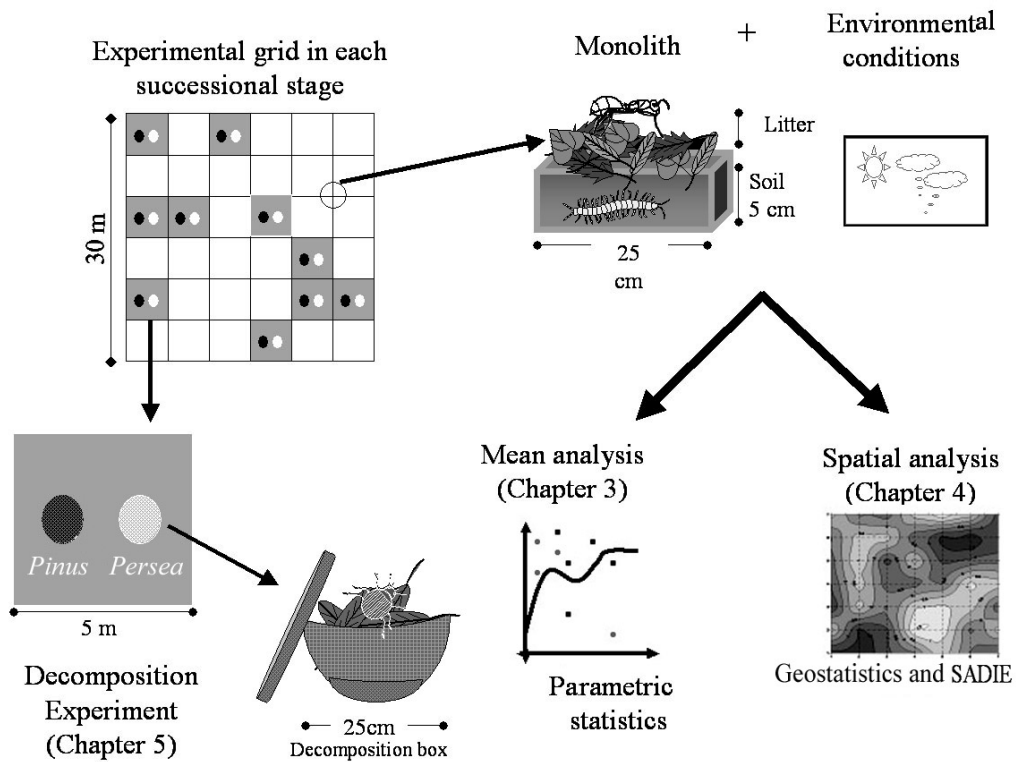


Figure 2.5. Diagram summarising the studies performed in sampling grids established in each study site. The chronosequences survey (Chapter 3), spatial study (Chapter 4) and the across-succession decomposition experiment (Chapter 5) were carried out in these square grids.

Tarantulas was selected for the intensive survey (part of Chapter 3), spatial study (Chapter 4) and decomposition experiments (Chapters 5 and 6) because it is the most accessible chronosequence. Within a couple of hours one can walk to the nearest road and therefore litter and soil samples could be carried back to the vehicle relatively easy. In contrast, to reach the Laguna sites requires walking at least three hours and during the rainiest part of the year (when the macroinvertebrate population is highest) the road is inaccessible and the walking time increases up to six hours, over difficult terrain.

Sampling and experimental designs

The body of data accumulated in this thesis was obtained from two different settings: (1) 30 m × 30 m sampling grids established in all successional stages of all chronosequences (Chapters 3, 4 and 5; figure 2.5) and (2) the area under the canopy

of 12 experimental trees in the 100-year-old forest of the Tarantulas chronosequence (Chapter 6; figure 2.6).

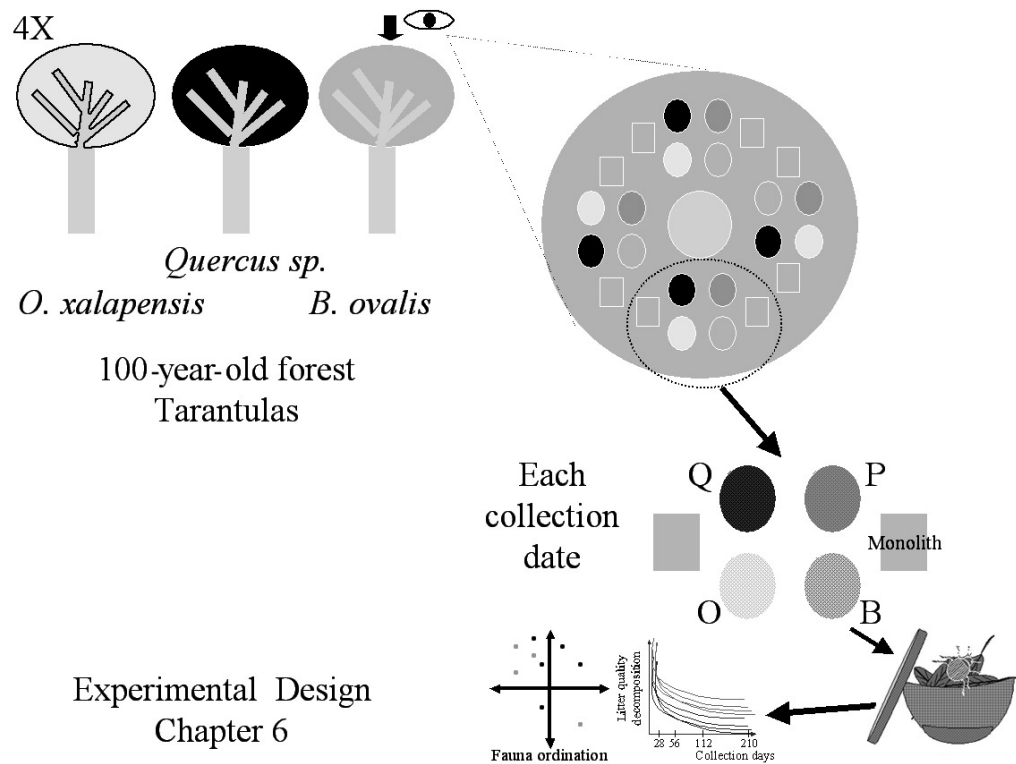


Figure 2.6. Diagram summarising the experimental design used in the between-trees decomposition experiment presented in Chapter 6. This experiment was carried out under the canopy of 12 experimental trees in the 100-year-old forest of the Tarantulas chronosequence. The litter used in decomposition boxes belonged to *Oreopanax xalapensis* (O), *Beilschmedia ovalis* (B), *Quercus spp.* (Q) and *Pinus chiapensis* (P) tree species

Sampling grids

The chronosequences survey (Chapter 3), spatial study (Chapter 4) and the across-succession decomposition experiment (Chapter 5) were carried out in sampling grids (figure 2.5). The study area selected in each successional stage consisted of a 30 m × 30 m quadrat divided into 5 m × 5 m squares that formed a 49 intersection grid. All of the areas were located at least 10 m away from the edge of the successional stage and 2 metres away from walking trails. Surveys (Chapter 3 and 4) were performed on the intersections of all grids. The across-succession decomposition experiment (Chapter 5) was carried out in the middle of sixteen randomly chosen squares formed

by the grid in each successional stage of the Tarantulas chronosequence only (figure 2.5).

Experimental trees

The between-tree species decomposition experiment (Chapter 6) was carried out under the canopy of 12 trees in the 100-year-old forest of the Tarantulas chronosequence (figure 2.6). Four trees of three species common in late succession (*Beilschmiedia ovalis*, *Oreopanax xalapensis* and *Quercus* sp.) were selected for this purpose. The dbh of all experimental trees was larger than 40 cm and the projection of their canopy on the floor was as symmetrical as possible in all directions.

Microclimate measurement

Soil temperature, volumetric soil water content and canopy cover were considered as indicators of soil microenvironmental conditions. For soil water content and temperature a Delta-T-Theta Probe soil moisture sensor attached to a Delta-T- HH1 meter (Delta-T Devices Ltd, Cambridge, UK) and a Taylor soil digital thermometer (model 9840; Taylor Precision Products LP, Oak Brook, USA) were used respectively. The final calculation of volumetric soil water content was based in a soil-specific calibration (Delta-T Devices Ltd, 1999) performed with soil cores obtained from each successional stage of the Tarantulas chronosequence. Both the temperature and humidity sensor probes were placed at a soil depth of 10 cm. Percent canopy cover was measured with a Convex Spherical Crown Densiometer (Forestry Suppliers Inc., Jackson, USA), facing north and holding the densiometer at breast height, above the sampling point. All canopy cover measures were made by the same observer.

Monolith extraction and processing

All monoliths extracted in this study consisted of 25 cm × 25 cm × 5 cm depth of soil, plus all the litter above it. To avoid disturbing the surrounding soil, the monoliths were extracted with a box corer and therefore did not follow the excavation

method recommended in the TSBF handbook (Anderson & Ingram, 1993). The litter and soil sample was hand sorted *in situ* for macroinvertebrates (defining macroinvertebrates as all invertebrate animals larger than 3 mm in any of its dimensions) and stored in black plastic bags. The macroinvertebrates found in the soil and litter of the monolith were preserved in 70% alcohol in individual vials (hand-sorting of samples always occurred within 24 hours of the extraction of the sample). In the laboratory the litter and soil samples were transferred to paper bags and dried in the oven at 80°C until they reached constant mass. The dry mass of the soil and litter in each monolith were recorded and soil bulk density calculated (Anderson & Ingram, 1993).

Experimental decomposition boxes

Both decomposition experiments (Chapters 5 and 6) were carried out in decomposition boxes (kitchen plastic colander: 25 cm top diameter × 15 cm bottom diameter × 10 cm depth; figures 2.5 and 2.6). These boxes were similar to decomposition bags, but were made out of hard plastic mesh (7 mm openings) that forms a rigid box. These boxes contained 30.025 ± 0.025 g (d.w.) of loose experimental leaves from different tree species (from here on referred to as leaf species). The lid and bottom of the boxes have a thin plastic mesh (1 mm openings) to prevent sample lose and new materials from entering the box. The boxes were located within the local litter and surface soil to disguise them. A quarter of the boxes were recovered 28, 56, 112 and 210 days after placement. Experimental boxes were hand-sorted *in situ* for macroinvertebrates (within 24 hours of collection) and their leaf content stored in black plastic bags. All handling of the experimental leaves was performed over wide white trays to assure that no material was lost. The macroinvertebrates found were preserved in 70% alcohol in vials. In the laboratory the experimental leaves were transferred to paper bags and dried in the oven at 80°C until they reached constant mass. The dry mass was recorded. Four experimental boxes per leaf species were carried to the field, placed and recovered immediately to assess mass loss due to handling.

Chemical analysis

Leaf samples

Leaf samples used for experimental purposes and extracted from decomposition boxes (Chapters 3, 5 and 6) were analysed for: (1) total C concentration using the loss on ignition method (Jackson, 1958); (2) total N concentration with sulphuric acid digestion followed by distillation and titration (Anderson & Ingram, 1993); (3) total P concentration using sulphuric acid digestion followed by colorimetric determination (Anderson & Ingram, 1993) and (4) cations concentration (Ca^{++} , Mg^{++} , K^+ and Na^+) using atomic absorption spectroscopy (Allan, 1971).

The fibrous contents in experimental leaves was analysed with a sequential procedure of Neutral Detergent Fibre (NDF) and Acid Detergent Fibre (ADF) extractions (Van Soest, 1994) followed by a 72% Sulphuric acid extraction through the method named Acid Detergent Lignin extraction in beakers (ADL; ANKOM Technology, 2000). All this was performed in filter bags simultaneously for 15 samples at a time in an ANKOM²⁰⁰ Technology Fiber Analyzer (ANKOM Technology, Fairport, NY; Vogel *et al.*, 1999). The fraction remaining after ADF minus the one extracted by ADL was named the acid soluble fraction (ASF), and the organic residual after ADL was named residual fraction (RF).

Macroinvertebrate identification and grouping

All macroinvertebrates collected were counted under a dissecting microscope and classified into one of the following 29 higher taxa and groups of immature stages. Taxonomic classification was performed following Brusca (2003) for higher taxa and Fragoso & Reynolds (1997) for the lower taxa of the Suborder Lumbricina:

Phylum Arthropoda
 Subphylum Myriapoda
 (1) Class Chilopoda

- (2) Class Diplopoda
 - Subphylum Cheliceriformes
 - Class Chelicerata
 - Subclass Arachnida
 - (3) Order Opiliones
 - (4) Order Pseudoscorpionida
 - (5) Order Acari
 - (6) Order Aranea
 - (7) Order Ricinulei
 - (8) Order Uropygi
 - Subphylum Hexapoda
 - Class Insecta
 - Subclass Pterygota
 - Infraclass Neoptera
 - (9) Order Coleoptera
 - (10) Order Orthoptera
 - (11) Order Blattodea
 - (12) Order Hemiptera
 - (13) Order Homoptera
 - (14) Order Dermaptera
 - (15) Order Diptera
 - (16) Order Hymenoptera (other than Formicidae)
 - Superfamily Formicoidea
 - (17) Family Formicidae
 - Subclass Zygneta
 - (18) Order Thysanura
 - Class Entognatha
 - (19) Order Collembola
 - (20) Order Diplura
 - Subphylum Crustacea
 - Class Malacostraca
 - Subclass Eumalacostraca
 - Superorder Peracarida
 - (21) Order Isopoda

Phylum Mollusca

- (22) Class Gasteropoda

Phylum Annelida

- Class Clitellata
 - Subclass Oligochaeta
 - Order Haplotaxida
 - Suborder Tubificina
 - (24) Family Enchytraeidae
 - (25) Suborder Lumbricina

Immature stages

- (26) Coleoptera larvae
- (27) Diptera larvae
- (28) Lepidoptera larvae
- (29) Other larvae and pupae

All the earthworms (Suborder Lumbricina) were identified to species by Dr. Carlos Fragoso, Instituto de Ecología, Xalapa, Mexico.

Hemiptera and Homoptera were kept as separate orders although in recent years most authors have adopted the convention of grouping them under the Order Hemiptera (Brusca, 2003)

When Collembola found in decomposition experimental boxes exceeded 200 individuals in a single sample, a counting grid was used to estimate the total number as recommended by Southwood (1984), who reports the counting error of this method to be between 5 and 15 percent.

Statistical analyses

Detailed tables of the statistical analyses performed in each chapter are included in the appendices at the end of this thesis (which have been named after the corresponding chapters Appendices CH3, CH5 and CH6).

Analyses of variance

All variations of analyses of variance (ANOVA) and tests of their assumptions were performed using the software STATISTICA v.6.0 (Statsoft Inc., Tulsa). When the assumptions of normality (Kolmogorov-Smirnov test) or homoscedasticity (Leven's test) were not met, a randomisation test with 10,000 iterations was performed (Legendre & Legendre, 1998; Edgington, 1995) using the software Genstat v.10.0 (VSN International Ltd., Hemel Hempstead Herts, UK). Dr. David Allcroft (BIOSS, Edinburgh) wrote the program that performs the randomisations. When the randomisation was performed, it was stated in the ANOVA tables and in those cases

where the P-value obtained from the randomisation curve differed from that obtained from standard F-tables, the value obtained from randomisation was adopted. Following some ANOVAs a Tukey's Honest Significant Difference post-hoc test (HSD; Legendre & Legendre, 1998) was performed in STATISTICA v.6.0. When the interactions between treatments were significant, this test accounted for the increase in probability of Type I error due to added consecutive testing. Following the suggestion by Underwood (1997), when treatments in an ANOVA interacted significantly, the treatment effects were only interpreted in terms of the interaction.

Multivariate analysis of variance (MANOVA) was only performed when the homoscedasticity (Box's M test) and multivariate normal distribution assumptions were met. Multivariate normality was assumed to be achieved when all dependent variables were themselves normally distributed (Kolmogorov-Smirnov test) (Legendre & Legendre, 1998). In the case of repeated measures analysis of variance (ReANOVA) additionally to the general MANOVA assumptions sphericity was tested with Bartlett's and Mauchly's test (Legendre & Legendre, 1998). In the case of Analysis of Covariance (ANCOVA) in addition to the general ANOVA assumptions the additional assumptions of (1) linear relationship between covariate and dependent variable and (2) homogeneity of covariate regression coefficients (no interaction effect between treatments and covariate) were tested.

Compositional diversity indices

For litter components, tree genera and macroinvertebrate taxa, I used three estimates of compositional diversity: the number of elements (macroinvertebrate taxa or tree genera), the equitability index or Shannon-Wiener evenness ($J=H'/\log(S)$, where H' is the observed Shannon-Wiener index and S the total number of elements observed over all samples) and the Shannon-Weiner index ($H'=-\sum p_i \ln p_i$ where p_i is the proportion of individuals found in the i th element) (Magurran, 1996). The number of elements and equitability were chosen as they constitute the core components of any diversity measure and H' was preferred to other indices because it facilitates comparison with other studies due to its widespread use.

As a result of the wide range of body sizes covered by the set of taxa considered here as Macroinvertebrates, changes in the values of a Shannon-Wiener diversity index constructed with counts of individuals cannot be assumed to correlate directly with functional changes of similar magnitude. Those organisms with higher biomass per individual like earthworms may play an essential role as ecosystem engineers and yet wrongly count as rare in an index that is based on counts of individuals. The reverse may also be true, small organisms like Collembola will be considered in the index as very common and yet their functional role may not be overall very influential since their body size is relatively small. For this reason, diversity indices of the soil community should ideally be based on biomass rather than number of individuals per taxon. However, calculating the biomass per taxon is a very laborious task when all macroinvertebrate taxa are being taken into consideration. Furthermore, within a single higher taxon, such as Formicidae or Coleoptera, the wide range of body sizes of different species does not allow for an easy extrapolation from the biomass of a few individuals. Therefore a more detailed taxonomic distinction would be needed within such taxon in order to produce a sufficiently accurate estimate of overall biomass.

Considering that the soil macroinvertebrate community in Sierra Norte had never been studied before and the limited time available, I decided that as a first approach this study should include counts of all Macroinvertebrate taxa, rather than biomass estimates of a few groups. The diversity indices presented here are used to compare communities in different successional stages and under different experimental conditions. They should not be considered in isolation as all discussions about community changes are accompanied by references to those changes in the abundance of individual taxa that determine the variation in diversity indices. Future research on the Macroinvertebrate community of Sierra Norte should focus on those groups that this study demonstrates to be sensitive to succession, and diversity indices should be constructed based on biomass estimates of lower taxa within those groups.

Multivariate relationships between macroinvertebrate communities and environmental, resource and experimental treatment variables

Canonical Correspondence Analysis (CCA) was used to explore the amount of variances in macroinvertebrate community composition explained by environmental, resource and experimental treatment variables. The amount of variance explained by subgroups of variables (such as microenvironmental, chemical, forest age, etc) was then explored through Variance Partitioning (Ter Braak & Smilauer, 1998). When partitioning the variance I did not extract (by the use of covariates) the shared variance between subgroups of variables. I chose not to do so because the main objective of this study is precisely to study the interaction between those variables during secondary succession. Furthermore, I considered that given the natural network of associations between explanatory variables (for example successional stage, litter components and litter chemistry) it would be difficult to find an ecological (and not stochastic) explanation of the variance explained outside this network. CCA biplots (of the first two axes extracted) were used as a means of reducing the dimensionality and providing a visual representation of the environmental, resource and chemical conditions in each successional stage or experimental setting. Simultaneously, they provided a picture of the macroinvertebrate community living under each combination of those conditions (Ter Braak & Smilauer, 1998). No statistical tests of significance were performed on these analyses.

I chose to use a direct gradient analysis (and not an indirect one) because the overall hypothesis to be tested by this study was that well-defined environmental and resource gradients associated with aboveground secondary succession lead to a succession of macroinvertebrate community composition below-ground. This meant that I was not exploring what sort of environmental conditions would determine the community composition (indirect gradient analysis) but I had specific candidate environmental and resource gradients (shown to change through succession), to explain changes in community composition.

The choice of an ordination technique that assumes a unimodal response of taxa abundance to environmental gradients (CCA) due to the fact that λ (the unconstrained length of the taxa gradient) was most often between 1.5 and 3 standard deviations (Ter Braak & Smilauer, 1998). CCA was also preferred because Monte-Carlo randomisation tests have been developed with it that allow formal hypothesis testing, which was performed for the experiments presented in Chapter 5 and 6. All of the CCAs and biplots were performed in the Canoco for Windows v.4.0 (Ter Braak & Smilauer, 1998).

Mass loss in decomposition boxes

ANOVAs were used to determine the effect of experimental treatments on the loss of mass through time in decomposition boxes. Treatments for the across-succession decomposition experiment (Chapter 5) were successional stage (four levels), species of leaf (two levels) and time spent in the field (four levels) and for the between-tree species decomposition experiment (Chapter 6) treatments were tree species (three levels), species of leaf (four levels) and time spent in the field (four levels). For both experiments the natural logarithm of fraction of mass remaining was regressed against time (fractions of year) to determine the exponential decay constant k (Swift *et al.*, 1979). The use of this model was chosen as a means of summarising overall rates of decomposition and allow comparison with other studies. It does not imply that it is the best representation of mass loss at any of the sites.

Chemical evolution in decomposing litter

A principal component analysis (PCA) was first performed on the nutrient, lignin and cellulose concentrations in decomposition boxes to reduce redundant information due to correlation between variables. This analysis was performed in SPSS v.9.0 (SPSS Inc., Chicago, USA). The first three axes extracted from this analysis were characterised as indicators of different aspects of foliar quality and were named foliar quality components. The foliar quality components were then individually analysed with three way-ANOVA to determine the effect of experimental treatments on the evolution of litter quality through time in decomposition boxes. Treatments for the across-succession decomposition experiment (Chapter 5) were successional stage

(four levels), species of leaf (two levels) and time spent in the field (four levels) and for the between-tree species decomposition experiment (Chapter 6), tree species (three levels), species of leaf (four levels) and time spent in the field (four levels).

The treatment effects tested by ANOVAs on foliar quality components (PCA scores) only apply to the variance extracted by the PCA from the data. This does not mean that the remaining variance is not explainable by the experimental treatments, but means that it is not being tested because this variation could not be represented by the first three PCA axes. This remaining variance most likely corresponds to variation in individual nutrient concentrations that is independent from the general trends of variation in all the nutrients simultaneously. If more PCA axes were added to the analyses of variance, then more of this variation could be accounted for. However it would also represent the addition of more consecutive ANOVAs and the consequent increase in the probability of Type I errors. Therefore, by performing a PCA followed by ANOVAs on the PCA scores, the proportion of variation that can be assured to be explained by experimental treatments is sacrificed in order to keep the probability of Type I errors as low as possible. This could be regarded as a subjective process, but it is not, because it is done through an optimisation technique, e.g. PCA extracts the most conspicuous trends in the data, maximising the amount of variation that can be explained by a single variable. The problem with this technique is that it will never be possible to know how much of the variation left out of the analysis can actually be explained by the experimental treatments. Out of the available techniques, I considered this to be the most conservative approach.

Net immobilisation and mineralisation of nutrients were presented in terms of percentage of the absolute initial amount remaining in the sample at the time of collection. This was determined by dividing the mass of any element at any collection (concentration times remaining litter mass) by the initial content of that element in the litter. And finally multiplied by 100 to calculate the percentage of the element remaining at a given collection time. Immobilisation was considered to happen once the percentage of an element surpassed 100 percent of the initial sample content and mineralisation to occur when the percentage of an element diminished to

less than 80% of the initial sample (considering a 20% loss through leaching, (Swift *et al.*, 1979).

Changes in macroinvertebrate diversity and most common taxa in decomposition boxes

ANOVAs were used to determine the effect of experimental treatments on the macroinvertebrate diversity indices and abundance of most common taxa in decomposition boxes (chapters 5 and 6). Taxa were considered common when they reached minimum mean abundance of 0.5 per decomposition box over the course of the experiment. For the across-succession decomposition experiment (Chapter 5) treatments were successional stage (four levels), species of leaf (two levels) and time spent in the field (four levels) and for the between-tree species decomposition experiment (Chapter 6) treatments were tree species (three levels), tree individual (nested within tree species, 12 levels) species of leaf (four levels) and time spent in the field (four levels).

CHAPTER 3.

THE EFFECT OF LOGGING AND SECONDARY SUCCESSION ON THE BIOGEOCHEMICAL CYCLE AND SOIL MACROINVERTEBRATE COMMUNITY

Introduction

The tendency of Tropical Montane Cloud forests (TMCF) to display efficient nutrient cycling and low productivity has been reported in an number of studies undertaken in different parts of the world (Vitousek, 1984; Proctor *et al.*, 1989; Veneklaas, 1990; Tanner *et al.*, 1992; Crews *et al.*, 1995; Tanner *et al.*, 1998; Miller *et al.*, 2001; Nomura & Kikuzawa, 2003). These characteristics have been attributed to a range of factors such as low solar radiation, temperature and evapotranspiration (Bruijnzeel & Veneklaas, 1998). However, there is very little information concerning the role that the soil biota plays in the cycling of nutrients in these forests and little is known about how changes in environmental conditions and resource availability associated with logging disturbance and secondary succession, affect productivity, nutrient cycling (Olander *et al.*, 1998; McDonald & Healey, 2000; Saenz & Guariguata, 2001) and soil biodiversity of TMCF.

Biogeochemical cycling in Tropical Montane Cloud forests

Tropical Montane Cloud forests (TMCF) have an unusual physiognomy that is a result of multiple factors acting synergistically (Waide *et al.*, 1998). These forests are known to have low productivity, poor soils, slow nutrient cycling, and slow decomposition rates together with low pH (Vitousek, 1984; Tanner *et al.*, 1998; Bruijnzeel & Proctor, 1995). These characteristics have largely been attributed to the continuous cloud that covers the forest, which diminishes the photosynthetic capacity. In ecosystems growing in conditions of low nutrient availability, a positive feedback between plants and soil is thought to occur. Because there is low nutrient availability in the soil, plants adapted to live under these conditions produce foliage with low nutrient and high lignin and phenol concentrations. These plants use nutrients efficiently, grow slowly, lose their leaves less frequently and allocate a relatively high proportion of resources to below-ground biomass (Hobbie, 1992). In TMCF the availabilities of N and P and often K, Ca, and Mg in the soil are lower than in more fertile lowland forests. This is a result of reduced litter fall combined

with low concentrations of N and P in litter fall especially in forests above 1500 m (Vitousek, 1984).

In forests growing on poor soils, most nutrients are sequestered in plant and microbial biomass (Hobbie, 1992). The slow cycling of nutrients in litter that occurs in TMCF can be aggravated by nutrient immobilisation in the soil, which in turn is attributable to a build-up of soil organic matter resulting from incomplete decomposition (Tanner, 1980; Tanner, 1981). In these forests pH lower than 5 often occurs simultaneously with low nutrient availability because they are caused by the same factors: leaching of bases and/or high cation-exchange capacity owing to high organic matter concentration (Tanner *et al.*, 1998).

When nutrients in forests are lacking in availability, mycorrhizas play an important role in nutrient acquisition for plants and populations of microbial grazers tend to be relatively abundant (Hobbie, 1992). Little is known about the importance of soil biota in mediating nutrient availability in cloud forests (Waide *et al.*, 1998), but nutrient limitation may be associated with bottom-up control of food-web complexity (Scheu & Schaffer, 1998; Neilson *et al.*, 2002; Halaj & Wise, 2002) that could potentially play an important role in the cycling of the limiting resources.

Consequences of logging disturbance for the soil system in a TMCF

Land-use change profoundly affects the biogeochemical cycles in a forest ecosystem (Wardle, 1992). Mexican TMCF is increasingly being transformed into agricultural land, and is being degraded by grazing and logging for timber and firewood (Ramírez-Marcial *et al.*, 2001; Velázquez *et al.*, 2003). In Mexico logging for firewood extraction, is of particular importance and in many areas this type of disturbance has become continuous pressure particularly involving harvesting of *Quercus* spp. trees (Ramírez-Marcial *et al.*, 2001). As a consequence of any type of logging, the opening of the canopy may lessen the ability of the cloud forest to retain cloud cover. Consequently, environmental temperature increases and air humidity diminishes (Romero-Nájera, 2000; González-Espinosa *et al.*, 1991). Also, in the short term, logging produces an above-ground flush of nutrient-rich organic matter

from harvested plant residues (Olsson *et al.*, 1996b; Olsson *et al.*, 1996a; Finér *et al.*, 2003) and a below-ground litter input from dead rooting systems.

The input of residues in a forest together with the increase of radiation reaching the soil may bring a temporary increase in the rate of nutrient cycling and microbial biomass turnover (Butterfield, 1999; Siira-Pietikäinen *et al.*, 2001; Finér *et al.*, 2003). The rise in availability of organic matter may also decrease the proportion of fungal-based over bacterial-based food-webs (Wardle, 1992; Siira-Pietikäinen *et al.*, 2001). Below-ground food-web responses to logging, given associated environmental and resource-availability changes, are poorly understood (Bengtsson *et al.*, 1997; Wardle *et al.*, 1998), particularly in nutrient-poor ecosystems such as TMCF.

Consequences of above-ground secondary succession for the soil system in TMCF

Above-ground it is possible to identify different plant species associated with different successional stages of TMCF in Mexico strongly related to specific differences in regeneration requirements (Blanco-Macias, 2001; Quintana-Ascencio & González-Espinosa, 1993; Galindo-Jaimes *et al.*, 2002). The succession of the multilayered community in montane forests in Mexico starts with the dominance of early successional species that tend to have Holarctic biogeographic origins (from now on referred to as Holarctic species), particularly *Pinus* spp. in early stages. Under the incomplete canopy of pine-dominated stands, *Quercus* spp. are able to regenerate and are commonly found to dominate mid-successional canopies. Under canopies dominated by *Quercus* spp. tree species of a tropical origin (from now on referred to as tropical species) are often successful in forming an understory (González-Espinosa *et al.*, 1991; Quintana-Ascencio & González-Espinosa, 1993; Ramírez-Marcial *et al.*, 2001). Even if the environmental and vegetation shifts associated with succession above-ground in TMCF have been studied in detail, less is known about the consequences that these dynamics have for processes below-ground. Productivity-limiting factors in TMCF may change during succession (Waide *et al.*, 1998). Soon after logging a temporal input of nutrient rich resources

enter the soil system and light-demanding and herbaceous species flourish (Walker *et al.*, 1996). In Mexican forests Holarctic species are often pioneers in TMCFs and are known to be more productive than tree species of a tropical phytogeographic origin (Williams-Linera & Toledo, 1996), therefore they can be expected to produce more abundant and more nutrient-rich litter that will increase the rate of decomposition process and enhance nutrient availability. Furthermore, after disturbance and in early succession, the diversity of tree species diminishes relative to older forests (Ramírez-Marcial *et al.*, 2001), and therefore the diversity of resources available. This together with the high quality and abundance of resources might lead to a more uniform soil community.

Given the extent of human disturbance to Mexican TMCF and the scarcity of knowledge about its impact on the biogeochemical cycling and biodiversity, I here support the suggestion made by Noss (1990) that it is important to assess the recovery potential of native forests with a holistic approach for assessment of stand conditions. This study presents an integrative study of the biogeochemical cycling and soil fauna in three chronosequences, two recently logged sites and two pristine TMCF sites in Oaxaca, Mexico. The objectives of the study were:

- To determine whether changes happening above-ground as a result of logging impact and subsequent secondary succession are coupled with changes in microenvironmental conditions, resource quality and availability and soil chemistry.
- To determine if the macroinvertebrate community composition and diversity reflect those changes and therefore can serve as good indicators of disturbance and degree of recovery of the system.
- To determine whether different aspects of the biogeochemical cycling and the soil macroinvertebrate community recover within 100 years of secondary succession, compared to pristine forests.

Methods

This chapter analyses surveys carried out in all of the field sites: Tarantulas, Tarbis and Laguna chronosequences, two recently logged sites (Tar0 and Tar 00) and two pristine sites (Pris and PrisII). Because the Tarantulas chronosequence was studied most intensively, I present a section entitled '*General survey*' that describes the activities that were performed (although at different intensities) in all sites and a section entitled '*Further studies in Tarantulas*' that describes those activities that were exclusive to the Tarantulas chronosequence.

General survey

First an intensive survey was carried out in the Tarantulas chronosequence between July 11 and August 17, 2000. In this period all 49 intersections of each of the four grids (15-, 45-, 75- and 100-year-old forests) were sampled. The following year, between June 25 and December 3, 2001, all of the successional stages of Laguna and Tarbis, recently logged sites (Tar0 and Tar00) and the Pristine sites (Pris and Pris II; [figure 2.1](#)) were sampled. On this occasion, only seven random vertices in each grid were selected for sampling. Both of these field seasons were included in the rainiest half of the year when macroinvertebrate populations reach their maximum size.

In all of the field sites except Tarantulas, sampling at each grid intersection consisted of the simultaneous extraction of a monolith and the measurement of microenvironmental conditions. All seven samples per successional stage were extracted within one hour and the sampling of each chronosequence within three days. Owing to unexpected technical difficulties soil temperature was not measured in the Laguna chronosequence.

In the Tarantulas chronosequence, microenvironmental measurements were carried out separately from the monolith extraction. Microenvironmental conditions were measured in each successional stage (in all 49 vertices of the grid) in four different sampling dates (July 11 and 18 and August 14 and 17, 2000). The point measurements for each sampling session were carried out within the same day. For

each sampling vertex all four repetitions of environmental measures were averaged. Monoliths in Tarantulas were extracted in all successional stages between July 7 and August 15, 2000.

Details of microenvironmental measurements, monolith extraction, litter and soil processing and macroinvertebrate sorting and identification can be found in Chapter 2.

Further studies in Tarantulas

Tree genera basal area

Within the boundaries of the Tarantulas sampling grids, as well as in a 5 m width frame around them, I recorded the genus and dbh of all the live trees (with a dbh > 5 cm). Assuming a cylindrical shape, the basal area per genus, per successional stage, was calculated.

Litter fall

On July 15 2000, ten litter traps were distributed evenly in each sampling grid of the Tarantulas chronosequence. The traps consisted of a wire ring (1 m in diameter) with a nylon mesh bag hanging from it. The ring and mesh were fixed at 1 m height on the top of four poles inserted in the soil. Litter that accumulated in the traps was collected on seven occasions between July 2000 and January 2002 (July 21, August 5 and August 17 in 2000, May 10, July 23 and December 12 in 2001 and January 24 in 2002). Every time a trap was stolen, which occurred repeatedly, it was replaced at the following sampling date. To calculate an estimate of the daily litter fall in each collection period, the total amount of litter found in each trap was divided by the number of days it was left open. Because littertraps are conspicuous and their material valuable for local population, their persistence on site was very variable and it was not possible to avoid pooling data over long periods of time.

Litter components

The litter of all the monoliths extracted from the Tarantulas chronosequence were sorted into six components: *Pinus* needles, *Quercus* leaves, Lauraceae leaves, woody and reproductive material, leaves from other genera and unrecognisable leaf material. The dry mass of these components was recorded separately.

Common leaf species chemistry

The litter caught in litter traps remained between 1 and 27 weeks in the field, and therefore it was susceptible to various degrees of leaching and decomposition. For this reason, I decided to concentrate the study of litter chemistry to the leaves of four species representative of different successional stages that were carefully collected from the forest floor. Recently fallen leaves of *Pinus chiapensis*, *Oreopanax xalapensis*, *Beilschmedia ovalis* and *Quercus* spp. were collected from the forest floor, dried to constant weight and analysed for nutrient, fibre content (acid soluble fraction (ASF) and residual fraction (RF)) as described in Chapter 2.

Chemical analyses of soil samples

All soil samples from the Tarantulas chronosequence were analysed for: (1) total C using the loss on ignition method to determine total organic matter and dividing by a 1.742 factor to calculate total carbon concentration (Jackson, 1958), (2) total P concentration using sulphuric acid digestion followed by calorimetric determination (Anderson & Ingram, 1993) (3) exchangeable cations (Ca^{++} Mg^{++} , K^+ and Na^+) with the ammonium acetate extraction method at pH 7 (Anderson & Ingram, 1993). Additionally 10 randomly chosen samples from each successional stage were analysed for total N with acid digestion followed by distillation and titration (Anderson & Ingram, 1993).

Statistical Analysis

Analyses of variance within grids and between sites

For microenvironmental conditions, soil bulk density, litter mass and taxa diversity indices, ANOVAs were used to determine significant differences between replicate sites and between forest ages. The configuration of some of the study areas in chronosequences and others in separate recently logged and pristine sites did not permit a single analysis of variance that would test the effect of site and forest age simultaneously for all studied areas. For this reason, I have fragmented the analyses into the following steps. First a one-way ANOVA was performed to determine whether there were differences among the pristine and recently logged sites (Pris, Pris II, Tar 0 and Tar 00). These analyses test whether differences between individual plots exist. They do not test for differences between forest ages because only two real replicates of recently logged sites and two replicates of pristine sites are available. The three chronosequences (Tarantulas, Tarbis and Laguna) were analysed with a 2-way ANOVA to determine the effect of Chronosequence (3 levels) and Forest age (4 levels). The interaction between chronosequence and forest age was not tested since no true replication of successional stage within each chronosequence was available. Measurements within a single grid are in this context only pseudoreplicates (Hurlbert, 1984). Lastly I analysed the overall effect of forest age with an ANCOVA (with sampling date as a covariate) using the mean value per grid as a replicate. In this manner I tested the effect of forest age simultaneously in the successional stages of the chronosequences, recently logged and pristine sites and removed the variance caused by differences in the sampling date. However, these analyses should be interpreted with caution as they ignore the fact that several successional stages and sites are grouped in different areas producing a site effect that is being ignored. Soil temperature was not available for the Laguna chronosequence and therefore when analysing this variable only data for Tarantulas and Tarbis were included.

Differences in litter fall per day between successional stages and collection periods in the Tarantulas chronosequence were analysed with a repeated measures ANOVA with collection date as the repetition factor. The collection period between December

7, 2001 and January 24, 2002 was analysed separately with a one-way ANOVA because in this period only one trap was left undisturbed in the 45-year-old forest and therefore this successional stage could not be considered in the analysis (forest age was a three level factor in this analysis).

Differences between successional stages (of the Tarantulas chronosequence) in the mass per sample of litter components (six variables: *Pinus* needles, *Quercus* leaves, Lauraceae leaves, woody and reproductive material, leaves from other genera and unrecognisable leaf material) and the chemical composition of soils (seven variables: concentration of total C, total N, total P, Ca⁺⁺, Mg⁺⁺, K⁺ and Na⁺) were tested with one-way multivariate analyses of variance (MANOVA) with age as a four level factor (15, 45, 75 and 100 years of age). The 49 samples extracted from the intersections of each of the Tarantulas grids were considered as replicates. Both Wilk's λ and Rao's R are reported in Appendix CH3. When the MANOVA turned out to be significant, the corresponding one-way ANOVAs for each individual variable were then performed and Bonferroni significance level was presented along with the P-values. In the text of this chapter Wilk's λ and P-values are reported when appropriate. The differences in the nutrient and fibre content (nine variables: concentration of total C, total N, total P, Ca⁺⁺, Mg⁺⁺, K⁺, Na⁺, ASF and RF) between the litter of different tree species (four levels: *Beilschmedia ovalis*, *Pinus chiapensis*, *Quercus* sp. and *Oreopanax xalapensis*) were also tested with a one-way MANOVA. For this analysis three replicates per leaf species were analysed (except for *Pinus chiapensis* for which four replicates were used). Each replicate consisted of a 30 g sample of dry leaves randomly drawn from the pool of leaves. Both Wilk's λ and Rao's R are reported in Appendix CH3. If the MANOVA turned out to be significant the same procedure described above for other MANOVAs was followed.

Relationship between macroinvertebrate community composition and environmental and resource variables in different successional stages

CCAs and Variance Partitioning were performed in two steps:

- (1) Ordinations of the litter and soil communities in Tarantulas with respect to successional stage (four dummy variables) and all the microenvironmental, litter component and soil chemistry variables available for this chronosequence. In these analyses all 49 vertices of each grid were included.
- (2) Ordinations of the litter and soil communities of Tarantulas, Tarbis, Laguna, Pris, Pris II, Tar0 and Tar00 with respect to successional stage (six dummy variables) and microenvironmental conditions. In this ordinations seven randomly selected vertices were included for each grid, achieved by random sub-sampling of the 49 vertices available for the Tarantulas grids. Because soil temperature was not available for Laguna sites, two runs of each of these analyses were performed, one including soil temperature and excluding Laguna chronosequence and a second one including Laguna and excluding soil temperature.

Details of the CCA and Variance Partitioning procedures can be found in Chapter 2. In this chapter, Monte-Carlo randomisations were not used for formal hypothesis testing because individual observations within a grid are pseudoreplicates (Hurlbert, 1984) with respect to successional stage. This implies that no real replication is available for the ordinations performed exclusively for Tarantulas and that for the ordinations including the other chronosequences, the recently logged sites and the pristine sites, there are only two or three replicates per successional stage.

Results

Soil microenvironmental conditions through secondary succession

Canopy cover

There were significant differences in canopy density between Tar0, Tar00, Pris and PrisII ($F=13.80$, $d.f.=3$, $P<0.0001$)¹; recently logged sites had lower mean canopy density than the pristine sites (figure 3.1a). When comparing the 3 chronosequences,

¹ ANOVA tables including the error degrees of freedom for all F ratios, are given in Appendix CH3.

there was no effect of age ($F=0.506$, $d.f.=3$, $P>0.05$) or chronosequence ($F=0.028$, $d.f.=2$, $P>0.05$) on canopy cover (figure 3.1a). When the mean canopy cover per site was compared in an ANCOVA considering sampling date as covariate, there was a significant difference between successional stages ($F=32.25$, $d.f.=5$, $P<0.0001$). Recently logged sites have a noticeably lower mean canopy cover than the other sites (figure 3.1a).

Soil Temperature

Soil temperature was significantly different when Tar0, Tar00, Pris and PrisII sites were compared ($F=45.91$, $d.f.=3$, $P<0.0001$; figure 3.1b). The recently logged sites had a higher mean soil temperature (15.4°C and 16.4°C) than the pristine sites (12.2°C and 11.5°C). In both Tarantulas and Tarbis chronosequences, temperature initially dropped with increasing forest age followed by a slight increase between the 75 and 100 years successional stages ($F=23.96$, $d.f.=3$, $P=0.013$ figure 3.1b). Although Tarantulas and Tarbis followed the same general trend, Tarbis displayed a constantly higher soil temperature by about 1°C ($F=181.10$, $d.f.=1$, $P=0.009$; figure 3.1b).

When the mean soil temperature per site was compared pooling all sites with an ANCOVA, considering sampling date as a covariate, there was a significant difference in soil temperature between successional stages ($F=19.31$, $d.f.=5$, $P=0.003$). Pristine forests had lower mean soil temperature than the other sites (figure 3.1b).

Volumetric soil water content

Both recently logged and pristine sites had low to intermediate mean values for volumetric soil water content (between 0.12 to $0.21 \text{ cm}^3\cdot\text{cm}^{-3}$). When sites were compared statistically there were significant differences ($F=6.71$, $d.f.=3$, $P<0.002$) The site named Pris had the highest mean volumetric soil water content ($0.21 \text{ cm}^3\cdot\text{cm}^{-3}$) and the smallest variance (figure 3.1c) recorded.

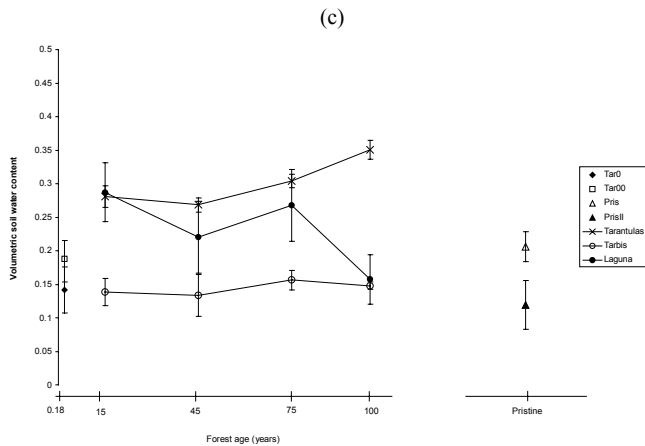
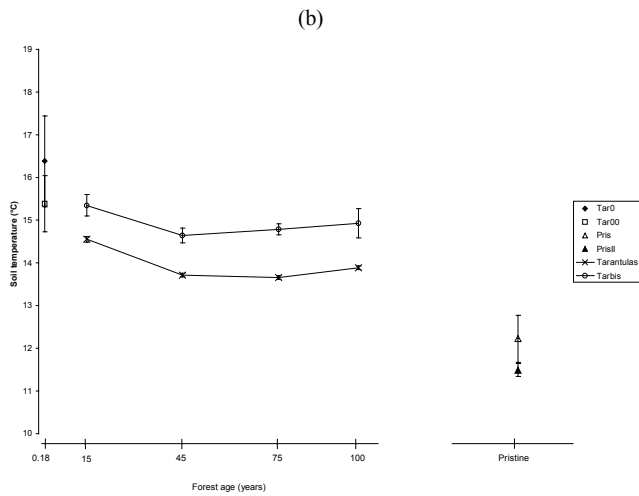
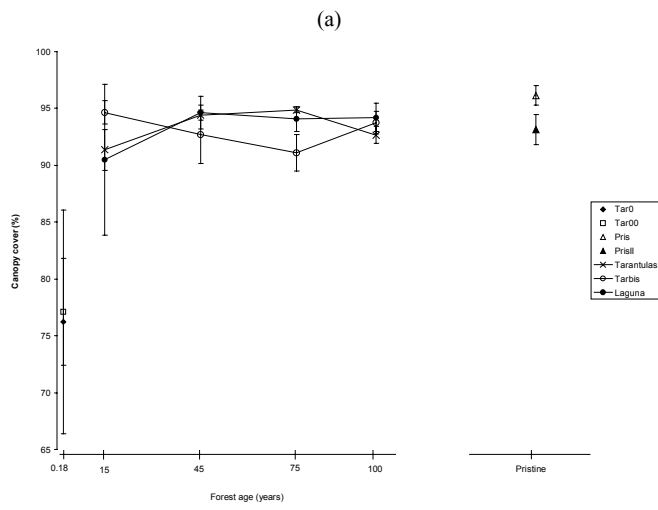


Figure 3.1. Changes in environmental conditions across three chronosequences, two recently logged sites and two pristine forests. (a) Canopy cover, (b) soil temperature (Laguna not available) and (c) volumetric soil water content. Values presented are mean \pm 95% confidence limits are represented. Sample size (n) is 7 except for Tarantulas where n=49.

For the three chronosequences studied, high variability in volumetric soil water content was recorded (figure 3.1c). Mean values ranged from 0.13 cm³·cm⁻³ to 0.35 cm³·cm⁻³. An ANOVA showed a significant effect of chronosequence (F=13.83, d.f.=2, P=0.006) but not of forest age. In general, Tarantulas displayed the highest values, followed by Laguna and then Tarbis (figure 3.1c). When the mean volumetric soil water contents per site were compared for all sites with an ANCOVA (considering date as a covariate), there was no significant difference between successional stages (figure 3.1c).

Litter resource quality and availability through secondary succession

Tree genera

The number of tree genera (DBH>5cm) present in each of the sampling grids of the Tarantulas chronosequence was between 20 and 23 (table 3.1). The total basal area irrespective of the genus differed between successional stages. The lowest total basal area was found in the 100-year-old forest (0.42%) and the 15-year-old forest (0.44%). The highest value of basal area was recorded in the 45-year-old forest (0.84%).

Successional stage	Total basal area (%)	Total number of tree genera	Equitability J	Shannon H'
15	0.44	20	0.73122	2.1905
45	0.84	22	0.71510	2.2106
75	0.60	20	0.80249	2.4040
100	0.42	23	0.7462	2.3398

Table 3.1. Dominance of tree genera in different successional stages of the Tarantulas chronosequence. Total basal area, number of genera and genera diversity indices are presented for trees (DBH>5 cm) in the survey plots (40 m x 40 m) of the Tarantulas chronosequence. The diversity indices are based on the basal area covered by each genus.

Figure 3.2 shows the total basal area covered by each tree genus in the survey plots of the Tarantulas chronosequence. The tree genus that dominated the basal area was different in each successional stage. In the early successional plot, there was a single genus that covered circa 40% of the total basal area. In the 15-year-old forest the dominant genus was *Clethra* (38.4%); while in the 45-year-old forest *Quercus* dominated (40.46%). In later successional stages, the basal area was shared between

more genera. In the 75-year-old forest the three most dominant genera were *Quercus* (26.04%), *Vaccinium* (11.56%) and *Temstroemia* (11.04%) while in the 100-year-old forest the three genera that accounted for most basal area were *Quetzalia* (19.05%), *Persea* (17.5%) and *Oreopanax* (15.09%). These differences in dominance between species are reflected in the Equitability (J) and Shannon (H') indices of diversity (table 3.1). The highest equitability and diversity according to these indices was found in the 75-year-old forest and the lowest in the 15-year-old.

Litter fall

A repeated measures ANOVA showed that there was a significant difference in daily litter fall between sampling periods ($F=49.90$, $d.f.=5$, $P<0.0001$) and this interacted with successional stage ($F=4.31$, $d.f.=15$, $P<0.0001$; figure 3.3). The first and second sampling periods had respectively the highest and lowest mean litter fall per day (1.83 and 0.56 g day^{-1} trap^{-1}). Paired comparison with Tukey's HSD showed that the interaction between the effects of age and sampling period were mainly driven by a significantly higher daily litter fall in the 45-year-old forest during the week comprised in the first sampling period (mean 2.4 g day^{-1} trap^{-1}). The other sampling periods showed no differences between successional stages.

Standing litter

There were no significant differences between Tar0, Tar00, Pris and PrisII sites in terms of the amount of standing litter per monolith (figure 3.4). All four sites had a low mean mass of litter per sample (between 50 g and 80 g). When the three chronosequences were compared there was no significant effect of the forest age or chronosequence. When the mean volume of standing litter per site was compared for all sites with an ANCOVA considering sampling date as a covariate, there were no significant differences between successional stages (figure 3.4)

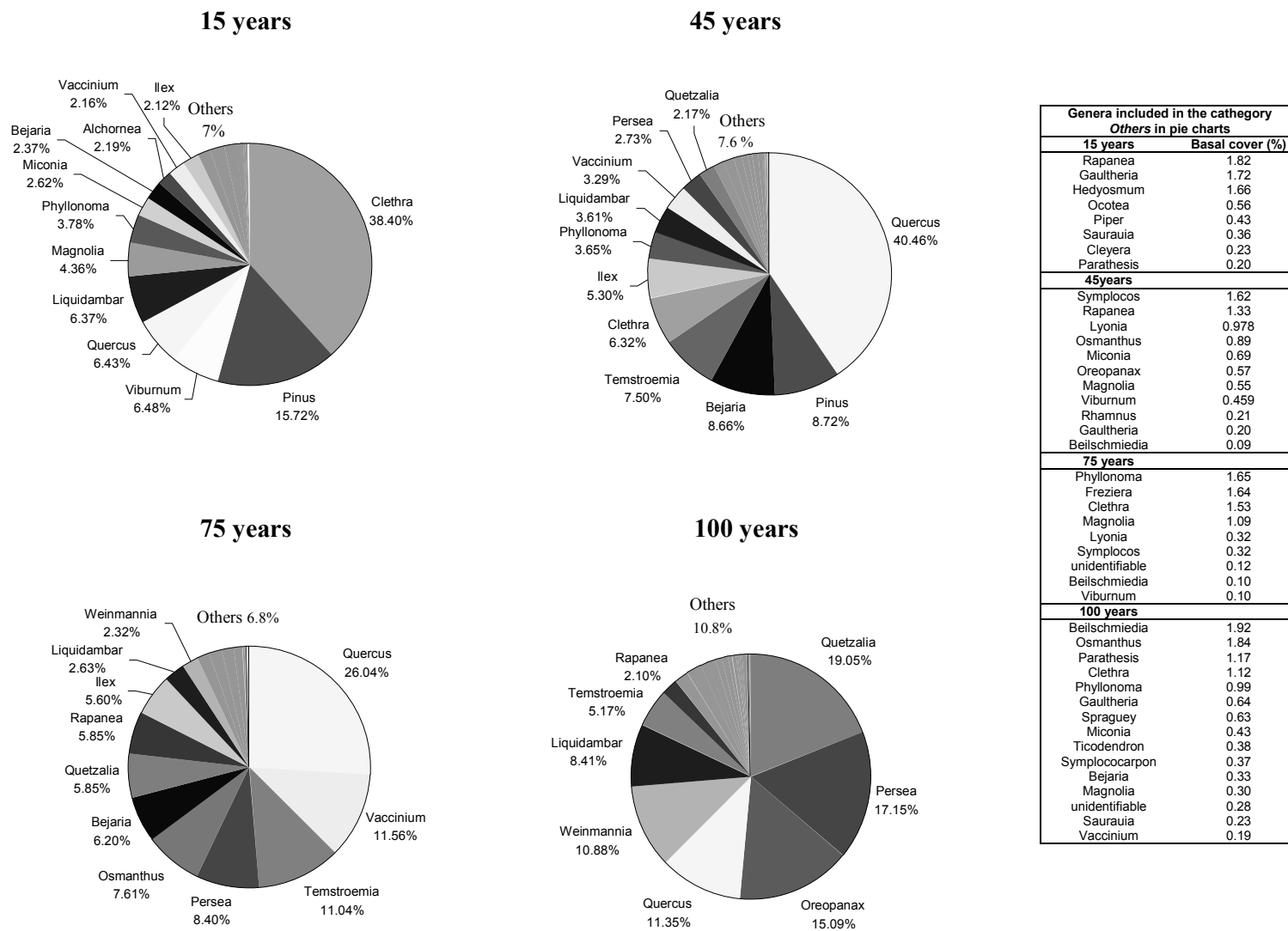
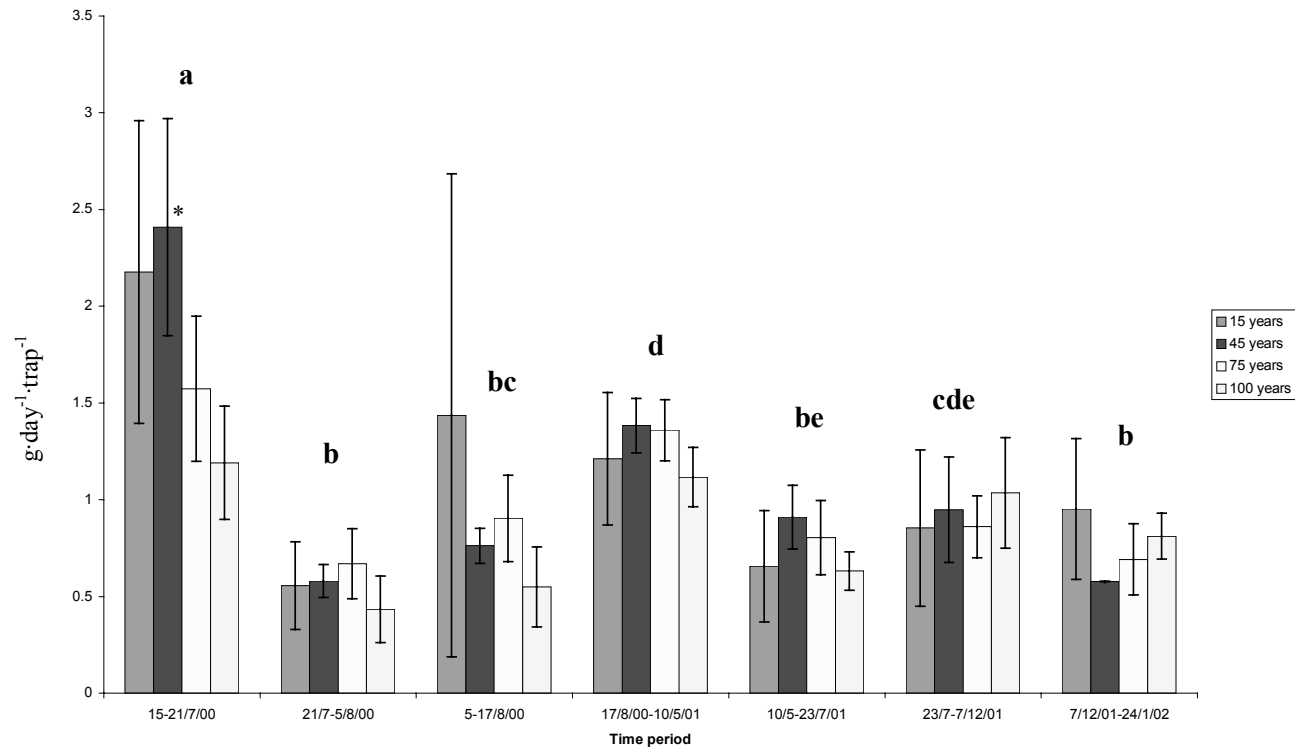


Figure 3.2. Total basal area covered by each tree genus in the successional stages of the Tarantulas chronosequence. Includes trees with a diameter at breast height of >5 cm. The percentage is calculated over the total area of each survey plot plus its 5 m border (40 x 40 m).



	January	February	March	April	May	June	July	August	Sept.	October	Nov.	Dec.
2000												
2001												
2002												

Figure 3.3. Litter fall per day in different successional stages of the Tarantulas chronosequence. The total amount of litter found in each trap was divided by the number of days it was left open. (weeks represented by each sample period are shown in the calendar). Mean \pm 95% confidence limits represented. Asterisk denotes significant differences ($p < 0.05$) between successional stages within one sampling period in paired comparisons with Tukey's HSD test. For the 7/12/01-24/1/02 time period, the 45-year-old forest was not considered in the comparison because only one litter trap was left undisturbed. Different letters denote differences between sampling periods when successional stages were pooled together. Sampling periods represented in bottom calendar.

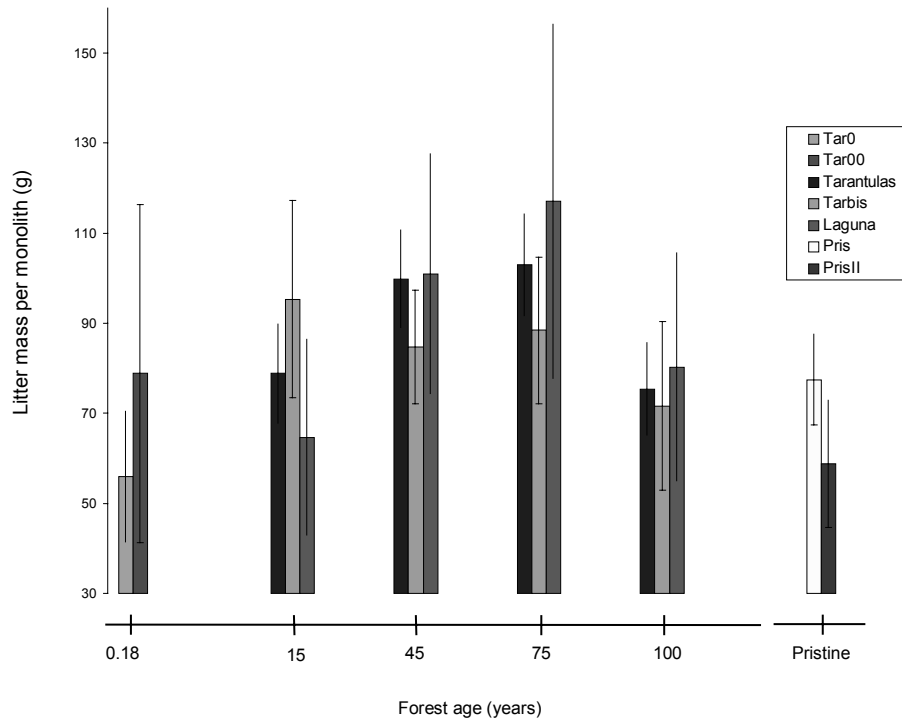


Figure 3.4. Changes in mass of standing litter across three chronosequences, two recently logged sites and two pristine forests. Mean \pm 95% confidence limits are represented. Sample size (n) is 7 except for Tarantulas where n = 49.

Components of standing litter

In the Tarantulas chronosequence, woody and reproductive plant parts together with unidentifiable leaf materials were the main components of the standing litter for all of the successional stages, accounting for 59 to 73% of the total litter mass in each forest (figure3.5a). Leaves that were recognisable composed the rest of the litter; they formed a greater proportion in the 45-year-old forest (41%) and the lowest proportion in the 100-year-old forest (27%). The three taxa identified (*Quercus* spp., Lauracea and *Pinus* spp.) made up between 55 and 90% of the recognisable leaves and between 18 and 23% of the total litter mass in each successional stage. Of the identifiable leaf material, pine needles formed the highest proportion (22.2%) in the 15-year-old forest and oak leaves in the other three successional stages (16.4-20.7%). Pine needles were the second-most abundant component in the 45-year-old forest (13.8%). Pine needles were absent from the 100-year-old forest and other genera were the second most abundant component in this successional stage (12.4%).

Lauracea leaves were absent from the 15-year-old forest and their presence was negligible in the 45 and 75 years successional stages (0.1 and 0.2% respectively).

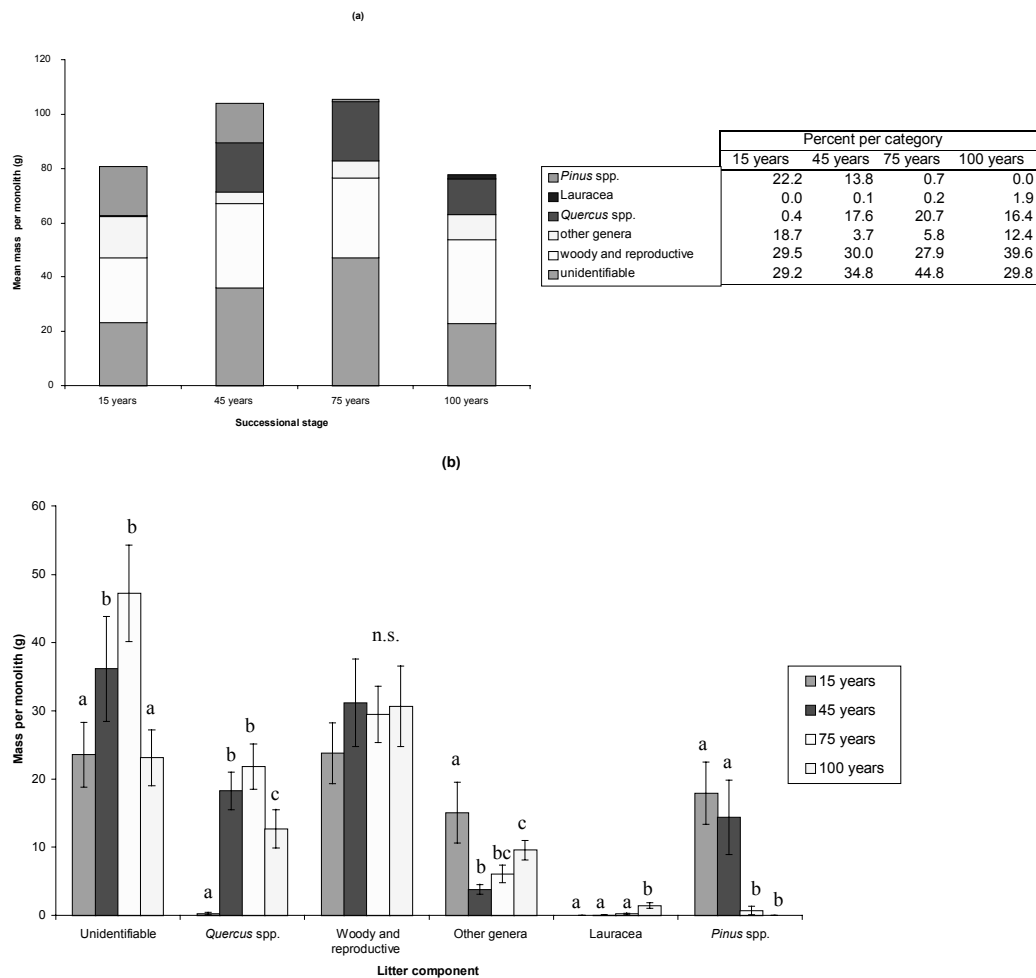


Figure 3.5. Components of standing litter in different successional stages of the Tarantulas chronosequence. (a) Mean percent of total mass accounted for by each litter category in each successional stage. (b) Mass of each litter category in different successional stages. Mean \pm confidence limits presented. Different letters indicate significant differences ($p < 0.05$) in paired comparisons (Tukey's HSD) within each litter category.

A Multivariate Analysis of Variance of the sorted standing litter showed that there was a significant difference between successional stages in the mass per litter component ($\lambda = 0.205$, $P = 0.001$, Appendix Table CH3.6). Figure 3.5b shows that the 45- and 75-year-old successional stages had significantly more total unidentifiable material and *Quercus* spp. leaves than the 15- or 100-year-old forest. There was no significant difference between successional stages in the amount of woody and reproductive material. Other genera of leaves that were not identified were most abundant in the 15-year-old forest. In the 45-year-old forest plot these genera were

the least abundant and increased with successional stage thereafter. The Lauracea leaves were the least abundant of the litter components, but reached their maximum relative abundance in the 100-year-old forest. The contribution of pine needles to the standing litter diminished with forest age, being relatively high in the 15- and 45-year-old successional stages and low and absent in the 75- and 100-year-old forest plots respectively.

Quality of main leaf litter genera

Some of the main leaf components of the litter in Tarantulas chronosequence (*Pinus*, *Quercus*, *Beilschmedia* and *Oreopanax*) differed in their nutrient and fibre RF compositions ($\lambda=0.0001$, $P<0.01$, Appendix CH3, Table CH3.7). The percentage of total carbon varied significantly among leaf genera (figure 3.6a). Values recorded were highest in *Pinus* and *Quercus* leaves (mean 57%), intermediate in *Beilschmedia* (mean 56%) and lowest in *Oreopanax* (mean 55%). Nitrogen concentration did not differ significantly between leaf genera (figure 3.6b), but mean phosphorus concentration was highest in *Pinus* leaves ($2.43 \text{ cmol}\cdot\text{kg}^{-1}$), intermediate in *Beilschmedia* ($1.50 \text{ cmol}\cdot\text{kg}^{-1}$) and *Oreopanax* ($1.83 \text{ cmol}\cdot\text{kg}^{-1}$) and lowest in *Quercus* ($0.95 \text{ cmol}\cdot\text{kg}^{-1}$; figure 3.6c).

The concentration of sodium was not significantly different between foliar species (figure 3.6d) and potassium occurred in higher concentration in *Oreopanax* leaves (mean $11.97 \text{ cmol}\cdot\text{kg}^{-1}$) than in the other genera (mean $1.28\text{-}4.80 \text{ cmol}\cdot\text{kg}^{-1}$; figure 3.6e). Overall there was no significant difference between leaf genera in the mean amount of calcium (figure 3.6f). The mean concentration of magnesium was lowest in *Pinus* needles ($5.24 \text{ cmol}\cdot\text{kg}^{-1}$), intermediate in *Quercus* and *Beilschmedia* (14.18 and $20.40 \text{ cmol}\cdot\text{kg}^{-1}$) and highest in *Oreopanax* ($35.05 \text{ cmol}\cdot\text{kg}^{-1}$; figure 3.6g).

In terms of fibre concentration, the percentage of ASF in the leaves was not significantly different between genera (figure 3.6h) but the RF concentration was lowest in *Oreopanax* (mean 49%) intermediate in *Pinus* and *Quercus* (mean 56 and 59%) and highest in *Beilschmedia* (mean 68%). The foliar carbon/nitrogen ratio was not significantly different between genera (figure 3.6i).

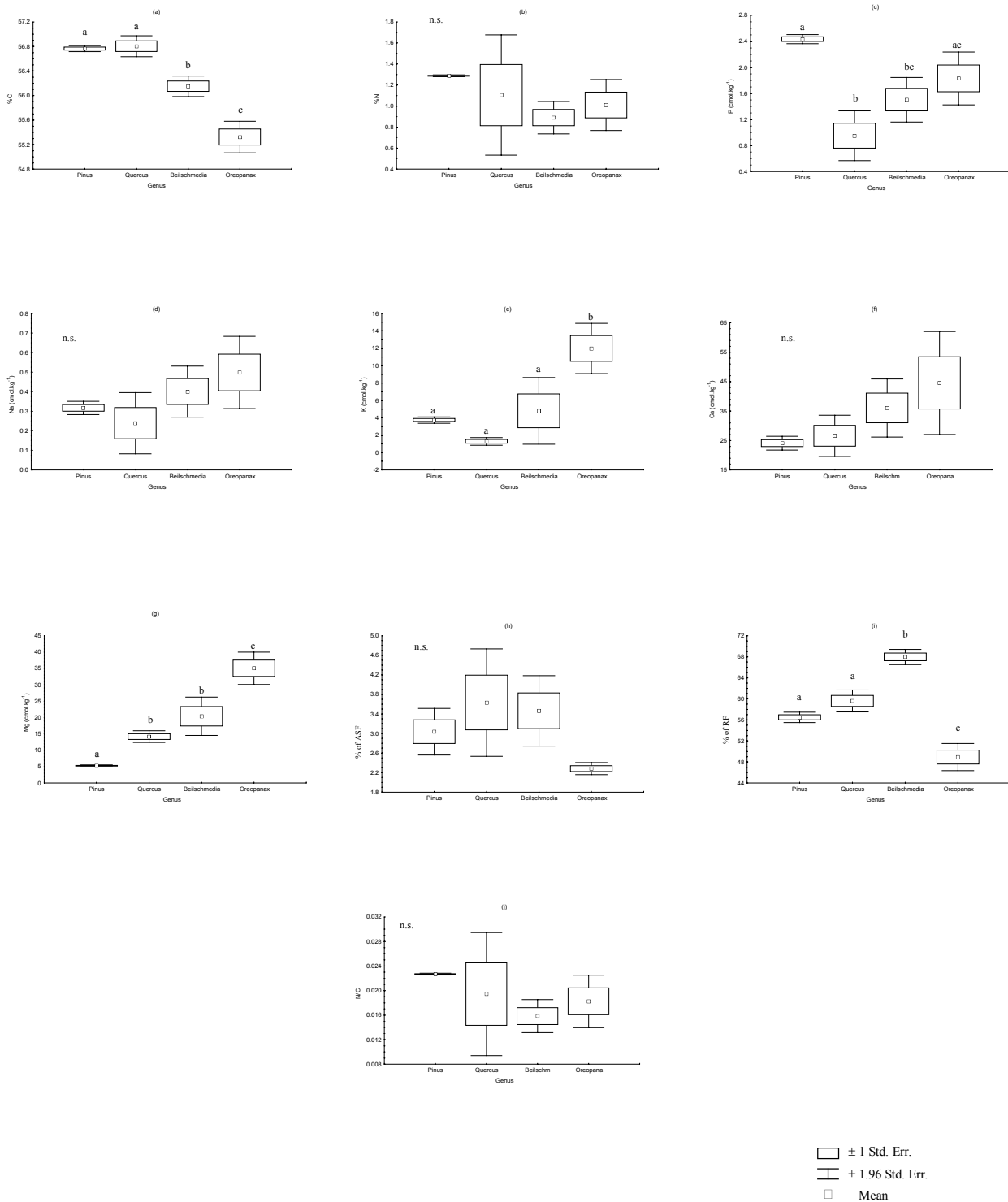
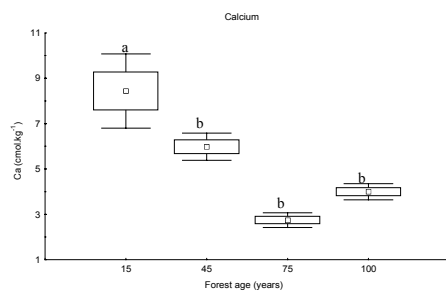
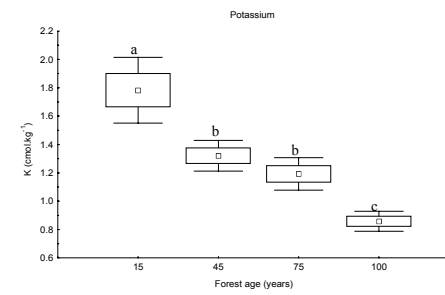
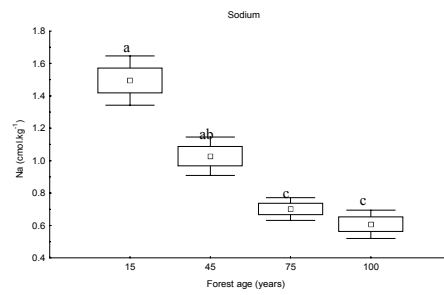
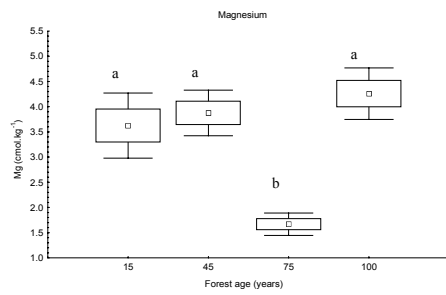
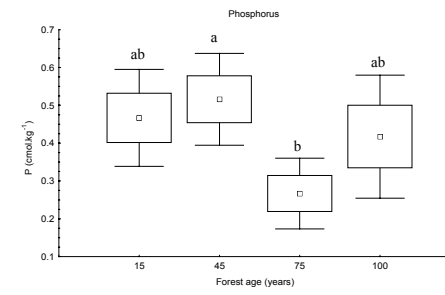
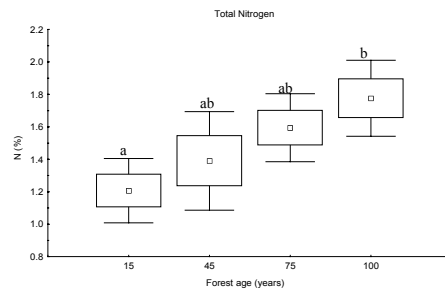
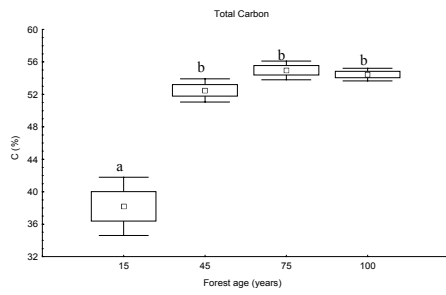


Figure 3.6. Nutrient, fibre ASF and RF concentration in the senescent leaves of four tree genera. Sample size (n) is three except for *Pinus* where n = 4. (a) percent of total carbon, (b) percent of nitrogen, (c) cmol.kg^{-1} of phosphorus, (d) cmol.kg^{-1} of sodium, (e) cmol.kg^{-1} of potassium, (f) cmol.kg^{-1} of calcium, (g) cmol.kg^{-1} of magnesium, (h) percent of ASF, (i) percent of RF, (j) N/C ratio. Different letters indicate significant differences ($p < 0.05$) in paired comparisons with Tukey's HSD test. n.s. indicates no significant difference in any paired comparison. It should be noted that the scale of the y-axis in some graphs has been truncated to improve presentation.



□ ± 1 Std. Err.
 ▭ ± 1.96 Std. Err.
 □ Mean

Figure 3.7. Nutrient concentration in the soils of the successional stages of the Tarantulas chronosequence. The first 5 cm of soil under the litter layer are considered. The sample size is 49 for each successional stage except for nitrogen where a subsample of 10 was analysed. Different letters denote significant differences ($p < 0.05$) in paired comparisons with Tukey's HSD test. It should be noted that the scale of the y-axis in some graphs has been truncated to improve presentation.

Nutrient concentration in the soil

The concentration of nutrients in the soil significantly differed between successional stages of the Tarantulas chronosequence ($\lambda=0.140$, $P<0.0001$; [figure 3.7](#), Appendix CH3, Table CH3.8). The total concentration of carbon was very low in the earliest successional stage (35.4%) and significantly higher in the 45-, 75- and 100-year-old successional stage (48.7-51.8 %).

Total soil nitrogen concentration increased along the successional chronosequence, from a mean of 1.2% in the 15-year-old forest to a mean of 1.8% in the 100-year-old forest ([figure 3.7](#)). In this sequence, only the extreme values (15 years and 100 years) differed significantly from each other, the intermediate stages did not differ from either extreme ([figure 3.7](#)). In the case of phosphorus the 45- and 75-year-old forest had the highest and lowest values (0.51 and 0.26 $\text{cmol}\cdot\text{kg}^{-1}$), which were significantly different from each other. The values for magnesium were similar (means between 3.55 and 4.30 $\text{cmol}\cdot\text{kg}^{-1}$) for all forests except for the 75-year-old which had a significantly lower concentration (*c.* 1.7 $\text{cmol}\cdot\text{kg}^{-1}$).

The concentrations of sodium, potassium and calcium decreased steadily along the successional sequence ([Figure 3.7](#)). For both sodium and calcium the concentration in the 75- and 100-year-old plots were the lowest, while in the case of potassium the value for the 75- and 45-year-old forest plots were intermediate and significantly higher than the 100-year-old successional stage.

Macroinvertebrate communities through succession

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

For the litter macroinvertebrate community the number of taxa, equitability and Shannon's H' were significantly different when Tar0, Tar00, Pris and PrisII sites were compared (number of taxa: $F=4.30$, $d.f.=3$, $P<0.05$, equitability: $F=4.94$, $d.f.=3$, $P<0.01$ and Shannon's H' : $F=4.95$, $d.f.=3$, $P<0.01$). All three variables were higher in Pris and PrisII sites than in the Tar0 and Tar00 sites ([figure 3.8a-c](#)). However, for

the soil community, there was no significant difference between pristine and recently logged sites for any of these variables; the values were relatively high for pristine as well as recently logged forests (figure 3.8d-f).

For the litter macroinvertebrate community, there was no significant difference between chronosequences in terms of the number of taxa, however there was a significant effect of forest age ($F=5.19$, $d.f.=2$, $P=0.049$) (figure 3.8a). The litter community in the 15-year-old forests had often a lower mean number of taxa than other successional stages. The equitability and Shannon's H' of the litter community were not significantly different between chronosequences or successional stages (figure 3.8b-c).

In the case of soil macroinvertebrate taxa, a two-way analysis of variance showed that for all three chronosequences the number of macroinvertebrate taxa increased along the successional sequence ($F=7.64$, $d.f.=3$, $P=0.018$), the number of taxa in 15- and 45-year-old forests being lower than in the 75- and 100-year-olds (figure 3.8d). However, the number of taxa in Tarbis was always higher than in the other two chronosequences ($F=15.08$, $d.f.=2$, $P=0.004$). The equitability and Shannon's H' of soil macroinvertebrate taxa were not significantly different between chronosequences or successional stages (figure 3.8e-f).

There was no significant difference between successional stages when the mean number of litter macroinvertebrate taxa and mean equitability and Shannon's H' indices per site were compared for all sites with an ANCOVA (considering sampling date as a covariate). When the same test was performed for the number of taxa in the soil macroinvertebrate community, there was a significant difference between successional stages ($F=3.47$, $d.f.=5$, $P=0.05$; figure 3.8e-f). Recently logged and pristine sites had a higher number of taxa than the 15-year-old forests. However there was no significant difference among successional stages in the mean equitability or Shannon's H' of soil macroinvertebrate taxa.

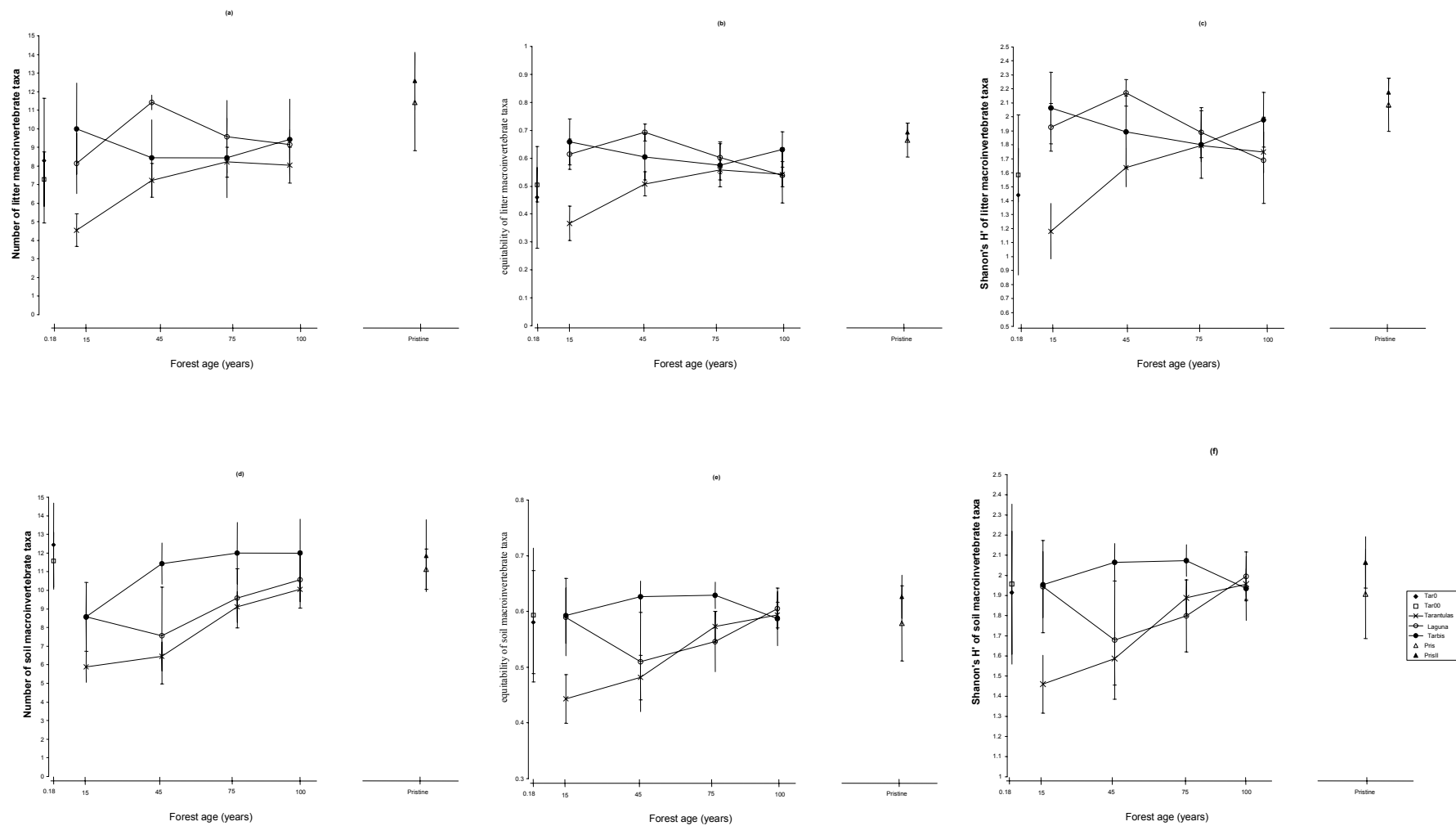


Figure 3.8. Number of taxa, equitability and Shannon's H' of macroinvertebrate taxa in three chronosequences, two recently logged sites and two pristine sites. (a-c) Litter macroinvertebrate community, (d-f) soil macroinvertebrate community. Mean \pm confidence limits are presented. Sample size (n) is 7 per successional stage except for Tarantulas where n=49.

The individual taxa of macroinvertebrates through succession

Of the total number of macroinvertebrates collected in the survey, 76.9% (9924) were located in the soil and 23.1% (2981) in the litter, and consequently individual taxa often occurred in higher numbers in the soil than in the litter (figure 3.9). However, there were some exceptions for which the reverse was true, such as Acari and Collembola. The most abundant taxa were Formicidae (15.3%), Coleoptera (adults, 12.4%) and Enchytraeidae (12.1%) in the soil and Coleoptera (adults, 14.4%), Collembola (14.2%) and Diplopoda (9.4%) in the litter. Four taxa were relatively rare: Dermaptera (2 individuals), Thysanura (8 individuals), Uropygi (10 individuals) and Blattaria (11 individuals). Further more, Uropygi and Thysanura occurred exclusively in the soil.

Macroinvertebrate taxa varied in abundance across successional stages but the pattern was not always the same for both the soil and the litter (figure 3.9). This was particularly evident for taxa such as Coleoptera, Homoptera, Orthoptera and Formicidae.

Often taxa displayed their highest mean abundance in the pristine forests. This was the case for Homoptera, Diplura, Gasteropoda, Diptera larvae, Coleoptera larvae and Enchytraeidae in the litter and Lumbricina in both litter and soil. For four out of the six taxa that reached their litter highest abundance in the pristine forests (Enchytraeidae, Diptera, Homoptera and Coleoptera) their abundance in the soil was high both in the pristine and recently logged sites. In contrast, the highest litter and soil abundance of Collembola was found solely in recently logged sites.

Frequently taxa displayed a relatively low abundance in particular forest ages, for example Coleoptera were low in the litter of 15- and 45-year-old forests and Collembola in the soils of 15-year-old forests, while Orthoptera were present in low numbers in the litter of 15- and 100-year-old successional stages. In some cases taxa were even completely absent from particular ages of the forest. This was the case for

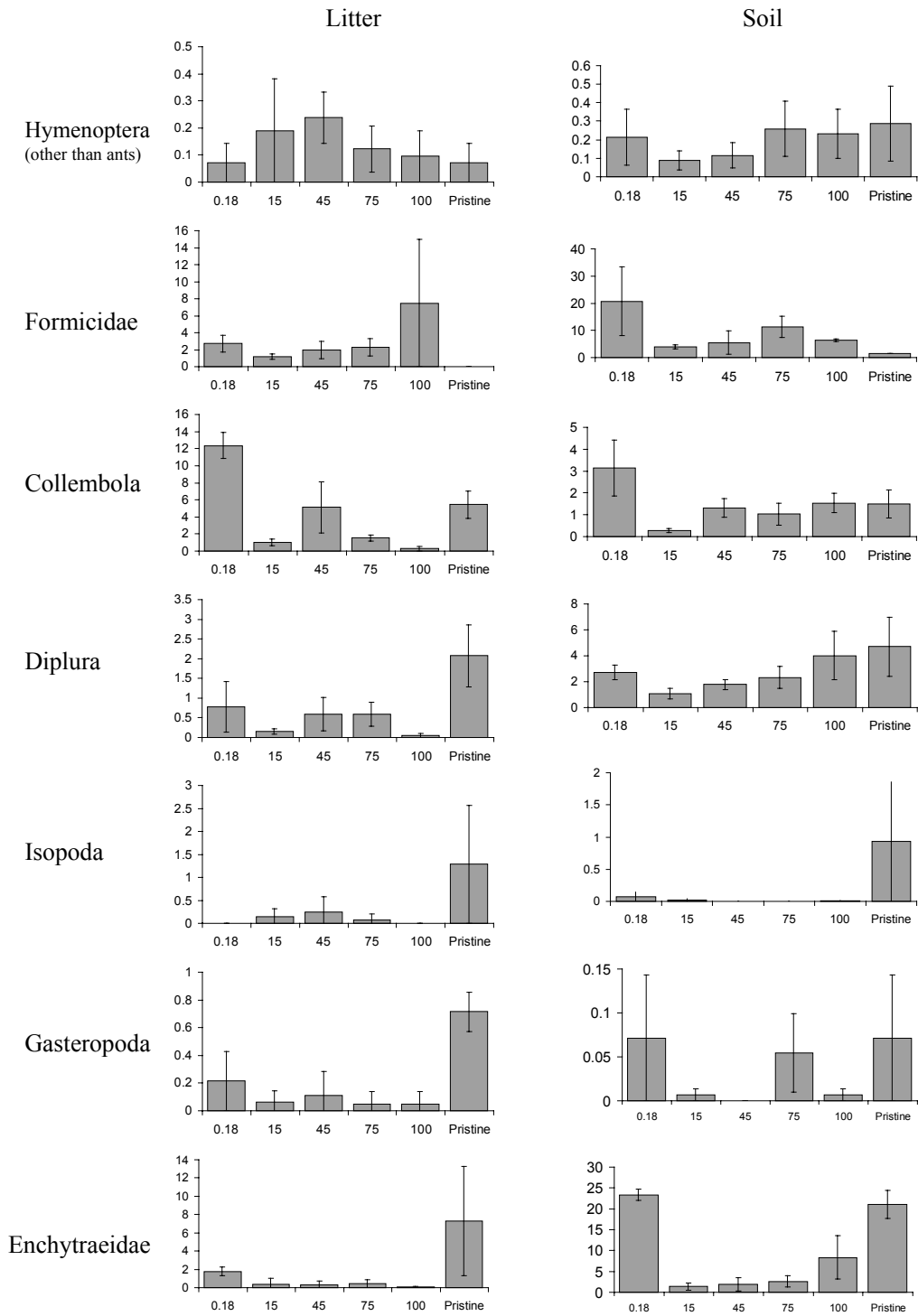


Figure 3.9. Mean abundance of macroinvertebrate taxa per monolith in the litter and soil of different successional stages. The mean \pm standard error of the abundance per successional stage is presented for Tarantulas, Laguna and Tarbis chronosequences, recently logged sites and pristine sites. The abundance per replicate successional stage was calculated averaging the abundance of all its monoliths. Sample size (n) is four for the 15- to 100-year-old forests and n=2 for the pristine and recently logged sites.

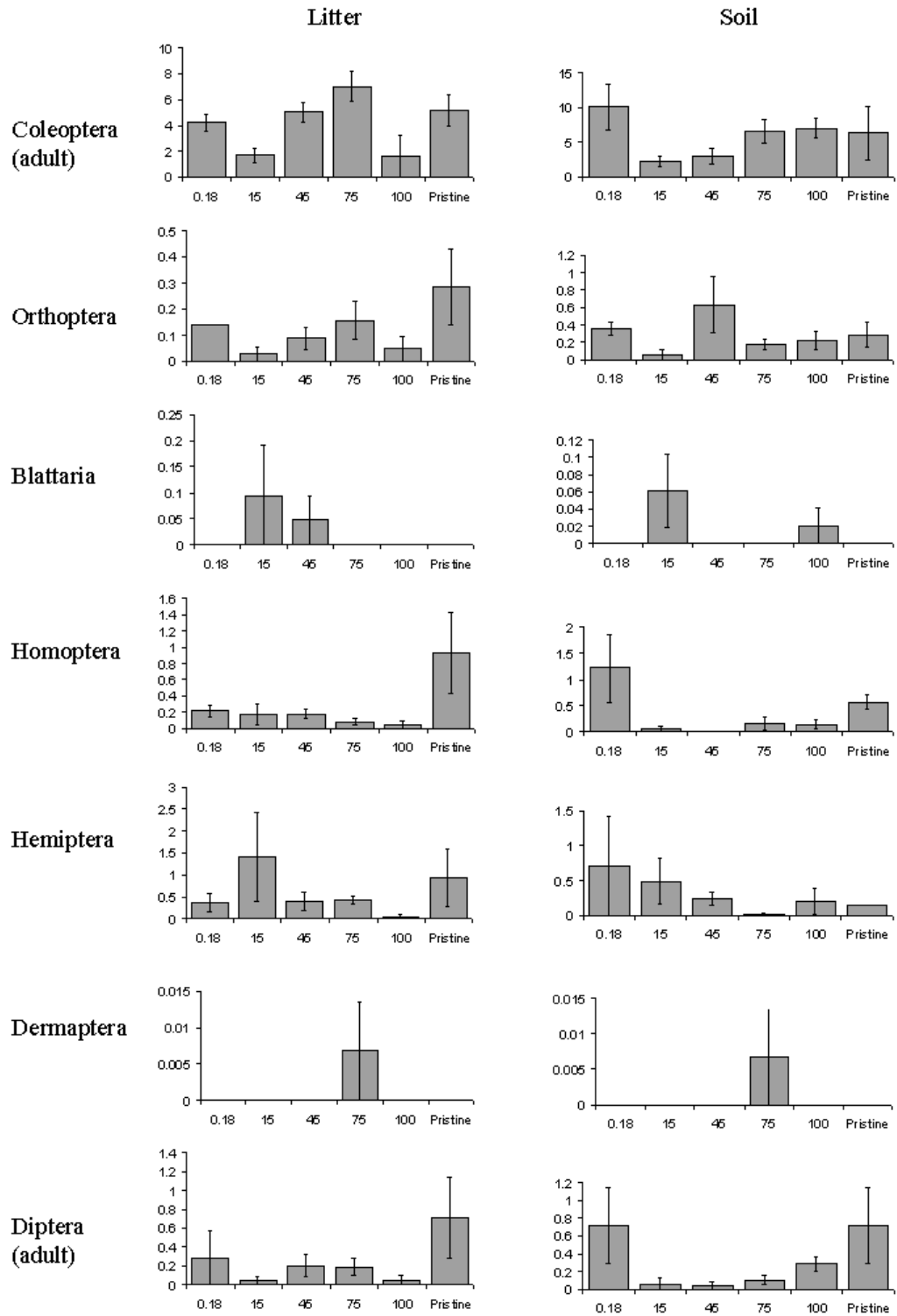


Figure 3.9 continuation...

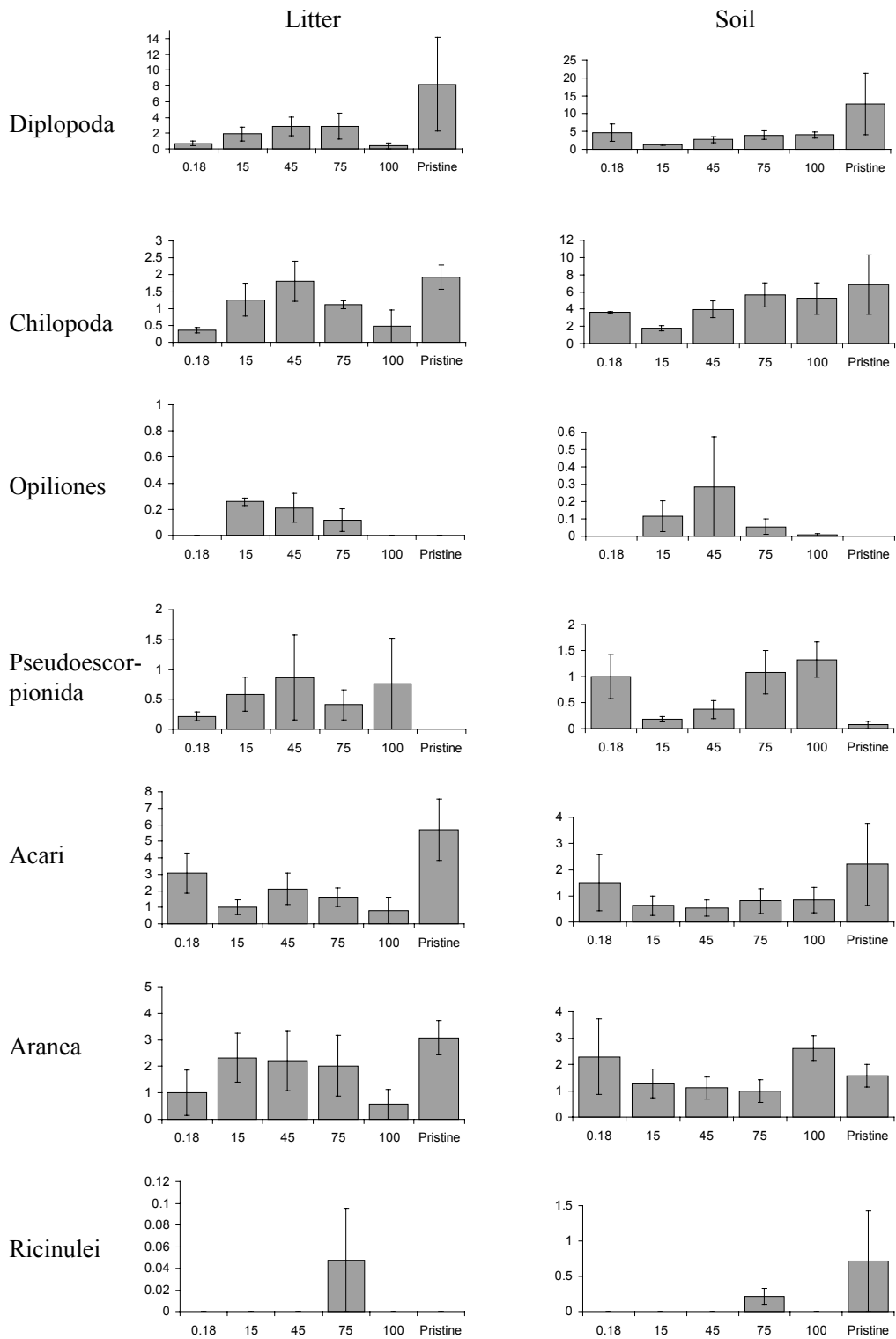


Figure 3.9 continuation...(ends)

Gasteropoda in the soils of the 45-year-old successional stage and Isopoda in the litter of recently logged sites and 100-year-old forests.

Some taxa, usually those that were rare overall, were only found in one or two successional stages. For example, Ricinulei were almost exclusively found in 75-year-old forests and only in one sample with 10 individuals in pristine forests. Opiliones only occurred in mid-successional stages both in the litter and the soil.

Several macroinvertebrate taxa did not vary noticeably in their abundance between forests of different age or the variation amongst replicates was so high that no pattern was detected across the successional sequence. These cases include Diplura in the soil and Aranea, Chilopoda, Hymenoptera and Lepidoptera larvae both in litter and soil.

All of the earthworms (Order Lumbricina) were identified as *Ramiellona wilsoni* (Annelida, Acanthodrilidae), a small litter dwelling species that is thought to be endemic to Oaxaca (Fragoso & Reynolds, 1997).

Relationship between macroinvertebrate communities and environmental and resource variables.

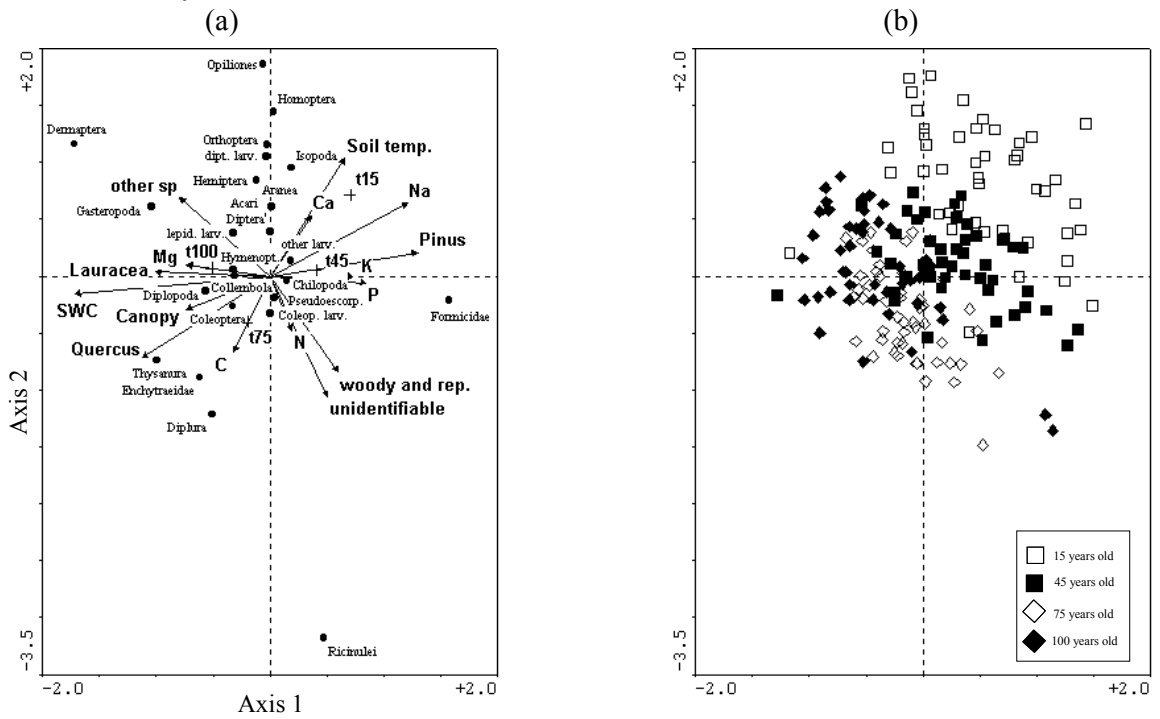
A canonical correspondence analysis of the litter macroinvertebrate community in the Tarantulas chronosequence with respect to successional stage and environmental variables (table 3.2 and figure 3.10a-b) showed that there were a number of associations between the community composition and the combination of soil microclimate, resource type and soil nutrient concentration in each successional stage of the chronosequence. The chosen variables explained about 11.4% of the total taxa variance, of which 7.6% is represented in the first two canonical axes (figure 3.10a-b).

Groups of explanatory variables included in CCA	Extracted inertia		% of taxa variance explained (3 or 4 axes)	
	Litter total:	Soil total:	Litter	Soil
Soil/litter community	3.042	2.332		
Successional stage	0.173	0.108	5.7	4.6
All environmental variables	0.520	0.354	12.9	10.8
Litter components	0.191	0.132	5.7	5.2
Physical variables	0.246	0.111	8.1	4.8
Soil chemistry	0.199	0.127	5.7	4.8
Successional stage and all environmental variables	0.607	0.438	14.1	13.2

Table 3.2 Partitioning of macroinvertebrate taxa total inertia in CCA amongst different groups of explanatory environmental variables. Includes all samples from the Tarantulas chronosequence. Notice that the CCAs have been 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.

In the canonical space of Tarantulas litter macroinvertebrate data (Figure 3.10b) successional shifts appear to be represented by a clockwise movement around the axes. The 15-year-old forest is the successional stage furthest from the origin, which denotes a more distinct community composition that includes Isopoda, Aranea, Homoptera, Opiliones and other larvae and pupae as distinctive components (Figure 3.10a). This community is also associated with a high mean soil temperature and concentration of calcium and sodium in the soil as well as a high proportion of pine needles in the litter. The next successional stage in the clockwise movement is the 45-year-old forest that has a community shift towards an increase in Chilopoda, Pseudoscorpionida, Formicidae and Coleoptera larvae. This shift is associated with an increase in the concentration of potassium and phosphorous in the soil and pine needles in the litter. The 75-year-old forest was characterised by an increase in Diplura, Enchytraeidae, Thysanura, Coleoptera and Diplopoda. These taxa appear to be associated with a high carbon concentration in the soil, a closer canopy and a high abundance of *Quercus* leaves in the litter. In the bottom right quadrant of the graph are those taxa and environmental conditions that are shared by a portion of the samples in both the 45 and 75-year-old forests figure 3.10b. These include Chilopoda, Pseudoscorpionida and Coleoptera larvae in terms of taxa, high concentration of nitrogen in the soil and high quantities of unidentifiable material and woody and reproductive materials in the litter. Rcinulei (the most isolated taxon in the bi-plot) is a rare taxon that occurred only in the 75-year-old forest, but seems

Litter community



Soil community

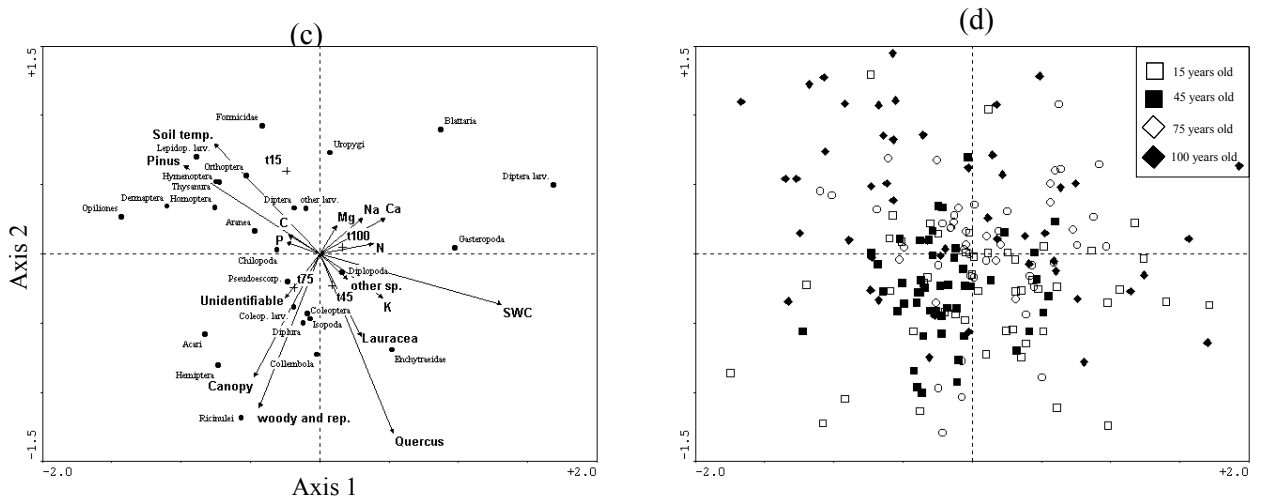
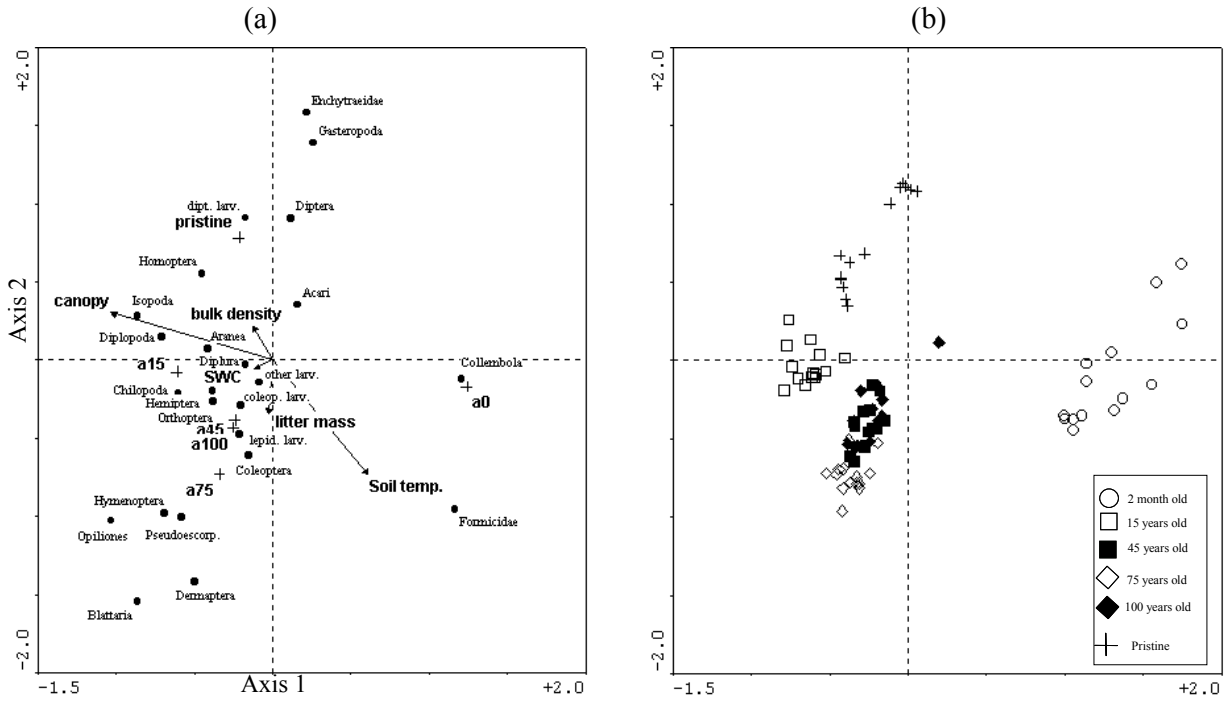


Figure 3.10 Ordination diagrams based on canonical correspondence analyses of community composition with respect to successional stage (dummy variables), soil microclimate, nutrient content in the soil and litter composition variables in Tarantulas chronosequence. In litter community ordination (top graphs) first two axes account for 7.6% of taxa variation, three extreme samples were excluded. In soil community ordination (bottom graphs) first two axes account for 8.3% of taxa variation, one extreme sample was excluded. (a) and (c) Biplot of taxa-explanatory variables and (b) and (d) sample scatterplots symbol coded per site. SWC stands for volumetric soil water content.

Litter community



Soil community

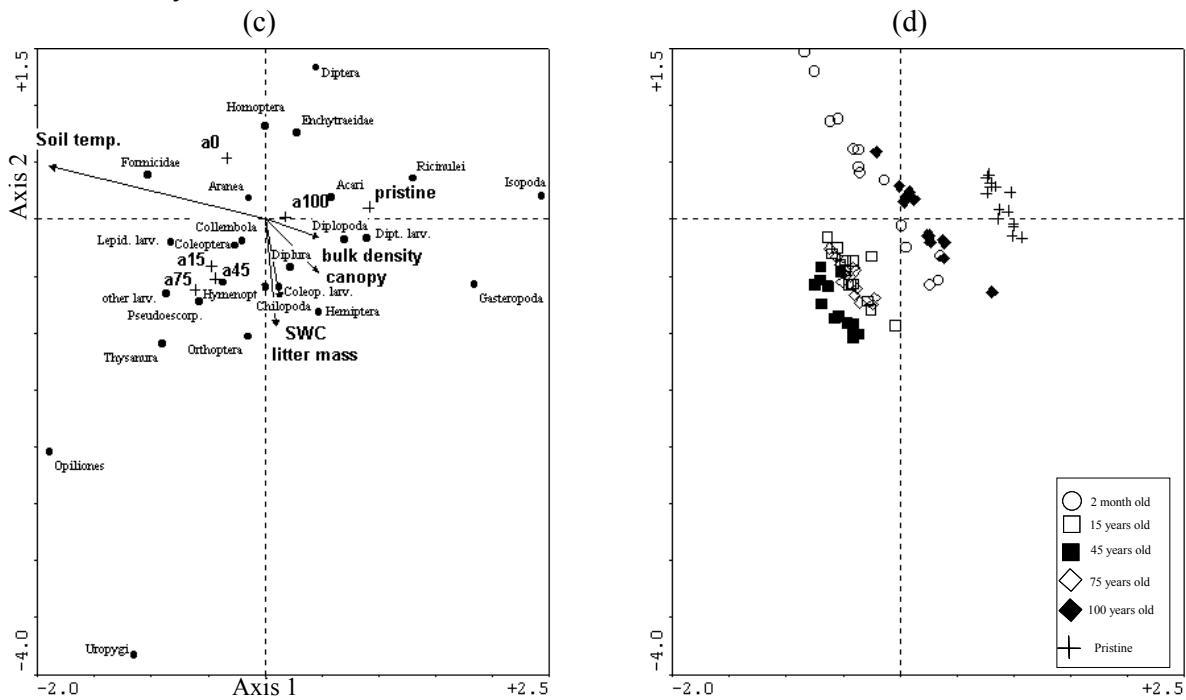


Figure 3.11 Ordination diagrams based on canonical correspondence analyses of community composition with respect to successional stage (dummy variables denoted as a0-100 and pristine), soil microclimate (soil temperature, volumetric soil water content (SWC) and canopy cover), litter mass and soil bulk density variables in Tarantulas (seven random subsamples) and Tarbis chronosequences plus recently logged sites (Tar0 and Tar00) and pristine sites (Pris and PrisII). In litter community ordination (top graphs) the first two axes account for 15.7% of taxa variation. In soil community ordination (bottom graphs) first two axis account for 11.1% of taxa variation. (a) and (c) Biplot of taxa-explanatory variables and (b) and (d) sample scatterplots with symbol coded per site.

to be associated with the environmental conditions shared by the 45- and 75-year-old forests which, explains its position in [figure 3.10a](#). Finally, the 100-year-old forest is the last step in the clockwise movement around [figure 3.10b](#). In this successional stage there are more Collembola, Hymenoptera, Diptera, Lepidoptera larvae and Gasteropoda, together with more Lauracea and other species of leaves in the litter, a higher concentration of magnesium in the soil and a higher volumetric soil water content. The 75- and 100-year-old forests share a high volumetric soil water content, canopy cover and a higher proportion of *Quercus* leaves in the litter. They also share higher numbers of Chilopoda and Diplopoda in the litter.

A similar canonical correspondence analysis of the soil macroinvertebrate community in the Tarantulas chronosequence ([table 3.2 and figure 3.10c-d](#)) showed that there is also a network of associations between the soil community composition and the combination of soil microclimate, resource type and soil nutrient concentration in each successional stage of the chronosequence. The chosen variables explained 13.4% of the total taxa variance, of which 8.3% is represented in the first two canonical axes ([figure 3.10c-d](#)).

In the case of the canonical soil macroinvertebrate space the samples of each successional stage appear in less compact groups denoting a greater diversity in soil community composition in each sample with relatively low association with overall trends in environmental variables.

Canonical correspondence analyses of litter and soil macroinvertebrate communities in two chronosequences (Tarantulas and Tarbis), recently logged sites (Tar0 and Tar00) and pristine sites (Pris and Pris II) with respect to successional stage and environmental variables ([table 3.3 and figure 3.11a-b](#)) showed that there is a strong association between succession, environmental variables and macroinvertebrate communities. The chosen variables explained 21% of the total litter invertebrate taxa variance, of which 15.7% is represented in the first two canonical axes ([table 3.3 and figure 3.11a-b](#)). In the case of the soil macroinvertebrate community, the environmental variables tested explained about 14.6% of the total litter invertebrate

taxa variance, of which 11.1% is represented in the first two canonical axes (table 3.3 and figure 3.11c-d).

In the canonical space of the litter community (figure 3.11a-b) the most important variables that distinguish successional stages are soil temperature and canopy cover. The most distinctive successional stage is that formed by the recently logged forests with high numbers of Collembola and Formicidae associated with high soil temperatures and low canopy cover. The samples from pristine sites also form a distinct group (figure 3.11b) with Enchytraeidae, Gasteropoda, Diptera, Acari and Diptera larvae as distinctive elements. These are associated with lower temperatures and to a lesser extent low volumetric soil water content and lower litter mass. The 15-year-old forests form a group of points close to the pristine sites with Chilopoda, Diplopoda, Aranea, Diplura and Coleoptera larvae as important elements. The samples from 45, 75 and 100-year-old forests form a compact group of points next to the 15-year-old forests in the canonical space. These forests have taxa such as Hemiptera, Orthoptera, Lepidoptera larvae and Coleoptera, and are loosely associated with higher litter mass. The samples in the 75-year-old forests are part of this group, however they lie slightly apart from it because they tend to have other distinctive elements such as Hymenoptera, Opiliones, Pseudoscorpionida, Blattaria and Dermaptera which are mostly rare taxa.

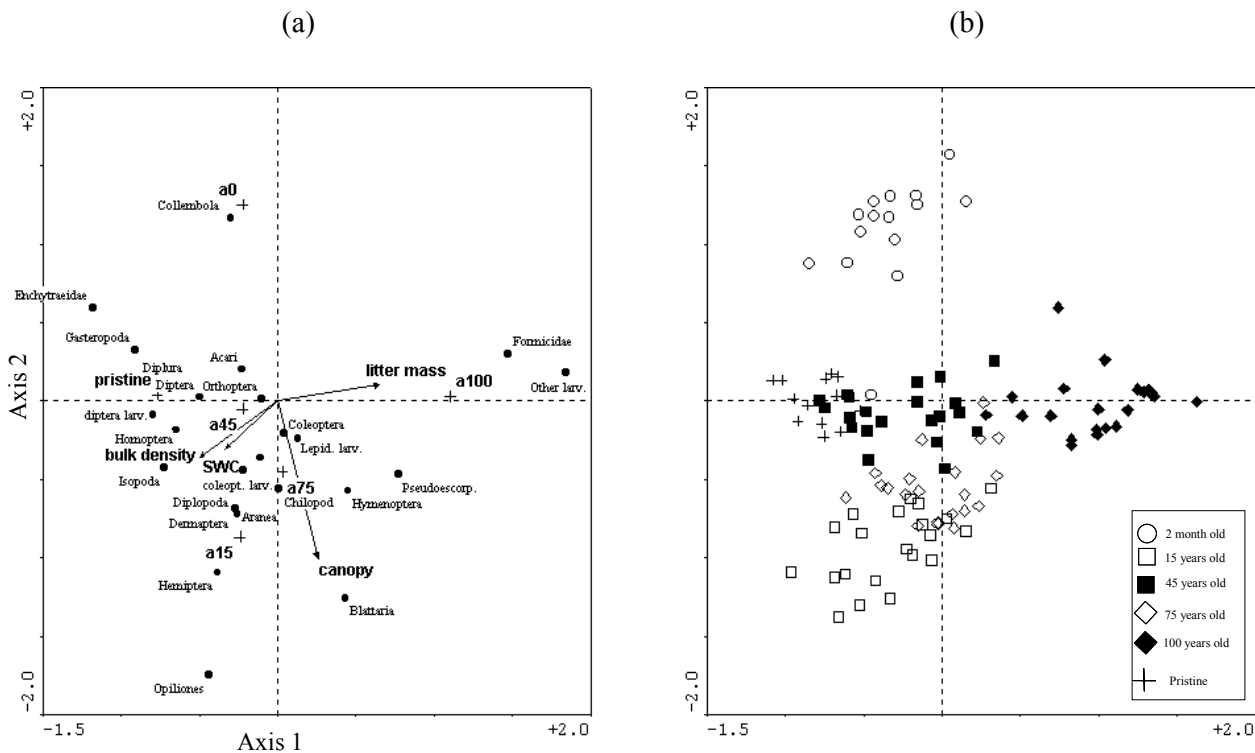
Groups of explanatory variables included in CCA	Inertia (total/extracted)		% of taxa variance explained (3 or 4 axes)	
	Litter	Soil	Litter	Soil
Successional stage	2.264/0.458	1.987/0.219	19.7	10.4
Environmental variables				
Including temperature and excluding Laguna	1.864/0.273	1.831/0.181	13.8	9.5
Including Laguna and excluding temperature	2.264/0.179	1.987/0.08	7.9	4.0
Successional stage and environmental variables				
Including temperature and excluding Laguna	1.864/0.485	1.831/0.342	21	14.6
Including Laguna and excluding temperature	2.264/0.558	1.987/0.290	22.1	12.0

Table 3.3. Partitioning of macroinvertebrate taxa total inertia in CCA amongst different groups of explanatory environmental variables. Includes samples from the Tarantulas (seven random subsamples per successional stage), Laguna (except when specified) and Tarbis chronosequences plus recently logged (Tar0 and Tar 00) and pristine (Pris and Pris II) sites. Notice that the CCAs have been 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.

In the canonical space formed by the soil community (figure 3.11c-d), mean soil temperature locates the recently logged sites apart from the rest of the successional stages. These sites have low canopy cover, litter mass and volumetric soil water content as well as higher numbers of Formicidae, Homoptera, Enchytraeidae and Diptera. Very close to the recently logged sites lies the group of points that corresponds to the 100-year-old forests with Diplopoda, Acari, Diptera larvae, Diplura and Chilopoda. The 100-year-old forests have lower mean soil temperature and higher canopy cover, and soil bulk density. Next to the 100-year-old forests there is a distinct group of points formed by the samples in the pristine sites. These have similar environmental conditions and community composition to the 100-year-old forests but also have other rare taxa such as Isopoda, Ricinulei and Gasteropoda. The 15, 45 and 75-year-old forests form a group of samples that have a community with taxa such as Coleoptera, Lepidoptera larvae, Collembola, Hymenoptera, Other larvae and pupae, Pseudoescorpionidae and Orthoptera. The 45-year-old forest forms a slightly separate group from this group because it also has some other rare elements such as Opiliones, Orthoptera, and Uropygi.

When a CCA was performed for the macroinvertebrate community excluding soil temperature (which was not available for Laguna) and incorporating data for the Laguna chronosequence, a strong association was also found between the soil and litter communities and the environmental variables (tables 3.3 and figure 3.12). The chosen variables explained 22.1% of the total litter invertebrate taxa variance, of which 16% is represented in the first two canonical axes (table 3.3 and figure 3.12a-b). In the case of the soil macroinvertebrate community, the environmental variables tested explained about 12% of the total litter invertebrate taxa variance, of which 9.4% is represented in the first two canonical axes (table 3.3 and figure 3.12c-d). In the case of the litter community, the recently logged sites were again the successional stage that forms the most isolated group of samples. High numbers of Collembola characterise the community of the litter in these sites, which have low canopy cover (figure 3.12a-b). The other successional stages have more closed canopies and their samples lie on the opposite side of the ordination. The communities in the litter of

Litter community



Soil community

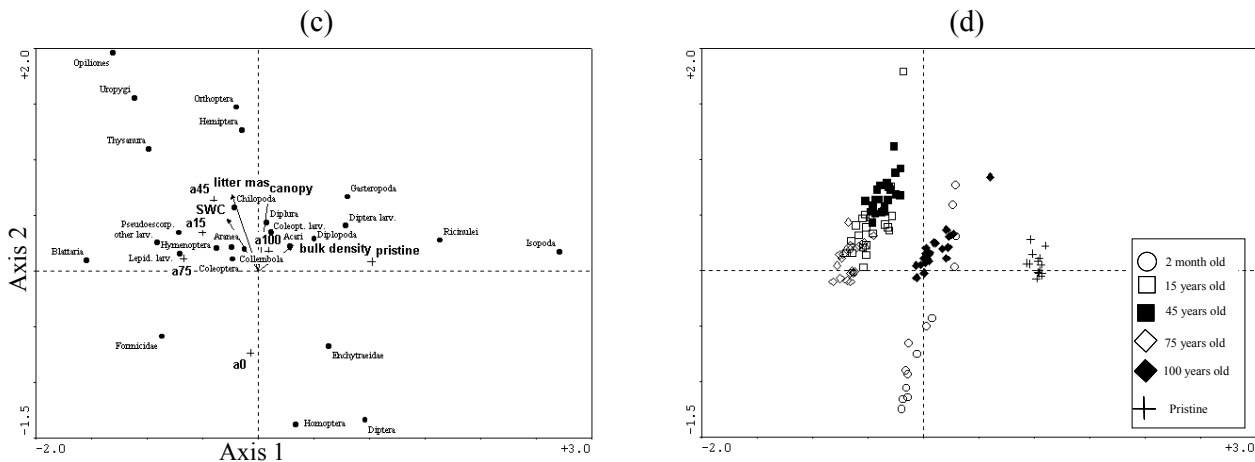


Figure 3.12 Ordination diagrams based on canonical correspondence analyses of community composition with respect to successional stage (dummy variables denoted as a0-100 and pristine), soil microclimate (volumetric soil water content (SWC) and canopy cover), litter mass and soil bulk density variables in Tarantulas (seven random subsamples), Laguna and Tarbis chronosequences plus recently logged sites (Tar0 and Tar00) and pristine sites (Pris and PrisII). In litter community ordination (top graphs) first two axis account for 16% of taxa variation. In soil community ordination (bottom graphs) first two axis account for 9.4% of taxa variation. (a) and (c) Biplot of taxa-explanatory variables and (b) and (d) sample scatterplots symbol coded per site.

the 100-year-old forests have Formicidae and other larvae and pupae as important elements and are associated with higher mass of litter per sample. The 75-year-old forests have higher canopy cover and their litter community has Chilopoda, Hymenoptera, Pseudoescorpionida and Coleoptera larvae as important elements. In the litter community of the 15-year-old forest taxa such as Aranea, Diplopoda, Hemiptera and Opiliones appear as distinctive components. There is no environmental variable in the ordination diagram that seems particularly associated with these forest plots. The 15- and 75-year-old forests seem to share some elements in their litter community such as Chilopoda, Diplopoda and Coleoptera larvae. The pristine forest litter communities are characterised by Enchytraeidae, Gasteropoda and Diplura. These forests are characterised by low litter weight. The 45-year-old forests have higher soil bulk density and volumetric soil water content. In these forests the litter macroinvertebrate community has Acari, Diptera and Orthoptera as dominant elements. The 45-year-old and pristine forests share some elements such as Diplura and Diptera larvae.

When the soil community was ordinated with respect to environmental variables including Laguna chronosequence and excluding soil temperature ([figure 3.12c-d](#)) the recently logged sites are drawn apart from the rest of the sites in the bottom half of the diagram. These sites are characterised by low canopy cover, litter mass, soil bulk density and volumetric soil water content. The soil macroinvertebrate community in these forests is characterised by high numbers of Formicidae, Homoptera, Diptera and Enchytraeidae. Four samples from recently logged sites lie on the top half of the diagram owing to their high values in canopy cover and a soil macroinvertebrate community similar to that found in 100-year-old forests. The environmental conditions in the other successional stages (top half of the ordination diagram) are relatively similar. High canopy cover, soil bulk density, litter mass and volumetric soil water content characterised these forest plots. The samples of pristine sites form a compact group to the right of the ordination owing to the presence of rare taxa such as Ricinulei and Isopoda. Pristine sites also share some elements with the 100-year-old forests such as Diptera larvae and Diplopoda. The 100-year-old forests have Coleoptera, Coleoptera larvae, Acari, Diplura and Gasteropoda as

distinctive elements. The samples from 15-, 45- and 75-year-old forests form a compact group with the samples from the 45-year-old forests situated slightly towards the top. The communities in these three successional stages have elements such as Chilopoda, Pseudoescorpionida, other larvae and pupae, Lepidoptera larvae and Hymenoptera as predominant. Additionally, the 45-year-old forest has some distinctive rare elements such as Thysanura, Uropygi, Opiliones, Hemiptera and Orthoptera (which draw the samples from these forests slightly apart from the ones of 15- and 75-year-old forests).

Tables 3.2 and 3.3 present the results of partitioning the explained variance in the canonical correspondence analyses presented above. For the Tarantulas chronosequence (table 3.2) forest age alone explained 5.7% of the variance in the litter and 4.6% in the soil communities. All environmental variables together without considering successional stage explained 12.9% and 10.8% of the variance in the litter and soil communities respectively. In the litter, physical environmental variables (soil temperature, volumetric soil water content and canopy cover) explained the highest amount of taxa variance (8.1%) followed by soil chemistry (nutrient concentrations) and litter components that each explained 5.7% of the taxa variance each. In the soil the litter components alone explained 5.2% of the variance and the physical environmental variables and soil chemistry 4.8% each. Note that the taxa variance explained by successional stage and environmental variables together presented in table 3.2 is higher than that presented in Appendix CH3 (tables CH3.15 and CH3.16) because, for the later CCAs, samples with extreme values were excluded from the analyses.

When all of the sites and chronosequences were included in the variance partitioning (table 3.3), successional stage alone explained 19.7% of the taxa variance in the litter and 10.4% in the soil communities. Environmental variables alone explained 13.9% of the variance in the litter community and 9.5% in the soil community when temperature was included but Laguna chronosequence is excluded. When the Laguna chronosequence was included and soil temperature was excluded, environmental

variables alone explained 7.9% of the variance in the litter community and 4.0% in the soil community.

Discussion

Consequences of logging and secondary succession for the soil microenvironment

If the canopy cover in Tar0 and Tar00 is compared with the one of the 100-year-old forest in Tarantulas (the nearest old forest), the relatively mild disturbance that was recorded for the recently logged sites in this study represented a mean 16% reduction of the canopy cover. The disturbance event that preceded establishment of the secondary forests in the chronosequences may have been more intense (Blanco-Macias, 2001) than this. In any case, for all three chronosequences by 15 years of succession, the cover of the canopy had recovered (and was sustained there-after) to a value similar to that of the pristine sites. A similar recovery time for canopy cover has been observed in similar montane forests in Mexico, where the complete floristic and structural substitution from herbaceous communities by a multilayered vegetation (three synusiae) occurs between 15 and 20 years of succession. (González-Espinosa *et al.*, 1991; Romero-Nájera, 2000).

The opening of the canopy through logging in a cloud forest constitutes an important disruption of the unusual physiognomy that sustains the TMCF as a unique ecosystem (Waide *et al.*, 1998). Even if the canopy cover has recovered within 15 years of succession, the chain of environmental changes that unfold after the canopy of a TMCF has been opened may have a longer-term impact. Opening of the canopy temporarily increases the radiation penetrating the forest, not only because of removal of the physical barrier provided by the canopy, but also because the simplification of the structure may hinder its capacity to retain fog (Bruijnzeel & Proctor, 1995; Cavalier *et al.*, 1997). The increase in radiation reaching the forest floor is thought to be responsible for higher soil temperatures (Bruijnzeel & Veneklaas, 1998; Romero-Nájera, 2000).

In this study the pristine sites (Pris and PrisII) had a soil temperature between 3 and 4°C lower than any other successional stage including recently logged sites (Tar0

and Tar00). This suggests that the elevation in soil temperature caused by logging in these forests may not be reversed through succession for at least 100 years. The reason for this might be that although the extent of canopy cover was reversed in only 15 years of succession, the vertical structural complexity that may be responsible for the capacity to retain fog, could take more than 100 years of succession to reform (Blanco-Macias, 2001). Visually it was evident that the pristine sites had higher and vertically thicker canopies than the secondary forests. The higher structural complexity of the vegetation in pristine sites might also be associated with the higher density of epiphytes (Cordova & del Castillo, 2001) that could be contributing significantly to the retention of fog (Waide *et al.*, 1998).

It is possible that at least part of the difference in soil temperature between pristine sites and the secondary forests is a result of the difference in altitude (100-200m). An increase in altitude is often associated with thicker cloud cover and lower environmental temperatures which cause a lower soil temperature (and often higher SWC) (Bruijnzeel and Veneklaas, 1998). However, evidence from the literature suggests that the difference in altitude between pristine sites and secondary forests is not large enough to explain a difference of 3 to 4°C in soil temperature. Considering that soil temperature mirrors mean environmental temperature (with a narrower daily variation), an adiabatic lapse rate of 15-20°C per 1000 m increase in elevation would be necessary to produce a difference of temperature of 3 to 4°C for a 200 m increase in altitude. As a generalisation Vitousek (1984) considered the intermediate between wet and dry adiabatic lapse rates (4.5°C per 1000 m increase in elevation) as a good approximation for tropical mountains. Specific examples of lapse rates per 1000 m increase in elevation in tropical mountains are 5.7°C in Hawaii (Vitousek *et al.*, 1994), 4.8 °C in Sabah (Proctor *et al.*, 1988) and 5.7°C in Puerto Rico (Lawrence *et al.*, 1996). Vitousek's generalisation and the three specific examples of lapse rates in other tropical areas produce a difference in temperature per 200 m increase in altitude less than half the one recorded between pristine sites and secondary forests. For this reason it is unlikely that the change in altitude between pristine sites and secondary forest is the prime explanation of the difference in soil temperature.

Another consideration is that the soil temperature (and SWC, see below) was only replicated on different days for Tarantulas. The plots in other chronosequences and sites were only sampled in a single day. Even if the cloud cap in tropical mountains provides a thick fog cover for most of the day in TMCF, there is some variation in the frequency of sunlight penetration during the day (Bruijnzeel and Veneklaas, 1998). The two pristine sites studied here were sampled in different days, but there is a risk that both were sampled on cloudier days than the other sites and therefore at least part of the difference in temperature could have been spurious and not a result of differences in the forest structure as is hypothesised above.

It has also been suggested that the opening of the canopy in TMCF promotes low humidity conditions in the soil because the thickness of the canopy in mature TMCF shelters the understory from wind and solar radiation (Olander *et al.*, 1998). In this study there was remarkable variability in soil volumetric water content between and along chronosequences. The water content in the soil may have been highly influenced by temporal variation, and therefore results do not support the hypothesis that selective logging or succession have an effect on soil water content.

The complex structure of the mature TMCF canopy may play a significant role in buffering extreme changes in soil temperatures and humidity in the soil. The results of this study cannot be used to test this hypothesis because most measurements were not replicated through time. However Romero-Nájera (2000) has shown that the temperatures (air and soil) and air humidity (at the week and season temporal scales) are progressively more variable in montane forests in Chiapas where the canopy is dominated by *Quercus* spp., a combination of *Quercus* spp. and *Pinus* spp and *Pinus* spp. alone. Considering that in these same forest fragments in Chiapas there was a significant negative linear relationship between the species richness of understory broad-leaved trees and the degree of dominance of *Pinus* spp., pine-dominated areas were less structurally complex (Galindo-Jaimes *et al.*, 2002) and their temperature (soil and air) and environment humidity were more variable (Romero-Nájera, 2000). In the TMCF of Oaxaca a similar trend of increased buffering of microenvironmental variability may be happening as succession proceeds, because the dominance of pine

in the forest diminishes with succession (shown for Tarantulas here and for other chronosequences by Blanco-Macias (2001) and the structural complexity of the canopy increases with succession (Blanco-Macias, 2001).

Consequences of vegetation changes for the quality and availability of litter resources

Logging debris and trees felled accidentally during stem extraction produce a flush of litter to the forest floor (Olsson *et al.*, 1996a; Finér *et al.*, 2003). In this study, I did not find any evidence of difference in the mass of standing litter on the forest floor of Tar0 and Tar00 (recently logged sites) and old forests (pristine or late successional stages). This is likely to be the case because two months after extraction, logging debris was still mostly intact in the form of whole fallen trees and oak crowns that did not enter the < 2 cm in diameter category that were collected as standing litter and therefore their contribution to the litter was not accounted for. However, it is important to consider that the input of resources by logging above-ground and below-ground may have consequences for the geochemical cycling in the systems at various temporal scales (see next section). Olsson *et al.* (1996a) found in a coniferous forest in Sweden that 15 years after clear-cutting a high proportion of the woody residues were still visible and the nutrients within them had not entered the soil pool. During stem extraction a higher proportion of C is removed with the stems than is left on site in harvesting residues. This is because residues consist mainly of leaves and twigs that have relatively high concentrations of N and cations, which when released to the soil through decomposition increase the exchangeable capacity per unit area (Olsson *et al.*, 1996b). For example, Finér *et al.* (2003) found in a mixed forest in Finland where three times more N was left in the form of residues than was removed in harvesting. This effect is most pronounced in the uppermost soil layer and humus layers and may result in an increase in the quality of litter produced by subsequent successional communities.

The quantity and quality of litter reaching the forest floor depends not only on the nutrient availability but also on the tree species dominating the canopy (Switzer & Shelton, 1979) and therefore changes in canopy dominance that occur during succession have an important influence in the geochemical cycles, particularly in

Cloud Forest, where litter fall forms the most important component of productivity (Tanner *et al.*, 1998). It has been frequently observed that once the canopy is opened in many tropical montane forests in Mexico, genera from Holarctic origin such as *Pinus* spp. establish and dominate for at least the initial part of secondary succession (González-Espinosa *et al.*, 1991; Blanco-Macias, 2001). Although *Pinus* was never the most dominant genus in terms of total basal area in the Tarantulas chronosequence, it constituted the second most important genus in the 15-year-old forest and its dominance diminished considerably by the 45-year-old forest. Pines were absent in the 75- and 100-year-old forests, however Blanco-Macias (2001), having surveyed 0.1 ha transects, found some old pine trees in this 75-year-old forest. Blanco (2001) also studied the vegetation succession in Laguna and Yotao (see chapter 2 for a summary of her findings). Comparing the succession described by the three chronosequences in El Rincón it appears that the dominance of pine trees in the canopy is sustained for different lengths of time: around 45 years for Yotao, 75 years for Tarantulas and more than 100 years for Laguna. In similar forests in the southern Highlands of Chiapas the sustained dominance of pine through succession has been associated with a continuous moderate disturbance of secondary forests through extraction of wood for firewood and that its presence threatens the recolonisation by broadleaved species (Ramírez-Marcial *et al.*, 2001). Blanco (2001) found in Laguna a higher proportion of branching in trees and attributed this character to the continuous extraction of firewood by local people. This evidence points towards a gradient of disturbance between the chronosequences in El Rincón, Yotao (the most isolated chronosequence) being the least disturbed followed by Tarantulas (and Tarbis in this study) and then Laguna being the most disturbed. The presence of continuous disturbance in some secondary forests in El Rincón, Oaxaca might be promoting the dominance by pine trees and sustaining an early-mid succession type of vegetation for longer periods of time, not only because the dominance of pines in the canopy is sustained for longer but also because the whole vegetation composition in the 75- and 100-year-old forests in Laguna is more similar to the 45-year-old forests in the other two chronosequences (see [figure 2.2](#)).

In this study in the Tarantulas chronosequence, the genus *Clethra*, of a North American-East Asiatic affinity, was highly dominant in the 15-year-old forest, with 60 out of 178 trees being *Clethra* spp. where they accounted for 38.4% of the total tree basal area. This result is not consistent with the trend in montane forests in Chiapas where this genus is more common in late successional forest (González-Espinosa *et al.*, 1991). Blanco (2001) in her study of El Rincón reports it as one of the three most abundant genera in the 15-year-old forest of Yotao, 45- and 75-year-olds in Laguna and 100-year-old in Yotao (see table 2.2). Even if the genus in her study does not figure as part of the three most abundant genera in any of the successional stages in Tarantulas, *Clethra suaveolens* and *C. integerrima* were both found exclusively in the 15-year-old forest in this chronosequence and in early successional sites overall. The regeneration strategies of the seven species of *Clethra* found in El Rincón deserve further study because at the genus level it does not seem to follow a consistent pattern with respect to succession. In other montane forests species of *Clethra* have a pioneer regeneration strategy, for example in Jamaica *Clethra occidentalis* acts as a pioneer after disturbance (Newton & Healey, 1989).

The canopies of the 45- and 75-year-old plots in Tarantulas were dominated by *Quercus*. This finding is consistent with studies in Chiapas where it has been found that oak species are capable of regenerating under the semi-open canopies of pine-dominated forests in early succession; oak tends to dominate over pine under low disturbance regimes (Ramírez-Marcial *et al.*, 2001; Galindo-Jaimes *et al.*, 2002). Only the basal area of the 100-year-old forest in Tarantulas was dominated by genera with a tropical affinity such as *Quetzalia*, *Persea* and *Oreopanax*. In the north of Chiapas those areas where the forest habitat is most humid (what is referred to as Evergreen Cloud Forest) other broad-leaved species from a tropical phytogeographic origin can reach dominance over oak trees (Ramírez-Marcial *et al.*, 2001).

Furthermore, there is evidence that under low disturbance conditions, in the highlands of Chiapas secondary succession proceeds with a gradual increase in the number of plant species (González-Espinosa *et al.*, 1991), which is consistent with

the increase in number of tree genera dominating the canopy in the succession of Tarantulas.

There is a proportion of variation in plant species composition between successional stages in Tarantulas that must be associated with site differences and not with the age of the forest. In this study there are no replicate sites of successional stages within Tarantulas and therefore it is only possible to speculate about the relative importance of site differences *vs.* the age of the forest in determining the plant community. The dissimilarities between tree communities in Tarantulas were partly a result of numerous rare genera that often occurred only in one of the grids. For example *Piper* and *Cleyera* in the 15-year-old forest, *Rhamnus* in the 45-year-old and *Symplocarpon* in the 100-year-old. The presence or absence of rare genera in small study plots like those in Tarantulas is likely to be random. Unless a replicated study is performed, little can be concluded about the role of forest age *vs.* site characteristics in explaining the distribution of rare genera. However there is a clear indication that the chronosequence in Tarantulas models appropriately the general vegetation changes that occur during succession in a single site. The successional trends described in this section with respect to dominant genera (*Quercus*, *Pinus*, *Quetzalia*, *Persea* and *Oreopanax*) and genera richness appear to explain an important part of the variation in species composition between plots and they are consistent with the successional trends described by Blanco (2001) for Oaxaca and other authors for similar forests in Mexico. Further evidence is given by the UPGMA analysis performed by Blanco (Figure 2.2, page 29). The similarity between any two sites within Tarantulas was inversely proportional to their difference in age (visually demonstrated by the arrangement in order by age in the dendrogram in [Figure 2.2](#)).

The most important component of net primary productivity in tropical montane forests is above-ground litter fall (Tanner *et al.*, 1998). Mean yearly production of fine litter fall per hectare at the study sites (extrapolated from the mean per litter trap and independently of the successional stage) was $4.7 \pm 3.3 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ which is in the low range of the figures published for the american neotropics for high altitude (1500-3350 m) TMCF, for instance in Venezuela ($4.3 \text{ Mg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$; Tanner *et al.*,

1992), Colombia (4.6-7.0 Mg·ha⁻¹·yr⁻¹; Veneklaas, 1991), and Jamaica (5.6-6.6 Mg·ha⁻¹·yr⁻¹, Tanner, 1980). The measure of litter fall for Tarantulas should be interpreted with caution as it may be an underestimation because litter was left on site in the traps for 1, 2, 2, 27, 9 and 18 weeks in the different collection periods and it must have lost mass thorough decomposition and leaching on-site. However, it is still possible that litter-fall is towards the lower limit of the range of values recorded for high altitude TMCFs because mass loss through decomposition was also found to be very slow (see Chapters 5 and 6). Furthermore, the two periods with the highest litter fall per day were those where litter was left on site for one week and where the litter was left for 27 weeks, suggesting that the effect of the time litter was left on the traps did not dominate the final mass per day calculation.

In a review made by McDonald & Healey (2000) of litter fall published data for secondary (9 studies) and non-secondary (11 studies) upper TMCFs, they found that the range of litter fall values for non-secondary forests (3.6-11.0 Mg·ha⁻¹) was lower than for secondary forests (7.0-27.0 Mg·ha⁻¹). If mature TMCF occur on nutrient poor soils, it is expected that they should have low productivity (Tanner, 1981) and that the dominant tree species are slow-growing and are capable of a highly efficient use of nutrients (Tanner *et al.*, 1998). Often, the efficient use of resources implies production of nutrient-poor litter (Vitousek, 1984) that is shed infrequently (Hobbie, 1992) and therefore promotes further scarcity of nutrients in the soil. This positive feed-back cycle may be disrupted by an increase in basal area dominance of genera such as Pine and Oak in early succession. In a low tropical montane forest in Veracruz, Mexico, (Williams-Linera & Toledo, 1996) found that tree species from a Holarctic origin (including oak) produced higher quantities of litter than those of tropical origin. If that is the case in Oaxaca, higher quantities of litter should be produced in early-mid successional stages where tree genera of Holarctic origin dominate. In this study no significant differences were found in the mean litter fall per day produced in different successional stages of the Tarantulas chronosequence (except for one week in July 2000 when litter fall was higher in the 45-year-old forest). Similarly, there was no statistical evidence of differences in volume of standing litter between successional stages. However, it is worthy of notice that the

45- and 75-year-old forests appear to have circa 30% more standing litter than the other successional stages, although this difference is not statistically significant probably as a consequence of the high variability between replicates ($F=3.91$, $d.f.=3$, $P=0.073$). In the pristine sites and 100-year-old forests the mean value of standing litter was ($4.2 \text{ Mg}\cdot\text{ha}^{-1}$ and $4.7 \text{ Mg}\cdot\text{ha}^{-1}$) and in the 45- and 75-year-old forests (6.1 and $6.4 \text{ Mg}\cdot\text{ha}^{-1}$) for all chronosequences pooled. In a study comparing a primary and an approximately 30-year-old secondary TMCFs in the Blue Mountains (Jamaica), McDonald and Healey (2000) found that secondary forests had different masses of standing litter than the primary forest, but the differences were not consistent. Their main secondary plots had higher (*c.* $5.4 \text{ Mg}\cdot\text{ha}^{-1}$) and their subsidiary secondary plots lower (*c.* $2.7 \text{ Mg}\cdot\text{ha}^{-1}$) litter standing crop than the primary forest (*c.* $4.3 \text{ Mg}\cdot\text{ha}^{-1}$). However, for all of them the standing litter was proportional to the litter fall, which was (with respect to standing crop), 204% in main secondary plots, 274% in subsidiary secondary plots and 215 % in primary forest. Considering mean litter fall in Tarantulas ($4.7 \text{ Mg}\cdot\text{ha}^{-1}$) as a reference (given that no differences were detected between successional stages), litter fall was between 99.2 and 110.4% of standing litter in 100-year-old forests and pristine forests respectively, and 79.0 and 73.1% of standing litter in the 45- and 75-year-old forests. These comparisons suggest that, contrary to what was found by McDonald and Healey (2000), in El Rincón intermediate successional stages may be accumulating undecomposed litter while late successional stages and pristine forests are not. In another study closer to the ridge-top in the Blue Mountains, Tanner (1980) found that forests were accumulating standing crop of litter because the proportion of litter fall over standing litter was between 62 and 83%, figures that resemble more closely those found here. A more detailed study (with intra-chronosequence replication of successional stages) of litterfall and litter accumulation in El Rincón is needed in order to corroborate that intermediate successional stages are accumulating undecomposed and semi-decomposed litter on their forest floor.

The hypothesised accumulation of standing litter in intermediate successional stages could be explained by a lower decomposition rate (this will be explored in Chapters 5 and 6) or a result of an undetected higher litter fall, or both. The litter fall means

compared in this study represent a very diverse range of values, from 1 to 27 weeks. It is very likely that differences in litter fall between successional stages were not detected in this study because the unevenness in the data collection combined with the marked seasonality in montane forest leaf shedding (Tanner, 1980; Vitousek, 1984; Williams-Linera & Toledo, 1996; Tanner *et al.*, 1992) caused a substantial error around the per-day mean. The unrecognisable material fraction of the litter was most abundant in the 45- and 75-year-old successional stages. This unrecognisable material constitutes the fraction of the litter that is already comminuted and semi-decomposed. Its high abundance in the litter of mid-stages of succession is an indicator of an organic matter accumulation in the fermentation layer, possibly a result of a slow decomposition rate (Tanner, 1980; Tanner, 1981).

Woody and reproductive parts were not significantly different between successional stages and they accounted for *c.* 35% of total litter. The standing crop of leaf litter (calculated as the total standing litter minus a mean 35% of woody and reproductive materials) is within the range of those reported for other high altitude TMCFs. The standing crop of leaf litter in all sites and chronosequences ranged between 2.0 and 4.2 Mg·ha⁻¹ while in the Blue Mountains in Jamaica it ranged between 2.1-7.9 Mg·ha⁻¹ (Tanner, 1980; McDonald & Healey, 2000) and in Sabah, Malaysia between 2.5 and 2.7 Mg·ha⁻¹ (Proctor *et al.*, 1989).

Recognisable leaves constituted between 27% and 41% of the standing litter. Independently of what the dominant genus in the canopy was, in all of the successional stages of the Tarantulas chronosequence the dominant leaf component in the standing litter was the leaves of an Holarctic tree genus, e.g. *Pinus* in the 15-year-old-year-old-forest and *Quercus* in the other stages. This suggests that, as a result of higher litter production, the presence Holarctic genera in the canopy of this TMCF has a determinant role in the organic matter cycle even if their dominance is as small as 11.4% of the total basal area, as it is in the 100-year-old forest in Tarantulas. Of particular note is the situation in the 45-year-old forest, where the highest proportion of recognisable leaves was found. In this successional stage oak trees accounted for 40% of the basal area and their leaves made-up 73% of the

recognisable leaves, while pine trees accounted for 8.7% of the basal area and their contribution to standing litter was 36.9% of the recognisable leaves.

In general, the mean concentrations of elements in recently fallen leaves of different genera collected from Tarantulas forest floor (0.8-1.28% N, 0.03-0.08% P, 0.005-0.011% Na, 0.05-0.46% K, 0.49-0.89% Ca, 0.06-0.42% Mg) were within the range of those reported for pooled leaf litter fall in other TMCF of similar altitude (0.59-1.32% N, 0.02-0.09% P, 0.0039-0.11% Na, 0.16-0.84% K, 0.16-1.64 % Ca, 0.17-0.37% Mg; 7 studies revised in Bruijnzeel & Proctor, 1995 plus McDonald & Healey, 2000; Vitousek *et al.*, 1992). An exception was the unusually low mean value of K concentration in oak leaves ($0.05 \pm 0.02\%$) and of Mg in pine needles ($0.06 \pm 0.003\%$). For this reason, the forests in the Tarantulas chronosequence can be considered to be as nutrient limited as other TMCF of high altitude around the world, and probably more K and Mg limited in early succession where oak and pine leaves dominate the litter. The importance of *Pinus* and *Quercus* dominance for the organic matter cycling in Tarantulas may therefore be determined not only by their high contribution to the standing litter, but also by differences between the nutrient content in leaves shed from these genera and those from late-successional species. For example, mature TMCFs above 1500 m.a.s.l. around the world have been found to have low concentrations of P in their litter (Vitousek, 1984; Tanner *et al.*, 1998), indicating that this nutrient is limiting in these forests. Because pine needles had the highest phosphorus concentration among the genera tested here and they constituted the most abundant leaf in the litter of the 15-year-old forest, the phosphorus availability in early successional soils may be greater than in late succession (see following section). This finding is consistent with that reported by McDonald and Healey (2000) for the Blue Mountains where phosphorus concentration in pooled litter fall in secondary plots (0.1%) was substantially higher than the value by Tanner *et al.*, (1990) for several primary forests in the same region (0.02-0.04%). The opposite is expected for magnesium, which was present at lower concentrations in pine needles than in any other leaf species.

The leaves of the two tropical genera that were examined had important differences in their chemical composition. *Oreopanax* leaves had a relatively high quality because they were relatively rich in P, K and Mg and had the lowest fibre RF content of all leaves tested. On the other hand, *Beilschmedia* leaves had a poor quality because they had low to intermediate values of all the nutrients and the highest measured fibre RF concentration. This is an indication that the quality of the leaves shed from the trees characteristic of late succession may vary substantially and therefore their effect on nutrient cycling, given their low contribution to the standing litter, may be localised under the canopy of each tree (see chapters 4 and 6). *Oreopanax* trees were the third most dominant genus in terms of basal area (15.09%) in the 100-year-old forest and therefore the overall influence of their leaves on the nutrient cycling should be greater than that of *Beilschmedia* which only accounted for 1.92% basal area in this forest (see next section).

The concentrations of the fibre fractions named here as ASF and RF are considered to correspond roughly to the concentrations of holo-cellulose and lignin in abscised leaves (Vogel et al., 1999). In this study the proportions found for these fibre fractions in the 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). In six studies (White et al., 1988; Gallardo and Merino, 1993; Vitousek et al., 1994; Sanger et al. 1998; Wardle et al., 2002; Sariyildiz and Anderson, 2003) the range of ASF (holo-cellulose) concentrations in the abscised leaves of 12 woody species varied between 18.6% and 50%. In the litter analysed here the mean concentration of ASF was between 2.28% and 3.46% (for a per-species comparison see table CH3.19 in Appendix CH3). In the case of RF (Lignin), nine studies (Melillo et al., 1982; Blair, 1988; White et al., 1988; Gallardo and Merino, 1993; Vitousek et al., 1994; Sanger et al. 1998; Wardle et al., 2002; Sariyildiz and Anderson, 2003; Satti et al., 2003) showed a range from 4.6% to 45.0% in 32 woody species. In contrast the mean RF concentration in the litter tested here was between 48.9% and 68.0% (see table CH3.19 in Appendix CH3). It is evident that the range of ASF values in this study is considerably lower and the one

of RF considerably higher than the concentrations reported in the literature. This surprising discrepancy may be explained by an unnoticed partial ADL digestion that could have caused an underestimate of the acid soluble fraction and an overestimate of the residual fraction of the fibre in leaves. In this study ASF and RF concentrations most probably do not correspond to the holo-cellulose and lignin concentrations, therefore they have only been interpreted as representing fibrous fractions of the litter that are relatively more and less labile.

The concentration of nutrients in litter is simultaneously a cause and effect of nutrient deficit in the soil (Tanner *et al.*, 1998). Therefore the significant differences in the nutrient concentration of pine needles are probably explained by both a species-specific characteristic and also by the prevailing situation in the soils during early succession. Furthermore, the high variability in the concentration of N in oak leaves (0.60–1.70%) can be explained by the mixture of proveniences of the leaves. Since oak leaves were collected from all successional stages and samples randomly chosen for the nutrient analyses, the N concentration in each sample must have been particularly dependent on the availability of N in the soil, which differed between successional stages (see next section).

Successional consequences for the soil chemistry

In general, the mean concentration of elements in the soils of the Tarantulas chronosequence (35.3-51.8% C_{total} , 1.2-1.7% N_{total} , 133.8-205.5 $mg \cdot kg^{-1}$ of P_{total} , 0.85-1.58 $cmol \cdot kg^{-1}$ of Na, 0.96-1.75 $cmol \cdot kg^{-1}$ of K, 2.44-7.79 $cmol \cdot kg^{-1}$ of Ca, 1.36-3.7 $cmol \cdot kg^{-1}$ of Mg) were within the range of those reported for other TMCF of similar altitude (3.6-47.44% C_{total} , 0.25-2.1% N_{total} , 280-500 $mg \cdot kg^{-1}$ of P_{total} , 0.07-2.82 $cmol \cdot kg^{-1}$ of Na, 0.02-1.67 $cmol \cdot kg^{-1}$ of K, 0.05-17.0 $cmol \cdot kg^{-1}$ of Ca, 0.005-11.3 $cmol \cdot kg^{-1}$ of Mg; 8 studies revised in Bruijnzeel & Proctor, 1995 plus McDonald & Healey, 2000; Romero-Nájera, 2000; Wilcke *et al.*, 2003). An exception was the particularly low mean concentration of P_{total} in the soils of all successional stages, which was well below those recorded in other studies. This suggests that independently of successional stage the nutrient concentration in forests in Tarantulas were as low or lower than in other high altitude TMCF around the world.

When considering the effect of human disturbance on soil nutrient pools, long-term signatures need to be taken into account. For example, Dupouey *et al.* (2002) found that the phosphorous concentration of oak leaves and soil nutrient availability in western European forests was determined by the spatial delimitation of Roman agricultural settlements that were abandoned more than 2000 years before hand. Therefore, the nutrient pools that were recorded any stage of secondary succession in Tarantulas are likely to strongly reflect changes in nutrient input caused by previous disturbance. The high availability of all cations (except Mg) in the soils of the 15-year-old forest and their steady decrease in concentration with succession may be a result of the long-term effect of the initial disturbance rather than simply a consequence of the current nutrient input by vegetation.

During logging more C is removed with the stems than it is left on the site with the debris. Harvesting residues have relatively high concentrations of N and cations and contribute significantly to the soil pool of exchangeable K, Ca, Mg, Mn and Zn and increase the exchangeable capacity per unit area (Olsson *et al.*, 1996b). The effect of logging on nutrient cycling may not be immediate, for example Olsson *et al.* (1996a) found in a coniferous forest in Sweden that, although about half of the nutrients of logging residues were concentrated in needles and half in the woody parts, the elevation in C/N ratio in the humus and surface mineral soil layers were detectable only between 8 and 16 years after harvest. Their results suggest that the effect of logging on the nutrient pools in the soil has a time delay and that woody debris left on site acts as a nutrient reservoir in the longer term. This time delay may explain the relatively high concentration of cations found in the 15-year-old forest. Furthermore, the accumulation of mineralised cations in the soil may be enhanced by the reduction in nutrient uptake with the removal of living trees (Finér *et al.*, 2003). Because rates of nitrogen and phosphorus mineralisation *in situ* were not measured, it is not possible to draw conclusions about what the availability of N or P was in each successional stage. However, the fact that both elements were in relatively high concentrations in the pine litter which dominates the 15-year-old forest is consistent

with the evidence (provided by the high concentration of cations) that nutrients were more available in this forest than in other successional stages.

Therefore, soon after logging, the increment in high quality organic matter, the decrease in nutrient uptake due to removal of canopy trees and the increase of radiation through the opening of the canopy are thought to speed decomposition to make nutrients more available in the soil (Finér *et al.*, 2003). Even if evidence was found of nutrients being more available in the 15-year-old forest, the decomposition rate was not higher in this successional stage (this will be discussed further in Chapter 5).

The increment in total carbon and nitrogen in the soil through succession indicates an accumulation of organic matter. TMCF are known to accumulate semi-decomposed organic matter in their soils (Tanner, 1980; Tanner, 1981) that is a result of slow decomposition rate (see chapter 5). The accumulation of semi-decomposed organic matter through succession is likely to be explained by the accumulation of standing litter crop that resulted from the initial domination of holactic species such as oak and pine which produce higher quantities of litter). Because there is no evidence of differences in decomposition rate between successional stages, and decomposition rate has been found to be slow (see Chapter 5) the accumulation of litter from early successional species is likely to be the origin of high concentrations of semi-decomposed organic matter in the mineral soil in late successional stages, even if the crop of standing litter started to diminish after 75 years of succession.

The results suggest that even if there is an initial pulse of nutrients available in the soil some years after a forest has been cleared, the tendency is for the nutrients to become sequestered again through succession. The increment in litter availability in early succession does not seem to produce an increase in decomposition rate, instead semi-decomposed organic matter accumulates in the mineral soil probably promoting nutrient immobilisation in the soil.

In Chiapas in a similar TMCF, the dominance of pine over oak in the canopy was found to be negatively correlated with the content of organic carbon, cation exchange capacity, total nitrogen content and acidity in the soil (Galindo-Jaimes *et al.*, 2002; Romero-Nájera, 2000) all indicators of an accumulation of organic matter. These results are consistent with those obtained in this study if the decline in pine dominance is assumed to be a rough indicator of the age of the forest since the last major disturbance. Although continuous disturbance in the forests of Chiapas (Galindo-Jaimes *et al.*, 2002) makes it difficult to adopt a direct relationship between pine dominance and forest age, the successional trend in the area has been shown to follow such a pattern (González-Espinosa *et al.*, 1991).

The availability of phosphorus may be playing a particularly important role in the geogeochemical cycling in these forests. In general the content of P in the litter was found to be in the low range of values obtained from other TMCF and the total content in the soil was well below the values recorded in other sites. These two results point towards this nutrient being particularly deficient. The fact that pine litter was found to have higher concentrations of P and to dominate early succession and total phosphorous was most abundant in mid-successional soils, indicates that logging and early succession might have released some of the P locked up in the mature forest and made its cycling less efficient.

Macroinvertebrate responses to logging and succession

In the short term, logging activities can disturb soil and litter communities by physically altering their habitat and also by changing microenvironmental conditions due to increased radiation after canopy opening. The number of taxa, diversity index and equitability in both litter and soil macroinvertebrate communities does not seem to be affected by logging in the short term, since no significant differences were found when Tar0 and Tar00 were compared with the pristine and oldest forest sites. However, the composition of the community was altered by logging as shown in the ordination diagrams by the recently logged sites being the most distant group of forests. This difference in the community composition was mostly explained by the more opened canopy and higher soil temperature in the recently logged sites.

However, the characteristic members of the community were not the same in the litter and the soil. The differences may be a reflection of a stronger impact of logging on the more exposed litter community and/or of a vertical migration as a response to environmental perturbation (Zaitsev *et al.*, 2002; Bezkorovainaya & Yashikhin, 2003). Comparing recently logged with pristine sites, for four out of six taxa (Enchytreidae, Diptera, Homoptera and Coleoptera) that reached their highest abundance in the soil and litter of pristine forest, their abundance was relatively high in the soil but low in the litter of the recently logged sites. This suggests that these taxa may have been drastically affected in the litter layer or that they migrated towards the mineral soil.

Few studies have found a detectable difference in the macroinvertebrate community composition in the short term after disturbance (Okwakol, 1994; Zaitsev *et al.*, 2002). For example Okwakol (1994) found an increase in the number of higher taxa six months after clear-cutting in a mid-altitude tropical forest. Many studies have found that the short-term impact on the invertebrate community is imperceptible if the intensity of extraction is low as in recently logged sites (Davies *et al.*, 1999) (termites), (Pietikäinen *et al.*, 2003) (macroarthropods). In conifer forests of central Finland, Siira-Pietikainen *et al.* (2003) found no differences in the higher taxa diversity of macroarthropod community structure and diversity in the following three years after selective logging (that extracted 30% of the stand volume), but did record significant effects after more intensive extractions such as clear felling. Furthermore, some studies have not found a short-term effect even after clear-cutting on the macroinvertebrate community (Theenhaus & Schaefer, 1995). This discrepancy may be explained by differences in the factors limiting productivity in the system. In forests that are not as nutrient or energy limited as TMCs, subtle changes in these factors caused by selective logging may not alter prevailing conditions to an extent that results in an impact on the composition of the macroinvertebrate community.

Collembola was the only taxon that appears to benefit from logging; its abundance in recently logged sites was higher than in any other forest including pristine sites. Collembola abundance has been found to decrease even with very mild forms of

experimental mechanical perturbation (Maraun *et al.*, 2003). The positive effect of logging to Collembola in our recently logged may be a result of their close association with microbial activity (Chauvat *et al.*, 2003). Selective logging produces low physical soil perturbation yet increases radiation and soil temperatures that benefit Collembola through increasing decomposition rate and microbial activity (Butterfield, 1999; Chauvat *et al.*, 2003). The opening of the canopy can be beneficial for Collembola in systems where radiation reaching the forest floor and soil temperatures are limiting factors for microbial metabolism, as seems to be the case for TMCF (Bruijnzeel & Veneklaas, 1998). However, the opening of the canopy can also produce a reduction in soil water content that is very detrimental for microorganisms and Collembola (Butterfield, 1999). Because logging and the survey were both carried out within the same rainy season, if drought affected the Collembola populations, it would have done so a few months after the survey, when the dry season occurred.

In terms of the number and diversity of higher taxa, the litter community in the 15-year-old forest did not follow the same trend for the three chronosequences and when effects of sampling date were removed (and the effect of site ignored) there were no differences between successional stages. However, in the soil, independently of sampling time, mean number of soil taxa was lowest in the 15-year-old forest and increased steadily with succession. On the other hand, when the community composition was ordinated against environmental variables, the litter community in the 15-year-old forest formed a distinct group while the soil community merged with other successional stages. This suggests that the environmental conditions prevailing in recently logged sites could explain the variation in the community composition of the litter community but not in the soil. Similar results were found for Oribatid mites by Zaitsev *et al.* (2002) in spruce forest stands in Germany. They found that in a 95-year-old chronosequence, the disturbance of the community composition was most intense in an early stage (25-year-old), but environmental variables in a constrained ordination failed to explain these changes. They hypothesised that the community had a delayed response to logging disturbance. Therefore, differences in the response of litter and soil community to early succession could be explained by the litter

community being driven by present environmental conditions, while the soil community could have been experiencing a delayed response to logging disturbance. One plausible hypothesis is that after logging, the substantial input of high quality residues and increase in temperature must have increased decomposition rate (Zaitsev *et al.*, 2002) and consumed the accumulated semi-decomposed organic matter that sustains the soil macroinvertebrate community in mature TMCF. In a lowland tropical forest in the Amazon basin, where the soils are also very nutrient deficient, Höfer *et al.* (2001) also found a very suppressed macroinvertebrate fauna 13 years after a clear-cut.

The long-lasting effect of logging residues on the macroinvertebrate communities was demonstrated by Bengtsson *et al.* (1997). They found in a *Pinus sylvestris* forest in Sweden that, in comparison with plots receiving twice the usual amount of clear-cut residues, plots that had no residues left on the ground had decreased numbers of springtails, gamasid mites, spiders, predatory insects and dipterous larvae 15-18 years later. Their results seem somewhat contradictory with my findings and the ones presented by Höfer *et al.* (2001), however comparison between studies is difficult because no information about the community before logging is available in the Swedish study and there are important differences in the type of forests and disturbances.

The number of higher taxa composing the macroinvertebrate community in the soil was the best univariate indicator of successional stage for all sites, except for the two recently logged site that had similar mean number of taxa to the old forests (pristine and 100-year-old). However, the 15-year-old forest had the least number of taxa and the number increased thereafter with succession for all chronosequences.

Microenvironmental changes were important correlates of the community composition through the succession. In particular, soil temperature was more closely associated with the soil community than it was in the litter community. In the soil, the community composition in recently logged sites and the 100-year-old forests was intermediate between the pristine sites and the early and mid-successional stages.

These results suggest that after 100 years of succession the macroinvertebrate community composition started to resemble that of pristine sites. A possible explanation for the resemblance of the soil communities in the recently logged sites and the 100-year-old forests may be that the sites that originated the recently logged sites were as old as the adjacent Tarantulas 100-year-old forest and there was no evident change in their community composition two months after logging. The macroinvertebrate community composition in early and intermediate successional stages was distant from old forests (pristine and 100-year-old), but no distinction could be made amongst them. The resemblance of the early and mid-successional stages in these chronosequences may have been a result of the dominance of pine and oak leaves in the litter, which would only diminish by the 100-year-old forest where other leaves form a more substantial component of the litter. This hypothesis will be explored further in Chapters 5 and 6.

The above hypothesis may explain the increasing number of taxa in the soil recorded through succession, but receives little support from the results obtained in the detailed study of the Tarantulas chronosequence. Even if detailed information about changes in resource quality and soil chemistry through succession were available, little variance could be accounted for in the macroinvertebrate communities in the soil (14.1%) and litter (13.2%). Environmental variables could explain more variation in the macroinvertebrate taxa in the recently logged and pristine sites, than they could in secondary forests. Furthermore, in the litter community, microenvironmental variables explained the highest amount of the taxa variance despite all the changes recorded in the availability and quality of resources in the litter. This is likely to be a result of the litter communities being a transient subset of the deeper soil community that moves vertically depending on the prevailing environmental conditions. In the soil, resource quality and availability may play a more important role in determining the macroinvertebrate community because, not only did the number of taxa increase with the age of the forest, but also the amount of taxa variance explained by microenvironmental variables, litter components and soil chemistry was more evenly distributed (4.8, 5.2 and 4.8% respectively) than in the litter (8.1, 5.7 and 5.7%).

The soil and litter macroinvertebrate community composition in the pristine forest was always distinct from any other secondary forest and therefore, even after 100 years of succession the macroinvertebrate community had not fully recovered from logging disturbance. Enchytraeidae, Gasteropoda, Diptera, Acari and Diptera larvae were distinctive members of the community in the litter and Isopoda and Ricinulei in the soil. Both in litter and soil, worms (Oligochaeta: Lumbricidae) were exclusive of the pristine forests except for two organisms found in the 45-year-old forest in Tarantulas. When identified to species all earthworms turned out to be the native litter dweller *Ramiellona willsoni* which was described by Righi (1972) from material collected in the same region (Sierra Norte) and then collected in a second occasion by Fragoso & Reynolds (1997) in the Sierra of Miahuatlan, regions only separated by the valley of Oaxaca. The record presented here is the third record of this native species and considering that it was only found in the pristine forests, attention should be paid and further studies carried out to determine the sensitivity of this species to human disturbance. The disappearance of earthworms as a result of forest clearing has also been observed in the humid tropics (Tian, 1998) where their absence is thought to be responsible for slower decomposition rates in severely disturbed habitats.

Conclusion

In conclusion results show that the macroinvertebrate community composition in both recently logged sites and pristine forests were distinct compared to secondary successional stages. A decrease in soil temperature and nutrient availability but an increase in litter diversity and soil organic matter recorded through succession were accompanied by an increase in the number of macroinvertebrate taxa in the soil. Collembola were most abundant in recently logged sites and earthworms (Megascolecidae) were almost exclusively found in the pristine forests. Overall the results indicate that mature cloud forests sustain a diverse macroinvertebrate community, but its composition and diversity are compromised by logging and full recovery may take more than 100 years.

