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by

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Factors affecting variation in forest community characteristics and leaf-litter decomposition in tropical montane forest of Chiapas, Mexico: a functional ecology approach

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ABSTRACT

A functional ecology approach was combined with floristic studies to seek increased ecological understanding of forest characteristics and processes in the Central Highlands of Chiapas State, Mexico. The study had two main aims: 1) to determine the major ecological factors driving the floristic and functional variation of forest ecosystems, with emphasis on the operation of either environmental (niche model) or spatial (dispersal limitation model) factors and 2) to determine the relationship of leaf-litter decomposition rates to both leaf functional traits and forest conditions. For this, the specific objectives were i), characterise both the dominant species and the forest stands they form using functional traits, determining also the trait-trait and species-trait relationships; ii), characterise the floristic and functional variation amongst forest stands, and the relationship of this variation with spatial and environmental variables; iii) determine the influence of spatial factors, climate variables, anthropogenic disturbance, forest canopy openness and the traits of species on the abundance of saplings and iv), determine the effect of species leaf trait values, forest type, and their interaction, on leaf-litter decomposition. The study area encompassed a narrow altitudinal range from 2100 to 2800 m a.s.l., located on a carboniferous limestone substrate with abrupt topography and a cool and humid climate. For objectives i), ii) and iii), both adult trees and saplings were counted, measured and identified in field plots in four previously-defined forest types –oak forest, pine-oak forest, pine forest and broadleaved forest– at seven study sites. Plots were characterised in terms of spatial location, altitude above sea level and climate variables from Worldclim climate surfaces. Leaf, stem and whole-plant traits, as well as leaf carbon fractions, were measured for dominant species, and saplings were sampled under both closed and open canopies. For objective iv), first, leaf litter decomposition rates of 20 dominant species were measured in a greenhouse experiment for the assessment of trait effects and second, decomposition rates of representative litter from each forest type, plus two standard species, were measured in a field experiment using forest type as the main factor. Forests of the study area are a mosaic in which three main functional groups of species were identified (objective i). Two groups were respectively dominated by *Quercus* species and *Pinus* species, which both reach the canopy or sub-canopy layers of the forests and had high wood density, leaf dry matter content (LDMC) and other trait values suggesting relatively slow growth. The third group contained a wide taxonomic range of species that generally develop in the forest understorey and had high specific leaf area, leaf nutrient contents and other trait values suggesting relatively high rates of growth and population turnover. These three functional groups of species form a variety of floristic assemblages, ranging from those of simple structure and low floristic diversity (mostly pine forests) to complex and diverse broad-leaved forests. Most oak and pine-oak forests had intermediate characteristics. Variation partitioning analysis showed that the floristic variation of both adults and saplings was related to climate but also to spatial factors, suggesting an important role of dispersal limitation in the shaping of species assemblages (objectives ii and iii). In contrast, variation partitioning also showed that forest functional characteristics –measured using weighted mean trait values– were strongly linked to human disturbance, suggesting that people have had strong effects on the ecological functions of these forests (objective ii). Additionally, floristic variation among forest stands was not always accompanied by functional variation, suggesting that floristics can change across space while forest functional characteristics remain relatively homogeneous. Regarding objective (iii), leaf area was the only species functional trait with a clear relationship to the absolute densities of saplings, suggesting that the abundance of regeneration increases with increasing leaf area, though the effect of canopy openness was small. Finally, for objective iv), the greenhouse experiment showed that *Quercus* spp. and *Pinus* spp. with tough leaves had relatively slow decomposition rates and species with lower LDMC and associated tradeoffs in trait values, such as high specific leaf area, had higher decomposition rates. In the field experiment (objective iv), decomposition rates did not vary significantly between the four different forest types, supporting the hypothesis that persistent leaf characteristics of species, rather than forest functional characteristics and environment, are the most important controls on decomposition. Nevertheless, there was evidence that litter mixtures tended to show higher decomposition rates in forest associations where they were collected, than in other forest associations (the "home-field advantage" hypothesis). This result suggests probable variations in leaf-litter substrates determined by forest functional composition. It is believed that this is the first study to apply a functional traits approach to understanding variation of forest ecological characteristics and processes in Mesoamerican mountains. The study shows that dispersal limitation, as well as environmental and anthropogenic factors, probably influences the characteristics of forest stands, and that the degree of functional variation may be smaller than that of floristic variation. The study demonstrates that leaf trait values of dominant tree species influence litter decomposition rates and therefore, potentially, nutrient cycling. Even though litter decomposition rates in the field were most likely to be affected by leaf and litter characteristics, not forest environment, there was evidence for a home-field advantage effect. In the current era of anthropogenic global change effects on the forests of Chiapas, this work sheds new light on forest function and forest change and has special relevance for the design of conservation strategies for the tropical montane ecosystems.

Keywords: functional traits; species distributions; species regeneration; dispersal limitation; after-life effects; home-field advantage.

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COMMONLY USED ACRONYMS

Ag	Site of Aguaje
AIC	Akaike information criterion
ANOVA	Analyses of variance
BA	Basal area
BIC	Bayesian information criterion
BLF	Broad-leaved forest
CONAGUA	Comisión Nacional del Agua
CWM	Community weighted mean value
DBH	Diameter at breast height
Dens	Density of individuals
Dist	Human disturbance level
ECOSUR	El Colegio de La Frontera Sur
En	Site of Encuentro
GPS	Global positioning system
H_{max}	Maximum height
Hu	Site of Huitepec
LA	Leaf area
LCC	Leaf organic carbon content
LDMC	Leaf dry matter content
LNC	Leaf nitrogen content
LPC	Leaf phosphorous content
LTS	Leaf tensile strength
m a.s.l.	Meters at sea level
Mo	Site of Moxviquil
NMS	Non-metric multidimensional scaling
OF	Oak forest
PCA	Principal component analysis
PCNM	Principal coordinates of neighbour matrices
PF	Pine forest
POF	Pine-oak forest
Preci drym	Precipitation of driest month
Preci mean	Mean annual precipitation
Preci season	Precipitation seasonality
RDW	Remaining dry weight
Rich	Species richness
RIV	Relative importance value
Sa	Site of San José
SLA	Specific leaf area
Temp maxw	Temperature of warmest month
Temp mean	Mean annual temperature
Temp minc	Temperature of coldest month
Temp season	Temperature seasonality
Tz	Site of Tzontehuitz
UTM	Universal Transverse Mercator coordinates
WD	Wood density
Zo	Site of Military zone

CHAPTER 1. GENERAL INTRODUCTION

1.1. GENERAL CONTEXT OF THE TROPICAL MONTANE FORESTS AND THE FUNCTIONAL ECOLOGY APPROACH

Tropical forests are amongst the most highly biodiverse terrestrial ecosystems in the world. They are a conspicuous feature of Latin America although far from being uniform since they are not only distributed at lower altitudes but also in mountains (Richter 2008). These ecosystems have been inextricably linked to the evolutionary and social history of humans; however, in the last five decades they have been severely affected by the intensification of new consumption practices and effective ways to extract resources. These human forces have caused rapid land-use change producing, in turn, forest fragmentation and rapid species loss; furthermore, it is expected that current global climate change will affect their structure, diversity and distribution (Theurillat & Guisan 2001; Bugmann *et al.* 2007). Many tropical forests are located in highly biodiverse zones called "hotspots" (Myers *et al.* 2000), predominantly within developing countries where the traditional uses of natural resources are intensive; nevertheless, the requirements for water, food, medicine, and timber, amongst others goods and services, are not only a characteristic of traditional societies but also of modern ones located in developed economies.

In this context, species assemblages of tropical montane forests interact not only with a particularly harsh surrounding environment but also with anthropogenic factors that, potentially, threaten the functions of these ecosystems and the ecosystem services that society receives from them (Chapin III *et al.* 2000). For this reason, understanding of the effects of drivers of change on ecosystems is a main goal in ecology; however, even when a considerable knowledge has been built up on the effects of disturbance agents on the biodiversity of terrestrial ecosystems, their effects on ecosystem functional properties are still rarely linked or associated (Díaz *et al.* 2007a; b). This bias can be partially attributed to biodiversity being considered just as species richness, which means that other important components frequently remain underestimated (Díaz & Cabido 2001).

The novel approach of functional ecology is part of the important quest to explore how changes in spatially and temporally complex forests can influence ecosystem processes and their concomitant effect on ecosystem services. This approach considers that the effects of biodiversity on ecosystem functionality should be attributed to the functional traits of individual species and their interactions with the biotic and abiotic environment, rather than to the species abundance by itself (Díaz & Cabido 2001). The approach allows the scaling-up from the functional traits of organisms to higher ecological levels (e.g. populations, communities or ecosystems; Violle *et al.* 2007). In the context of global change, functional ecology is considered the link between species and the delivery of ecosystem services and, consequently, the inherent link between ecology and socioeconomics.

1.2. GENERAL SCOPE OF THE STUDY, OBJECTIVES AND HYPOTHESIS

Based on the functional ecology approach, the present thesis aims to contribute to the understanding of factors that determine first: the abundance and distribution of tree species, examining both tree and sapling life stages; second, the functional properties of the forest stands that these species make up; and finally, the leaf-litter decomposition process. The study area is the tropical mountains of the region of the Central Highlands, State of Chiapas, Mexico.

The different forest associations of this region (mainly oak, pine, pine-oak, and broad-leaved forests; González-Espinosa *et al.* 1991, 1997) are a very important resource for both the indigenous Mayan and *mestizo* (mixed-race) peoples. As a consequence of the intensive activities of people, the landscapes of the Central Highlands present forest fragments within a matrix of secondary vegetation, settlements, pasturelands and crop fields (Ramírez-Marcial, González-Espinosa & Williams-Linera 2001). The ecological studies so far undertaken have found that the characteristics of the extant forests (e.g. floristic composition, structure) and their dynamics (successional development, early species recruitment, establishment) may best be explained by the interaction of species' physiological restrictions, environmental factors and anthropogenic disturbance (e.g. González-Espinosa *et al.* 1991, 2004; Cayuela, Golicher & Rey-Benayas 2006a; Golicher *et al.* 2008). However, in spite of this relative consensus, the role of dispersal limitation (*sensu* Hubbell 1999, 2001) in the determination of the floristic and functional variation of the forest of this mountainous region has not been determined. If dispersal limitation plays a role, it is critically important to determine how great is its influence with respect to that of other factors, and whether its influence is similar in adult trees and in saplings. In addition, it is not known whether the floristic variation of forests is related to functional variation. Finally, the continued development of the functional ecology requires work that determines how the functional traits of species and the floristic and functional variation in forests influence important ecological processes like leaf-litter decomposition.

In order to contribute to filling these knowledge gaps, this thesis proposes the following specific objectives:

i) characterise both the dominant species and the forest stands they form using functional traits, determining also the trait-trait and species-trait relationships;
ii) characterise the floristic and functional variation amongst forest stands, and the relationship of this variation with spatial and environmental variables;
iii) determine the influence of the traits of species on the abundance of their saplings,
iv) determine the effect of species leaf trait values, forest type, and their interaction, on leaf-litter decomposition.

Given the mountainous and heterogeneous environmental conditions of the region and the high floristic variation already documented, it is expected to find 1) prevalence of environmental factors over spatial factors in the explanation of floristic and functional variation amongst forest stands and 2), a strong association between floristic and functional variation. The prevalence of human impacts in the forests of the Central Highlands led us to expect 3), a strong influence of the functional traits of species on sapling abundances. It was also expected that there would be 4) strong effects of functional traits of leaves on leaf-litter decomposition rates, and finally, due to the marked variation of forest structure and composition, 5) strong effects of forest type on leaf-litter decomposition rates.

In line with the objectives proposed, the investigation is divided into five main sections or chapters. The present introduction (Chapter 1) deals with the scope of the investigation, its conceptual basis and the general characteristics of the study area; Chapter 2 presents an evaluation of the floristic and functional variations amongst forest stands, assessing their relationship with spatial and environmental variables. Chapter 3, presents an assessment of the influence of spatial and environmental factors on floristic variation amongst sapling assemblages but, additionally, assesses the associations of functional traits of dominant species with their sapling abundances. Chapter 4 assesses both the effects of leaf traits of dominant species and forest conditions on leaf-litter decomposition rates. A final discussion is presented in Chapter 5 with the intention of providing an integrated analysis, linking the general findings and presenting the general conclusions and an evaluation of the approaches used.

1.3. GENERAL APPROACH AND METHODS OF THE THESIS

In order to achieve the objectives of this investigation, field and laboratory assessments were performed in different phases during the period from July 2010 to June 2012, in different stands of pine, oak, pine-oak and broad-leaved forests of the Central Highlands, located within the altitudinal range of 2100 to 2800 m a.s.l. Methods used were the following:

For objectives i), ii) and iii), adult trees were counted, measured and identified in 48 0.1 ha plot in the four previously-defined forest types –oak forest, pine-oak forest, pine forest and broadleaved forest– at seven study sites. The same data were taken for saplings in 96 0.05 ha plots, equally divided between stands with open and closed canopies. Plots were characterised in terms of geographical location, altitude above sea level, aspect, anthropogenic disturbance level, and seven climatic variables (mean average temperature and precipitation, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, precipitation of driest month, and precipitation seasonality) taken from Worldclim climate surfaces.

Nine functional traits (leaf area, specific leaf area, leaf tensile strength, leaf dry matter content, leaf nitrogen and phosphorous contents, maximum height and wood density) were measured for the dominant tree species, defined for each individual plot as the species making up 70% of the basal area. Leaf carbon fractions were obtained from leaf-litter of species selected for the decomposition experiments.

For objective iv), leaf litter decomposition rates were measured in a greenhouse experiment for the assessment of trait effects and in a field experiment for the assessment of the effects of conditions in the four forest types.

Statistical analyses for objectives i), ii) and iii) (Chapters 2 and 3) included a) Non-metric multidimensional scaling (NMS) ordination to explore patterns of forest species composition, b) Mantel correlograms to determine the degree of spatial autocorrelation of species composition and environmental factors, and c) variation partitioning analyses to extract individual and combined effects of environmental and spatial factors on floristic and functional variation. Additionally, for the case of adult trees, Pearson's correlations and Principal Components Analysis (PCA) ordination were used to establish relationships between traits, between traits and species and between plot-level community weighted means (CWM) of traits. For the determination of factors affecting the abundances of saplings, analyses of variance (ANOVA) were used to identify differences of species' abundances between stands with open and closed canopies, as well as variation of total sapling abundances between combinations of sites and forest types, both in open and closed canopies.

For the study of decomposition (objective iv), Chapter 4), general mixed models were used to look for significant differences in decomposition rates amongst species, forests and in relation to other factors. Also, Pearson correlation analyses were used to find trait-trait and trait-decomposition rates relationships; PCA ordination to explore species-traits relationships, and Partial Least Squares (PLS) regression to relate species, traits and decomposition rates.

1.4. SOME BASIC CONCEPTS OF THE FUNCTIONAL ECOLOGY APPROACH

1.4.1. Biodiversity, plant functional traits and ecosystem functioning

The term biodiversity encompasses a broad spectrum of biotic scales, from genetic variation within species to biome distributions on the planet (Purvis & Hector 2000). However, in spite of this variety of levels, species richness continues to be the main measure of diversity, even though the existence of strong links between the presence and abundance of certain plant characteristics and types and the rate and magnitude of ecosystem processes has been known for quite a time (Díaz & Cabido 2001; Díaz *et al.* 2013). These links, for example, can be seen in a forest ecosystem where the presence of tree species with certain characteristics of wood, leaves and roots, has important consequences for soil and water retention, as well for climate buffering, animal diversity and nutrient cycling (Díaz & Cabido 2001; Pérez-Harguindeguy *et al.* 2013). In this way, there is a growing consensus that the effects of species diversity on ecosystem properties, processes and functions should be attributed to the functional characteristics or *functional traits* of the species and their interactions rather than to species number *per se* (Tilman 1997; Díaz & Cabido 2001; Hooper *et al.* 2005; Petchey & Gaston 2006; Díaz *et al.* 2006, 2007a). However, although it has recently been shown that community weighted mean values of leaf traits of dominant tree species are correlated with the production of above ground biomass in lowland tropical rain forests (Finegan *et al.* 2015), much more work is required to move tropical forest ecology away from a taxonomic towards a trait-based (McGill *et al*. 2006) approach.

Biodiversity across the different ecological levels is affected in different ways by biotic and abiotic factors. Changes in climate, atmospheric composition, land-use and disturbance regime, and biotic exchanges (deliberate or accidental introduction of organisms to an ecosystem) all have non-random effects on functional diversity, i.e. they select for or against species bearing certain traits (Díaz *et al.* 2006). For example, traits that can determine the performance of a species in a given environment are lifespans, body size, dispersal capacity, resource use and reproductive rate. With this, species with a particular set of trait values will be favoured in particular environments and, therefore, there will be species more vulnerable or susceptible than others to changes.

Changes in the functional structure of species assemblages may affect properties, functions and ecosystem processes and, most importantly for human societies, may affect the provision of ecosystem services (Díaz *et al.* 2006). Such services encompass all the benefits to human material and cultural life and are not restricted to the species *per se*, for example: pollination and seed dispersal, regulation of climatic conditions, control of agricultural pests and diseases, biomass production, nutrient and water cycling, and soil formation and retention (Tilman 1997); as well as provisioning of food, fibre, potable water, shelter and medicines.

1.4.2. Functional traits, functional diversity and related concepts

Violle *et al.* (2007) define a trait as "any morphological, physiological or phenological feature measurable at the individual level, from cell to the whole-organism level, without reference to the environment or any other level of organisation". In contrast, these same authors define a *functional* trait as "any trait which impacts fitness indirectly via its effects on growth, reproduction and survival" (see also Reich *et al.* 2003). On the other hand, Díaz & Cabido (2001) define a functional trait as "the characteristic of an organism that is considered relevant to its response to the environment and/or its effects on ecosystem functioning".

In terms of their usefulness in a particular methodology, plant functional traits can be grouped as whole-plant traits (e.g. growth form, life form, plant height), leaf traits (e.g. specific leaf area, leaf size, leaf dry matter content), stem and belowground traits (e.g. stem specific density, bark thickness, specific root length) or regenerative traits (e.g. dispersal mode, dispersule size, seed mass) amongst others (Cornelissen *et al.* 2003). Sometimes functional traits can be divided into soft and hard traits (Lavorel & Garnier 2002; Cornelissen *et al.* 2003; Violle *et al.* 2007). Soft traits are those relatively easy and quick to quantify for a large number of species and sites, but that are not necessarily explicitly related to a particular functional mechanism; whereas hard traits are usually less accessible but with a direct functional role (Hodgson *et al.* 1999; Lavorel & Garnier 2002). Despite their origin, soft traits can usually be good correlates of other hard traits (Cornelissen *et al.* 2003) and, sometimes, a combination of soft traits can provide a good indicator of a hard trait (for example, soft traits such as seed mass and seed shape providing an idea of seed persistence, a hard trait (Thompson, Band & Hodgson 1993)).

According to their relationship to ecosystem functioning, traits can also be classified into "response" or "effect traits". Response traits are that reflect species responses to variation in environmental conditions whereas effect traits are those that reflect the effects of a species on ecosystem properties.

Functional diversity is a central concept in functional ecology. It refers to the value, range, and relative abundance of functional traits present in a given ecosystem (Díaz & Cabido 2001; Díaz *et al.* 2007a). The value of traits refers to the presence and relative abundance of certain values (or kinds) of, for example, leaf size, nitrogen content, canopy height, seed dispersal and dormancy characteristics, vegetative and reproductive phenology (Díaz & Cabido 2001). The range of traits refers to the difference between extreme values of functional traits, for example, the range of leaf sizes, canopy heights, or rooting depths deployed by different plants in an ecosystem.

Another important concept is plant functional type. It is a set of species showing similar responses to the environment and similar effects on ecosystem functioning (Díaz & Cabido 2001). Functional types can also be divided into functional response and functional effect types (Díaz & Cabido 2001; Hooper *et al.* 2002; Lavorel & Garnier 2002). Functional response types are groups of plant species that respond in similar ways to the biotic and abiotic environment, such as resource availability, climatic conditions, or disturbance regime (e.g. xerophytic versus mesophytic species, gap versus understory species, fire tolerant versus fire intolerant, drought or frost resistant versus susceptible and grazing tolerant versus grazing intolerant). Functional effect types are groups of plants that have similar effects on the dominant ecosystem processes, such as primary productivity, nutrient cycling and trophic transfer (for example nitrogen fixers, ecosystem engineers, nurse species and fire-promoting species).

Functional response and effect types often coincide, particularly in the case of resource use; for example, traits that confer high resistance to environmental stress and herbivory (i.e. response) are also associated with slow decomposition and thus a slower rate of nutrient cycling (i.e. effect). As Díaz & Cabido (2001) have pointed out, these groupings tend to be based on common attributes rather than on phylogenetic relationships. There is no universal functional type classification and functional types are, like most categories used to simplify the natural world, arbitrary divisions of a relatively continuous trait space.

1.4.3. Functional diversity, resource dynamics and ecosystem stability

Ecosystem resource dynamics comprise the magnitude (how much) and rate (how fast) of inputs, outputs, and internal cycling of key resources (carbon, water, mineral nutrients) within an ecosystem, at a particular time (Petchey 2000; Díaz & Cabido 2001). There are two mechanistic explanations for the role of plant diversity in ecosystem resource dynamics: the selection effect and the niche complementarity effect. The selection effect states that with high species richness in a community there would be more possibilities to find species with important traits that can dominate ecosystem functioning. Conversely, the niche complementarity effect states that with higher diversity there would be a greater range of functional traits providing opportunities for more efficient resource use in a spatially or temporally variable environment. The selection effect stresses the presence of certain key trait values whereas the niche complementarity effect stresses the presence of a range of different traits (Díaz & Cabido 2001).

Ecosystem stability is the capacity of a given ecosystem to persist in the same state (Díaz & Cabido 2001). It has two components: ecosystem resistance and ecosystem resilience. Ecosystem resistance is the ability to persist in the same state in the face of a perturbation. Ecosystem resilience is the capacity of a system to absorb perturbation and reorganise while undergoing change resulting in it retaining essentially the same function, structure, identity, and feedbacks (Walker *et al.* 2004). In terms of functional diversity, it implies that the presence of several different functional groups and the interactions amongst them can offer ecological resilience to a community against disturbances (Peterson *et al.* 1998).

Another important concept is functional redundancy. This mechanism is responsible for the maintenance of long-term ecosystem functioning (Díaz & Cabido 2001). Two or more species are considered redundant when the disappearance of one or more of those species does not affect a particular ecosystem process in a significant way. This is because the species removed represents "redundant information" with respect to that particular process. In terms of functional diversity a high functional redundancy occurs when species overlap in their trait values (Flynn *et al.* 2009). It implies that the larger the number of functionally similar species in a community the greater the probability that at least some of these species will survive changes in the environment and maintain the properties of the ecosystem. It can be seen as an insurance policy against the loss of function in the event that species are lost.

In the context of changes in species assemblages, an accurate measure of functional diversity can then explain and predict changes in ecosystem functioning.

1.5. ECOLOGICAL SIGNIFICANCE OF THE FUNCTIONAL TRAITS USED IN THIS STUDY

The eight functional traits of tree species determined in this study are all continuous measures and represent important parameters to tackle ecological questions at the scale of species, ecosystems, landscapes or biomes (Cornelissen *et al.* 2003). Their ecological significances are briefly described below.

Leaf area (LA). Leaf area is the most common metric for leaf size and is defined as the one-sided or projected area of an individual leaf (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013). Leaf area has important consequences for leaf energy and water balance. Variation in LA amongst species has been related to climatic variation, geology, altitude and latitude, where stress (e.g. caused by heat, cold, drought, nutrient shortage, excessively high-radiation) tends to select for relatively small leaves. Within climatic zones, variation in LA may also be linked to allometric factors (plant size, branch size, anatomy and architecture, leaf number, number of lateral buds produced) and ecological strategy with respect to environmental nutrient stress and disturbances, and phylogenetic factors can also play an important role.

Specific leaf area (SLA). Specific leaf area is the light-capturing foliar area per unit of leaf biomass invested (Larcher 2003; Poorter *et al.* 2008). This trait is a positive correlate of the potential relative growth rate of species or its mass-based maximum photosynthetic rate (Cornelissen *et al.* 2003). Leaves with low values of SLA tend to be thick and dense, and thus physically robust and less attractive to herbivores than leaves with high SLA (Coley 1983; Wright & Westoby 2002); that is, low values of SLA are associated with relatively high investments in leaf "defences" (particularly structural ones). Moreover, these kinds of leaves tend to be longer-lived, which by itself may lead to longer plant life spans (Sterck, Poorter & Schieving 2006). On the other hand, species in resource-rich environments tend to have larger SLA than those in environments with resource stress, although some shade-tolerant woodland understorey species are known to have remarkably large SLA as well (Cornelissen *et al.* 2003). Species with high SLA tend to have high nutrient concentrations and mass-based photosynthesis and respiration rates (Reich, Walters & Ellsworth 1992; Wright *et al.* 2004; Poorter & Bongers 2006). Interspecific variation in seedling growth rate is largely driven by variation in SLA (Wright & Westoby 1999).

Leaf dry-matter content (LDMC). Sometimes referred to as tissue density, LDMC is simply the ratio of leaf dry mass to fresh mass (Wilson, Thompson & Hodgson 1999; Garnier *et al.* 2001). Leaf dry matter content is an indicator of a plant species' resource use strategy, i.e. its position in a fundamental trade-off between a rapid assimilation and growth at one extreme, and efficient conservation of resources within well-protected tissues at the other (Wilson *et al.* 1999; Garnier *et al.* 2001; Vaieretti *et al.* 2007). In general, it correlates negatively with potential relative growth rate and positively with leaf life-span, but the strengths of these relationships are usually weaker than those involving SLA (Cornelissen *et al.* 2003). Leaves with high LDMC tend to be relatively tough (i.e. highly related with physical strength) and are thus assumed to be more resistant to physical hazards (e.g. herbivory, wind, hail) and to have slower decomposition rates than leaves with low LDMC. Moreover, species with low LDMC tend to be associated with productive, often highly disturbed environments.

Leaf tensile strength (LTS). This trait basically represents leaf toughness (Cornelissen & Thompson 1997; Balsamo *et al.* 2006). It is a good indicator of the carbon investment in structural protection relative to photosynthetic tissues (Cornelissen *et al.* 2003). As a general tendency, physically stronger leaves are better protected against mechanical damage (e.g. wind, hail, even herbivory), contributing to longer leaf lifespans. These stronger leaves are also better protected against herbivory, although other kinds of defences are important too (e.g. spines, secondary metabolites for chemical defence). On the other hand, physical investments in leaf strength tends to have afterlife effects in the form of poor litter quality for decomposition (Cornelissen *et al.* 2003).

Leaf nitrogen and phosphorus concentration (LNC, LPC). These foliar concentrations have been used in several studies of litter decomposition in order to understand both the particularities of biogeochemical cycles in ecosystems and the nutrient status of plants (for instance, Cornelissen & Thompson 1997; Pérez-Harguindeguy *et al.* 2000; Liu, Fox & Xu 2000; Vaieretti *et al.* 2005). Grime *et al.* (1997) found that high foliar concentrations of N and P (as well of K, Ca, Mg) are highly correlated with the capacity of plants for rapid growth under productive conditions and an inability to sustain yield under a limiting supply of nutrients. In particular, across species, LNC tends to be closely correlated with mass-based maximum photosynthetic rate (Garnier *et al.* 2004). Interspecific variations of these traits are frequently correlated and the LNC:LPC (N:P) ratio is used as a tool to assess whether the availability of N or P is more limiting for carbon cycling processes in ecosystems (Cornelissen *et al.* 2003).

Wood density (WD). Wood density represents the biomass invested per unit of wood volume (Poorter *et al.* 2008). Wood density is closely linked to plant species' growth rate (in general, high growth rate with low WD). Low WD can contribute to higher stem volume growth rate because more volume is produced per unit biomass (King *et al.* 2005). Conversely, high-density woods are formed of small cells with thick walls and limited intercellular space (Castro-Díez *et al.* 1998), therefore a dense stem provides the structural strength that a plant needs to stand upright (in a broad sense, greater stem densities are related to taller plants (Cornelissen *et al.* 2003)). In general, there is a correlation between high defence and high wood density: dense stems are more resistant to breakage (van Gelder, Poorter & Sterck 2006) and to fungal and pathogen attack (Augspurger 1984), thus contributing to enhanced plant survival (Muller-Landau 2004) In combination with plant size-related traits, high wood density also plays an important global role in the above-ground storage of carbon (Chave 2001; Cornelissen *et al.* 2003; Chave *et al.* 2008).

Maximum adult height (H_{max}). This trait is tightly correlated with competition amongst plants to access light (Reich *et al.* 2003; Poorter *et al.* 2005, 2008). In general, taller plant species have the possibility to capture more light and thus potentially achieve faster growth rates. Competition for light is asymmetrical therefore height tell us about the position of a plant in the light hierarchy of the canopy (Reich *et al.* 2003). Moreover, Cornelissen *et al.* (2003) have mentioned that plant height is associated with plant fecundity, with growth time intervals, and with tolerance or avoidance of environmental stress due to climate, disturbance or nutrient shortage. On the other hand, plant height is well correlated allometrically with other traits in interspecific comparisons, for instance aboveground biomass, rooting depth, lateral spread and leaf size (Gaudet & Keddy 1988; Westoby 1998; Thomas & Bazzaz 1999; Cornelissen *et al.* 2003).

1.6. GENERAL CHARACTERISTICS OF THE STUDY AREA

1.6.1. State of Chiapas, physiography and montane forests

The state of Chiapas is located in the southernmost part of Mexico, on the Pacific Coast between the border with Guatemala and the Isthmus of Tehuantepec, covering more than 74,000 km^2 (Fig. 1.1). Chiapas is the second richest Mexican state in biodiversity and this feature is in part attributable to the complex topography arranged within the seven physiographic regions defined by Mullerried (1957): Pacific Coastal Plain, Sierra Madre, Central Depression, Central Plateau (or Central Highlands), Northern Highlands, Eastern Highlands and Gulf Coastal Plain (Fig. 1.1). Climate varies from warm to temperate and vegetation varies from semi-desert to rainforest, as well from mangrove forests at sea level to sub-alpine vegetation on peaks as high as 4,000 m (Breedlove 1981).

The montane forests in Chiapas are mainly situated along the Sierra Madre, the Central Highlands (Central Plateau) and the Northern Highlands, distributed from 1,000 m to above 2,000 m a.s.l., associated with cooler conditions, with marked dry and wet seasons and an important supplement of horizontal precipitation (Breedlove 1981; Challenger 1998). According to the classification of Breedlove (1981), this altitudinal range includes at least four forest communities: *Pinus-Quercus*, *Pinus-Quercus-Liquidambar*, montane rain forest and evergreen cloud forests. In general, forest patches of each of these communities within one of these regions are more similar to each other than to patches of the same floristic community in a different physiographic regions (Breedlove 1981). This means, for instance, that two pine-oak communities from the same region are more alike in structure and composition than two pine-oak forest communities from two different regions.

Figure 1.1 State of Chiapas, and its physiographic regions.

1.6.2. Montane forests of the Central Highlands of Chiapas

The most exhaustive information about floristic and ecological issues on montane forests of Chiapas is probably available for the Central Highlands. Forests of this region exist in a landscape as a mosaic of vegetation fragments embedded in a matrix of agricultural fields, livestock pasture and settlements (González-Espinosa *et al.* 1997). Vegetation in general shows a wide superposition both in distribution and successional age, making it difficult to delimit in time and space. Relatively conserved communities are restricted to mountain summits, gullies or canyons or the scarce protected areas administrated by indigenous communities, municipalities or military authorities.

Miranda (1952) and Breedlove (1973, 1981, 1986) made early studies of the composition and structure of the different forest associations of the Central Highlands. More recently, González-Espinosa *et al.* (1997) proposed to divide the local montane forests into four general types: cloud forest, oak forest, pine-oak forest and pine forest. Cloud forests occur in the vicinity of humid summits (mostly above 2400 m), in relatively small and isolated patches. Trees here maintain a great number of bromeliads, ferns, mosses, lianas and vines. The canopy is frequently dominated by a wide diversity of broad-leaved species, mainly individuals of 20-30 m height. The lower arboreal stratum and shrub and herbaceous strata are, as well, highly diverse.

Oak forests frequently occupy the humid areas adjacent to the montane cloud forest which they resemble in composition and structure, including an abundance of epiphytes. *Quercus* species dominate the canopy but there is high species diversity in the lower strata. Pine-oak forests are the most extensive forest type of the Central Highlands. Trees here can reach 20-40 m in height and vascular epiphytes are common in more dense forests. The canopy is dominated by several species of oaks and pines. Pine forest is the least diverse vegetation type with the simplest composition and structure, almost without lower arboreal strata. This vegetation type is frequently located in the least humid places of the region and its distribution has been maintained through succession following deforestation by farming and livestock (extensive grazing, periodic fires to renew pasturelands and selective extraction of oaks for firewood and charcoal).

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CHAPTER 2. DRIVERS OF TREE COMMUNITY COMPOSITION AND TURNOVER OF MONTANE FORESTS OF THE CENTRAL HIGHLANDS OF CHIAPAS, MEXICO: EVIDENCE FROM TAXONOMIC AND FUNCTIONAL VARIATION

2.1. ABSTRACT

There is an active debate in ecology about the influence of niche and dispersal factors on species distributions and assemblages. Our overall aim was to define their relative importances in the configuration of tree species assemblages of the montane forest ecosystems of the Central Highlands, state of Chiapas, Mexico. Specifically, we sought to 1) describe and quantify floristic and functional variation amongst different forest remnants, 2) assess the degree of spatial autocorrelation of floristic and functional composition and climatic variables at a range of spatial scales, and 3) compare the relative influences of spatial variables, climatic variables, altitude above sea level, aspect and human disturbance on floristic and functional variation. We hypothesised that environmental factors and human disturbance would play the most important roles in the determination of forest variation in this very heterogeneous landscape with its long history of human disturbance. An intensive sampling of adult trees (> 5 cm DBH) was carried out in 48 plots (0.1 ha each) and an accurate determination of nine functional traits (leaf area, specific leaf area, leaf tensile strength, leaf dry matter content, and leaf nitrogen, phosphorous and carbon contents; wood density and maximum height) was done for each of 26 dominant species. Each of the sample plots was floristically, environmentally and spatially characterised, and functional characteristics of each one were determined using basal-area weighted mean trait values (CWMs). Ordination, cross-species correlations of trait values and spatial statistics were used to analyse the resulting data. The landscape was found to contain a mosaic of floristically and functionally differentiated forest stands in which three main functional groups of tree species were identified: *Quercus* species and *Pinus* species, which both reach the forest canopy or sub-canopy, and a third group of a wide taxonomic range of species that generally develop in the understorey. Variation partitioning showed that the floristic variation was more related to spatial variables derived from Principal Components of Neighbour Matrices ($R^2 = 0.11$, $P < 0.005$) than to climate ($R^2 = 0.06$, $P < 0.005$), whereas human disturbance was the factor most strongly linked to functional variation ($R^2 = 0.21$, $P < 0.005$) although spatial variables were also important ($R^2 = 0.07$, $P < 0.005$). The strong relationship of spatial variables with floristic variation suggests the need to consider the potential effect of dispersal limitation and stochastic factors, as well as climate variation and human disturbance, as drivers of the forest composition of the Central Highlands. The results also emphasise the strong effect of human disturbance on the functional variation amongst forest stands. Thus, floristic composition and functional characteristics of these forests appear to respond to different drivers. Floristic change may occur due to spatial factors without corresponding functional change, so that a major characteristic of these forests is broad patterns of functional characteristics imposed by human disturbance, to an extent independently of floristic composition.

Keywords: Functional traits; tropical mountains; beta diversity; niche assembly; dispersal limitation.

2.2. INTRODUCTION

To understand how species are distributed through space and form communities is a major goal in ecology (Weiher *et al.* 2011; Götzenberger *et al.* 2012). For decades there was a consensus about the importance of deterministic factors in defining plant distributions and assemblages until the case made by Hubbell (1999) for the importance of stochastic factors. This questioned the status of environmental equilibrium as a dominant factor and, for a time, polarised the debate between either niche or dispersal theory. Niche theory indicates that environmental conditions and competitive exclusion mainly determine the presence of a species at a given point in space and time and, therefore, species assemblage is a non-random characteristic of ecological communities (de Blois, Domon & Bouchard 2002; Austin 2002; Jones *et al.* 2006). On the other hand, the dispersal assembly concept proposes that the presence of a given species in a given community is mainly a result of its own dispersion capacity (dispersal limitation), i.e. the species assemblage is a more or less stochastic phenomenon and is strongly defined by the composition of surrounding communities, greatly affected by distance-dependent processes (Hubbell 2001; Weiher *et al.* 2011).

Since the niche and dispersal models are not mutually exclusive (Götzenberger *et al.* 2012), there is a current tendency to include both explanations (Barot 2004; Adler, Hillerislambers & Levine 2007) suggesting an integrative hypothesis (continuum hypothesis, Gravel *et al.* 2006). However, research on how species assemble throughout landscapes is still far from producing definitive answers (Hubbell 2005; Liu *et al.* 2013), primarily because of two challenging aspects. Firstly, many studies still see communities as ecological units with individual integrity (Harrison & Cornell 2008; Ricklefs 2008) and fail to integrate influences of large-scale patterns, regional processes and historical factors (Ricklefs 1987, 2007, 2008; Chase 2003; Jenkins & Ricklefs 2011). Secondly, the scale of this regional-historical viewpoint is less amenable to experimentation than are local processes in ecological time, although non-experimental testing of hypotheses and many mathematical and statistical tools have recently been developed to disentangle the effects of ecological factors on species distribution and coexistence (e.g. Ricklefs 1987; Legendre & Legendre 1998; Legendre 2007).

The use of the metacommunity concept (a set of local communities linked by dispersal of multiple potentially interacting species (Gilpin & Hanski 1991; Sloan Wilson 1992; Leibold *et al.* 2004)) and its related terms beta diversity (a quantitative measure of the amongst-site variation in community composition (Tuomisto 2010)) and gamma diversity (the regional source pool of species (Ricklefs 1987; Huston 1999)) has been helpful for studies at the landscape scale. In addition, in recent years the species' functional traits approach has been incorporated into research on community assembly since traits (such as toughness and size of leaves, wood density, maximum plant height) may indicate where a species can occur in the landscape relative to the properties of the local environment, and whether it has an advantage over competitors in those locations (Sokol *et al.* 2011). This new focus is considered more ecologically meaningful than assessments based solely on extant taxonomic composition (Sokol *et al.* 2011) allowing scaling-up from organisms to higher ecological levels, permitting more direct understanding of how species assemblages interact with environmental factors (Keddy 1992; Díaz & Cabido 2001; Violle *et al.* 2007; Díaz *et al.* 2007).

Studies of community species composition and turnover have been particularly prolific in the highly diverse forest systems of tropical America. While some of them find evidence for the role of processes linked to species' niches in community assembly (e.g. Pyke *et al.* 2001; Duque *et al.* 2002; Phillips *et al.* 2003; Tuomisto *et al.* 2003; Jones *et al.* 2006, 2008; Sesnie *et al.* 2009) others find more evidence for the role of dispersal (e.g. Chust *et al.* 2006; Normand *et al.* 2006; Duque *et al.* 2009; Chain-Guadarrama *et al.* 2012). However, few of these studies have incorporated important environmental factors such as altitude (as do Chain-Guadarrama *et al.* 2012) or natural or anthropogenic disturbance. Additionally, even when some studies include the functional approach, they have mostly been carried out in lowlands where the environment could be relatively uniform over wider areas. In contrast, the environment in tropical mountains abruptly changes over relatively short distances affecting such important factors as temperature, soil, solar radiation and wind (Grubb 1977; Larcher 2003; Körner 2004; Becker *et al.* 2007; Richter 2008; Malhi *et al.* 2010), and under these conditions the evolution, dispersal and establishment of species have formed well-defined distinct communities.

In the context of the diverse montane forest ecosystems of the Central Highlands region, state of Chiapas, Mexico, this study aims to evaluate the influence of different important drivers on the spatial variation of both species and their functional traits. Due to the mountainous topography of the region, highly affected by pre-Columbian and contemporary human activities (González-Espinosa *et al.* 1991, 1997), local ecological studies have found that the composition of the extant forest associations (mixed broad-leaved, pine-oak, oak, and pine dominated forests), their characteristics (e.g. composition, structure) and their dynamics successional development, early species recruitment, establishment) may be well explained by the interaction of species' physiological restrictions, environmental factors and anthropogenic disturbance (e.g. González-Espinosa *et al.* 1991, 2004; Cayuela, Golicher & Rey-Benayas 2006a; Golicher *et al.* 2008). This leads to a key ecological question: how great is the role of stochastic events in determining variation in species composition in these heterogeneous conditions? From this, do spatial variation in species and their functional traits respond more, equally or less to environmental differences amongst sites (in support of the niche theory) than to geographical distance amongst sites (in support of the dispersal limitation theory)? Furthermore, how do the changes in floristic and functional similarity differ in their response to environmental or distance gradients?

In order to answer these questions, we 1) characterise the floristic and functional variation of the extant tree associations and 2) characterise forest sites in terms of climate variables, altitude, geographical position, aspect and human disturbance level. From this, we proceed to i) evaluate the degree of spatial autocorrelation of floristic and functional composition at a range of spatial scales and ii) assess and compare the single and combined influence of spatial and environmental factors on the floristic and functional variation. By using a spatial statistics approach (Legendre & Legendre 1998), we expect to find evidence of the importance of environment (climate, aspect and altitude) in determining floristic and especially functional variation. In contrast, the role of dispersal limitation will be indicated when this variation is more closely related to geographical distance, independently of other factors.

2.3. METHODS

2.3.1. Study sites, sampling and forest types description

The Central Highlands in the state of Chiapas, Mexico, extend over 11,000 km^2 with an elevation range from 600 to 2900 m a.s.l., mostly above 1500 m (Cayuela *et al.* 2006c; b). The topography is highly abrupt with moderately steep slopes (mean = 14.8°, SD = 9.6°) whereas the underlying geology is carboniferous limestone with many rocky outcrops. The soils are a mixture of thin lithic rendzinas, deeper humic acrisols in forested areas, and infertile chromic luvisols (Cayuela *et al.* 2006c; a; b).

The sampling was performed in the middle portion of the region, within an altitudinal range of 2200-2900 m a.s.l., between 16° 36'-16° 50' N and 92° 30'-92° 44' W, covering an approximate area of 230 km^2 (Fig. 2.1). The general climate of the central part of the study area is cool (mean annual temperature ranges from 13 to 15 °C) and humid (mean annual rainfall ranges between 1000 and 1300 mm), with a 5-6 month dry season, from the records of the climatic stations of Chamula, La Cabaña and Chilil of the National Commission of Water (CONAGUA 2012) (Table 2.1. See approximate locations in the Fig. 2.1).

The first stage of the sampling strategy was identifying potential sites in terms of their forest cover, their forest types defined in previous studies (if applicable), their conservation status, and the ease of access and permission for the fieldwork. In order to encompass the four forest associations recognized in the study area, in each of the selected sites we carried out an *a priori* forest identification based on the definitions of González-Espinosa *et al.* (1997), mainly based on the dominant genera (*Pinus* forests, PF; *Quercus* forests, OF; *Pinus*-*Quercus* forests, POF, or broad-leaved and not dominated by *Quercus*, BLF). With this, a design of three sites per forest type, giving 12 combinations between forest type and site (Fig. 2.1). Four rectangular sample plots were established at each site giving a total of 48 rectangular plots each of 0.1 ha (20 × 50 m). These forest type-site combinations allowed the characterisation of the dominant species for each group of four plots, necessary for the subsequent trait determination. The floristic and structural characteristics are summarised in Table 2.2 and the procedures for the traits determination in the next section.

Only stands with ≥ 5 m canopy height and ≥ 30 m between the sample plot edge and forest edge were included in the sampling; additionally, a separation distance of at least 300 m amongst plots, achieved by direct measurement in the field and use of Google Earth maps, was defined in order to reduce local-scale autocorrelation as much as possible (Sesnie *et al.* 2009). With these criteria applied, a total of seven different sites unevenly distributed along the irregular terrain of the region were identified that contained the range of four forest types (Fig. 2.1, Table 2.2): private forest reserves of Huitepec (BLF, OF), Moxviquil (OF) and El Encuentro (PF); state forest reserve of San José (POF), military forest reserve of 31 Military zone (BLF, POF, PF), and communal indigenous forest reserves of El Aguaje (POF, PF) and of Tzontehuitz mountain (BLF, OF). Due to the size of some of these reserves, a few plots had to be placed as close as possible outside their boundary, trying to sample the range of floristic and structural associations as much as possible.

Figure 2.1 The Central Highlands (circled in blue within the box) in the state of Chiapas, Mexico, and the location of the 48 0.1 ha sample plots and their corresponding sites and forest types (compare with Table 2.2). Broad-leaved forests (BLF) are in green dots, pine-oak forests (POF) in yellow, oak forests (OF) in light blue and pine forests (PF) in red. The location of three climatic stations (Table 2.1) is shown as orange dots.

Table 2.1 Precipitation and temperature values given by nine climate stations of the National Commission of Water (CONAGUA) located within or in the vicinity of the study area. The corresponding climatic values obtained from WorldClim data layers (Hijmans *et al.* 2005), for the same geographic locations, are also shown for comparison purposes. The approximate locations of the three nearest stations (Chamula, Cabaña and Chilil) are shown in Figure 2.1. The stations of Tzontehuitz and Ollas, denoted with an asterisk (*) are also located within the study area although their short-period data was considered unreliable because of many inconsistences observed. Temp mean = mean annual temperature, Temp max = mean annual maximum temperature, Temp min = mean annual minimum temperature, Preci mean = mean annual precipitation.

Climatic station name and years registered	Altitude (m)	Location (latitude, longitude)	Preci mean (mm)	Temp mean (°C)	Temp max (°C)	Temp min (°C)	WorldClim data	
							Preci mean (mm)	Temp mean (°C)
Chamula 44 years	1930	16°47'49" 92°41'48"	1288.0	13.7	20.7	6.6	1204	14.2
Cabaña 55 years	2113	16°42'51" 92°37'44"	1084.7	15.0	21.9	8.1	1193	15.1
Chilil 42 years	2266	16°40'40" 92°29'21"	1220.0	14.0	20.5	7.4	1142	14.2
Larrainzar 38 years	2000	16°53'13" 92°42'56"	1737.9	15.4	21.6	9.2	1565	16.3
Chenalho 40 years	1537	16°53'37" 92°37'32"	1596.3	17.4	23.4	11.4	1939	19.0
Amatenango 66 years	1950	16°33'10" 92°28'30"	1351.0	16.5	23.3	9.6	1364	17.4
Chiapilla 42 years	550	16°34'39" 92°42'55"	1032.7	24.9	32.0	17.8	1204	23.5
Tzontehuitz * 18 years	2570	16°50'02" 92°34'49"	2062.0	17.0	22.6	11.4	1305	13.0
Ollas * 4 years	2450	16°46'60" 92°32'60"	1700.2	12.6	17.5	7.6	1212	13.4

Table 2.2 Structural and environmental characteristics (in ranges) and sets of dominant species (70% of basal area in each sample plot) of each of 12 forest type-site combinations of the study area (four plots of 0.1 ha per combination, stems $\geq$ 5 cm dbh). The locations of the forest types defined *a priori*, their sites and plots, are shown in Fig. 2.1. BLF = broad-leaved forest, POF = pine-oak forest, OF = oak forest, PF = pine forest; Hu = Huitepec, Tz = Tzontehuitz, Zo = Military zone, Ag = Aguaje, Sa = San José, Mo = Moxviquil, En = Encuentro; Temp mean = mean annual temperature, Preci mean = mean annual precipitation.

Forest	Site	Species number	Basal area (m^2 ha^{-1})	Density (ind ha^{-1})	Dominant species	Altitude (m)	Temp mean (°C)	Preci mean (mm)
BLF	Hu	16 - 24	53.78 - 67.95	1200 - 1760	*Quercus laurina, Q. rugosa, Clethra macrophylla, Styrax magnus, Arbutus xalapensis, Quetzalia contracta*	2533 - 2698	12.9	1249
	Tz	17 - 26	48.79 - 85.60	1570 - 3110	*P. americana, Q. ocoteaefolia, Symplocos breedlovei, Quetzalia contracta, Miconia glaberrima, Prunus rhamnoides, Ternstroemia lineata, Clethra oleoides, Weinmannia pinnata, Oreopanax xalapensis*	2651 - 2777	11.7 - 12.6	1309 - 1396
	Zo	14 - 19	47.41 - 61.09	880 - 1200	*Q. laurina, Cornus disciflora, Q. rugosa, Chiranthodendron pentadactylon, P. ayacahuite*	2488 - 2527	12.9	1187
POF	Ag	5 - 10	25.08 - 38.88	1240 - 1520	*P. montezumae, Q. crispipilis, Q. rugosa, Arbutus xalapensis, P. tecunumanii, Q. segoviensis*	2363 - 2449	13.1 - 14.1	1121 - 1177
	Sa	6 - 15	31.28 - 51.64	1060 - 1680	*P. tecunumanii, Q. rugosa, Q. crassifolia, P. pseudostrobus var apulcensis , Q. crispipilis*	2314 - 2399	13.8 - 14.0	1144 - 1167
	Zo	12 - 13	49.31 - 54.28	770 - 1080	*Q. rugosa, Q. laurina, P. tecunumanii*	2663 - 2735	11.8 - 12.0	1267 - 1293
OF	Hu	8 - 15	46.56 - 52.02	870 - 1680	*Q. crassifolia, Q. rugosa, Q. laurina*	2317 - 2396	13.9 - 14.1	1138 - 1146
	Mo	9 - 11	26.59 - 44.68	1100 - 2110	*Q. segoviensis, Q. rugosa, Q. crispipilis*	2213 - 2337	13.6 - 15.1	1166 - 1230
	Tz	10 - 17	37.84 - 50.70	750 - 2820	*Q. ocoteaefolia, P. pseudostrobus var. pseudostrobus, Buddleja cordata, Persea americana*	2646 - 2817	11.7 - 12.7	1289 - 1396
PF	Ag	1 - 7	29.91 - 34.57	430 - 1200	*P. montezumae*	2280 - 2370	13.8 - 14.0	1115 - 1123
	En	3 - 11	31.65 - 55.01	1050 - 1150	*P. tecunumanii*	2290 - 2331	14.3	1135 - 1141
	Zo	1 - 6	36.18 - 66.00	320 - 1020	*P. montezumae, P. tecunumanii*	2354 - 2395	13.6 - 13.9	1116 - 1138

All tree individuals ≥ 5 cm in diameter at breast height (DBH) within each plot were counted, identified and measured for DBH. Identification was carried out in the field using a catalogue with morphospecies identified by the expert knowledge of local researchers and parataxonomists in the field team for those individuals that could be reliably identified by those means. For others, voucher specimens were collected and identified by a member of the field team at the herbarium of ECOSUR (San Cristóbal de Las Casas) using local floras and comparison with specimens. Once identified, the species were assigned to their corresponding forest strata according to our field observations and the descriptions given by the species list included in González-Espinosa *et al.* (1997).

The geographical position of each sample plot was determined by a Garmin GPS whereas altitude (in m a.s.l.) and slope angle (in degrees) were obtained with a Suunto altimeter and clinometer, respectively. The plots were also qualitatively characterised by general aspect (north, south, east or west-facing slope, or flat) and their degree of anthropogenic disturbance in five ordinal levels: 1, 2, 3, 4 and 5 (with 5 being the most disturbed). This classification was formed by several recorded characteristics of each plot: protection status, land-use history, and intensity and frequency of current anthropogenic disturbance of the site, together with estimated percentages of canopy, shrub and herbaceous cover, the diameter and height of the sampled trees and occurrence of cut stumps.

2.3.2. Functional traits measurement and functional characterisation

Nine functional traits were measured as continuous variables: leaf area (LA) in mm^2, specific leaf area (SLA) in $mm^2\ mg^{-1}$, leaf dry matter content (LDMC) in mg g^{-1}, leaf tensile strength (LTS) in N mm^{-1}, leaf nitrogen concentration (LNC) in mg g^{-1}, leaf phosphorus concentration (LPC) in mg g^{-1}, leaf organic carbon concentration (LCC) in mg g^{-1}, wood density (WD) in g cm^{-3}, and maximum plant height (H_{max}) in m. These traits were selected not only for their relative ease of measurement in the field or laboratory but mainly because they are known to be well linked to the plant functions of potential relative growth rate (LA, SLA, WD), plant and leaf life spans (LA, SLA, LDMC, WD), photosynthetic rate (LA, SLA), nutrient conservation in resource-rich or resource-poor environments (SLA, LDMC, LNC, LPC, WD), above-ground biomass (WD, H_{max}), access of plant to light (H_{max}, WD), protection, defence and resistance to physical or mechanical damage (SLA, LDMC, LTS, WD), amongst others (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013). Given these associations, this trait set is predicted to correlate with species relative abundance along the gradients of distance, altitude, climate and disturbance.

Following the mass ratio hypothesis (Grime 1998), these trait determinations were completed only for the set of dominant species of each of the twelve forest type-site combinations (Table 2.2). For this, the basal area of each species was calculated in each of the 48 plots, and for each plot the species were ranked by basal area in order to identify the set of most dominant species comprising 70% of the total basal area. Subsequently, these plot-dominant species sets were grouped by their corresponding forest-site combination (four plots per combination). This produced a primary set of 26 dominant species. However, because several species were present in the dominant set in more than one forest type-site combination, we made two or more determinations of their values of each trait. This resulted in a total of 49 data sets which enabled a more accurate characterisation of forest functional variation in relation to environment and spatial factors (Appendix 2.1).

Measurement methods are briefly explained in Appendix 2.2 and followed the protocols of Cornelissen *et al.* (2003) and Pérez-Harguindeguy *et al.* (2013), with minor modifications where required. In general, the five healthiest and sun-exposed trees per species per forest type-site combination were sampled for trait determination. Leaf samples attached to twigs (five per individual) were selected based on being the healthiest, complete, fully expanded and sun-exposed. Both the wood and the leaf samples obtained were tagged and stored in cool conditions until measurement in the laboratories of ECOSUR. Oven-dry weight was determined using a standard of 60 °C and a minimum of 96 hours with periodic verification of the constant weight (Cornelissen *et al.* 2003).

A community weighted mean value (CWM) of each of the nine traits was determined for each of the 48 plots by means of f-Diversity software (Casanoves *et al.* 2011) (Appendix 2.3). This community-aggregated metric represented the expected value of a given functional trait for a tree selected at random in a given plot (Garnier *et al.* 2004; Violle *et al.* 2007; Díaz *et al.* 2007; Lavorel *et al.* 2008) and was calculated as the sum of the resulting products between the trait values of the plot's dominant species and those species' relative basal area.

2.3.3. Climatic characterisation

Average annual temperature and precipitation for each of the 48 plot locations were taken from 30 arc-second (approx. 1 km^2) resolution grids, from the WorldClim Webpage (http://www.worldclim.org/) (Appendix 2.4). Other climate variables were obtained from BIOCLIM, a section of WorldClim: temperature seasonality (standard deviation of monthly mean temperature x 100), maximum temperature of warmest month, minimum temperature of coldest month, precipitation of driest month, and precipitation seasonality (coefficient of variation of monthly mean temperature). These bioclimatic variables are derived from the monthly temperature and rainfall values and were used as indicators of potentially extreme or limiting climatic factors at the forest locations. Hijmans *et al.* (2005) present a comprehensive description of the methods used to produce the WorldClim data layers.

The 48 sample plots were all within a narrow altitudinal range of 604 m from 2213 to 2817 m a.s.l., and according to the WorldClim data varied little in mean annual temperature (11.7 to 15.1 °C) and mean annual precipitation (1115 to 1396 mm), with only minor differences in the temperature ranges of the warmest and coldest months (Appendix 2.4). Most of these results were coincident with those from three climatic stations of CONAGUA located at the centre of the study area (Chamula, Cabaña, and Chilil, Fig. 2.1, Table 2.1), already validated by Díaz Hernández *et al.* (2000). However, it was not possible to directly verify the slightly higher precipitation in the WorldClim data of the northern portion corresponding to the Tzontehuitz site (Fig. 2.1) since the two nearest climatic stations (Tzontehuitz and Ollas) have highly overestimated and inconsistent data. Nevertheless, the climatic stations of Larrainzar and Chenalho, 10 km further distant but located in this same zone with an easterly aspect exposed to the winds of Gulf of Mexico, supported a higher precipitation of this zone (Table 2.1).

WorldClim data layers may be considered to be a reliable source of climatic information, comparable or even better than the local sources in this area (Golicher & Cayuela 2007; Golicher 2014), which is partially corroborated by their similarity to the data obtained from the nearest and most reliable climatic stations of the study area (Table 2.1); however, owing to their coarse resolution, they have mostly been used for envelope modelling at larger regional scales (e.g Golicher *et al.* 2012). This resolution led to some of the sample plots sharing the same WorldClim pixel and, therefore, climatic sets (Appendix 2.4); nevertheless, in these cases we assumed that they share the same climate. In total, 26 plot locations were sufficiently distant to have different climates in the WorldClim data.

2.3.4. Data analysis

In order to explore floristic relationships between sample plots, a non-metric multidimensional scaling (NMS) ordination analysis was performed by means of PC-ORD ver. 4.25 (McCune & Mefford 1999) using Euclidean distances, with 50 iterations, 10 runs with real data but 0 runs with randomized data. This procedure was followed in order to get an acceptable final stress value to exert an appropriate analysis of three principal ordination axes (Clarke 1993). NMS was executed using the abundance data of 65 species that were recorded in two or more plots.

Cross-species correlations (Pearson's r) were used to define significant bivariate relationships ($P < 0.05$) amongst the nine functional traits and a Principal Component Analysis (PCA) was executed to explore both the associations amongst traits and the species distribution within the functional space, as well as the associations amongst CWMs and the resulting distribution of sample plots within the ordination. These routines were executed with the Infostat statistical package (Di Rienzo *et al.* 2008).

Individual matrices of sample plots with species abundances and with CWM data, as well as altitude, geographical coordinates (in Universal Transverse Mercator coordinates, UTM), and climatic variables, were prepared for subsequent analyses with spatial statistics.

Multivariate Mantel correlograms (Borcard & Legendre 2012) were produced to summarise spatial turnover patterns in taxonomic and functional composition (*sensu* Sokol *et al.* 2011) but also to observe variation of altitude and climate across space. In this kind of analysis, the Mantel statistic (r_M) constitutes a metric of inter-plot similarity that is drawn against distance classes; therefore it quantifies the level of spatial autocorrelation of a particular variable through increasing distances (Chain-Guadarrama *et al.* 2012). The distance classes used ranged from 0.7 to 18 km divided into 1-km intervals previously defined from the maximum distance limits obtained from plot pairs. Statistical significances were determined from the probability value resulting from each Mantel correlation coefficient; however, following Legendre & Legendre (1998), a progressive Bonferroni correction was applied to each distance class to get adjusted p values. Calculations were carried out with R statistical software ver. 2.15.1 (R Development Core Team

2014), by means of *mantel.correlog* given by the *vegan* library (Oksanen *et al.* 2014).

Variation partitioning analyses (Borcard, Legendre & Drapeau 1992; Legendre, Borcard & Peres-Neto 2005; Peres-Neto *et al.* 2006) were performed to assess the joint and separate effect of explanatory variables on taxonomic and functional variation. This technique is used when two or more complementary sets of hypotheses can be invoked to explain the variation of an ecological response variable (Legendre 2007). Apart from the matrices of altitude, space and climate, we include those of aspect and disturbance level.

Several statistical procedures were performed to prepare the data for partitioning analysis. A principal coordinates of neighbour matrices (PCNM) analysis was applied to the matrix of geographical coordinates to get eigenvalues that could represent the spatial structure (Borcard & Legendre 2002). In this case, the significance ($P < 0.05$) of the resulting positive vectors was defined using Moran's I statistic. A principal coordinates analysis (PCoA or multidimensional scaling, MDE) with Jaccard´s similarity index was applied to the exposure data in order to get distance matrices. The species abundance data were transformed with the Hellinger method to down-weight common species (Legendre & Gallagher 2001; Jones *et al.* 2008) whereas CWMs were standardized. A log-transformation was used for altitude and environmental variables whereas the same untransformed ordinal scale (1–5) was used for disturbance level. A forward selection procedure was separately applied to each set of the explanatory variables in order to select those that were significant ($P < 0.05$ with 999 random permutations) in explaining the variation in both taxonomic and functional composition. Only the selected components of each set of variables were used in the final variation partitioning analysis.

The PCNM analysis generated a total of 19 eigenvectors of which nine were positive, and of these only four had significant Moran's I ($P < 0.05$). The procedure of forward selection retained these four significant PCNM eigenvectors for the final tests with floristic variation and it also selected five of the seven possible climate variables: temperature seasonality, temperature of the warmest month, mean annual precipitation, precipitation of the coldest month, and precipitation seasonality. In the case of functional composition, forward selection retained three PCNM eigenvectors and only three climate variables: temperature seasonality, mean annual precipitation and precipitation seasonality. The *var.part* function of the *vegan* library was executed for variation partitioning analysis and the *anova.cca* function of the same library was used to make significance tests (999 permutations) for testable fractions. The PNCM analysis was executed with the *pcnm* function of *vegan* whereas the forward selection was completed with the *forward.sel* function of the *packfor* library. All these R segments were executed through an interface implemented in Q-eco software (Di Rienzo *et al.* 2010).

2.4. RESULTS

2.4.1. Taxonomic and functional variation across the landscape

2.4.1.1. Floristics of the forests

Eighty four tree species ≥5 cm dbh were recorded across the 48 0.1 ha sample plots, corresponding to 6086 individuals. They represented 41 genera and 31 families and, except for three morphospecies, all were identified to the species level (Appendix 2.5). Mature individuals of the species recorded dominated the canopy, middlestorey and shrub strata, with a majority in the middlestorey. *Pinus* and *Quercus* contributed the highest number of species (5 and 7 respectively) in the canopy stratum, dominating in almost all the sample plots (Appendix 2.5, compare with Table 2.2).

The forest in the sample plots ranged from simple structured (low floristic richness, basal area and tree density, PF plots) to complex (high species richness, basal area and density, BLF plots) with most of the OF and POF plots being intermediate (Table 2.2). Analysis by NMS provided a three-dimensional solution with a final stress of 12.6 and a total explained variance of 89%; axis 2 was the most important (43%) followed by axis 1 (27%) and axis 3 (19%). The NMS biplots (Fig. 2.2) showed a strong superimposition of sample plots from different locations and in some cases of different forest types, corroborating the complex variation in species composition throughout the study area. It was evident that the *a priori* forest classification did not correlate strongly with floristic composition, though there was a stronger tendency for closely located plots in the same site to be grouped.

Axis 2 showed strong negative correlation values for species associated with the BLF plots in the Huitepec and Military zone sites and with the POF plots and OF plots of the Huitepec and Moxviquil sites: *Q. rugosa* (*r* = −0.70), *Q. laurina* (*r* = −0.57, *Garrya laurifolia* (r = −0.46), *Prunus serotina* (*r* = −0.35), *Clethra macrophylla* (*r* = −0.31), *Viburnum jucundum* (*r* = −0.31) and *Arbutus xalapensis* (*r* = −0.31) (Fig. 2.2a). Axis 2 was positively correlated with *Pinus montezumae* (*r* = 0.67), a dominant species in the PF plots of the Military zone and Aguaje sites, and with species occurring at a high density in the BLF plots of the Tzontehuitz site: *Drimys granadensis* (*r* = 0.43), *Persea americana* (*r* = 0.40), *Deppea grandiflora* (r = 0.38), *Solanum aligerum* (r = 0.35), *Prunus rhamnoides* (*r* = 0.35) and *Quetzalia contracta* (*r* = 0.30). In contrast, for axis 1 there were negative correlation values for species dominant in the POF plots and the PF plots of the Encuentro site: *P. tecunumanii* (*r* = −0.57), *Q. crassifolia* (r = −0.37) and *P. pseudostrobus* var. *apulcensis* (r = −0.35); and for species dominant in the BLF plots of the Tzontehuitz site such as *Oreopanax arcanus* (*r* = −0.43) (Fig. 2.2a). Conversely, there was a positive correlation with axis 1 for species dominant in the OF plots of the Tzontehuitz site such as *Q. ocoteaefolia* (*r* = 0.40) and *P. pseudostrobus* var. *pseudostrobus* (r = 0.31).

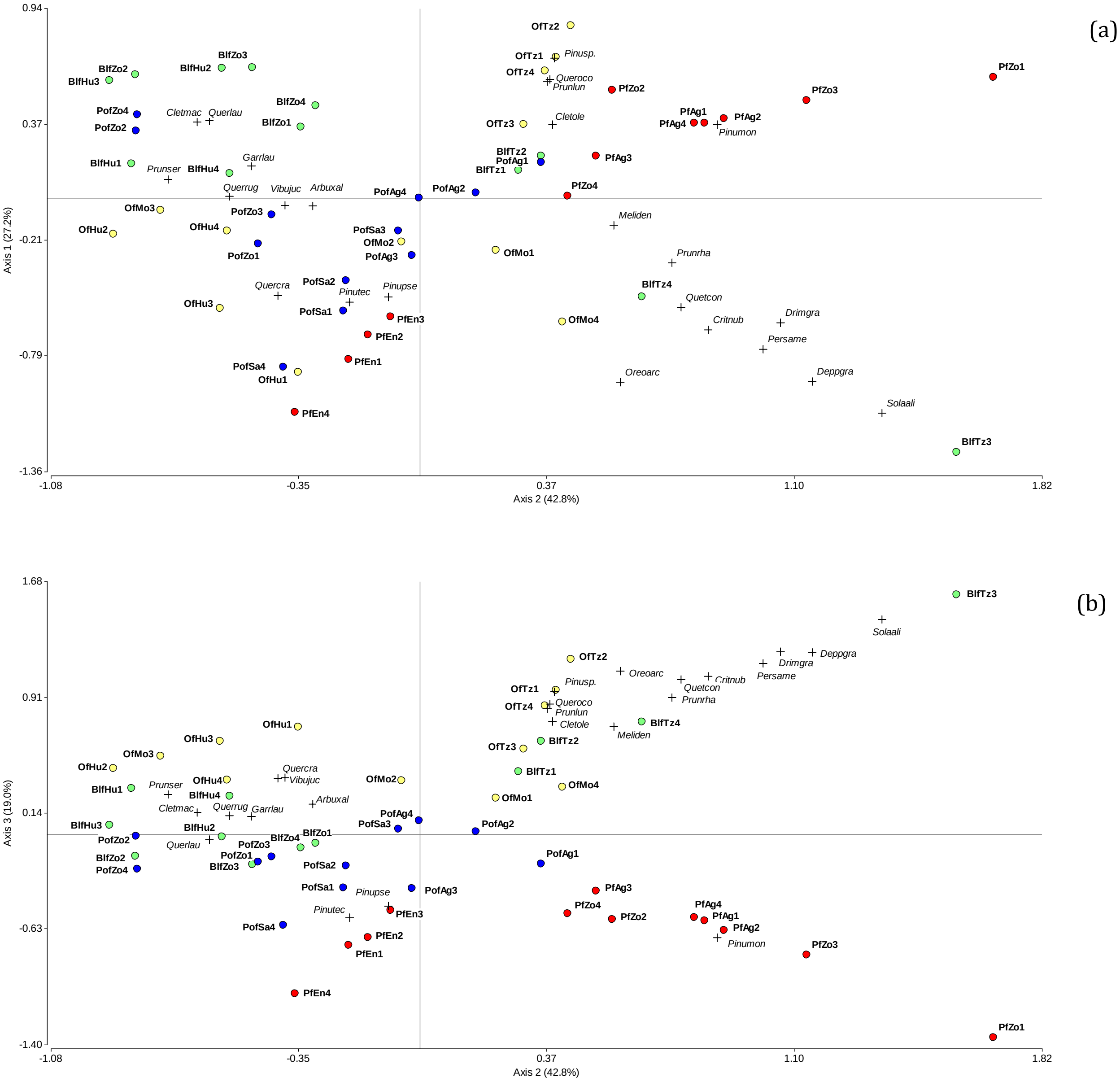

Figure 2.2 Non-metric multidimensional scaling ordination of species composition for the 48 sample plots showing (a) axes 2 and 1 and (b) axes 2 and 3. Plots are shown as an acronym in bold (defined in Appendix 2.3) and represented as dots with different colours in order to distinguish the four forest types identified *a priori* (broad-leaved forests = green, pine-oak forests = blue, oak forests = yellow, pine forests = red). The species better correlated (r > 0.30) are shown as a seven letter acronym and represented with a cross symbol: *A. xalapensis* (Arbuxal), *C. macrophylla* (Cletmac), *C. oleoides* (Cletole), *C. nubigenus* (Critnub), *D. grandiflora* (Deppgra), *D. granadensis* (Drimgra), *G. laurifolia* (Garrlau), *M. dentata* (Meliden), *O. arcanus* (Oreoarc), *P. americana* (Persame), *P. montezumae* (Pinumon), *P. pseudostrobus* var. *apulcensis* (Pinupse), *P. pseudostrobus* var. *pseudostrobus* (Pinusp.), *P. tecunumanii* (Pinutec), *P. lundelliana* (Prunlun), *P. rhamnoides* (Prunrha), *P. serotina* (Prunser), *Q. crassifolia* (Quercra), *Q. laurina* (Querlau), *Q. ocoteaefolia* (Queroco), *Q rugosa* (Querrug), *Q. contracta* (Quetcon), *S. aligerum* (Solaali), *V. jucundum* (Vibujuc).

Axis 3 (Fig. 2.2b) separated the PF plots (all in the Encuentro, Military zone and Aguaje sites) from those of OF and BLF in the Tzontehuitz site. Negatively correlated with this axis were *P. montezumae* (*r* = −0.57), *P. tecunumanii* (*r* = −0.54) and *P. pseudostrobus* var. *apulcensis* (r = −0.30); positively correlated were *D. granadensis* (*r* = 0.52), *Q. ocoteaefolia* (*r* = 0.51), *P. americana* (*r* = 0.48) and other species associated with OF and BLF. The rest of the species and plots formed a separate relatively compact group on axis 3.

Across the two biplots, the biggest distinction in floristic association was between the PF plots of the Military zone and Aguaje sites and the BLF and OF plots of the Tzontehuitz site, located at the northernmost part of the study area (Fig. 2.1), with the highest number of distinctive species (Table 2.2, Appendix 2.5).

2.4.1.2. Trait-trait relationships and species distribution in the functional space

The 26 dominant species had high variation in their trait values (Table 2.3, Appendix 2.1), varying from soft to hard leaves and wood, small to big leaves, with a variety of heights at maturity. Except for the understorey species *Miconia glaberrima*, all belonged either to the middlestorey or canopy strata groups. The total set of species included six species of *Quercus* and five of *Pinus*; of these *Q. rugosa* was dominant in seven forest type-site combinations, *P. tecunumanii* in five, *Q. laurina* in four, *Q. crispipilis* in three and *P. montezumae* in three.

Pearson correlations (Table 2.4) performed on the trait data indicate that the foliar nutrient concentrations LNC and LCC were strongly and positive correlated with each other (r = 0.91) and both were positively correlated with LTS. These three traits, but particularly LTS (r = −0.54), were negatively correlated with SLA. LDMC was also (but weakly) negatively correlated with SLA (r = −0.28), however it was not correlated with LTS. In contrast to the other two nutrients, LPC was only correlated (positively and weakly) with LA (r = 0.34). Stem traits were well correlated with leaf traits: WD was positively and strongly positively correlated with LDMC (r = 0.59) and negatively with LTS (r = −0.34), whereas H_{max} was positively correlated with LTS (r = 0.43) and negatively with SLA (r = −0.38).

In the PCA biplot of species distribution within the traits' space the first two ordination axes together explained 51% of the species' variation (32% for axis 1 and 19% for axis 2; Table 2.5, Fig. 2.3). LCC, LNC and LTS were positively related and SLA negatively related to axis 1. This axis provided a good differentiation of species according to their specialisation in leaf traits. In contrast, LDMC, and to a lesser extent to WD and more weakly still H_{max}, were positively correlated with axis 2, with only SLA showing any notable negative correlation. For the species with samples from different forest type-site combinations the PCA ordination showed that for most their replicates were quite clustered, however for some (e.g. *Q. rugosa*) there was notable scatter (Fig. 2.3). There is insufficient evidence to determine if this intraspecific trait variation (Appendix 2.1) is ecotypic or just phenotypic in its origin. The similarity in most trait values (particularly WD, LA, SLA, and LDMC) amongst the six *Quercus* species was notable, leading to them forming a relatively compact group within the ordination (Fig. 2.3). There was, however, greater distinction amongst the four *Pinus* species, mainly because of their differences in LTS and SLA.

Table 2.3 Descriptive statistics of functional traits obtained for 26 tree species (scored independently in each of the 12 forest type-site combinations in which they were abundant) and community weighted mean (CWM) values for 48 plots. Full data sets are in Appendices 2.1 and 2.3.

Variable	Description	Mean ± SD	Range
Trait	LDMC, leaf dry matter content (mg g^{-1})	439.79 ± 64.64	284.45 - 617.27
	LA, leaf area (mm^2)	5509.74 ± 7225.39	477.13 - 43224.67
	SLA, specific leaf area (mm^2 mg^{-1})	8.61 ± 2.78	4.32 - 14.76
	LTS, leaf tensile strength (N mm^{-1})	1.31 ± 1.56	0.12 - 7.71
	H_{max}, maximum height (m)	21.34 ± 6.83	5.72 - 35.34
	WD, wood density (g mm^{-1})	0.60 ± 0.12	0.41 - 0.8
	LPC, leaf phosphorous content (mg g^{-1})	1.17 ± 0.24	0.73 - 1.83
	LNC, leaf nitrogen content (mg g^{-1})	24.77 ± 2.76	17.5 - 31.3
	LCC, leaf organic carbon content (mg g^{-1})	424.85 ± 41.59	318.9 - 532.7
CWM	LDMC	456.35 ± 49.8	390.52 - 584.89
	LA	4713.96 ± 3872.08	552.38 - 19220.77
	SLA	7.81 ± 2.12	4.32 - 11.96
	LTS	2.02 ± 2.09	0.43 - 6.53
	H_{max}	25.05 ± 5.93	15.27 - 32.49
	WD	0.61 ± 0.09	0.47 - 0.78
	LPC	1.18 ± 0.22	0.78 - 1.63
	LNC	25.36 ± 2.52	21.27 - 31.3
	LCC	433.65 ± 40.97	363.59 - 532.7

Table 2.4 Pearson correlations (r-value and (p)) amongst traits for the complete set of 26 species (scored independently in each of 12 forest type-site combinations in which they were abundant). Significant correlations ($P < 0.05$) are shown in bold. Trait abbreviations are defined in Table 2.3.

	LA	SLA	LTS	H_{max}	WD	LPC	LNC	LCC
LDMC	0.08 (0.61)	**−0.28 (0.05)**	−0.05 (0.73)	0.26 (0.07)	**0.59 (7.50E-06)**	1.80E-04 (1.00)	−0.14 (0.35)	−0.19 (0.20)
LA		0.14 (0.35)	−0.24 (0.10)	−0.11 (0.43)	0.15 (0.31)	**0.34 (0.02)**	−0.13 (0.36)	−0.19 (0.20)
SLA			**−0.54 (6.00E-05)**	**−0.38 (0.01)**	0.14 (0.34)	0.24 (0.10)	**−0.35 (0.01)**	**−0.36 (0.01)**
LTS				**0.43 (1.80E-03)**	**−0.34 (0.02)**	−0.1 (0.49)	**0.37 (0.01)**	**0.44 (1.50E-03)**
H_{max}					−0.05 (0.75)	−0.18 (0.22)	0.09 (0.53)	0.18 (0.22)
WD						0.16 (0.27)	−0.08 (0.57)	−0.16 (0.28)
LPC							−0.1 (0.52)	−0.07 (0.65)
LNC								**0.91 (0)**

Table 2.5 Loadings of species traits and community weighted means of the first two axes of their respective principal components analyses; see also Figs. 2.3 and 2.4. The most important correlations (> 0.30) are shown in bold.

	Functional traits		Community weighted means	
	Loadings on axis 1	Loadings on axis 2	Loadings on axis 1	Loadings on axis 2
Total variation explained by axis	32%	19%	53%	15%
Variables				
Basal area BA			−0.09	**−0.45**
Leaf dry matter content LDMC	−0.07	**0.70**	**−0.31**	−0.05
Leaf area LA	−0.23	0.05	−0.28	0.04
Specific leaf area SLA	**−0.40**	**−0.32**	**−0.35**	0.17
Leaf tensile strength LTS	**0.45**	0.06	**0.40**	0.14
Maximum height H_{max}	0.28	**0.38**	0.28	**−0.39**
Wood density WD	−0.23	**0.48**	**−0.37**	0.17
Leaf phosphorous content LPC	−0.20	−0.05	−0.06	**0.68**
Leaf nitrogen content LNC	**0.44**	−0.10	**0.40**	0.22
Leaf organic carbon content LCC	**0.47**	−0.12	**0.40**	0.21

On the negative side of axis 1, characterised by high SLA, were broadleaf species with soft, fragile and big leaves typical of humid and old growth forests, which frequently belong to the middlestorey or lower strata, such as *Chiranthodendron pentadactylon*, *P. rhamnoides*, *Cornus disciflora*, *Q. contracta* and *M. glaberrima* (Fig. 2.3). In contrast, most of the species on the positive side of axis 1 (linked to high LCC, LNC and LTS) are typical of naturally- or human-disturbed sites, including *Pinus* species (except *P. ayacahuite*) together with broadleaf species such as *Buddleja cordata* and the overstorey species *Ternstroemia lineata* and *Clethra oleoides*. The compact group of *Quercus* species were mainly found on the positive side of axis 2, linked to high LDMC and WD. The species clustered in the centre of the ordination, *P. americana*, *C. macrophylla*, *Styrax magnus*, *Oreopanax xalapensis*, *Symplocos breedlovei*, *Weinmania pinnata* and *A. xalapensis*, all had intermediate values of WD, LA, SLA, LDMC and LTS (Appendix 2.1), and mainly belonging to the middle-storey stratum of broad-leaved, pine-oak and oak forests (Appendix 2.5).

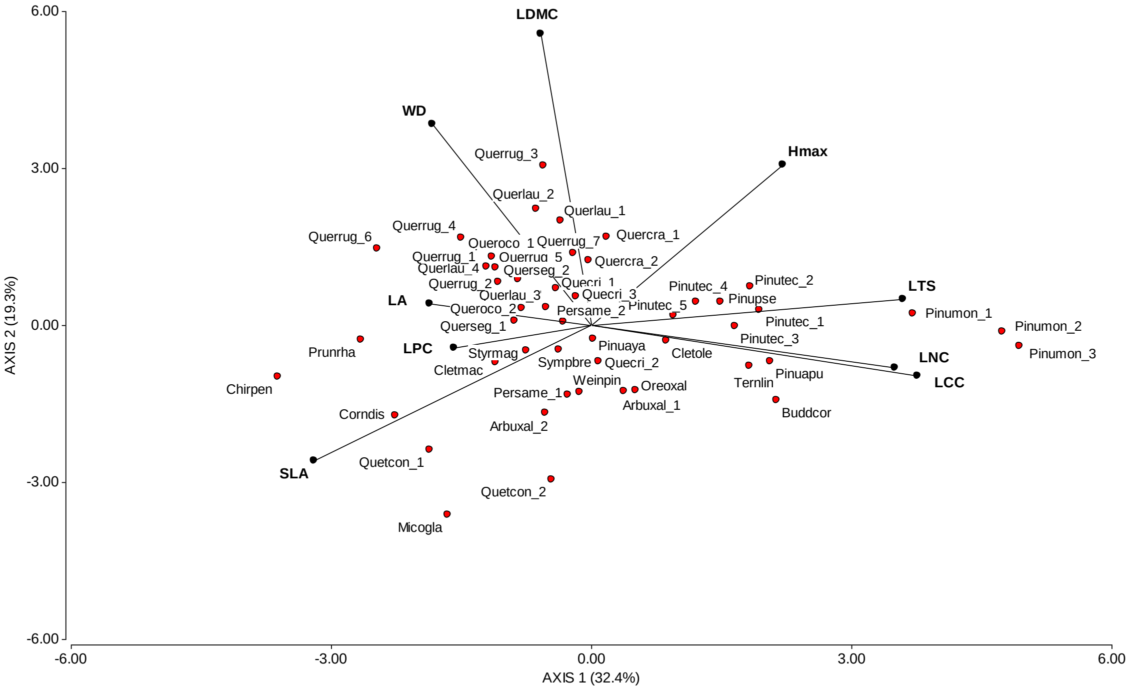

Figure 2.3 Principal components analysis ordination of nine functional traits of dominant tree species shown as vectors, with 26 species (separating their samples in different forest types) shown as a seven letter acronym defined in Appendix 2.1. Loadings of traits on axes and definitions of trait acronyms are shown in Table 2.5.

2.4.1.3. Forest functional composition

The PCA with CWM values (Table 2.5, Fig. 2.4) summarizes and simplifies the floristic variation (NMS ordination, Fig. 2.2) and species functional variation (PCA ordination, Fig. 2.3) amongst plots. In particular, it groups the BLF and OF sample plots in the Tzontehuitz site, so distinct in the NMS ordination, with the BLF and OF plots in other sites. It also creates a clearer grouping of the PF plots and some POF plots, whose CWM trait values reflect the dominance of *Pinus* species.

The first two axes of the PCA explained 68% of the CWM variation, with that explained by axis 1 being considerable higher (53%) than axis 2 (15%) (Table 2.5). The traits LTS, LNC and LCC were equally positively related to axis 1, whereas WD, SLA and LDMC were weakly negatively related (Table 2.5, Fig. 2.4); it therefore provides only a partial representation of both the wood and leaf economics spectra, because of the association between high CWM SLA and high CWM WD in forests dominated by broadleaved species (negative values on Axis 1) and the particular combination of high CWM LTS, LCC and LNC in *Pinus* species. Axis 2 was dominated by a positive linkage with LPC and negative with basal area and H_{max}. In terms of forest type, axis 1 represented a gradient from PF (in particular the eight plots dominated by *P. montezumae*, with high CWM values for LTS, LNC, and LCC) to BLF and OF (with high CWM values for WD, SLA and LDMC) (Appendix 2.3). Most of the POF plots were intermediate, except those in the Military zone where *Quercus* species were more dominant and, therefore, they were more associated with the BLF and OF plots.

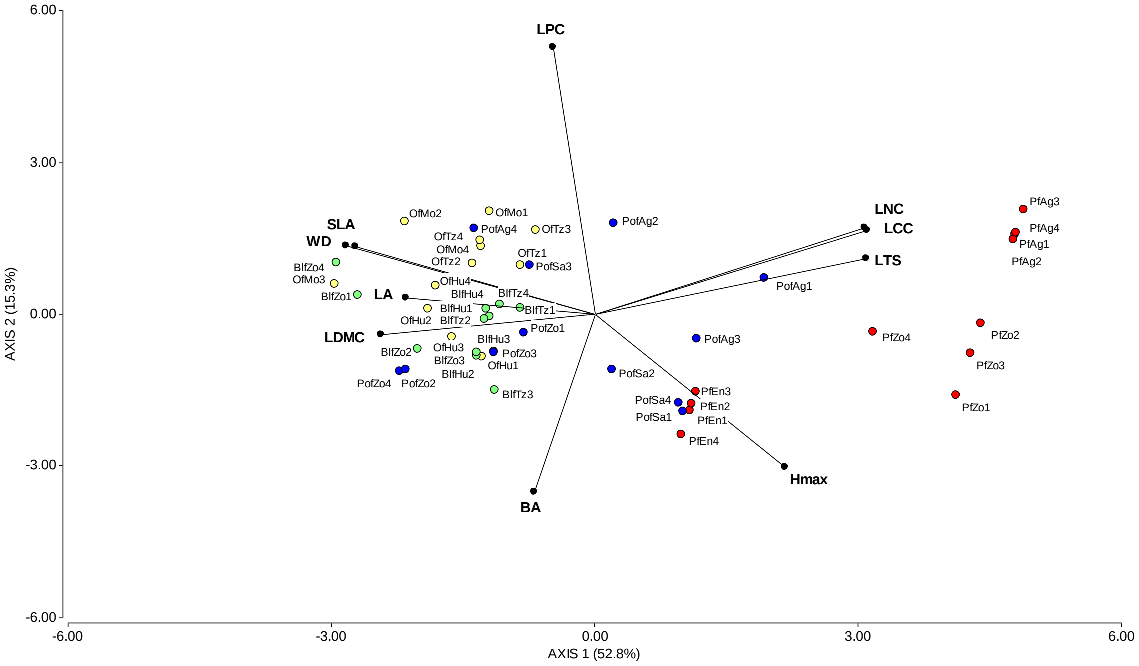

Figure 2.4 Principal components analysis ordination of community weighted means of nine functional traits shown as vectors, with 48 plots shown as an acronym defined in Appendix 2.3. Each of four forest types is shown by dots with different colours (green = broad-leaved forest, blue = pine-oak forest, yellow = oak forest, red = pine forest). Loadings of traits on axes and definitions of trait acronyms are shown in Table 2.5.

2.4.2. Floristic and functional turnover and spatial autocorrelation of variables

The Mantel correlograms indicate that floristic and functional similarity amongst plots decays abruptly in the first kilometre, matching a similarly rapid change in altitude and climate (Fig. 2.5). Functional composition showed a more rapid change in autocorrelation with distance than did floristic composition. The significant positive autocorrelation of functional composition ceased after the 0–1-km class, then suffered a continuing and pronounced fall towards negative autocorrelations, reaching negative significance until the 12–13-km class. The positive autocorrelation of floristic composition was significant only in the 1–2-km class and it was followed by a lagged fall until the 5–6-km class where the shift to negative correlation happened. Significance of the negative correlation was reached in the 12–13-km class and retained until the 14–15-km class. Significances of altitude and climate were also transient, although both had similar patterns with distance which were closely linked to the pattern of autocorrelation with distance for floristic turnover.

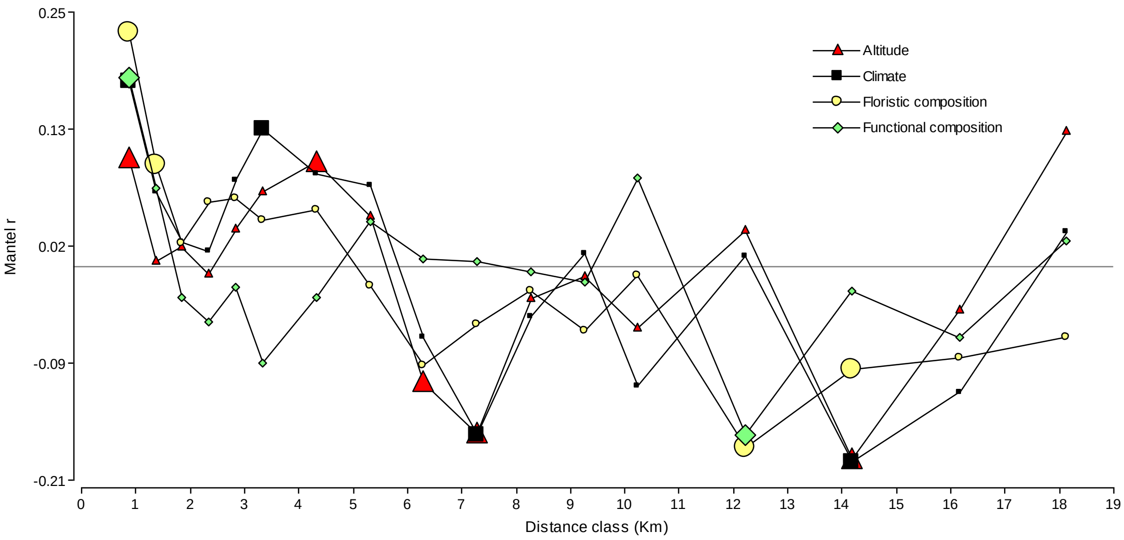

Figure 2.5 Spatial autocorrelation coefficients of Mantel correlograms of sample plot pairs for 19 geographical distance classes. Mantel comparisons of distance matrices of altitude, climate, floristic composition and functional composition are shown as different symbols and lines. Large symbols denote significant correlations ($P < 0.05$). The x axis shows the maximum geographical distance in each class.

2.4.3. Variation partitioning of taxonomic and functional composition

The variation partitioning analysis showed both pure (individual) and combined (joint) contributions of climate, spatial variables, disturbance level and altitude to variation in both floristic and functional composition amongst the sample plots (Table 2.6). Preliminary tests included "aspect" as an explanatory variable but it contributed a minimal jointly explained variance both for floristic ($R^2_{adj} = 0.09$) and functional ($R^2_{adj} = 0.17$) composition; its pure contributions were also very low ($R^2_{adj} = 0.02$ and $R^2_{adj} = 0.07$, respectively). Even though the pure effects of aspect were slightly higher than those reported by altitude, we decide to include only altitude in the final analysis because of its importance as an ecological gradient (Grubb 1977; Körner 2007) .

The four tested predictor matrices together explained almost half of the total floristic variation ($R^2_{adj} = 0.47$) but only an adjusted R^2 of 0.20 of this joint variance was attributed to their pure effects, the remaining 0.27 in combined or masked contributions. This is evidenced clearly when the effect of the variables is individually controlled (Table 2.6). Of the pure effects, the best predictor was geographical distance ($R^2_{adj} = 0.11$), followed by climate and disturbance. When controlling for the effect of one or two variables, the effect of spatial variables on floristic variation is shared with climate ($R^2_{adj} = 0.22$ when controlling for altitude and disturbance) and to a lesser extent with disturbance ($R^2_{adj} = 0.16$) and altitude ($R^2_{adj} = 0.12$). The explained variance of climate was similarly more related to spatial variables (shared $R^2_{adj} = 0.16$) than to altitude (shared $R^2_{adj} = 0.08$) and disturbance (shared $R^2_{adj} = 0.05$). Both disturbance and altitude had weak relationships with other variables; nevertheless, disturbance shared more effects with spatial variables, and altitude was more related to climate.

Table 2.6 Results of variation partitioning analysis on floristic and functional composition. Adjusted R^2 statistics (Adj R^2) and F statistics are presented for all measured predictors. Significant correlations are marked in bold (* P < 0.05, ** P < 0.005). The effect of predictors controlling for any combinations of other predictor is denoted by the symbol │. Null fractions are denoted with a dash.

	Predictor	Floristic composition		Functional composition	
		Adj R^2	F	Adj R^2	F
Total effects per predictor	Altitude	**0.11****	7.04	**0.10****	6.28
	Spatial variables	**0.28****	5.46	**0.17****	4.13
	Climate	**0.28****	4.63	**0.22****	5.45
	Disturbance	**0.11****	6.92	**0.35****	26.05
Pure effects per predictor	Altitude│Other 3 predictors	0.002	1.14	0.01	1.86
	Spatial variables│Other 3 predictors	**0.11****	3.14	**0.07****	3.12
	Climate│Other 3 predictors	**0.06****	1.86	**0.03***	1.89
	Disturbance│Other 3 predictors	**0.03****	3.24	**0.21****	18.56
Total pure effects		0.20	-	0.32	-
Combined effects		0.27	-	0.20	-
All the effects of predictors		**0.47****	4.80	**0.52****	7.27
Residuals		0.53	-	0.48	-
Effects controlling one predictor	Altitude│Spatial variables	**0.12****	9.26	**0.12****	8.01
	Altitude│Climate	0.003	1.17	0.01	1.62
	Altitude│Disturbance	**0.09****	6.03	0.01	1.55
	Spatial variables│Altitude	**0.28****	6.26	**0.18****	4.88
	Spatial variables│Climate	**0.16****	3.98	**0.08***	2.67
	Spatial variables│Disturbance	**0.28****	6.16	**0.14****	5.15
	Climate│Altitude	**0.17****	3.14	**0.13****	3.61
	Climate│Spatial variables	**0.16****	3.49	**0.13****	3.81
	Climate│Disturbance	**0.24****	4.40	**0.08****	3.23
	Disturbance│Altitude	**0.09****	5.92	**0.25****	19.15
	Disturbance│Spatial variables	**0.11****	8.84	**0.32****	28.43
	Disturbance│Climate	**0.07****	5.75	**0.21****	17.19
Effects controlling two predictors	Altitude│Climate, Disturbance	0.01	1.07	0.01	1.20
	Altitude│Spatial variables, Disturbance	**0.03****	3.03	−0.001	0.92
	Altitude│Spatial variables, Climate	0.001	1.39	0.003	1.98
	Spatial variables│Climate, Disturbance	**0.12****	3.88	**0.08***	2.49
	Spatial variables│Altitude, Disturbance	**0.22****	5.15	**0.13****	4.80
	Spatial variables│Altitude, Climate	**0.16****	3.26	**0.07****	3.19
	Climate│Altitude, Disturbance	**0.16****	1.70	0.09	1.45
	Climate│Spatial variables, Disturbance	**0.08****	3.22	**0.02****	3.37
	Climate│Altitude, Spatial variables	**0.05****	2.30	0.02	1.56
	Disturbance│Spatial variables Climate	**0.03****	2.67	**0.21****	18.00
	Disturbance│Altitude, Climate	**0.08****	5.89	**0.21****	17.33
	Disturbance│Altitude, Spatial variables	**0.02****	3.23	**0.20****	18.03

More than half of the variance in functional composition (R^2_{adj} = 0.52) was explained substantially by the four tested variables (Table 2.6). The total contribution of their pure effects was considerably higher than in the case of floristic variation (R^2_{adj} = 0.32) leaving less (R^2_{adj} = 0.20) for their combined or masked effects. In marked contrast to taxonomic composition, for functional composition disturbance (R^2_{adj} = 0.21) was the best predictor distantly followed by spatial variables (R^2_{adj} = 0.07) and climate (R^2_{adj} = 0.03). The combined effects of disturbance are, however, strongly related to altitude, climate and spatial variables, being difficult to separate as indicated by the analyses controlling for one and two variables. However, the combined effect of climate was again higher with spatial variables (R^2_{adj} = 0.09) than with altitude and disturbance, and the same was true for spatial variables: they were more related to climate (R^2_{adj} = 0.13) than to altitude and disturbance. The combined effects of altitude were statistically significant only when controlling for spatial variables (R^2_{adj} = 0.12), indicating that it is highly interrelated with climate and disturbance.

Combining these effects for floristic composition, the total effects of climate and spatial variables were greatest, whereas for functional composition the greatest effect was of disturbance, followed by climate and spatial variables.

2.6. DISCUSSION

2.6.1. Relationships of traits amongst the dominant species

While they only account for 35% of the total number of tree species, the 26 dominant species of the study area represented 80% of the individuals and 94% of the basal area across the 48 sample plots. It is therefore highly probable that they control the functioning of the four forest types that were compared (Grime 1998), conforming with the concept "hyperdominant" species of ter Steege *et al.* (2013). Despite their taxonomic diversity, these 26 species were divided into three main functional groups on the basis of the PCA (Fig. 2.3): *Quercus* species and *Pinus* species, which both reach the canopy or sub-canopy layers of the forests, and a third group of a wide taxonomic range of species that generally only reach the lower strata. Species in the third group have a higher SLA but lower WD, H_{max}, LTS, and LDMC, indicating higher potential growth rates and preference for environments with less stress from heat, cold, drought, and shortage of nutrients and light (Pérez-Harguindeguy *et al.* 2013).

The measured traits of the *Quercus* species (high WD, high LDMC, and relatively high LTS and H_{max}, with relatively low SLA and low leaf nutrient concentrations) are indicative of high resource conservation and slow growth rates (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013). Traits of these *Quercus* species recorded in other studies, including high resprouting capacity, animal seed dispersal, medium seed size and high rates of fruit production amongst others, are likely to make them resilient not only to natural but also to anthropogenic disturbances (Quintana-Ascencio, González-Espinosa & Ramírez-Marcial 1992; López-Barrera & Manson 2006; Ramírez-Marcial *et al.* 2006). In contrast, the measured traits of the *Pinus* species (mainly low WD, LDMC and SLA, but high LTS and H_{max}, LNC and LCC) may indicate rapid resource acquisition and growth, but also the investment in some forms of leaf tissue defence. Other studies have recorded these *Pinus* species as having a much lower resprouting capacity, and distinctive functional characteristics of their needles: they are perennial with a waxy surface and a thick cuticle that greatly reduce moisture loss, and they have a high resistance to fire (e.g. González-Espinosa *et al.* 1991; González-Espinosa, Ramírez-Marcial & Galindo-Jaimes 2006; Galindo-Jaimes *et al.* 2002). The *Pinus* species share with *Quercus* a high rate of seed production, though their seeds are winged and dispersed by wind. Together these characteristics make these *Pinus* species highly invasive of highly disturbed sites with low soil nutrient levels (e.g. González-Espinosa *et al.* 1991; González-Espinosa, Ramírez-Marcial & Galindo-Jaimes 2006; Galindo-Jaimes *et al.* 2002).

The traits described indicate that *Quercus* and *Pinus* species are resource conservative and acquisitive, respectively, as defined by Díaz *et al.* (2004). The large number of species of these genera and their interspecific trait variation means that they are able to colonize a wide range of conditions in the mountainous environment of the study area. As pointed out by Quintana-Ascencio & González-Espinosa (1993), these two Holarctic genera form a canopy which appears to provide the more mesic sub-canopy environment that may be required by a majority of the other tree species occurring in forests of the Central Highlands.

In terms of trait relationships, the positive correlation found between WD and LDMC, as in *Quercus* species, can be related to high investment in tissue protection (Wilson, Thompson & Hodgson 1999; Garnier *et al.* 2001; Balsamo *et al.* 2006; Vaieretti *et al.* 2007). In contrast, the negative correlation found between WD and LTS, basically in *Pinus* species, can be related to a combination of high stem growth rate and high leaf tissue protection corresponding to the integration between leaf and stem morphology observed by Santiago *et al.* (2004) and Easdale *et al.* (2007). The abundance and richness of *Pinus* and *Quercus* species in the study area (and thus their strong representation amongst the studied abundant species), together with their particular sets of traits, means that the trait relationships found across the whole community differ from some of those observed in other Neotropical forests. The negative correlations that we found between SLA and both LTS and LDMC do correspond with the predictions of Cornelissen *et al.* (2003) and are indicative of a linkage between investment in leaf tissue mass and leaf survival typical of species occurring in environments that impose a high level of stress (Sterck, Poorter, & Schieving 2006). However, although LTS was found to be correlated with LCC it was not with LDMC. This is likely to be because the high resistance to tearing of *Pinus* species' leaves is associated with mechanisms independent of LDMC. Moreover, the high LDMC of the *Quercus* species in this study cannot be associated with long leaf lifespan since (in contrast to most of the studied species) they are deciduous.

Likewise, we did not find the positive relationships amongst SLA, LNC and LPC that had been reported by Reich, Walters, & Ellsworth (1992), Wright *et al.* (2004) and Poorter & Bongers (2006) and grouped as components of high potential photosynthetic rate by Cornelissen *et al.* (2003) and Wright *et al.* (2004). This is primarily because of the combination of low SLA and high LNC in the leaves of most of the *Pinus* species (see Cornelissen *et al.* (1997) for nitrogen content in other *Pinus* species). In addition, we did not find the positive relationship between LA and SLA described by Díaz *et al.* (2004) nor the negative correlation between LA and WD found in some other studies (e.g. Wright *et al.* 2006; Easdale *et al.* 2007; Easdale & Healey 2009; Salgado-Negret *et al. unpublished*). This may be a result of the high variety of SLA and LA of species, going from needle to tender leaves, as well that *Quercus* species presented both high LA and high WD. The negative relationship found between SLA and H_{max}, but positive relationship between LTS and H_{max} were both also strongly influenced by the abundance of tall *Quercus*, and especially *Pinus*, species in the study. In this way, the study finds that *Pinus* species don´t seem to fit on the leaf economics spectrum and this needs further research.

2.6.2. Relationship of floristic and functional variation with climate, altitude and distance

The Mantel correlograms and the variation partitioning suggested that the floristic variation in the study area is well related to climate and to a lesser extent to altitude (Table 2.6, Fig. 2.5). In particular, climate was well linked to altitude and spatial variables indicating a spatial structure of this factor, varying both vertically and horizontally, within the complex topography of the study area.

Over a wider range, altitude constitutes an important co-variable which reflects important changes in temperature and humidity and it, therefore, constitutes an important factor related to floristic change (Grubb 1977; Körner 2004). However, high altitude did not by itself explain the particular composition of the oak and broad-leaved forests in the Tzontehuitz site, the most distinct plots in the study (Fig. 2.2). Whilst this site had some of the highest altitudes in the study it was also the most north-easterly (Table 2.2, Fig. 2.1), with the highest exposure to the humid winds from the Gulf of Mexico, with the highest precipitation as well as the lowest temperature according to the WorldClim data (Appendix 2.4, corroborated by the two nearest climatic stations, Larrainzar and Chenalho (Table 2.1)). In this way, a combination of altitude and location may be the responsible for this major floristic variation that makes possible the identification of two different species source pools (*sensu* Sokol *et al.* 2011) across the study area as a whole: 1) represented by the Tzontehuitz site, with species associated with high precipitation, together with high altitude and therefore low temperature and high humid exposure; 2) represented by the remaining sites at the centre of the study area, with species associated with lower precipitation and lower altitude, and therefore higher temperature.

On the other hand, within each of these two floristic provinces there is a small altitudinal range of the sample plots, which is associated with only a low absolute range of climatic variation (WorldClim data in Appendix 2.4). In this way, the altitudinal factor did not appear to affect the distribution and abundance of canopy dominant species such as *Quercus laurina*, *Q. rugosa*, *Q. crassifolia* and *Pinus tecunumanii* that are present in different forests (Table 2.2). Even though no data were available on local topographically-linked variation in microclimate, this narrow climatic range is the likely explanation for the small horizontal and vertical variation of floristics amongst the plots of the two source pools.

In contrast to floristic composition, functional composition of the tree communities was less related to the variation in climate, altitude and spatial variables (Table 2.6, Fig. 2.5) suggesting a general consistency in functional trait composition across the landscape. Together with the PCA using CWMs (Fig. 2.4), this result shows, at the landscape level, a decoupling of functional composition from floristic composition, where a spatial floristic change associated with climate and altitude does not necessarily mean a functional change: very different floristic associations shown by the NMS analysis (such as those of OF and BLF of Tzontehuitz and the PF dominated either by *P. montezumae* or *P. tecunumanii*) were closely grouped with the other floristic associations by functional trait criteria.

Other studies have found evidence of changes in functional beta diversity along big altitudinal ranges and broad geographical areas (Swenson, Anglada-Cordero & Barone 2011; Siefert *et al.* 2013; Liu, Tang & Fang 2015) indicating vertical and horizontal functional variation along the associated environmental gradients. However, the small altitudinal range and the size of the area of the present study are probably the reasons for the lack of strong associations between functional change and environmental factors, suggesting that in this landscape the different tree species assemblages have similar mechanisms for tolerating its high stress environmental conditions.

The possible causes of the relatively high rate of species turnover (variation in community composition) amongst the sample plots, despite the low rate of variation in functional traits amongst the communities is addressed in the following sections.

2.6.3. Disturbance and species assemblages

Variation partitioning analysis indicated a minimal role of disturbance level as a factor by itself in explaining floristic variation, probably because of the high degree in which species were shared amongst the different forest associations across the landscape of the study area (Table 2.6). In marked contrast, disturbance was the factor that best explained the functional variation between plots, both overall and in terms of its pure effect. This result is possibly due to the large differences of CWM trait values found between the disturbed pine forests (and to a lesser extent most of the pine-oak forests) and the other two forest types (Fig. 2.4).

Human disturbance is the main factor invoked by previous studies in the region to explain both the existence of pure stands of *Pinus* species and the increasing abundance of *Pinus* in pine-oak and broad-leaved forest associations (González-Espinosa *et al.* 1991; Galindo-Jaimes *et al.* 2002; Zavala, Galindo-Jaimes & González-Espinosa 2007). Despite the difficulty of determining pre-human forest composition due to the pre-Columbian human presence in the Central Highlands, the research of González-Espinosa *et al.* (1991) indicates that pine-oak associations are the most likely natural assemblage of most of the landscapes of the region. However, intensive productive and extractive activities of contemporary people have greatly increased the abundance of *Pinus* in the forests, causing a reduction of species richness, tree density and basal area amongst other factors, which is apparent along the pronounced gradient of *Pinus* abundance between the least and most disturbed forests (Galindo-Jaimes *et al.* 2002). Our study has added the important finding of a notable functional difference between low and high-disturbance stands associated with the abundance of *Pinus* species leading to a reduction in the CWM values of biomass-partitioning linked traits (such as WD and LDMC) accompanied by a reduction of the range of each functional trait because of dominance by a set of tree species that share similar trait values.

2.6.4. Spatial variables and floristic variation

The variation partitioning analyses indicated that floristic composition is strongly associated with spatial variables. It should be taken into account, however, that topographically linked variation in microclimate not detected at the scale of the WorldClim data, and other environmental variables, might be linked to spatial factors. Other studies in Neotropical forests (e.g. Pyke *et al.* 2001; Duque *et al.* 2002; Tuomisto, Ruokolainen & Yli-Halla 2003b; Tuomisto *et al.* 2003a; Phillips *et al.* 2003; Jones *et al.* 2006, 2008; Poulsen, Tuomisto & Balslev 2006; John *et al.* 2007; Macía *et al.* 2007; Sesnie *et al.* 2009; Costa *et al.* 2009; Swenson, Anglada-Cordero & Barone 2011; Swenson *et al.* 2012b; a) have found evidence of the effect of a wide range of other environmental factors on species distribution which were not recorded in our study but could be important given the high environmental heterogeneity of the area. These factors include soil physics, soil chemistry, terrain inclination, relative humidity, evapotranspiration, sun and wind exposure, fog frequency and cloudiness, amongst others (Grubb 1977).

In contrast, the effect of spatial variables on floristics found at the scale of this study could, instead, indicate that part of the variation can be explained by less deterministic processes such as dispersal capacity of the species (Sokol *et al.* 2011). The general lack of discrete floristic associations and the continuous distribution of sample plots in the NMS ordination would support this explanation. Dispersal limitation of tree species is certainly possible in the complex topographical environment of the study area. In this scenario, an individual of any tree species would have the same chance to colonize any geographical space, except in as much it is limited by the surrounding vegetation and its own reproductive and functional capacity in that location (Hubbell 2001). There is increasing evidence from other tropical areas of strong or partial effects of dispersal limitation on species turnover (e.g. Hubbell 1999; Condit *et al.* 2002; Vormisto *et al.* 2004; Chust *et al.* 2006; Normand *et al.* 2006; Bohlman *et al.* 2008; Duque *et al.* 2009; Chain-Guadarrama *et al.* 2012; Liu *et al.* 2013). It is therefore necessary to consider the potential combination of effects of deterministic and stochastic factors driving the vegetation composition of the Central Highlands of Chiapas (compare Barot 2004; Adler *et al.* 2007; Haegeman & Loreau 2011; Mutshinda & O'Hara 2011; Weiher *et al.* 2011; Liu, Tang & Fang 2015).

2.6.5. Contributions of the study and final reflections

The present study, based on the rigorous use of multivariate analyses and spatial statistics, complements the previous ecological knowledge obtained in the Central Highlands of Chiapas and is one of the first to address the relationships of floristic and functional trait variation, and their environmental correlates, in Neotropical mountains at altitudes above 2000 m a.s.l. Because of the particular combination of latitude and altitude, the composition and dominance structure of the forests of this region differs greatly from most other tropical forests, showing particular species assemblages varying spatially and with environmental factors and those linked to the type and intensity of anthropogenic disturbance. Nevertheless, an important finding of the study was that a floristic change does not necessarily imply a functional change.

Given that the functional variation is highly associated to human disturbance, our results stress on the importance of reducing the impact of human activities to maintain resilient forest ecosystems with high functional diversity (Laliberté *et al.* 2010; Carreño-Rocabado *et al.* 2012). This is crucial to sustain forests during future disturbance impacts with the functionality to deliver the quantity and quality of ecosystem services required by large human populations in mountain environments (Körner 2004; Becker *et al.* 2007; Bugmann *et al.* 2007).

Likewise, the possibly important role of tree species dispersal limitation shown by our study has implications for conservation policy. It indicates a potential limitation to species capacity to respond to either future deforestation or climate change through migration, or even rapid evolution promoted by gene flow. This will greatly reduce our capacity to predict future distributions of both species and communities (Dullinger, Dirnböck & Grabherr 2004; Anderson *et al.* 2012). The regional character of such stochastic processes supports the "ecosystem" approach to forest conservation and sustainable forest management, with integrated conservation of the landscape and the region, including all the floristic and functional elements, instead of emphasizing the conservation of particular species or communities (Jamoneau *et al.* 2012; Chain-Guadarrama *et al.* 2012). In a human disturbance context, this conservation must recognize the regional species pool and its phytogeography, and must emphasize communities' connectivity and the effects on fragmentation. In addition, if the current distribution of species is to some extent restricted by dispersal limitation (more than by their physiological tolerances) then climate envelope models could underestimate species real distributions (Dullinger *et al.* 2004; Anderson *et al.* 2012). In a scenario of climate change, this implies that future species' distributions could be partly determined by dispersal capacities rather than by environmental conditions alone. Conservation management therefore will need to incorporate the uncertainty of such stochastic factors in the predictions on which decisions are based.

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2.8. APPENDICES

Appendix 2.1 Twenty six tree species and their replicates, in the forests where they were dominant, with their functional traits. BLF = broad-leaved forest, POF = pine-oak forest, OF = oak forest, PF = pine forest; LDMC = leaf dry matter content, LA = leaf area, SLA = specific leaf area, LTS = leaf tensile strength, H_{max} = maximum height, WD = wood density, LPC = leaf phosphorous content, LNC = leaf nitrogen content, LCC = leaf organic carbon content.

Number	Species	Acronym	Forest type	Site	LDMC (mg g^{-1})	LA (mm^2)	SLA (mm^2 mg^{-1})	LTS (N mm^{-1})	H_{max} (m)	WD (g mm^{-1})	LPC (mg g^{-1})	LNC (mg g^{-1})	LCC (mg g^{-1})
1	*Arbutus xalapensis*	Arbuxal_1	BLF	Huitepec	389.79	4,016.44	9.37	0.59	17.10	0.56	1.28	27.10	460.40
2	*Arbutus xalapensis*	Arbuxal_2	POF	Aguaje	343.20	4,895.35	9.57	0.54	14.97	0.54	0.98	24.55	399.84
3	*Buddleja cordata*	Buddcor	OF	Tzontehuitz	380.26	6,726.37	5.20	0.31	14.71	0.54	1.33	31.20	528.90
4	*Chiranthodendron pentadactylon*	Chirpen	BLF	Military zone	381.60	43,224.67	13.07	0.16	22.27	0.54	1.83	21.70	369.10
5	*Clethra macrophylla*	Cletmac	BLF	Huitepec	412.87	6,898.92	10.32	0.48	22.70	0.44	0.93	21.50	369.10
6	*Clethra oleoides*	Cletole	BLF	Tzontehuitz	446.89	962.02	5.34	1.47	16.84	0.46	0.88	24.50	418.50
7	*Cornus disciflora*	Corndis	BLF	Military zone	348.95	3,932.13	14.16	0.51	17.19	0.58	1.32	20.20	389.00
8	*Miconia glaberrima*	Micogla	BLF	Tzontehuitz	284.45	3,020.00	14.76	0.12	5.72	0.52	1.28	24.50	418.80
9	*Oreopanax xalapensis*	Oreoxal	BLF	Tzontehuitz	386.19	21,351.50	8.33	1.01	15.71	0.53	1.03	27.70	471.80
10	*Persea americana*	Persame_1	OF	Tzontehuitz	416.44	9,122.97	8.08	0.72	13.97	0.46	1.43	25.70	437.60
11	*Persea americana*	Persame_2	BLF	Tzontehuitz	443.22	8,616.33	7.89	0.56	23.61	0.55	1.28	24.20	415.00
12	*Pinus ayacahuite*	Pinuaya	BLF	Military zone	403.75	533.20	8.17	2.29	29.68	0.43	1.16	17.50	421.00
13	*Pinus montezumae*	Pinumon_1	POF	Aguaje	427.44	1,138.10	5.40	7.71	29.00	0.46	1.08	26.60	453.40
14	*Pinus montezumae*	Pinumon_2	PF	Military zone	393.44	1,322.91	4.32	6.53	31.52	0.47	0.98	29.50	502.20
15	*Pinus montezumae*	Pinumon_3	PF	Aguaje	390.52	1,367.22	4.67	6.53	32.39	0.47	1.48	31.30	532.70
16	*Pinus pseudostrobus* var. *apulcensis*	Pinuapu	POF	San José	418.52	885.24	4.81	1.57	27.73	0.56	0.81	25.67	418.30
17	*Pinus pseudostrobus* var. *pseudostrobus*	Pinupse	OF	Tzontehuitz	422.24	704.45	4.51	2.57	21.07	0.41	1.38	27.00	460.40
18	*Pinus tecunumanii*	Pinutec_1	POF	San José	404.64	728.05	6.13	1.04	34.06	0.54	0.78	26.30	449.60
19	*Pinus tecunumanii*	Pinutec_2	POF	Military zone	498.54	890.32	5.88	3.03	26.10	0.49	1.13	26.10	445.20
20	*Pinus tecunumanii*	Pinutec_3	POF	Aguaje	399.14	477.13	6.68	1.07	32.73	0.52	1.03	26.30	449.60
21	*Pinus tecunumanii*	Pinutec_4	PF	Encuentro	433.53	552.38	6.29	1.44	31.21	0.50	0.83	24.30	414.70
22	*Pinus tecunumanii*	Pinutec_5	PF	Military zone	429.64	937.86	6.05	1.27	26.91	0.54	1.23	25.30	430.00
23	*Prunus rhamnoides*	Prunrha	BLF	Tzontehuitz	433.38	1,359.53	9.44	0.32	19.05	0.50	1.53	18.50	318.90

Number	Species	Acronym	Forest type	Site	LDMC (mg g^{-1})	LA (mm^{2})	SLA (mm^{2} mg^{-1})	LTS (N mm^{-1})	H_{max} (m)	WD (g mm^{-1})	LPC (mg g^{-1})	LNC (mg g^{-1})	LCC (mg g^{-1})
24	*Quercus crassifolia*	Quercra_1	POF	San José	515.86	14,847.61	6.31	1.20	22.49	0.69	0.73	24.90	426.50
25	*Quercus crassifolia*	Quercra_2	OF	Huitepec	485.03	11,643.37	6.82	0.89	22.45	0.69	0.88	24.80	422.70
26	*Quercus crispipilis*	Quecri_1	POF	San José	493.22	1,905.68	10.92	0.60	22.66	0.72	1.38	26.10	445.20
27	*Quercus crispipilis*	Quecri_2	POF	Aguaje	425.30	2,616.86	11.82	0.61	15.78	0.71	1.18	28.00	476.50
28	*Quercus crispipilis*	Quecri_3	OF	Moxviquil	488.97	2,641.47	9.17	0.66	19.62	0.66	1.13	25.50	434.20
29	*Quercus laurina*	Querlau_1	BLF	Military zone	566.71	2,243.27	9.12	0.74	25.47	0.72	1.13	24.70	422.30
30	*Quercus laurina*	Querlau_2	POF	Military zone	560.57	2,479.72	9.56	0.89	27.61	0.73	0.98	23.50	399.50
31	*Quercus laurina*	Querlau_3	OF	Huitepec	461.47	1,790.44	11.59	0.67	24.48	0.66	1.03	24.50	418.80
32	*Quercus laurina*	Querlau_4	BLF	Huitepec	450.30	1,768.81	12.92	0.61	35.34	0.69	1.08	23.10	395.80
33	*Quercus ocoteaefolia*	Queroco_1	BLF	Tzontehuitz	536.13	2,223.99	9.28	0.78	17.52	0.70	1.03	23.00	391.90
34	*Quercus ocoteaefolia*	Queroco_2	OF	Tzontehuitz	497.12	1,219.16	8.93	1.24	15.65	0.61	1.43	23.90	407.10
35	*Quercus rugosa*	Querrug_1	POF	Aguaje	490.47	10,748.48	6.95	0.95	15.16	0.73	1.18	23.10	395.80
36	*Quercus rugosa*	Querrug_2	POF	San José	453.86	10,552.52	8.62	0.85	18.91	0.78	1.23	24.10	411.10
37	*Quercus rugosa*	Querrug_3	POF	Military zone	617.27	14,898.62	5.51	1.40	25.00	0.69	1.18	23.50	399.50
38	*Quercus rugosa*	Querrug_4	BLF	Military zone	488.62	8,520.35	6.75	1.38	19.18	0.76	1.08	21.10	361.50
39	*Quercus rugosa*	Querrug_5	OF	Huitepec	499.37	8,623.14	8.46	0.77	20.78	0.71	1.43	23.80	407.30
40	*Quercus rugosa*	Querrug_6	OF	Moxviquil	491.24	7,491.87	7.36	1.01	15.22	0.78	1.43	20.20	345.80
41	*Quercus rugosa*	Querrug_7	BLF	Huitepec	469.55	11,444.20	8.83	0.68	32.14	0.76	1.58	26.10	445.20
42	*Quercus segoviensis*	Querseg_1	POF	Aguaje	458.91	4,697.49	11.41	0.55	15.25	0.80	1.53	26.70	457.20
43	*Quercus segoviensis*	Querseg_2	OF	Moxviquil	469.37	4,672.23	10.29	0.70	20.40	0.78	1.48	26.20	445.70
44	*Quetzalia contracta*	Quetcon_1	BLF	Tzontehuitz	337.14	1,250.92	12.53	0.87	12.82	0.44	1.18	20.90	357.30
45	*Quetzalia contracta*	Quetcon_2	BLF	Huitepec	338.03	1,747.68	13.28	0.62	10.72	0.42	0.92	25.67	418.30
46	*Styrax magnus*	Styrmag	BLF	Huitepec	486.93	9,778.33	10.11	0.35	16.54	0.46	1.28	24.70	422.30
47	*Symplocos breedlovei*	Sympbre	BLF	Tzontehuitz	396.61	1,852.83	7.72	0.86	13.84	0.69	1.28	24.90	426.50
48	*Ternstroemia lineata*	Ternlin	BLF	Tzontehuitz	399.74	1,015.87	6.14	1.77	14.43	0.58	0.78	28.00	475.60
49	*Weinmannia pinnata*	Weinpin	BLF	Tzontehuitz	383.47	3,639.27	13.11	0.60	20.14	0.57	0.88	25.50	434.20

Appendix 2.2 General measurement methods used to determine functional traits.

Maximum adult height (H_{max}). This was the shortest distance (in metres) between the upper boundary of the main photosynthetic tissues and ground level (Cornelissen *et al.* 2003). It was determined by using basic trigonometric calculations applied to the angles formed by the top and the base of a tree (taken with a Suunto clinometer) and the distance used to make the angle measurements. Corrections of distance and height were applied in sloping terrain.

Wood density (WD). This is expressed in mg cm^{-3} and was the oven-dry mass of a stem section divided by the volume of the section when still fresh (Cornelissen *et al.* 2003). Wood samples (1015 cm length) were taken with a 40 cm Suunto increment borer, at 1.3 m height, on trees of at least 10 cm DBH. The sample fresh volume was determined by using the water-displacement method (Chave 2005) obtaining the displaced weight of water in grammes but later converted to cm^3 (1 g = 1 cm^3). The sample was then oven-dried to obtain the wood dry-weight that was measured.

Leaf area (LA) and **specific leaf area** (SLA). A flat image of each leaf was obtained from a flatbed scanner adjusted to the most appropriate grey scale, at 600 dots per inch (dpi); subsequently, leaf area software (UCPE 2009) was used to give a complete leaf area in mm^2. The same leaf sample was then oven-dried to get a leaf dry-weight. SLA was then taken as the one-sided area of a fresh leaf divided by its dry mass, expressed in mm^2 mg^{-1}. As pointed out by Cornelissen et al. (2003), special procedures were followed for pine needles (Kloeppel *et al.* 2000; Hans Cornelissen and Lourens Poorter pers. comm.) and other special cases (for instance non-flat leaves, very large leaves, compound leaves). The LA and SLA averages of five leaves per tree constituted a single individual observation (Garnier *et al.* 2001).

Leaf dry matter content (LDMC). Twigs with leaves collected from each of five individuals per species were rehydrated for six hours with deionized water (Garnier *et al.* 2001). Five water-saturated leaves from each tree individual were fresh weighed and then oven-dried. The LDMC value was taken as the dry mass (mg) of the leaf divided by its fresh mass (g) (Cornelissen *et al.* 2003).

Leaf tensile strength (LTS). This was the force (in N) used to tear a leaf cross section divided by the width (in mm) of the leaf fragment. For most species we used a rectangular fragment (10 mm width, 40 mm length) taken from the leaf central section, however special procedures were used for tiny leaves (such as *Weinmania pinnata* leaflets) and *Pinus* species needles. The measurements were made with a leaf tensiometer obtaining the value in grammes but later converting to Newtons (1 N = 100 g). The average of five leaf measurements per tree constituted a single observation.

Leaf nitrogen (N), leaf phosphorus (P) and leaf organic carbon (OC) concentrations. These traits were the total amounts of N, P, and organic C per unit of dry leaf mass, expressed in mg g^{-1}. They were determined from oven-dried and ground leaves in a composite sample (approx. 200 g) for each of five individuals per species. Leaf samples were processed without any petiole or rachis traces. Total concentrations of N and P were determined by the semi-micro Kjeldahl method whereas organic carbon was determined by the Walkley and Black method, following the protocols detailed in Etchevers-Barra (1992).

Appendix 2.3 Community weighted mean values (CWM) for each of the 48 sample plots. LDMC = Leaf dry matter content, LA = Leaf area, SLA = Specific leaf area, LTS = Leaf tensile strength, H_{max} = Maximum height, WD = Wood density, LPC = Leaf phosphorous content, LNC = Leaf nitrogen content, LCCC = Leaf organic carbon content.

Forest	Site	Plot	Acronym	LDMC (mg g^{-1})	LA (mm^2)	SLA (mm^2 mg^{-1})	LTS (N mm^{-1})	H_{max} (m)	WD (g mm^{-1})	LPC (mg g^{-1})	LNC (mg g^{-1})	LCC (mg g^{-1})
Broad-leaved forest	Huitepec	1	BlfHu1	458.25	8,189.79	9.99	0.62	29.67	0.69	1.40	25.35	432.79
		2	BlfHu2	445.99	4,127.39	11.84	0.60	32.49	0.65	1.12	23.23	397.85
		3	BlfHu3	448.74	5,168.14	11.51	0.64	32.39	0.69	1.24	24.34	414.83
		4	BlfHu4	454.92	8,023.55	10.21	0.63	31.47	0.69	1.34	24.52	419.05
	Tzontehuitz	1	BlfTz1	423.62	4,278.95	10.43	0.80	17.70	0.62	0.99	25.14	428.55
		2	BlfTz2	471.09	3,207.31	8.17	0.83	17.61	0.64	1.13	23.90	408.52
		3	BlfTz3	427.25	7,507.50	8.59	0.61	21.98	0.53	1.26	23.70	406.31
		4	BlfTz4	417.58	6,682.16	9.16	0.46	20.20	0.54	1.32	23.40	401.25
	Military zone	1	BlfZo1	452.33	13,286.84	11.12	0.62	21.58	0.64	1.34	22.26	392.26
		2	BlfZo2	524.08	3,949.96	9.09	0.87	23.05	0.71	1.14	23.34	403.93
		3	BlfZo3	480.25	1,922.58	9.55	1.22	25.65	0.60	1.17	21.64	416.95
		4	BlfZo4	459.26	18,928.01	11.47	0.47	22.92	0.62	1.44	22.81	395.89
Pine-oak forest	Aguaje	1	PofAg1	426.71	1,644.67	7.60	5.28	24.47	0.55	1.11	27.08	461.31
		2	PofAg2	421.85	3,317.89	9.49	2.54	19.11	0.64	1.23	26.54	449.56
		3	PofAg3	423.85	2,766.81	6.49	2.33	28.31	0.55	1.07	25.68	439.02
		4	PofAg4	440.70	6,395.42	9.61	0.70	15.27	0.71	1.23	25.31	428.94
	San José	1	PofSa1	430.65	3,721.65	5.91	1.17	30.42	0.57	0.78	25.88	438.75
		2	PofSa2	440.68	6,133.18	6.75	1.03	27.99	0.63	0.87	25.48	435.55
		3	PofSa3	462.93	4,196.56	8.71	0.92	22.83	0.70	1.19	25.40	428.42
		4	PofSa4	414.74	2,742.81	6.64	1.00	30.96	0.59	0.87	25.85	441.70
	Military zone	1	PofZo1	565.58	8,800.24	5.67	2.11	25.48	0.60	1.16	24.63	419.40
		2	PofZo2	584.89	7,806.45	7.82	1.11	26.49	0.71	1.07	23.50	399.50
		3	PofZo3	566.60	7,755.48	6.46	1.83	25.89	0.63	1.12	24.36	414.56
		4	PofZo4	578.14	6,329.10	8.30	1.05	26.81	0.72	1.04	23.50	399.50
Oak forest	Huitepec	1	OfHu1	480.54	9,764.07	7.73	0.85	22.84	0.68	0.91	24.74	421.96
		2	OfHu2	495.21	9,500.25	7.98	0.80	21.27	0.70	1.27	24.09	411.77
		3	OfHu3	490.37	10,520.49	7.43	0.84	21.83	0.70	1.08	24.43	416.97
		4	OfHu4	495.20	9,501.83	7.98	0.80	21.27	0.70	1.27	24.09	411.78
	Moxviquil	1	OfMo1	475.08	4,080.85	9.96	0.69	20.17	0.75	1.38	26.00	442.35
		2	OfMo2	477.96	5,779.82	9.14	0.82	18.37	0.78	1.46	23.84	406.46

Forest	Site	Plot	Acronym	LDMC (mg g^{-1})	LA (mm^{2})	SLA (mm^{2} mg^{-1})	LTS (N mm^{-1})	H_{max} (m)	WD (g mm^{-1})	LPC (mg g^{-1})	LNC (mg g^{-1})	LCC (mg g^{-1})
		3	OfMo3	490.78	6,515.72	7.72	0.94	16.10	0.76	1.37	21.27	363.59
		4	OfMo4	476.05	3,979.93	9.91	0.68	20.14	0.74	1.36	25.96	441.78
	Tzontehuitz	1	OfTz1	485.87	1,141.87	8.27	1.44	16.47	0.58	1.42	24.37	415.10
		2	OfTz2	497.12	1,219.16	8.93	1.24	15.65	0.61	1.43	23.90	407.10
		3	OfTz3	470.09	3,033.74	8.29	1.04	15.30	0.58	1.42	25.16	428.20
		4	OfTz4	497.12	1,219.16	8.93	1.24	15.65	0.61	1.43	23.90	407.10
Pine forest	Aguaje	1	PfAg1	390.51	1,367.22	4.67	6.53	32.39	0.47	1.48	31.30	532.70
		2	PfAg2	390.51	1,367.22	4.67	6.53	32.39	0.47	1.48	31.30	532.70
		3	PfAg3	390.51	1,367.22	4.67	6.53	32.39	0.47	1.48	31.30	532.70
		4	PfAg4	390.51	1,367.22	4.67	6.53	32.39	0.47	1.48	31.30	532.70
	Encuentro	1	PfEn1	433.53	552.38	6.29	1.44	31.21	0.50	0.83	24.30	414.70
		2	PfEn2	433.53	552.38	6.29	1.44	31.21	0.50	0.83	24.30	414.70
		3	PfEn3	433.53	552.38	6.29	1.44	31.21	0.50	0.83	24.30	414.70
		4	PfEn4	433.53	552.38	6.29	1.44	31.21	0.50	0.83	24.30	414.70
	Military zone	1	PfZo1	393.44	1,322.91	4.32	6.53	31.52	0.47	0.98	29.50	502.20
		2	PfZo2	393.44	1,322.91	4.32	6.53	31.52	0.47	0.98	29.50	502.20
		3	PfZo3	393.44	1,322.91	4.32	6.53	31.52	0.47	0.98	29.50	502.20
		4	PfZo4	405.87	1,190.71	4.92	4.73	29.94	0.49	1.07	28.06	477.41

Appendix 2.4 Environmental variables obtained from WorldClim data layers (Hijmans *et al.* 2005) assigned to each of the 48 sample plots. BLF = broad-leaved forest, POF = pine-oak forest, OF = oak forest, PF = pine forest. Temp mean = mean annual temperature, Temp season = temperature seasonality, Temp maxw = temperature of warmest month, Temp minc = temperature of coldest month, Preci mean = mean annual precipitation, Preci drym = precipitation of driest month, Preci season = precipitation seasonality.

Number	Forest	Site	Plot	Acronym	Altitude	Latitude	Longitude	Temp mean	Temp season	Temp maxw	Temp minc	Preci mean	Preci drym	Preci season
1	BLF	Huitepec	1	BlfHu1	2533	533701	1851886	12.9	110.5	20.9	3.9	1249	17	76
2			2	BlfHu2	2668	532997	1851326	12.9	110.5	20.9	3.9	1249	17	76
3			3	BlfHu3	2639	533290	1851455	12.9	110.5	20.9	3.9	1249	17	76
4			4	BlfHu4	2593	533441	1851692	12.9	110.5	20.9	3.9	1249	17	76
5		Tzontehuitz	1	BlfTz1	2681	543689	1858379	11.7	103.9	19.5	3.1	1396	27	69
6			2	BlfTz2	2777	543867	1858158	11.7	103.9	19.5	3.1	1396	27	69
7			3	BlfTz3	2773	543967	1858321	11.7	103.9	19.5	3.1	1396	27	69
8			4	BlfTz4	2651	545474	1858312	12.6	105.4	20.5	3.9	1309	24	69
9		Military zone	1	BlfZo1	2512	544086	1841340	12.9	110.6	20.9	3.9	1187	15	77
10			2	BlfZo2	2527	544163	1841141	12.9	110.6	20.9	3.9	1187	15	77
11			3	BlfZo3	2491	544054	1841027	12.9	110.6	20.9	3.9	1187	15	77
12			4	BlfZo4	2488	543923	1841303	12.9	110.6	20.9	3.9	1187	15	77
13	POF	Aguaje	1	PofAg1	2449	543844	1843829	13.8	112.5	21.9	4.7	1123	13	78
14			2	PofAg2	2384	543445	1846038	14.1	116.0	22.4	4.9	1121	13	78
15			3	PofAg3	2363	543282	1846222	14.1	116.0	22.4	4.9	1121	13	78
16			4	PofAg4	2422	543529	1844212	13.1	108.5	21.2	4.1	1177	15	76
17		San José	1	PofSa1	2376	532036	1848989	13.9	117.6	22.0	4.7	1150	11	82
18			2	PofSa2	2375	531770	1848718	13.8	115.9	21.9	4.6	1167	12	81
19			3	PofSa3	2399	531862	1848515	13.8	115.9	21.9	4.6	1167	12	81
20			4	PofSa4	2314	532562	1847717	14.0	118.1	22.1	4.7	1144	11	82
21		Military zone	1	PofZo1	2700	546011	1839995	11.8	99.8	19.7	3.2	1293	20	73
22			2	PofZo2	2663	545807	1839749	12.0	103.2	19.9	3.2	1272	19	74
23			3	PofZo3	2735	546201	1839624	12.0	103.2	19.9	3.2	1272	19	74
24			4	PofZo4	2699	546390	1839913	12.0	104.8	19.9	3.3	1267	19	74
25	OF	Huitepec	1	OfHu1	2396	534092	1852086	14.1	116.9	22.2	4.9	1138	14	77
26			2	OfHu2	2343	533810	1852402	14.1	116.9	22.2	4.9	1138	14	77
27			3	OfHu3	2367	534006	1851739	13.9	119.0	22.0	4.7	1146	13	78
28			4	OfHu4	2317	534231	1851985	14.1	116.9	22.2	4.9	1138	14	77

Number	Forest	Site	Plot	Acronym	Altitude	Latitude	Longitude	Temp mean	Temp season	Temp maxw	Temp minc	Preci mean	Preci drym	Preci season
29		Moxviquil	1	OfMo1	2334	539002	1852971	13.6	114.4	21.7	4.5	1183	16	75
30			2	OfMo2	2337	539144	185300	13.7	117.2	21.8	4.5	1166	16	75
31			3	OfMo3	2314	539292	1852885	13.7	117.2	21.8	4.5	1166	16	75
32			4	OfMo4	2213	539159	1852661	15.1	121.9	23.4	5.8	1230	25	70
33		Tzontehitz	1	OfTz1	2776	543918	1857743	11.7	103.9	19.5	3.1	1396	27	69
34			2	OfTz2	2646	542418	1856121	12.7	112.8	20.6	3.8	1289	22	71
35			3	OfTz3	2817	543995	1857866	11.7	103.9	19.5	3.1	1396	27	69
36			4	OfTz4	2767	543943	1857531	11.7	103.9	19.5	3.1	1396	27	69
37	PF	Aguaje	1	PfAg1	2280	544440	1843148	14.0	114.4	22.3	4.8	1115	13	78
38			2	PfAg2	2285	544585	1843413	14.0	114.4	22.3	4.8	1115	13	78
39			3	PfAg3	2370	543982	1844385	13.8	112.5	21.9	4.7	1123	13	78
40			4	PfAg4	2312	544098	1844085	13.8	112.5	21.9	4.7	1123	13	78
41		Encuentro	1	PfEn1	2292	542349	1850457	14.3	122.1	22.6	5.0	1141	16	75
42			2	PfEn2	2331	542601	1850366	14.3	122.1	22.6	5.0	1141	16	75
43			3	PfEn3	2290	542523	1849450	14.3	121.3	22.5	5.0	1135	15	77
44			4	PfEn4	2267	542286	1849575	14.3	121.3	22.5	5.0	1135	15	77
45		Military zone	1	PfZo1	2388	547244	1841178	13.9	113.2	22.0	4.7	1116	14	76
46			2	PfZo2	2395	547267	1841559	13.9	113.2	22.0	4.7	1116	14	76
47			3	PfZo3	2354	546976	1841749	13.7	115.1	21.8	4.4	1127	14	77
48			4	PfZo4	2374	547186	1842011	13.6	110.8	21.7	4.5	1138	15	76

Appendix 2.5 The 84 tree species recorded in the 48 sample plots with the maximum stratum height of each species and the forest types and sites in which they were located. BlfHu = Broad-leaved forest of Huitepec, BlfTz = Broad-leaved forest of Tzontehuitz, BLFZo = Broad-leaved forest of Military zone, PofAg = Pine-oak forest of Aguaje, PofSa = Pine-oak forest of San José, PofZo = Pine-oak forest of Military zone, OfHu = Oak forest of Huitepec, OfMo = Oak forest of Moxviquil, OfTz = Oak forest of Tzontehuitz, PfAg = Pine forest of Aguaje, PfEn = Pine forest of Encuentro, Pfzo = Pine forest of Military zone.

CLASS /FAMILY	Scientific name	Stratum	Forest type and site
GIMNOSPERMAE			
CUPRESSACEAE	*Pinus ayacahuite* var. *ayacahuite* C. Ehrenb. ex Schltdl.	Canopy	BlfZo, PofZo, PfZo
	Pinus montezumae Lamb.	Canopy	PofAg, PofZo, PfAg, PfZo, PfEn
	Pinus pseudostrobus var. *apulcensis* (Lindl.) Shaw	Canopy	PofSa, PfAg, PfEn
	Pinus pseudostrobus (Lindl.) var. *pseudostrobus*	Canopy	OfTz
	Pinus tecunumanii F. Schwerdtf. ex Eguiluz & J.P.Perry	Canopy	BlfZo, PofAg, PofSa, PofZo, PfAg, PfEn, PfZo
ANGIOSPERMAE			
ADOXACEAE	*Viburnum acutifolium* Benth.	Shrub or small tree	BlfTz
	Viburnum elatum Benth.	Shrub or small tree	BlfTz, OfHu, OfMo
	Viburnum jucundum Morton ssp. *jucundum*	Understory tree	BlfHu, BlfTz, BlfZo, PofSa, PofZo, OfHu, OfTz
	Viburnum obtusatum D.N. Gibson	Understory tree	BlfTz
ARALIACEAE	*Oreopanax arcanus* A.C. Sm.	Understory tree	BlfHu, BlfTz, OfHu
	Oreopanax peltatus Linden ex Regel	Understory tree	BlfZo
	Oreopanax xalapensis (Kunth) Decne. & Planch	Understory tree	BlfHu, BlfTz, BlfZo, PofSa, PofZo, OfHu, OfTz
ASTERACEAE	*Baccharis vaccinioides* Kunth	Shrub or small tree	PfAg
	Critoniadelphus nubigenus (Benth.) R.M. King & H. Rob.	Shrub or small tree and understory tree	BlfHu, BlfTz, PofZo
	Eupatorium ligustrinum DC.	Shrub or small tree	BlfHu, BlfTz, PofAg, OfMo
	Eupatorium pycnocephalum Less.	Shrub	BlfZo
	Roldana acutangula (Bertol.) Funston	Shrub or small tree	BlfTz, PofZo
	Senecio uspantanensis Greenm.	Shrub	BlfTz
	Verbesina perymenioides Sch. Bip. ex Klatt.	Shrub or small tree	BlfHu, BlfTz, PofSa

CLASS /FAMILY	Scientific name	Stratum	Forest type and site
	Vernonia leiocarpa DC.	Shrub or small tree	OfMo
	Asteracea sp1	Shurb	BlfZo
BETULACEAE	*Alnus acuminata* subsp. *arguta* (Schltdl.) Furlow	Canopy	BlfZo, PofSa, PofZo, OfTz
	Ostrya virginiana var. guatemalensis (H.J.P. Winkl.) J.F. Macbr.	Understory tree	BlfHu, BlfZo, OfHu
BUDDLEJACEAE	*Buddleja cordata* Kunth	Shrub or small tree and understory tree	BlfHu, BlfTz, BlfZo, PofAg, PofSa, PofZo, OfHu, OfMo, OfTz, PfAg, PfEn
	Buddleja nitida Benth.	Understory tree	BlfHu, BlfTz, BlfZo, OfTz
CELASTRACEAE	*Celastrus vulcanicola* Donn. Sm.	Vine	BlfTz
	Crossopetalum tonduzii (Loes.) Lundell	Shrub or small tree	BlfTz
	Quetzalia contracta Lundell	Understory tree	BlfHu, BlfTz, OfTz
CLETHRACEAE	*Clethra macrophylla* M. Martens & Galeotti	Understory tree	BlfHu, BlfTz
	Clethra mexicana DC.	Understory tree	BlfTz
	Clethra oleoides L.O. Williams	Shrub or small tree	BlfTz, OfTz
CORNACEAE	*Cornus disciflora* DC.	Understory tree	BlfTz, BlfZo, OfHu
	Cornus excelsa Kunth	Understory tree	OfHu, OfMox, PfEn
CUNONIACEAE	*Weinmannia pinnata* L.	Shrub or small tree	BlfTz
ERICACEA	*Arbutus xalapensis* Kunth	Understory tree and canopy tree	BlfHu, PofAg, PofSa, PofZo, OfHu, OfMo, OfTz, PfEn, PfZo
FAGACEAE	*Quercus candicans* Humb. & Bonpl.	Canopy	OfHu, PfEn
	Quercus crassifolia Humb. & Bonpl.	Canopy	BlfHu, PofAg, PofSa, OfHu, OfMo, OfTz, PfEn, PfZo
	Quercus crispipilis Trel.	Canopy	PofSa, OfMo, PfAg, PfEn
	Quercus laurina Bonpl.	Canopy	BlfHu, BlfZo, PofAg, PofZo, PofSa, OfHu, OfMo, PfZo
	Quercus ocoteaefolia Liebm.	Canopy	BlfTz, OfTz
	Quercus rugosa Née	Canopy	BlfHu, BlfZo, PofAg, PofSa, PofZo, OfHu, OfMo, OfTz, PfEn, PfZo
	Quercus segoviensis Liebm.	Canopy	PofAg, PofSa, OfMo, PfEn
	Quercus skutchii Trel.	Canopy	PofSa, PfEn
GARRYACEAE	*Garrya laurifolia* Hartw. ex Benth.	Understory tree	BlfHu, BlfZo, PofAg, PofZo, OfHu, OfMo, PfEn
LAURACEAE	*Litsea glaucescens* Kunth	Shrub or small tree	BlfTz, PofAg, PofZo, OfMo, OfTz

CLASS /FAMILY	Scientific name	Stratum	Forest type and site
		and understory tree	
	Persea americana Mill.	Understory tree and canopy tree	BlfHu, BlfTz, OfTz
MALVACEAE	*Malvaviscus arboreus* Cav.	Shrub or small tree	OfMo, OfHu
MELASTOMATACEAE	*Miconia glaberrima* (Schltdl.) Naudin	Shrub or small tree	BlfHu, BlfTz, OfTz
MYRICACEAE	*Morella cerifera* (L.) Small	Understory tree	BlfTz, PofSa, OfTz
MYRSINACEAE	*Myrsine juergensenii* (Mez) Ricketson & Pipoly	Understory tree	BlfHu, BlfTz, BlfZo, PofSa, OfHu, OfTz
	Synardisia venosa (Mast.) Lundell	Shrub or tree	BlfZo
OLEACEAE	*Forestiera reticulata* Torr.	Understory tree	BlfTz
PENTAPHYLACACEAE	*Cleyera theoides* (Sw.) Choisy	Understory tree	BlfHu, BlfZo, PofZo, PofSa, OfTz
	Ternstroemia lineata DC.	Understory tree	BlfTz, BlfHu, BlfZo, OfTz
PRIMULACEAE	*Parathesis chiapensis* Fernald	Shrub or understory	BlfHu
	Parathesis leptopa Lundell	Shrub or small tree	BlfTz, BlfZo
RHAMNACEAE	*Rhamnus mcvaughii* L.A. Johnst. & M.C. Johnst.	Shrub	OfHu
	Rhamnus sharpii M.C. Johnst. & L.A. Johnst.	Understory tree	BlfHu, BlfTz, OfHu
ROSACEAE	*Crataegus pubescens* (C. Presl.) C. Presl.	Understory tree	PofAg, OfHu, OfMo, PfAg, PfEn
	Photinia microcarpa Standl.	Small tree	BlfTz, BlfZo
	Prunus lundelliana Standl.	Understory tree	BlfTz, OfTz
	Holodiscus argenteus (L. f.) Maxim.	Shrub or small tree	BlfTz, PofZo, OfHu, OfTz
	Prunus brachybotrya Zucc.	Understory tree	BlfHu, OfHu
	Prunus rhamnoides Koehne	Understory tree	BlfHu, BlfTz, OfTz
	Prunus serotina Ehrenb. subsp. *capuli* (Cav.) McVaugh	Understory tree	BlfHu, BlfTz, OfHu, PfEn
RUBIACEAE	*Deppea grandiflora* Schltdl.	Shrub or small tree	BlfHu, BlfTz
RUTACEAE	*Zanthoxylum melanostictum* Schltdl. & Cham.	Understory tree	BlfHu, BlfTz, BlfZo, OfTz
SABIACEAE	*Meliosma dentata* (Liebm.) Urb.	Understory tree	BlfHu, BlfTz
SOLANACEAE	*Cestrum aurantiacum* Lindl.	Shrub or small tree	BlfZo
	Cestrum guatemalense C.V. Morton	Shrub or small tree	BlfHu
	Solanum aligerum Schltdl.	Shrub or small tree	BlfHu, BlfTz
	Solanum nigricans M. Martens & Galeotti	Shrub or small tree	BlfHu, BlfTz
STERCULIACEAE	*Chiranthodendron pentadactylon* Larreat.	Understory tree	BlfZo

CLASS /FAMILY	Scientific name	Stratum	Forest type and site
		and canopy tree	
STYRACACEAE	*Styrax magnus* Lundell	Understory tree	BlfHu, OfHu
SYMPLOCACEAE	*Symplocos breedlovei* Lundell	Understory tree	BlfHu, BlfTz, OfTz
THYMELAEACEAE	*Daphnopsis radiata* Donn. Sm.	Shrub	BlfHu
VERBENACEAE	*Lippia umbellata* Cav.	Shrub	BlfZo, PofZo
WINTERACEAE	*Drimys granadensis* var. *mexicana* (DC.) A.C. Sm.	Understory tree	BlfHu, BlfTz, OfTz
Unidentified	Plant 1	Shrub	PofAg
	Plant 2	Shrub	PofSa
	Plant 3	Shrub	PofSa
	Plant 4		PofSa
	Plant 5		PofSa
	Plant 6		PofAg

CHAPTER 3. FACTORS AFFECTING THE DISTRIBUTION AND ABUNDANCE OF SAPLINGS OF TREE SPECIES IN FORESTS OF THE CENTRAL HIGHLANDS OF CHIAPAS, MEXICO

3.1. ABSTRACT

Variation of the characteristics of tree species assemblages in forests is defined at multiple scales by spatial and biophysical factors, as well as disturbance regimes, which affect not only the composition and structure of adults but also their regeneration. We sought to determine the factors affecting the distribution and abundance of saplings of tree species of tropical montane forests of the Central Highlands (state of Chiapas, Mexico). First, it was hypothesised that climate factors and human disturbance would play the most important roles in the determination of composition and abundance of saplings at the landscape level. Second, it was hypothesised that canopy openness would be a major factor at the local scale. Finally, we asked what were the relationships between the functional traits of the dominant tree species and their sapling abundances, hypothesising that tree species with more acquisitive trait values would have more abundant saplings in this highly human disturbed landscape. For this, an intensive sampling of the sapling assemblages (individuals < 5 cm DBH, ≥ 30 cm height) was carried out in 96 plots equally divided between open and closed canopies. Each sample plot was floristically, spatially and environmentally characterised and, additionally, for 26 previously defined dominant species of large tree assemblages (> 10 cm DBH), eight functional traits were measured (leaf area, specific leaf area, leaf dry matter content, leaf tensile strength, leaf nitrogen content, leaf phosphorous content, wood density, and maximum height). Results indicate that the distribution of the sapling species and their abundances was not uniform across the study area, with floristic changes occurring over very short distances. Anthropogenic disturbance together with altitude explained differences in species richness and abundances between the saplings of pine-dominated and broad-leaved forests, whereas canopy openness had an effect for only nine of the 84 species analysed. Variation partitioning indicated that climate is the main factor explaining floristic variation in the sapling assemblages although spatial variables (PCNM eigenfunctions) were also related to sapling composition, suggesting a complementary effect of dispersal limitation. Leaf area was the only functional trait related to sapling abundance, having a positive correlation suggesting that regeneration of the dominant species in the study area is greater for those species that have big leaves, which may be associated with acquisitiveness. Overall, these results suggest that as hypothesised, distribution and abundance of sapling assemblages at the landscape scale are controlled by climatic variation and human disturbance, with a small contribution of spatial factors. The local-scale effect of canopy openness was smaller than expected, suggesting that due to generalised human disturbance in forests, light availability is not a major limiting factor on sapling regeneration. The positive relationship between species leaf area and sapling abundance, however, indicates that this point requires further research.

Keywords: montane forests, disturbance, functional traits, climate, spatial factors, dispersal assembly.

3.2. INTRODUCTION

Understanding of how tree species are adapted to grow, reproduce, survive and form community assemblages in their particular environments is an essential goal in plant ecology. In particular, comprehension of the processes that affect regeneration, the process by which trees and forest survive over the time (Ballabha, Tiwari & Tiwari 2013), becomes critical within the new contexts imposed by global change, especially in the hot spots of biodiversity represented by tropical montane forests (Richter 2008).

Mountains are conspicuous elements of tropical landscapes and represent evolutionary laboratories and ecological challenges for the species distributions (Körner 2004; Becker *et al.* 2007; Richter 2008). The regional source pool of species (gamma diversity) of these geological formations can be seen as a result of large-scale patterns, regional processes and historical factors (*sensu* Ricklefs 1987, 2007, 2008; Chase 2003; Jenkins & Ricklefs 2011) producing a variety of plant associations. Nevertheless, at local scales, montane forests are affected by spatial and environmental factors that, to a lesser or greater extent, affect not only their composition and structure but also the regeneration of their species. At this scale, understanding on how these different drivers interact to control spatial patterns and dynamics of biological communities is necessary (Vayreda *et al.* 2013); however, at the species level, the use of functional traits is compulsory in order to comprehend how vital rates may be related to the presence of a particular species in a given space (Ackerly 2003; Poorter & Bongers 2006; Poorter *et al.* 2008).

A functional trait is any morphological-physiological-phenological trait which impacts fitness indirectly by means of its effects on performance traits (Violle *et al.* 2007). In general, fitness is the extent to which an organism is adapted to its environment whereas the performance is understood by the ability of a sample of individuals to grow, reproduce or survive (fitness components) in particular ecological habitat; therefore, performance is a direct measure of fitness. Following Violle *et al*. (2007), three performance traits can be identified and measured to assess the three components of plant fitness: vegetative biomass, reproductive output (e.g. seed biomass, seed number) and plant survival. Investigations to elucidate the influence of functional traits on fitness are ongoing (Ackerly *et al.* 2000; Geber & Griffen 2003; Violle *et al.* 2007) but within this research effort, several key functional traits have been proposed to be universally important for plant performance and to represent relatively independent aspects of ecological strategies of plants (Cornelissen *et al.* 2003; Reich *et al.* 2003; Poorter *et al.* 2008).

Many of the tropical montane forests systems are far from pristine, they are highly related to the human activities and therefore anthropogenic variables are acting to shape the sapling distribution (Mayfield, Ackerly & Daily 2006). This is the case for the mountainous region of Central Highlands, in state of Chiapas, south-east Mexico, whose forests are currently distributed in fragments of different successional stages within a complex landscape of crop fields, pastureland and human settlements (González-Espinosa *et al.* 1991, 1997; Galindo-Jaimes *et al.* 2002), a phenomenon that possibly has led to an increased predominance of pines (*Pinus* spp.) at the expense of broad-leaved forests (González-Espinosa *et al.* 1991, 1997; Quintana-Ascencio *et al.* 2004). Due to this, many local ecological studies have dealt with species regeneration with a special concern on forest restoration, focusing mainly but not exclusively on vital aspects of species of *Quercus* and *Pinus* and others: seed dispersal, survival and growth of seedlings across successional or land-use gradients, and the effects of fragmentation, leaf-litter cover, forest canopy or seed predation on early establishment or germination (Ramírez-Marcial, González-Espinosa & Quintana-Ascencio 1992; Ramírez-Marcial, González-Espinosa & García-Moya 1996; Ramírez-Marcial *et al.* 2006; Quintana-Ascencio, González-Espinosa & Ramírez-Marcial 1992; Quintana-Ascencio *et al.* 2004; Camacho-Cruz *et al.* 2000; López-Barrera & González-Espinosa 2001; Ramírez-Marcial 2003; López-Barrera & Newton 2005; López-Barrera, Newton & Manson 2005; López-Barrera *et al.* 2006, 2007a; b; López-Barrera & Manson 2006). However, the associations between spatial and environmental factors and the floristic variation of sapling assemblages across the landscape have not been assessed yet, nor the possible relationship between species' abundances and their functional traits.

It is in this tropical but mountainous context of the Central Highlands that we ask what are the main factors influencing the floristic composition of sapling assemblages at the landscape level. In order to answer this question we 1) describe the floristic variation of the sapling assemblages, 2) assess the associations between structural descriptors of species and disturbance, 3) determine the relationships between the functional traits of dominant tree species with their sapling abundances, and 4) assess the relative contribution of geographic location, climate, altitude, canopy openness and human disturbance to floristic variation of the sapling assemblages.

From a floristic, environmental and geographical characterisation of the sapling assemblage of forests, and using an approach of spatial statistics (Legendre & Legendre 1998), we expect both to determine the spatial variation of floristic composition and to define the joint and the pure contributions of spatial and environmental factors to this variation. On the other hand, under the assumption that sapling abundance might be a relative measure of species survival and performance after germination, we expect to find associations between the sapling abundances of 26 dominant species and their eight functional traits previously determined in Chapter 2. In particular, based on the relationships between trait values and growth and mortality rates found by Poorter *et al.* (2008), we hypothesised that high wood density (WD) and maximum height (H_{max}) of species will be related to high abundance of saplings. Additionally, consistent with a hypothesis of greater construction costs of species and greater resistance to damage (Cornelissen *et al.* 2003; Pérez-Harguindeguy *et al.* 2013) in these mountainous and restrictive conditions (Körner 2004), we hypothesised that high sapling abundances would be related to high leaf tensile strength (LTS) and leaf dry matter content (LDMC) but low specific leaf area (SLA) and leaf area (LA), and generalized low leaf nutrient content.

3.3. METHODS

3.3.1. Study area and sampling of regeneration

This study was carried out in different forested sites of the Central Highlands, Chiapas, Mexico, between 16° 36'-16° 50' N and 92° 31'-92° 43' W, within an approximate area of 230 km^2 and an altitudinal range of 2200-2900 m a.s.l. (Fig.

3.1). Climate of this area is cool (mean annual temperature ranges from 13 to 15 °C) and humid (mean annual rainfall ranges between 1000 and 1300 mm), with a 5-6 month dry season (CONAGUA 2012) (Table 3.1). Topography is in general complex and abrupt with an underlying geology of carboniferous limestone with many rocky outcrops where the soils are a mixture of thin lithic rendzinas, deeper humic acrisols in forested areas, and infertile chromic luvisols (Cayuela *et al.* 2006c; Cayuela, Golicher & Rey-Benayas 2006a; Cayuela *et al.* 2006b).

We sampled four forest types as described by González-Espinosa *et al.* (1997) (pine forest PF, oak forest OF, pine-oak forest POF and broad-leaved forest BLF), using a design of three sites per forest type (12 sites) (Table 3.2); these are the same sites used in Chapter 2 in which were dominant a total set of 26 species (the species that made up 70% of the basal area in each sample plot). All saplings (individuals < 5 cm DBH, ≥ 30 cm height) were counted and identified in each of 96 rectangular plots of 500 m^2 (20 m × 25 m) each, 48 of them placed in closed forests and 48 in open areas. With this, eight plots (four in open and four in closed forest) were placed in each of the 12 sites. Canopy openness was evaluated in the four corners and the centre of each plot using a qualitative method based in Clark & Clark (1992) and adapted to percentages: open areas had canopy openness in the range 31-60% and closed forests, 61-90%.

Individuals sampled included both saplings of tree species and those typical of the understory. Preliminary identifications were carried out in the field using morphospecies. A posterior and complete identification was done by the expert knowledge of local researchers and parataxonomists for those individuals that could be reliably identified by those means. For others, voucher specimens were collected and identified by a member of the research team at the herbarium of ECOSUR (San Cristóbal de Las Casas) using local floras and comparison with specimens.

Altitude (in m a.s.l.) and geographical position of each sample plot were determined by a Suunto altimeter and by a Garmin GPS, respectively. Plots were also qualitatively characterised by their degree of anthropogenic disturbance in five ordinal levels (with 5 being the most disturbed) (Appendix 3.1). This classification was informed by several recorded characteristics of each plot: protection status, land-use history, and intensity and frequency of current anthropogenic disturbance of the site, together with the estimated percentages of canopy, shrub and herbaceous cover, the diameter and height of the sampled trees (Chapter 2) and occurrence of cut stumps.

3.3.2. Functional traits measurements

Based on the mass ratio hypothesis (Grime 1998), eight different vegetative traits (Table 3.3) were measured as continuous variables for the 26 dominant species in order to relate them with sapling densities: leaf area (LA) in mm^2, specific leaf area (SLA) in $mm^2\,mg^{-1}$, leaf dry matter content (LDMC) in mg g^{-1}, leaf tensile strength (LTS) in N mm^{-1}, leaf nitrogen concentration (LNC) in mg g^{-1}, leaf phosphorus concentration (LPC) in mg g^{-1}, wood density (WD) in g cm^{-3}, and maximum plant height (H_{max}) in m. These traits were obtained following the general procedures detailed in Chapter 2, based on the protocols of Cornelissen *et al.* (2003) and Pérez-Harguindeguy *et al.* (2013).

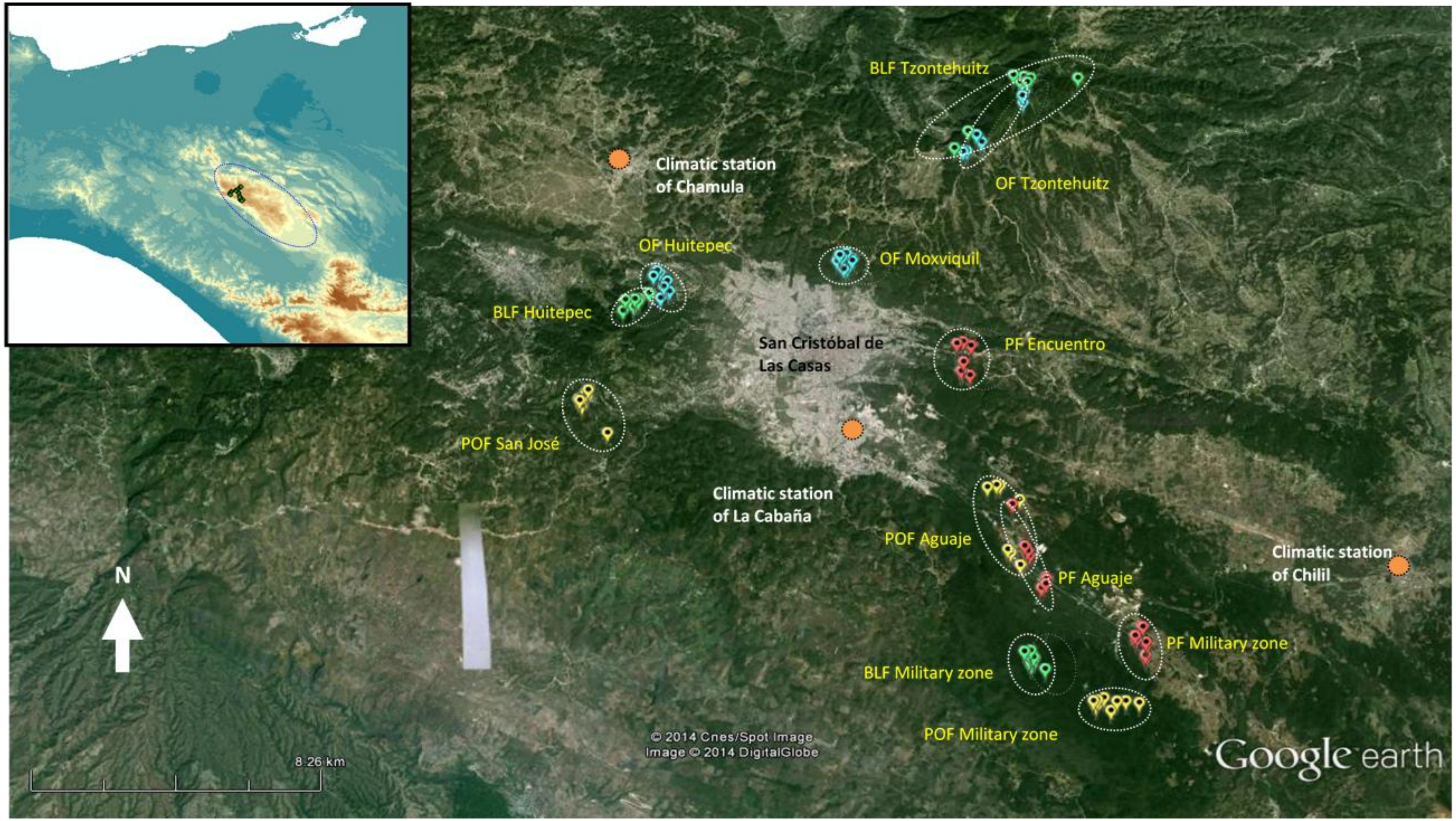

Figure 3.1 The Central Highlands (circled in blue within the box) in the state of Chiapas, Mexico, and the location of the 96 sample plots and their corresponding sites and forest types. Broad-leaved forests (BLF) are shown in green dots, pine-oak forests (POF) in yellow, oak forests (OF) in light blue and pine forests (PF) in red. The location of three climatic stations (Table 3.1) is also shown as orange dots.

Table 3.1 Precipitation and temperature values given by five climate stations of the National Commission of Water (CONAGUA) located within or in the cinity of the study area. The corresponding climatic values obtained from WorldClim data layers (Hijmans *et al.* 2005), for the same geographic locations, are also shown for comparison purposes. The locations of the three nearest stations (Chamula, Cabaña and Chilil) are shown in Figure 3.1. Temp mean = mean annual temperature, Temp max = mean maximum temperature, Temp min = mean minimum temperature, Preci mean = mean annual precipitation.

Climatic station name and years recorded	Altitude (m)	Location (latitude, longitude)	Preci mean (mm)	Temp mean (°C)	Temp max (°C)	Temp min (°C)	WorldClim data	
							Preci Mean (mm)	Temp Mean (°C)
Chamula 44 years	1930	16°47'49" 92°41'48"	1288.0	13.7	20.7	6.6	1204	14.2
Cabaña 55 years	2113	16°42'51" 92°37'44"	1084.7	15.0	21.9	8.1	1193	15.1
Chilil 42 years	2266	16°40'40" 92°29'21"	1220.0	14.0	20.5	7.4	1142	14.2
Larrainzar 38 years	2000	16°53'13" 92°42'56"	1737.9	15.4	21.6	9.2	1565	16.3
Chenalho 40 years	1537	16°53'37" 92°37'32"	1596.3	17.4	23.4	11.4	1939	19.0

Table 3.2 Some environmental characteristics (in ranges) and sets of dominant species (identified in Chapter 2 as the contributors of 70% of basal area in each sample plot) of each of 12 forest type-site combinations of the study area (eight plots per combination equitably divided in open and closed forests). The locations of the forest types, their sites and plots, are shown in Fig. 3.1. Preci mean = mean annual precipitation, Temp mean = mean annual temperature.

Forest	Site	Altitude (m)	WorldClim data		Dominant species
			Preci ann (mm)	Temp mean (°C)	
Broad-leaved forests	Huitepec	2516 - 2668	1249	12.9	*Quercus laurina, Q. rugosa, Clethra macrophylla, Styrax magnus, Arbutus xalapensis, Quetzalia contracta*
	Tzontehuitz	2600 - 2785	1262 - 1396	11.70 - 13.00	*Persea americana, Q. ocoteaefolia, Symplocos breedlovei, Quetzalia contracta, Miconia glaberrima, Prunus rhamnoides, Ternstroemia lineata, Clethra oleoides, Weinmannia pinnata, Oreopanax xalapensis*
	Military zone	2472 - 2613	1187 - 1225	12.9	*Q. laurina, Cornus disciflora, Q. rugosa, Chiranthodendron pentadactylon, Pinus ayacahuite*
Pine-oak forests	Aguaje	2326 -2449	1121 - 1123	13.10 - 14.10	*P. montezumae, Q. crispipilis, Q. rugosa, Arbutus xalapensis, P. tecunumanii, Q. segoviensis*
	San José	2314 - 2405	1144 - 1167	13.8 - 14.00	*P. tecunumanii, Q. rugosa, Q. crassifolia, P. pseudostrobus* var. *apulcensis* , *Q. crispipilis*
	Military zone	2546 - 2741	1267 - 1293	11.8 - 12.00	*Q. rugosa, Q. laurina, P. tecunumanii*
Oak forests	Huitepec	2317 - 2396	1138 - 1146	13.9 - 14.1	*Q. crassifolia, Q. rugosa, Q. laurina*
	Moxviquil	2213 - 2337	1166 - 1235	13.6 - 15.1	*Q. segoviensis, Q. rugosa, Q. crispipilis*
	Tzontehuitz	2634 - 2817	1289 - 1396	11.7 - 12.7	*Q. ocoteaefolia, P. pseudostrobus* var. *pseudostrobus, Buddleja cordata, Persea americana*
Pine forests	Aguaje	2312 - 2370	1115 - 1168	13.8 - 14.00	*P. montezumae*
	Encuentro	2267 - 2356	1135 - 1141	14.3	*P. tecunumanii*
	Military zone	2340 - 2396	1116 - 1138	13.6 - 13.9	*P. montezumae, P. tecunumanii*

Table 3.3 Eight functional traits of 26 dominant species of the study area (see Table 3.2) and some structural atributes of adults (from the study in Chapter 2) and saplings (results of this study, Appendix 3.3). LA = leaf area (mm^2), SLA = specific leaf area ($mm^2\,mg^{-1}$), LDMC = leaf dry matter content ($mg\ g^{-1}$), LTS = leaf tensile strength ($N\ mm^{-1}$), LPC = leaf phosphorous content ($mg\ g^{-1}$), LNC = leaf nitrogen content ($mg\ g^{-1}$), WD = wood density ($g\ mm^{-1}$), H_{max} = maximum height (m); BA = Basal area ($m^2\ ha^{-1}$), Dens = Density (ind ha^{-1}), Freq = Frequency (%).

Species	Traits								Adults			Saplings	
	LA	SLA	LDMC	LTS	LPC	LNC	WD	H_{max}	BA	Dens	Freq	Dens	Freq
Arbutus xalapensis	4455.90	9.47	366.50	0.56	1.13	25.82	0.55	16.04	40.95	750	54.17	1860	22.92
Buddleja cordata	6726.37	5.20	380.26	0.31	1.33	31.20	0.54	14.71	13.42	850	56.25	3140	42.71
Chiranthodendron pentadactylon	43224.67	13.07	381.60	0.16	1.83	21.70	0.54	22.27	26.17	50	6.25	0	0.00
Clethra macrophylla	6898.92	10.32	412.87	0.48	0.93	21.50	0.44	22.70	22.22	820	12.50	10640	14.58
Clethra oleoides	962.02	5.34	446.89	1.47	0.88	24.50	0.46	16.84	10.74	320	12.50	820	7.29
Cornus disciflora	3932.13	14.16	348.95	0.51	1.32	20.20	0.58	17.19	28.32	860	12.50	1780	11.46
Miconia glaberrima	3020.00	14.76	284.45	0.12	1.28	24.50	0.52	5.72	8.13	1110	12.50	19020	14.58
Oreopanax xalapensis	21351.50	8.33	386.19	1.01	1.03	27.70	0.53	15.71	23.21	1530	45.83	47080	53.13
Persea americana	8869.65	7.98	429.83	0.64	1.35	24.95	0.51	18.79	107.54	1180	20.83	30100	26.04
Pinus ayacahuite	533.20	8.17	403.75	2.29	1.16	17.50	0.43	29.68	38.72	340	22.92	420	6.25
Pinus montezumae	1276.08	4.80	403.80	6.92	1.18	29.13	0.47	30.97	309.99	5150	33.33	3700	15.63
Pinus pseudostrobus var. *apulsensis*	885.24	4.81	418.52	1.57	0.81	25.67	0.56	27.73	35.56	690	14.58	0	0.00
Pinus pseudostrobus var. pseudostrobus	704.45	4.51	422.24	2.57	1.38	27.00	0.41	21.07	10.98	50	6.25	0	0.00
Pinus tecunumanii	717.15	6.21	433.10	1.57	1.00	25.66	0.52	30.20	301.19	5030	43.75	8540	20.83
Prunus rhamnoides	1359.53	9.44	433.38	0.32	1.53	18.50	0.50	19.05	15.40	480	16.67	6320	20.83
Quercus crassifolia	13245.49	6.57	500.45	1.05	0.81	24.85	0.69	22.47	117.01	3060	35.42	7060	34.38
Quercus crispipilis	2388.01	10.63	469.16	0.62	1.23	26.53	0.70	19.36	66.49	2860	31.25	5060	33.33
Quercus laurina	2070.56	10.8	509.76	0.73	1.05	23.95	0.70	28.23	253.06	3070	47.92	11940	41.67
Quercus ocoteaefolia	1721.58	9.10	516.63	1.01	1.23	23.45	0.66	16.59	148.93	5220	14.58	3300	12.50
Quercus rugosa	10325.60	7.50	501.48	1.01	1.30	23.13	0.74	20.91	339.55	6300	64.58	17480	61.46
Quercus segoviensis	4684.86	10.85	464.14	0.62	1.50	26.45	0.79	17.83	79.19	4570	18.75	4000	23.96
Quetzalia contracta	1499.30	12.91	337.58	0.74	1.05	23.28	0.43	11.77	18.39	700	14.58	5640	17.71
Styrax magnus	9778.33	10.11	486.93	0.35	1.28	24.70	0.46	16.54	8.38	880	10.42	7280	18.75
Symplocos breedlovei	1852.83	7.72	396.61	0.86	1.28	24.90	0.69	13.84	19.45	1310	14.58	2640	10.42
Ternstroemia lineata	1015.87	6.14	399.74	1.77	0.78	28.00	0.58	14.43	14.22	890	16.67	4280	18.75
Weinmannia pinnata	3639.27	13.11	383.47	0.60	0.88	25.50	0.57	20.14	19.54	860	6.25	140	2.08

As pointed out by Cornelissen *et al.* (2003) and Pérez-Harguindeguy *et al.* (2013), these traits are well associated to the plant functions like potential relative growth rate (LA, SLA, WD), plant and leaf life spans (LA, SLA, LDMC, WD), photosynthetic rate (LA, SLA), nutrient conservation in resource-rich or resource-poor environments (SLA, LDMC, LNC, LPC, WD), above-ground biomass (WD, H_{max}), access of plant to light (H_{max}, WD), protection, defence and resistance to physical or mechanical damage (SLA, LDMC, LTS, WD), amongst others. In particular, leaf traits have been identified by Poorter & Bongers (2006) as important to understand the sapling performance and survival of species. Therefore, it is predicted that some or several of the traits assessed will correlate with juvenile densities.

Additionally, and accordingly to our field observations and the descriptions given in the species list included in González-Espinosa *et al.* (1997), we define the life form and the forest stratum reached for plants at maturity as a way to relate them with light requirements (Appendix 3.2).

3.3.3. Climatic variables

Averages of annual temperature and precipitation were taken for each of the 96 plot locations from the 30 arc-second resolution grids (approx. 1 km^2 resolution) developed by Hijmans *et al.* (2005) and available in the WorldClim Webpage (http://www.worldclim.org/) (Appendix 3.1). Plots were also characterised by another six climatic variables taken from BIOCLIM, a section of WorldClim: temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, precipitation seasonality, precipitation of driest month, and precipitation of the wettest month. Owing to the coarse resolution of these data, some of the plots shared the same pixel and, therefore, climatic sets. In total, 30 plot locations were sufficiently distant to have different climatic data sets. For the cases sharing the same pixel we assumed the same climate.

The 96 plots varied from 11.7 to 15.1 °C in mean annual temperature and in mean annual precipitation, although most of the plots were in the range 1121 to 1293 mm yr^{-1}), there was slightly higher precipitation at the Tzontehuitz site (1262 to 1396 mm) (Table 3.2). This site is located at higher altitudes of the northernmost portion of the study area, coincident with a more exposure to the winds of Gulf of Mexico (Fig. 3.1). The precipitation and temperature obtained from WorldClim were consistently similar with those obtained from climatic stations situated within the corresponding pixel (Table 3.1), although there was no reliable station to corroborate the climatic variation of the Tzontehuitz site. Nevertheless, the stations of Larrainzar and Chenalho, located outside of the study area, at lower altitudes but in that northern exposure, presented as well higher precipitations.

3.3.4. Data analysis

A Non-metric Multidimensional Scaling (NMS) ordination analysis was performed to explore floristic relationships between plots based on the composition of their sapling assemblage. This was carried out by means of PC-ORD ver. 4.25 m (McCune & Mefford 1999) with the sapling abundance data of 125 species recorded in two or more plots (Greig-Smith 1983). We used the following procedures in order to get an acceptable final stress value (Clarke 1993) to exert an appropriate analysis of three principal ordination analysis: Euclidean distances, 50 iterations, 10 runs with real data but 0 runs with randomized data.

Pearson correlations were calculated to assess relationships ($P < 0.05$) between the structure of the tree stratum (basal area, density and frequency) and sapling abundances (density, frequency and relative importance value (RIV)) in open or closed sites separately. The same analysis was used to determine correlations between the functional traits of dominant species and the abundances of their saplings and the resulting ratio between the proportion of saplings and adults (saplings: adult ratio), both in open and close canopies. Additionally, analyses of variance (ANOVA) with a post-hoc multiple comparison test (Fisher´s LSD) were executed to assess density differences ($P < 0.05$) amongst plots located in different combinations of forest types and sites, as well to assess density differences in the regeneration located both in open and closed canopies. This set of statistics was executed with the Infostat statistical package (Di Rienzo *et al.* 2008).

Matrices of plots with all their species abundances, as well as their altitudes, geographical coordinates (in Universal Transverse Mercator coordinates –UTM–), and climatic variables were prepared for subsequent analyses with spatial statistics using R statistical software ver. 2.15.1 (R Development Core Team 2014).

The turnover patterns of floristic composition (*sensu* Sokol *et al.* 2011) and the changes of altitude and environmental variables throughout the space were represented with multivariate Mantel correlograms (Borcard & Legendre 2012) created from the function *mantel.correlog*, a library of *vegan*. The distances classes used to determine and graph the inter-plot distances of floristic composition and environmental variables ranged from 0.7–18 km, divided into 1–km intervals previously defined from the maximum distance limits obtained from plot pairs. The statistical significances were defined from the probability value resulting from each Mantel correlation coefficient (r_M) although a progressive Bonferroni correction was applied to get adjusted p values (Legendre & Legendre 1998).

A variation partitioning analysis (Borcard, Legendre & Drapeau 1992; Legendre 2008, Legendre *et al.* 2005) was performed to evaluate the joint and separate effect of climate, geographic location, altitude, canopy openness and human disturbance level on floristic variation. For this, the *var.part* and the *anova.cca*, functions of *vegan* library, were executed both to perform the analysis and to make significance tests (999 permutations) for testable fractions. Densities of species were previously transformed with the Hellinger method to downweight common species (Legendre & Gallagher 2001; Jones *et al.* 2008) whereas a log-transformation was used for altitude and environmental variables. For the case of disturbance level and canopy openness, the untransformed ordinal scale (1–5) and percentages were used. Additionally, a principal coordinates of neighbour matrices (PCNM) analysis (*pcnm* function of *vegan*) was applied to the matrix of geographical coordinates to get significant eigenvalues ($P < 0.05$, Moran's I statistic) representing the spatial structure. A forward selection procedure (*forward.sel* function of *packfor* library) was then applied both on the resulting eigenvalues and on the environmental variables in order to select those with a relevant level of significance ($P < 0.05$ with 999 random permutations) to explain the floristic variation. At the end, two significant PCNM eigenvectors (spatial structure factor) and the complete set of eight climatic variables were retained for the analysis. All these R routines were executed through an interface implemented in Q-eco software(Di Rienzo *et al.* 2010).

3.4. RESULTS

3.4.1. Floristics

3.4.1.1. General

41751 sapling individuals were recorded in the 96 sample plots. They represented 80 genera, 45 families, and 133 species (Appendix 3.2). From these species, 116 were fully identified to species level, ten recognized to family level and three to genus level. Very well represented families in terms of genera and species were Asteraceae (17 genera, 27 species), Rosaceae (5 genera, 9 species), Celastraceae (4 genera, 4 species), Ericaceae (3 genera, 4 species), Solanaceae (3 genera, 7 species) and Adoxaceae (2 genera and 5 species). In terms of number of species per genus, *Quercus* presented eight species although the genera *Eupatorium*, *Fuchsia*, *Prunus* and *Viburnum* had also four species each. Excepting the monocotyledon species *Chusquea nubicola* (Poaceae), an understorey bamboo, all the morphospecies were dicotyledonous. Gymnosperms were only represented by *Pinus* (3 species) and *Cupressus* (1 species).

50% of the species recorded as saplings belonged to the understorey layer (shrubs and small trees) and included the genera *Fuchsia*, *Eupatorium*, *Roldana*, and *Solanum*. 30% belonged to the middlestorey, in which *Prunus*, *Oreopanax*, *Cornus*, *Clethra* and *Viburnum* were important. 15% belonged to the canopy stratum in which *Pinus* and *Quercus* were the genera with most species. Only 5% of species were either perennial or annual herbs. Abundances varied widely: from the total number of species, 51% of the total of individuals was made up by 15 species (Appendix 3.3). The remaining 49% was shared between the 118 remaining species. The most abundant (> 15040 ind ha^{-1}) and frequent (> 50% of sample plots) saplings were the small trees *Viburnum jucundum* and *Litsea glaucescens* and the shrubs *Garrya laurifolia*, *Eupatorium ligustrinum* and *Fuchsia microhylla*. Other very abundant sapling species (> 30000 ind ha^{-1}) but with more restricted distributions across the landscape were the shrubs *Ageratina mairetiana*, *Lippia umbellata*, *Myrsine juergensenii*, and *Gaulteria chiapensis*.

The regeneration of each of the 26 dominant species of the tree stratum ranged from non-existent, rare to abundant (Table 3.3, Appendix 3.3): species such as *Pinus pseudostrobus* var. *pseudostrobus*, *P. pseudostrobus* var. *apulcensis* and *Chirantodendron pentadactylon* did not show any regeneration but that of *Oreopanax xalapensis*, *Persea americana* and *Miconia glaberrima* was particularly abundant. As it was difficult to identify many *Pinus* individuals to species, I present only data at the genus level; *Pinus* presented an appreciable but still low abundance in relation to the other species. Conversely, saplings of *Quercus* species were abundant although some of them had restricted geographical distributions – such as *Q. ocoteaefolia,* found only at Tzontehuitz.

3.4.1.2. Non-metric Multidimensional Scaling (NMS) ordination

Analysis by NMS provided a three-dimensional solution with a final stress of 15.8, with a high total explained variance of 89%, axis 1 being the most important (42%) followed by axis 2 (28%) and axis 3 (19%). Given their cumulated explained variance (70% in total), axis 1 and 2 were chosen to represent the floristic variation amongst our plots (Fig. 3.2). It showed a complex floristic scenario where species and their sapling abundances are diversely associated and grouped. Despite some overlapping of plots from different *a priori* forest types, plots tended to be grouped by the same site, forest type and canopy condition (open or closed) indicating stand similarities in short distances.

The two axes represented continuous spectra of variation in which plots and species were sorted. Nevertheless at the centre of the ordination diagram, plots from the pine forests (PF) and to some extent, the pine-oak forests (POF), were compactly grouped. They were the simplest structured and the most floristically similar plots of the study area. On the contrary, much more sapling floristic heterogeneity was found amongst the remaining plots. The differences appeared even in forest types of the same site, as in OF and BLF of both Tzontehuitz and Huitepec, although it was not the case for the BLF and POF in Military zone, well associated between them and with OF Huitepec. Plots of OF Moxviquil were quite separated from the others but more or less associated with the condensed group formed by most of plots of POF and PF. On their part, plots of BLF Huitepec were quite related to BLF Tzontehuitz.

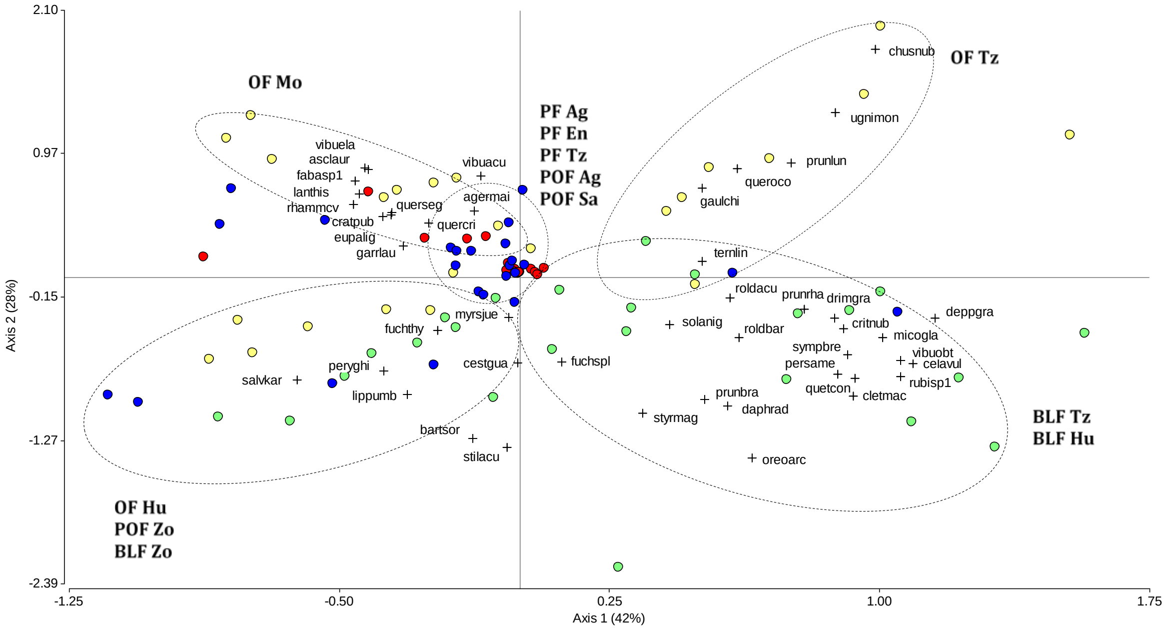

Figure 3.2 NMS ordination for 96 sample plots on the basis of sapling abundances showing axis 1 and 2. The species better correlated to each axis (r > 0.30) are shown as a seven letter acronym and represented with a cross symbol. Plots are represented as dots with different colours to distinguish the four forest types identified *a priori* (broad-leaved forests (BLF) = green, pine-oak forests (POF) = blue, oak forests (OF) = yellow, pine forests (PF) = red). Ellipses denote major groups of plots within forest types and sites. Sites: Hu= Huitepec, Ag = Aguaje, Sa = San José, Tz = Tzontehuitz, Zo = Military zone, En = Encuentro, Mo = Moxviquil. Species: *Ageratina mairetiana* (agermai), *Asclepias auriculata* (asclaur), *Bartlettina sordida* (bartsor), *Celastrus vulcanicola* (celavul), *Cestrum guatemalense* (cestgua), *Chusquea nubicola* (chusnub), *Clethra macrophylla* (cletmac), *Crataegus pubescens* (cratpub), *Critoniadelphus nubigenus* (critnub), *Daphnopsis radiata* (daphrad), *Deppea grandiflora* (deppgra), *Drimys granadensis* (drimgra), *Eupatorium ligustrinum* (eupalig), *Fabaceae* sp1 (fabasp1), *Fuchsia splendens* (fuchspl), *F. thymifolia* (fuchthy), *Garrya laurifolia* (garrlau), *Gaultheria chiapensis* (gaulchi), *Lantana hispida* (lanthis), *Lippia umbellata* (lippumb), *Miconia glaberrima* (micogla), *Myrsine juergensenii* (myrsjue), *Oreopanax arcanus* (oreoarc), *Persea americana* (persame), *Perymenium ghiesbreghtii* (peryghi), *Prunus brachybotrya* (prunbra), *P. lundelliana* (prunlun), *P. rhamnoides* (prunrha), *Quercus crispipilis* (quercri), *Q. ocoteaefolia* (queroco), *Q. segoviensis* (querseg), *Quetzalia contracta* (quetcon), *Rhamnus mcvaughii* (rhammcv), *Roldana acutangula* (roldacu), *R. barba-johannis* (roldbar), *Rubiaceae* sp1 (rubisp1), *Salvia karwinskii* (salvkar), *Solanum nigricans* (solanig), *Stillingia acutifolia* (stilacu), *Styrax magnus* (styrmag), *Symplocos breedlovei* (sympbre), *Ternstroemia lineata* (ternlin), *Ugni montana* (ugnimon), *Viburnum acutifolium* (vibuacu), *V. elatum* (vibuela), *V. obtusatum* (vibuobt).

3.4.2. Correlates of sapling density and species richness

An expected strong positive relationship was found between sapling density and species richness (r = 0.79) but both descriptors (r = 0.41 and r = 0.36 respectively) were positively related to altitude suggesting that stands at higher altitudes show higher density and richness (Table 3.4). On their part, disturbance and canopy openness were strongly negative related (r = −0.72) although disturbance also showed significant negative relationships with altitude (r = −0.35) as well with richness (r = −0.49) and density (r = −0.48), suggesting that the variation in richness and densities with altitude is a function of disturbance.

The 96 plots greatly varied in terms of juvenile densities (Table 3.5): PF plots, as well those in POF of Aguaje, showed significantly lower sapling densities than plots of POF, OF and, particularly, BLF. These characteristics of PF coincided in general with low number of species, high canopy openness and high disturbance (Appendix 3.1).

Canopy openness had no effect on sapling (Table 3.5). Nevertheless, nine of 84 species showed significant differences of abundance between open and closed sites (Table 3.6, Appendix 3.4). From them, only *A. xalapensis*, *C. macrophylla* and *P. americana* were part of the group of 26 dominant species. The remaining six were a tree (*Zanthoxylum melanostictum), a* small tree (*Drimys granadensis*), a vine (*Celastrus vulcanicola*), and different shrubs (*Eupatorium areolare*, *Fuchsia paniculata*, *Roldana barba-johannis*). None of the individual species of *Quercus* and *Pinus* presented significant differences between the two canopy openness conditions. However *Pinus*, as a genus, showed more saplings under open canopies (Table 3.4).

Furthermore, basal area and density of adults for 74 species were not correlated with density of saplings although they were weakly correlated with frequency and RIV (Table 3.7). By contrast, frequency and RIV of adults showed high positive correlation with frequency and RIV of saplings and, to some extent, with their density and sapling: adult ratio.

3.4.3. Regeneration of the dominant species and relationships with functional traits

Regeneration of the 26 dominant species also showed a range of proportions with respect to their adult individuals (Table 3.3, Appendix 3.3): some species had low abundance of adults and no saplings (*Pinus pseudostrobus* in their varieties *apulcencis* and *pseudostrobus*, *Chirantodendron pentadactylon*) or with uncommon regeneration (*P. ayacahuite*, *Clethra oleoides*), although some species uncommon as adults had abundant regeneration (*Prunus rhamnoides*, *Arbutus xalapensis*, *Ternstroemia lineata*, *Buddleja cordata*, *Oreopanax xalapensis*, *Clethra macrophylla*, *Quetzalia contracta*). Conversely, there were species with abundant adults but relatively uncommon regeneration (*P. montezumae*, *Q. ocoteaefolia*) or, on the contrary, with abundant regeneration (*Persea americana*, *Miconia glaberrima*). Another nine species presented a more equilibrated relationship, being common both as adults and as saplings (*Styrax magnus*, *Cornus disciflora*, *Symplocos breedlovei*, *P. tecunumanii*, *Q. crassifolia*, *Q. laurina*, *Q. crispipilis*, *Q. segoviensis*, *Q. rugosa*).

The Pearson correlations did not show any significant relationship between the eight functional traits and the regeneration of the complete set of dominant species. However, by removing *P. pseudostrobus* var. *apulcensis* and var. *pseudostrobus*, as well as *C. pentadactylon*, three locally distributed species with no regeneration (Table 3.3), a significant positive relationship (r = 0.74) appeared between sapling densities and LA (Table 3.8). The correlation was also significant (from r = 0.59 to r = 0.68) for saplings under open and closed canopies separately, as well for their frequency, relative importance value (RIV) and sapling: adult ratio. This suggests that the surviving regeneration of the dominant species in the study area is more abundant for those species that have big leaves, such as *O. xalapensis*, *P. americana*, *S. magnus* and some *Quercus* species (Table 3.3). On the contrary, less abundant and small-leaved species were *P. ayacahuite*, *C. oleoides*, *T. lineata*, *P. montezumae*, *Q. ocoteaefolia*, *S. breedlovei*, amongst others.

Other traits with significant although lower correlations were LDMC (r = 0.43) and WD (r = 0.48) with sapling frequency in open areas, and WD (r = 0.42) with the total frequency.

Table 3.4 Pearson correlations (r-value and (P)) between structural descriptors of sapling assemblages.

	Richness	Percentage of canopy cover	Disturbance level	Altitude
Density	**0.79 (0.0001)**	0.17 (0.09)	**−0.48 (0.0001)**	**0.41 (0.0001)**
Richness		0.16 (0.11)	**−0.49 (0.0001)**	**0.36 (0.0001)**
Percentage of canopy cover			**−0.72 (0.0001)**	0.12 (0.26)
Disturbance				**−0.35 (0.0004)**

Table 3.5 Results of Fisher's LSD test (α = 0.05) of ANOVA (F = 7, D.F. = 95, P = 0.0001) performed to test for effects of canopy type and combination of forest type and site on the density of individuals of plots. Means (SE = 1690.4) of densities of individuals for 24 combinations of forest type, site and canopy condition are shown. Means with different letters are significantly different. BLF = broad-leaved forest, POF = pine-oak forest, OF = oak forest, PF = pine forest.

Forest_Site_Canopy	Means	Comparisons								
BLF_Huitepec_Open	15905	A								
BLF_Huitepec_Closed	13895	A	B							
BLF_Tzontehuitz_Closed	13595	A	B	C						
OF_Huitepec_Open	13515	A	B	C	D					
BLF_Military zone_Closed	12975	A	B	C	D	E				
OF_Moxviquil_Open	11695	A	B	C	D	E				
OF_Tzontehuitz_Closed	11555	A	B	C	D	E				
BLF_Tzontehuitz_Open	11275	A	B	C	D	E				
POF_San José_Open	11255	A	B	C	D	E				
BLF_Military zone_Open	10985		B	C	D	E				
OF_Moxviquil_Closed	10465		B	C	D	E				
OF_Huitepec_Closed	10410		B	C	D	E				
POF_Military zone_Open	9660		B	C	D	E	F			
POF_Military zone_Closed	8945			C	D	E	F	G		
OF_Tzontehuitz_Open	8760				D	E	F	G		
POF_San José_Closed	8530					E	F	G		
POF_Aguaje_Open	5485						F	G	H	
PF_Encuentro_Closed	4835							G	H	I
POF_Aguaje_Closed	4725							G	H	I
PF_Encuentro_Open	4485							G	H	I
PF_Military zone_Open	2865								H	I
PF_Military zone_Closed	2075								H	I
PF_Aguaje_Open	735								H	I
PF_Aguaje_Closed	145									I

Table 3.6 Results for ANOVA to test for effects of canopy condition on densities of individuals of nine species, as well of *Quercus* spp. and *Pinus* spp. Complete set of analyses in Appendix 3.4. Means with different letters are significantly different (Fisher LSD test; α = 0.05).

	Total number of plots analysed	Open canopies			Closed canopies			F value	P value
		Mean	SE		Mean	SE			
Species									
Arbutus xalapensis	36	75.56	15.33	**A**	27.78	15.33	**B**	4.9	0.034
Celastrus vulcanicola	20	24.00	163.87	**B**	602.00	163.87	**A**	6.2	0.023
Clethra macrophylla	18	88.89	315.39	**B**	1093.33	315.39	**A**	5.1	0.039
Drimys granadensis	16	67.50	73.57	**B**	295.00	73.57	**A**	4.8	0.046
Eupatorium areolare	16	302.5	89.56	**A**	17.50	89.56	**B**	5.1	0.041
Fuchsia paniculata	12	480.00	107.58	**A**	0.00	-------	**B**	10.0	0.010
Persea americana	34	427.06	307.8	**B**	1343.53	307.80	**A**	4.4	0.043
Roldana barba-johannis	20	30.00	10.24	**B**	132.00	10.24	**A**	8.5	0.009
Zanthoxylum melanostictum	12	0.00	-------	**B**	213.33	57.12	**A**	7.0	0.025
Genera									
Pinus spp.	64	516.88	120.23	**A**	145.63	120.23	**B**	4.7	0.033
Quercus spp.	90	655.56	88.32	A	461.78	88.32	A	2.4	0.124

Table 3.7 Pearson Correlations (r-value and (P)) amongst adult and sapling abundances for 74 species. Significant correlations are marked in bold (* P < 0.05, **P < 0.005). RIV = relative importance value.

Adults	Saplings									Sapling: adult ratio
	Density (ind ha^{-1})			Frequency (%)			RIV (%)			
	open	closed	Total	open	closed	Total	open	closed	Total	
Basal area (m^2 ha^{-1})	0.14	0.07	0.11	**0.33****	0.20	**0.27***	**0.32***	0.19	**0.27***	−0.15
Density	0.19	0.15	0.18	**0.38****	**0.30***	**0.35****	**0.37****	**0.3***	**0.34****	−0.2
Frequency	**0.33****	**0.34****	**0.36****	**0.63****	**0.6****	**0.63****	**0.62****	**0.6****	**0.62****	**−0.29***
RIV	**0.31***	**0.30***	**0.33****	**0.6****	**0.55****	**0.59****	**0.59****	**0.54****	**0.58****	**−0.28***

Table 3.8 Pearson correlations (r-value and (P)) amongst functional traits of adults and sapling abundances for 26 dominant species. Significant correlations are marked in bold (* P < 0.05, ** P < 0.005). LA = leaf area (mm^2), SLA = specific leaf area (mm^2 mg^{-1}), LDMC = leaf dry matter content (mg g^{-1}), LTS = leaf tensile strength (N mm^{-1}), LNC= leaf nitrogen content (mg g^{-1}), LPC= leaf phosphorous content (mg g^{-1}), WD = wood density (g mm^{-1}), H_{max} = maximum height (m), Dens = Density (ind ha^{-1}), Freq = Frequency (%), RIV = relative importance value (%).

Traits	Saplings							Sapling: adult ratio
	Dens			Freq			RIV	
	open	closed	total	open	closed	total		
LA	**0.72****	**0.68****	**0.74****	**0.56***	**0.68****	**0.64****	**0.67****	**0.59****
SLA	−0.10	0.00	0.01	−0.23	−0.24	−0.24	−0.23	0.13
LDMC	0.14	−0.17	−0.05	**0.43***	0.20	0.34	0.32	−0.27
LTS	−0.09	−0.15	−0.14	−0.13	−0.15	−0.15	−0.15	−0.24
LNC	0.21	0.09	0.15	0.29	0.33	0.32	0.32	0.00
LPC	−0.01	0.07	0.04	0.09	0.15	0.12	0.12	0.1
WD	0.16	−0.16	−0.04	**0.48***	0.33	**0.42***	0.40	−0.34
H_{max}	0.04	−0.24	−0.14	0.18	−0.12	0.04	0.03	−0.32

3.4.4. Effects of distances, climate, altitude, canopy openness and disturbance level on floristic composition

Mantel correlograms indicate that floristic change is abrupt in very short distances (Fig. 3.3). Floristic composition showed a more rapid change in autocorrelation with distance than did altitude and climate, since their significant autocorrelations were positive in the 0−2-km class and negative in the 2−4-km class, matching similar, although less consistent, changes both in closed and open canopies (Fig. 3.3b). Altitude and climate had similar patterns along the distances presenting significant and positive autocorrelations within the 0−5-km class. They were followed by a lagged fall until the 5−6-km class where the shift to negative correlation happened.

The variation partitioning analysis showed that almost one third of the total variation of sapling composition (R^2_{adj} = 0.32) may be jointly explained by spatial variables, climate, altitude and canopy openness (Table 3.9). However only a fraction of this explained variance (R^2_{adj} = 0.19) could be assigned to pure effects, leading to an adjusted R^2 of 0.13 for combined or masked contributions. Of the pure effects, climate was the predictor with the strongest effect on floristic composition (R^2_{adj} = 0.11), followed by spatial variables (R^2_{adj} = 0.06) with small pure effects of altitude and canopy openness. When controlling for the effects of one or two variables, the combined effects of climate were quite related to altitude and to a lesser extent, to spatial variables (Appendix 3.5); in similar way, spatial variables were more related to climate and to a lesser extent to altitude and canopy openness.

The overall adjusted R^2 of the analysis including disturbance level instead of canopy openness was similar, 0.33, though the pure effect of this factor (R^2_{adj} = 0.01) was also very small (Table 3.9). The results of this second variation partitioning analysis suggest that the effects of disturbance level and canopy openness on sapling composition are very similar.

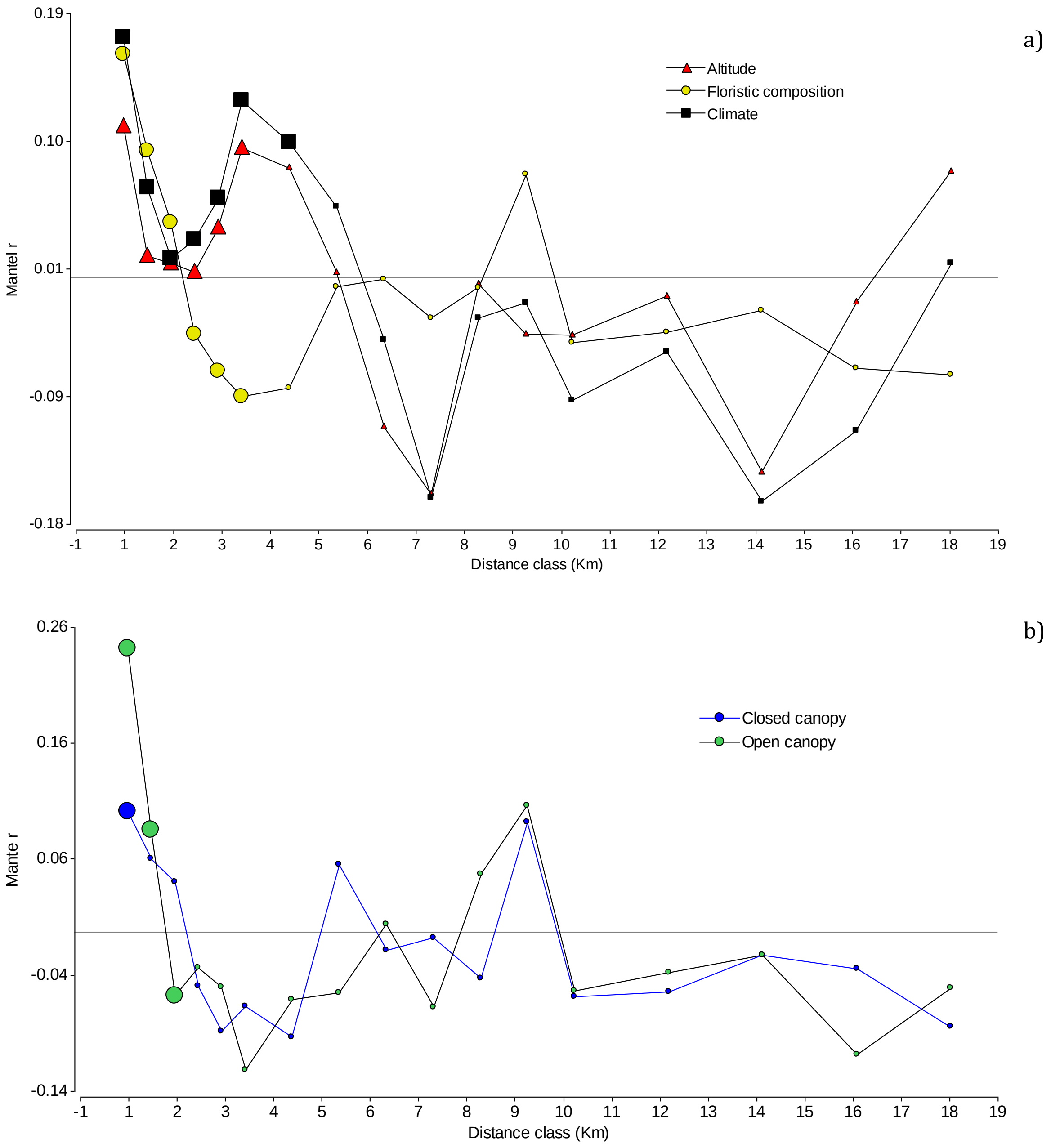

Figure 3.3 Spatial autocorrelation coefficients of Mantel correlograms of sample plot pairs for 19 geographical distance classes, for a) altitude, climate and total floristic composition, and b) floristic composition both in open and closed canopies. Mantel comparisons of distance matrices of the variables used are shown as different symbols and lines. Large symbols denote significant correlations ($P < 0.05$). The x axis shows the maximum geographical distance in each class.

Table 3.9 Results of variation partitioning analysis on taxonomic composition, including either canopy openness or disturbance level. Adjusted R^2 statistics (Adj R^2) and F statistics are presented for all measured predictors. Significant correlations are marked in bold (* $P < 0.05$, ** $P < 0.005$). The effect of predictors controlling for any combinations of other predictor is denoted by symbol │. Null fractions are denoted with a dash. Complementary results are in Appendix 3.5.

	Predictor	Including canopy openness		Including disturbance level	
		Adj R^2	F	Adj R^2	F
Total effects per predictor	Spatial variables	0.11**	6.66	0.11**	6.66**
	Climate	0.24**	4.68	0.24**	4.68
	Altitude	0.09**	10.66	0.09**	10.66
	Canopy openness	0.02**	2.49		
	Disturbance level			0.05**	5.66
Pure effects per predictor	Spatial variables │ Other 3 variables	0.06**	4.89	0.06**	4.66
	Climate │ Other 3 variables	0.11**	2.77	0.11**	2.82
	Altitude │ Other 3 variables	0.02**	3.28	0.02**	3.35
	Canopy openness │ Other 3 variables	0.004*	1.52		
	Disturbance level │ Other 3 variables			0.01**	2.38
Total pure effects		0.19	-	0.20	-
Spatial variables ∩ Climate ∩ Altitude ∩ Canopy openness		0.13	-		
Spatial variables ∩ Climate ∩ Altitude ∩ Disturbance level				0.13	-
Spatial variables U Climate U Altitude U Canopy openness		0.32**	4.80		
Spatial variables U Climate U Altitude U Disturbance level				0.33**	4.92
Residuals		0.68	-	0.67	-

3.5. DISCUSSION

3.5.1. Floristic variation, disturbance and characteristics of the sapling assemblage

The distribution of the species and abundances of saplings is far from uniform across the study area. As showed by NMS analysis, species were associated in a variety of contrasting assemblages and, as Mantel correlograms indicate, plots with certain composition may pass to other very different in adjacent forests (for instance, from POF to PF in sites as Military zone and Aguaje or from OF to BLF forests in sites of Huitepec or Tzontehuitz). This phenomenon occurs over the short altitudinal range of our study area and is coincident with the vegetation mosaic described by González-Espinosa *et al.* (1991, 1997) for spaces of the Central Highlands, being the human disturbance the main explanatory factor (González-Espinosa *et al.* 1991).

The sapling assemblage varied from poor in species and sparse (most of PF and some POF) to rich and dense (those in POF, OF and BLF) and as correlation analyses showed (Table 3.4), reductions in richness and density were correlated with high disturbance levels and low percentage of canopy cover. This same pattern was found by González-Espinosa *et al.* (1991) and Ramírez-Marcial, González-Espinosa & Williams-Linera (2001). In addition, the positive relationships of density and richness with altitude and the negative relationship of this with disturbance indicates that, in general, altitude may well constitute a gradient of access of local people to forest resources, revealing the pattern and impact of human activities: lower altitudes and flat terrains historically devoted to productive activities, higher altitudes and abrupt sites most times related to private, communal, municipal or military reserves.

3.5.2. Canopy openness and the composition and abundance of saplings

Canopy openness, a surrogate effect of human disturbance on forests, did not show any relationship with overall species richness or density of individuals but it had significant effects on the abundances of nine species including as well the genus *Pinus*. The case of *Pinus* is emblematic because the increased abundance of its regeneration in open areas has been widely documented for the study area (e.g. González-Espinosa *et al.* 1991; López-Barrera & González-Espinosa 2001; Quintana-Ascencio *et al.* 2004) leading to the hypothesis that human disturbance is producing an abundance of individuals of this genus in local forests.

On the other hand, despite the abundance and diversity of *Quercus* species, they were not significantly more abundant in a particular canopy condition. This was also in accordance with the general observations of González-Espinosa *et al.* (1991), Quintana-Ascencio, González-Espinosa & Ramirez-Marcial (1992), Quintana-Ascencio *et al.* (2004) and Camacho-Cruz *et al.* (2000) who, in general, have found that *Quercus* species have the capacity to survive in different light conditions although they show a high survival in open areas. Nevertheless, at the level of seedlings, López-Barrera *et al.* (2006) found that *Q. crassifolia* is markedly shade-intolerant whereas *Q. laurina* and *Q. rugosa* displayed more tolerance to high and low light conditions.

Less robust information is available from our study area to corroborate the significant effects of canopy openness on sapling densities found for the other nine species. Nevertheless, our results must be interpreted with care since a high density of individuals in a particular light condition may not be an accurate indicator of species performance over the whole life cycle. We may take the example of *Persea americana* that showed a significantly higher abundance of saplings under closed canopies suggesting certain performance in low light conditions; however, we need to consider that the fruits and seeds of this species are large (seed size = 3-4 cm (Camacho-Cruz *et al.* 2000)) and, even when fruits are edible by mammals, seeds are probably only dispersed over short distances. Having that the high sapling density of *P. americana* in closed canopies coincided with a high density of adult trees, the significant relationship with closed canopies may be more a result of that low dispersal capacity rather than a physiological intolerance to open areas, an interpretation coincident with the dispersal limitation model (Hubbell 2005). Thus, the abundance of a species in a particular light condition must be validated with factors such as seed viability, dispersion capacity, the distribution of mother trees, resprouting capacity, amongst others.

Contrary to the expected in such a highly fragmented space as the study area, the number of tree species showing marked effects of light condition on sapling abundance is quite low considering the total number of species. Lieberman *et al.* (1995) found in tropical forests of Costa Rica that only a fraction (14%) of the species indeed occurred in significantly darker or brighter conditions than expected at random, whereas 86% had a random distribution with respect to light. Our results suggest also that possibly most of the tree species of montane forests in the highlands of Chiapas are generalists rather than specialists.

This possibility seems to contradict the numerous local studies that use a classification based on the successional stages of tree species (e.g. González-Espinosa *et al.* 1991; Quintana-Ascencio & González-Espinosa 1993), more in accordance to the classical ideas about pioneer light-demanding species and shade tolerants (cf. Swaine & Whitmore 1988). For example, species found in this study as *Baccharis vaccinioides* has been classified as a pioneer; *Arbutus xalapensis*, *Q. crispipilis*, and *P. montezumae* as early successional; *V. jucundum* and *Ostrya virginiana* as intermediate; *Persea americana*, *Oreopanax xalapensis* and *Quercus laurina* as late successional (Quintana-Ascencio & González-Espinosa 1993).

The basis of this local arrangement has been the result of detailed observations in different forest associations and this leads us to consider that, despite the high number of plots used, the landscape approach of our study as well as the qualitative and coarse classification of canopy cover may impede us from observing more detailed relationships between species and light environment. However, we need also to take into account that experimental evidence has shown that both pioneer and non-pioneer species may germinate under a wide range of environmental conditions (Kyereh, Swaine & Thompson 1999; Peña-Claros 2001; Pearson *et al.* 2002), as well that tree species have different height-light trajectories when they grow from seedling to adulthood (Poorter *et al.* 2005). In this way, as Poorter *et al.* (2005) have pointed out, it is necessary to take subjective species classifications with care as they may restrict our assessments to deterministic trajectories leading us to underestimate the plasticity and adaptation of tree species. Here we may add the restrictive approach of chronosequences that assign successional stages to species but do not necessarily depict the course of change in a plant stand (Johnson & Miyanishi 2008 but see Walker *et al.* 2010).

3.5.3. Factors related to floristic variation and factors of change

Despite the noticeable relationship of disturbance, canopy openness and altitude with characteristics of the forest stands sampled, their effects on the variation of sapling species composition at the landscape level of our study were weak. The well known relationship of altitude with climatic factors (Grubb 1977; Körner 2007) was well depicted by variation partitioning analysis; however, possibly because of the narrow range used this factor alone did not have any important effect on floristic variation. On the contrary, climate showed sufficient independence both from altitude and spatial variables to explain to some extent the existing floristic variation. This seems particularly important to clarify the floristic differences of the sapling assemblage found amongst plots located at the centre and south of the study area and those located in the northernmost part (OF and BLF stands of the site Tzontehuitz), more related to higher precipitations and lower temperatures, with more exposure to the winds of the Gulf of Mexico (Table 3.2, Appendix 3.1); matching with a different floristic province within the region (*sensu* Sokol *et al.* 2011) as was discussed for adult trees in Chapter 2. Nevertheless, despite these climatic differences, there was a high overlapping of sapling composition observed between plots of BLF of Tzontehuitz with BLF Huitepec, as well of plots of different sites and geographical areas (for instance OF Huitepec with POF and BLF of Military zone); consequently, altitude or climate are not the sole factors defining the species distribution.

Spatial variables showed certain relevance to explain the floristic variation which implies a more controversial explanation: it suggests that communities may follow a dispersal assembly rule rather responding according to niches determined by environmental variables. It follows that species assemblages of the study area are more or less a stochastic phenomenon, strongly defined by the composition of surrounding communities, more affected by distance-dependent processes rather than deterministic (Hubbell 2001; Weiher *et al.* 2011). Given that saplings are part of the understorey stratum, subjected to more stable and uniform microclimate, the composition could be explained by factors other than deterministic ones. We propose then that even when niche assembly is the strongest factor (climate), there is a complementary role of dispersal assembly.

We need to consider that the explanatory power of the variables used for the variation partitioning is low (32%), leaving a high proportion of unexplained variation (68%). Besides, microclimate and other important factors of change, such as chemical and physical properties of soils, may be a crucial factors of change and theirs effects could be masked by spatial factors (Sesnie *et al.* 2009; Chain-Guadarrama *et al.* 2012). Nevertheless, the potential relevance of spatial factor in our study supports the suggestion of Zavala, Galindo-Jaimes & González-Espinosa (2007) that neutral processes explain part of the floristic variation in the Central Highlands.

3.5.4. Regeneration of dominant species and functional traits

The 26 dominant species displayed a variety of functional traits that reveal a variety of ecological strategies to face up the local conditions. Given the wide variation of sapling abundance amongst these species, it would be expected that several functional traits were correlated to some extent with structural descriptors of populations of saplings. However, except for LA, the relationships between traits and juvenile abundances were weak (as in LDMC and WD) or non-existent. Three possible factors may be invoked to explain this generalized lack of correlation: 1) we did not measure reproductive traits, 2) the lack of functional traits specifically measured for saplings, 3) the small number of species used. Nevertheless, the correlation of LA with species abundances was strong, suggesting that big-leaved species tend to have higher sapling abundance in the study area. Big-leaved species such as *O. xalapensis*, *P. americana* and *Q. rugosa* had abundant regeneration (Table 3.3); on the contrary, some small-leaved species with relatively low sapling abundances were *Clethra oleoides*, *Ternstroemia lineata* and most of the *Pinus* species.

The 26 species display a wide range of leaf sizes (Table 3.3) however the possible interpretations for a relationship between high leaf area and saplings abundance are at the moment limited (compare with Niinemets *et al.* (2007)). LA is strongly indicative of light requirements of species; in this way, big leaves are common in species in early successional stages, more related to a rapid acquisition of resources (Cornelissen *et al.* 2003). It is generally assumed that variation in LA amongst species is related to climatic variation, geology, altitude and latitude, where stress (heat, cold, drought, low nutrient availability, high-solar radiation) tends to select for relatively small leaves (Díaz *et al.* 2004). Stress has also been associated with the canopy layer of forests explaining in this way the tendency towards small leaves of their species in relation with understorey species (Niinemets *et al.* 2007; Niinemets, Keenan & Hallik 2015; Pérez-Harguindeguy *et al.* 2013). However, many dominant and big-leaved species of our study area are tall as adults leading to the question whether big leaves at the sapling stage may represent an advantage in terms of acquisition of resources. This would be useful for species to survive after germination and to proliferate in the dark understorey conditions, being comparable in performance to shade-tolerant species. On the other hand, high sapling abundance of big leaved species may simply indicate a possible high correlation with high production of seeds (which is the case for *P. americana* and most of *Quercus* species) or that the surrounding environmental conditions are not so restrictive to the species survival. In any case, more exhaustive sampling on species and their functional traits are needed to discard false relationships and to better understand the ecology of saplings in the mountainous conditions of the study area.

3.5.5. Conclusions

Predictor variables used in this study as density, richness, disturbance and canopy cover well predicted the structural and floristic changes of sample plots and the abundances of saplings. On the other hand, vegetative functional traits showed potential to be good indicators of sapling abundance although more critical assessments are needed to validate the relationships.

Our study finds as well a heterogeneous landscape with high species richness and a variety of associations where the species distribution is driven not only by deterministic factors but, potentially, by stochastic ones. Anthropogenic disturbance is an important factor that decisively changes the composition and structure of local associations driving to simple forests as those dominated by *Pinus* spp. Nevertheless, the abundance and dominance of *Pinus* species was found only in restricted highly disturbed areas; the uncomfortable truth for the study area is that even pine-dominated stands are losing spaces in favour of human activities that are free of forests (agriculture, livestock farming, settlements)(see Fig. 3.1). This situation forces to conserve as much as possible the different plant associations of the Central Highlands facilitating their connectivity and the species colonisation. This will preserve not only the evolutionary legacy of species but also the linked ecosystem services, important for the human well-being.

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3.7. APPENDICES

Appendix 3.1 Environmental and structural variables obtained for each of the 96 sample plots. PF = pine forest, OF = oak forest, POF = pine-oak forest, BLF = broad-leaved forest. Preci ann (mm) = annual precipitation, Preci sea (mm) = precipitation seasonality, Preci dry (mm) = precipitation of the driest month, Preci wet (mm) = precipitation of the wettest month, Temp mean (°C) = annual mean temperature, Temp sea (°C) = temperature seasonality, Temp warm (°C) = temperature of the warmest month, Temp cold (°C) = temperature of the coldest month, % cover = percentage of canopy cover, Dist = human disturbance level, Rich = species richness, Dens = density of individuals (ind ha^{-1}).

Forest type	Site	Canopy type	Plot	Alti-tude (m)	Location (UTM)		WorldClim's data								Structural attributes			
					Latitude	Longitude	Preci ann	Preci sea	Preci dry	Preci wet	Temp mean	Temp sea	Temp warm	Temp cold	% cov	Dist	Rich	Dens
BLF	Huitepec	Closed	1	2533	533701.00	1851886.00	1249	76	17	232	12.90	110.50	20.90	3.90	90	1	18	9400
			2	2668	532997.00	1851326.00	1249	76	17	232	12.90	110.50	20.90	3.90	70	1	29	13320
			3	2639	533290.00	1851455.00	1249	76	17	232	12.90	110.50	20.90	3.90	80	1	28	16100
			4	2593	533441.00	1851692.00	1249	76	17	232	12.90	110.50	20.90	3.90	70	1	23	16760
		Open	1	2584	533313.78	1851688.69	1249	76	17	232	12.90	110.50	20.90	3.90	50	3	38	15580
			2	2556	533402.67	1851618.14	1249	76	17	232	12.90	110.50	20.90	3.90	55	4	35	24340
			3	2513	533722.05	1851858.37	1249	76	17	232	12.90	110.50	20.90	3.90	50	3	33	16140
			4	2516	533056.20	1851663.73	1249	76	17	232	12.90	110.50	20.90	3.90	55	3	32	7560
	Tzonte-huitz	Closed	1	2681	543689.00	1858379.00	1396	69	27	245	11.70	103.90	19.50	3.10	85	1	38	10320
			2	2777	543867.00	1858158.00	1396	69	27	245	11.70	103.90	19.50	3.10	85	2	34	18680
			3	2773	543970.49	1858321.09	1396	69	27	245	11.70	103.90	19.50	3.10	80	1	31	14580
			4	2651	545474.00	1858312.00	1309	69	24	232	12.60	105.40	20.50	3.90	80	2	26	10800
		Open	1	2681	542452.34	1856717.01	1262	71	21	228	13.00	110.40	21.00	4.10	40	3	35	11180
			2	2600	542086.22	1856224.55	1289	71	22	231	12.70	112.80	20.60	3.80	31	3	25	9180
			3	2777	544056.63	1858149.14	1396	69	27	245	11.70	103.90	19.50	3.10	40	3	19	13380
			4	2785	544151.09	1858275.34	1396	69	27	245	11.70	103.90	19.50	3.10	50	3	23	11360
	Military zone	Closed	1	2512	544086.00	1841340.00	1187	77	15	217	12.90	110.60	20.90	3.90	90	1	23	11500
			2	2527	544163.00	1841141.00	1187	77	15	217	12.90	110.60	20.90	3.90	90	1	25	16320

Forest type	Site	Canopy type	Plot	Alti-tude (m)	Location (UTM)		WorldClim's data								Structural attributes			
					Latitude	Longitude	Preci ann	Preci sea	Preci dry	Preci wet	Temp mean	Temp sea	Temp warm	Temp cold	% cov	Dist	Rich	Dens
	Military zone		3	2491	544054.00	1841027.00	1187	77	15	217	12.90	110.60	20.90	3.90	90	1	26	14940
			4	2488	543923.00	1841303.00	1187	77	15	217	12.90	110.60	20.90	3.90	70	1	23	9140
		Open	1	2472	544110.29	1840887.22	1187	77	15	217	12.90	110.60	20.90	3.90	50	3	26	14080
			2	2510	544097.91	1841149.93	1187	77	15	217	12.90	110.60	20.90	3.90	50	3	23	9880
			3	2613	544465.90	1840806.54	1225	75	17	222	12.50	103.80	20.50	3.70	40	3	19	10880
			4	2506	544181.01	1841085.49	1187	77	15	217	12.90	110.60	20.90	3.90	60	3	27	9100
POF	Aguaje	Closed	1	2449	543844.00	1843829.00	1123	78	13	207	13.80	112.50	21.90	4.70	80	2	14	2380
			2	2410	543854.36	1845752.61	1168	76	15	214	13.30	112.00	21.40	4.30	70	2	18	5920
			3	2401	543332.26	1846169.48	1121	78	13	208	14.10	116.00	22.40	4.90	80	3	20	4940
			4	2424	543507.97	1844286.13	1177	76	15	216	13.10	108.50	21.20	4.10	80	3	16	5660
		Open	1	2430	543864.24	1843856.64	1123	78	13	207	13.80	112.50	21.90	4.70	40	4	12	1020
			2	2367	543234.57	1846184.55	1121	78	13	208	14.10	116.00	22.40	4.90	31	4	17	9500
			3	2326	542985.86	1846119.55	1121	78	13	208	14.10	116.00	22.40	4.90	40	4	13	6620
			4	2415	543585.16	1844187.94	1123	78	13	207	13.80	112.50	21.90	4.70	40	4	13	4800
	San José	Closed	1	2376	532036.00	1848989.00	1150	82	11	222	13.90	117.60	22.00	4.70	70	2	26	5980
			2	2375	531770.00	1848718.00	1167	81	12	224	13.80	115.90	21.90	4.60	80	2	39	8080
			3	2399	531862.00	1848515.00	1167	81	12	224	13.80	115.90	21.90	4.60	70	2	27	14300
			4	2314	532562.00	1847717.00	1144	82	11	221	14.00	118.10	22.10	4.70	65	3	23	5760
		Open	1	2405	531802.32	1848678.07	1167	81	12	224	13.80	115.90	21.90	4.60	40	3	34	14440
			2	2379	531938.34	1848819.54	1167	81	12	224	13.80	115.90	21.90	4.60	40	3	37	13000
			3	2403	532000.54	1848785.89	1150	82	11	222	13.90	117.60	22.00	4.70	31	3	25	10120
			4	2401	532000.32	1848933.35	1150	82	11	222	13.90	117.60	22.00	4.70	31	3	22	7460
	Military zone	Closed	1	2700	546011.00	1839995.00	1293	73	20	231	11.80	99.80	19.70	3.20	70	1	18	4640
			2	2663	545807.00	1839749.00	1272	74	19	228	12.00	103.20	19.90	3.20	80	2	20	14200
			3	2670	545726.85	1839905.74	1272	74	19	228	12.00	103.20	19.90	3.20	70	1	17	10580
			4	2735	546201.39	1839624.00	1272	74	19	228	12.00	103.20	19.90	3.20	70	1	20	6360
		Open	1	2546	546994.93	1839831.61	1267	74	19	227	12.00	104.80	19.90	3.30	60	3	23	6500

Forest type	Site	Canopy type	Plot	Altitude (m)	Location (UTM)		WorldClim's data								Structural attributes			
					Latitude	Longitude	Preci ann	Preci sea	Preci dry	Preci wet	Temp mean	Temp sea	Temp warm	Temp cold	% cov	Dist	Rich	Dens
OF		Open	2	2651	546624.42	1839889.20	1267	74	19	227	12.00	104.80	19.90	3.30	60	3	26	12740
			3	2648	546375.62	1839885.56	1267	74	19	227	12.00	104.80	19.90	3.30	60	3	22	12160
			4	2741	545830.45	1839930.52	1272	74	19	228	12.00	103.20	19.90	3.20	60	3	16	7240
	Huitepec	Closed	1	2396	534092.00	1852086.00	1138	77	14	217	14.10	116.90	22.20	4.90	70	1	18	10740
			2	2343	533810.00	1852402.00	1138	77	14	217	14.10	116.90	22.20	4.90	80	1	25	8780
			3	2367	534006.00	1851739.00	1146	78	13	219	13.90	119.00	22.00	4.70	80	1	30	11380
			4	2317	534231.00	1851985.00	1138	77	14	217	14.10	116.90	22.20	4.90	80	1	30	10740
		Open	1	2335	534251.85	1851945.28	1138	77	14	217	14.10	116.90	22.20	4.90	55	3	28	20360
			2	2335	534183.24	1852261.67	1138	77	14	217	14.10	116.90	22.20	4.90	55	3	27	13140
			3	2319	533981.50	1852510.25	1138	77	14	217	14.10	116.90	22.20	4.90	60	3	30	13340
			4	2321	533910.42	1852568.54	1138	77	14	217	14.10	116.90	22.20	4.90	60	3	21	7220
	Moxviquil	Closed	1	2334	539002.00	1852971.00	1183	75	16	220	13.60	114.40	21.70	4.50	70	1	19	12440
			2	2337	539128.98	1853099.91	1166	75	16	217	13.70	117.20	21.80	4.50	75	1	24	10240
			3	2314	539292.00	1852885.00	1166	75	16	217	13.70	117.20	21.80	4.50	70	1	19	8540
			4	2213	539159.00	1852661.00	1230	70	25	215	15.10	121.90	23.40	5.80	75	1	21	10640
		Open	1	2314	538942.57	1853044.25	1183	75	16	220	13.60	114.40	21.70	4.50	55	3	26	15020
			2	2231	539064.71	1852638.82	1235	70	25	216	15.10	120.40	23.40	5.80	45	3	20	7680
			3	2324	539306.94	1852943.48	1166	75	16	217	13.70	117.20	21.80	4.50	60	3	20	13160
			4	2314	538877.76	1852872.00	1183	75	16	220	13.60	114.40	21.70	4.50	55	3	21	10920
	Tzontehuitz	Closed	1	2776	543918.00	1857743.00	1396	69	27	245	11.70	103.90	19.50	3.10	70	2	16	11600
			2	2646	542418.00	1856121.00	1289	71	22	231	12.70	112.80	20.60	3.80	61	2	23	8320
			3	2817	543995.00	1857866.00	1396	69	27	245	11.70	103.90	19.50	3.10	65	1	25	9760
			4	2767	543943.00	1857531.00	1396	69	27	245	11.70	103.90	19.50	3.10	75	2	18	16540
		Open	1	2650	542823.00	1856385.88	1299	71	22	232	12.60	108.70	20.50	3.80	31	3	20	13760
			2	2691	542680.51	1856603.75	1357	70	25	240	12.10	105.10	19.80	3.40	40	4	25	7540
			3	2654	542787.39	1856447.21	1299	71	22	232	12.60	108.70	20.50	3.80	50	4	21	3980
			4	2634	542317.37	1856108.30	1289	71	22	231	12.70	112.80	20.60	3.80	40	4	21	9760

Forest type	Site	Canopy type	Plot	Altitude (m)	Location (UTM)		WorldClim's data								Structural attributes			
					Latitude	Longitude	Preci ann	Preci sea	Preci dry	Preci wet	Temp mean	Temp sea	Temp warm	Temp cold	% cov	Dist	Rich	Dens
PF	Aguaje	Closed	1	2320	544440.00	1843148.00	1115	78	13	207	14.00	114.40	22.30	4.80	61	5	0	0
			2	2325	544585.00	1843413.00	1115	78	13	207	14.00	114.40	22.30	4.80	61	5	1	60
			3	2370	543982.00	1844385.00	1123	78	13	207	13.80	112.50	21.90	4.70	61	4	5	300
			4	2312	544098.00	1844085.00	1123	78	13	207	13.80	112.50	21.90	4.70	61	4	2	220
		Open	1	2330	544561.53	1843265.03	1115	78	13	207	14.00	114.40	22.30	4.80	40	5	1	20
			2	2325	544575.92	1843470.93	1115	78	13	207	14.00	114.40	22.30	4.80	40	5	1	100
			3	2358	544064.87	1844235.06	1123	78	13	207	13.80	112.50	21.90	4.70	40	5	4	280
			4	2320	543659.21	1845617.03	1168	76	15	214	13.30	112.00	21.40	4.30	40	5	12	2540
	Encuentro	Closed	1	2292	542349.00	1850457.00	1141	75	16	208	14.30	122.10	22.60	5.00	70	3	7	1640
			2	2331	542601.00	1850366.00	1141	75	16	208	14.30	122.10	22.60	5.00	80	3	3	960
			3	2290	542523.00	1849450.00	1135	77	15	208	14.30	121.30	22.50	5.00	65	4	22	11260
			4	2267	542286.00	1849575.00	1135	77	15	208	14.30	121.30	22.50	5.00	80	3	18	5480
		Open	1	2329	542565.76	1850337.82	1141	75	16	208	14.30	122.10	22.60	5.00	40	5	5	2200
			2	2278	542177.73	1850404.63	1141	75	16	208	14.30	122.10	22.60	5.00	50	5	12	2600
			3	2275	542356.52	1849854.96	1135	77	15	208	14.30	121.30	22.50	5.00	40	5	19	6480
			4	2356	542280.11	1849578.25	1135	77	15	208	14.30	121.30	22.50	5.00	40	5	16	6660
	Military zone	Closed	1	2388	547244.00	1841178.00	1116	76	14	206	13.90	113.20	22.00	4.70	70	2	10	2600
			2	2395	547267.00	1841559.00	1116	76	14	206	13.90	113.20	22.00	4.70	70	3	7	2620
			3	2354	546976.00	1841749.00	1127	77	14	207	13.70	115.10	21.80	4.40	70	2	6	2520
			4	2374	547186.00	1842011.00	1138	76	15	207	13.60	110.80	21.70	4.50	70	3	6	560
		Open	1	2396	547258.76	1841092.09	1116	76	14	206	13.90	113.20	22.00	4.70	40	5	21	7420
			2	2340	547311.17	1841500.97	1116	76	14	206	13.90	113.20	22.00	4.70	40	5	4	720
			3	2360	547001.00	1841626.28	1127	77	14	207	13.70	115.10	21.80	4.40	40	5	4	2520
			4	2365	547148.51	1842050.63	1138	76	15	207	13.60	110.80	21.70	4.50	50	5	8	800

Appendix 3.2 133 species recorded in the 96 sample plots including the life form of each species.

CLASS / FAMILY	Scientific name	Life form
GIMNOSPERMAE		
CUPRESSACEAE	*Pinus ayacahuite* var. *ayacahuite* C. Ehrenb. ex Schltdl.	Canopy tree
	Pinus montezumae Lamb.	Canopy tree
	Pinus tecunumanii F. Schwerdtf. ex Eguiluz & J.P.Perry	Canopy tree
	Pinus sp1	Canopy tree
	Pinus sp2	Canopy tree
	Pinus sp3	Canopy tree
	Pinus sp4	Canopy tree
	Cupressus sp.	
ANGIOSPERMAE dicotiledonaceae		
ACTINIDIACEAE	*Saurauia oreophila* Hemsl.	Shrub or small tree
ADOXACEAE	*Viburnum acutifolium* Benth.	Shrub or small tree
	Viburnum elatum Benth.	Shrub or small tree
	Viburnum jucundum Morton ssp. *jucundum*	Understory tree
	Viburnum obtusatum D.N. Gibson	Understory tree
	Sambucus mexicana C. Presl ex DC.	Shrub or small tree
AMARANTHECEAE	*Iresine celosia* L.	Herbaceous
ANACARDIACEAE	*Rhus schiedeana* Schltdl.	Shrub or small tree
	Rhus terebinthifolia Schltdl. & Cham.	Shrub or small tree and vine
APOCYNACEAE	*Asclepias auriculata* Kunth	Perennial herb
ARALIACEAE	*Oreopanax arcanus* A.C. Sm.	Understory tree
	Oreopanax peltatus Linden ex Regel	Understory tree
	Oreopanax xalapensis (Kunth) Decne. & Planch	Understory tree
ASTERACEAE	*Ageratina mairetiana* (DC.) R.M. King & H. Rob.	Shrub
	Alloispermum integrifolium (DC.) H. Rob.	Shrub
	Archibaccharis asperifolia (Benth.) S.F. Blake	Shrub or small tree
	Baccharis serraefolia DC.	Shrub or small tree
	Baccharis vaccinioides Kunth	Shrub or small tree
	Bartlettina sordida (Less.) R.M. King & H. Rob.	Shrub or small tree
	Chromolaena odorata (L.) R.M. King & H. Rob.	Shrub
	Clibadium arboreum Donn. Sm.	Perennial herb or shrub

CLASS / FAMILY	Scientific name	Life form
	Critoniadelphus nubigenus (Benth.) R.M. King & H. Rob.	Shrub or small tree and understory tree
	Eupatorium areolare DC.	Shrub or small tree
	Eupatorium aschenbornianum S. Schauer	Shrub or small tree
	Eupatorium ligustrinum DC.	Shrub or small tree
	Eupatorium pycnocephalum Less.	Shrub
	Hebeclinium macrophyllum (L.) DC.	Herbaceous or annual bush
	Perymenium ghiesbreghtii B.L. Rob. & Greenm.	annual herb
	Roldana acutangula (Bertol.) Funston	Shrub or small tree
	Roldana barba-johannis (DC.) H. Rob. & Brettell	Shrub or small tree
	Roldana sp.	Shrub or small tree
	Senecio uspantanensis Greenm.	Shrub
	Smallanthus maculatus (Cav.) H. Rob.	Perennial herb
	Stevia lucida Lag.	Perennial herb
	Verbesina perymenioides Sch. Bip. ex Klatt	Shrub or small tree
	Vernonia leiocarpa DC.	Shrub or small tree
	Asteraceae sp1	
	Asteraceae sp2	
	Asteraceae sp3	
	Asteraceae sp4	
BETULACEAE	*Alnus acuminata* subsp. *arguta* (Schltdl.) Furlow	Canopy tree
	Ostrya virginiana var. *guatemalensis* (H.J.P. Winkl.) J.F. Macbr.	Understory tree
BUDDLEJACEAE	*Buddleja cordata* Kunth	Shrub or small tree and understory tree
	Buddleja nitida Benth.	Understory tree
CAMPANULACEAE	*Lobelia laxiflora* Kunth	Shrub or small tree
CELASTRACEAE	*Celastrus vulcanicola* Donn. Sm.	Vine
	Crossopetalum tonduzii (Loes.) Lundell	Shrub or small tree
	Quetzalia contracta Lundell	Understory tree
	Rhacoma tonduzii (Loes.) Standl. & Steyerm.	Shrub or small tree
CLETHRACEAE	*Clethra macrophylla* M. Martens & Galeotti	Understory tree
	Clethra mexicana DC.	Understory tree
	Clethra oleoides L.O. Williams	Shrub or small tree
CORNACEAE	*Cornus disciflora* DC.	Understory tree
	Cornus excelsa Kunth	Understory tree
CUNONIACEAE	*Weinmannia pinnata* L.	Shrub or small tree

CLASS / FAMILY	Scientific name	Life form
ERICACEA	*Arbutus xalapensis* Kunth	Understory tree and canopy tree
	Gaultheria chiapensis Camp	Shrub
	Comarostaphylis discolor (Hook.) Diggs	Shrub
	Ericaceae sp.	
EUPHORBIACEAE	*Stillingia acutifolia* (Benth.) Benth. ex Hemsl.	Shrub or small tree
FABACEAE	Fabaceae sp.	
FAGACEAE	*Quercus candicans* Humb. & Bonpl.	Canopy tree
	Quercus crassifolia Humb. & Bonpl.	Canopy tree
	Quercus crispipilis Trel.	Canopy tree
	Quercus laurina Bonpl.	Canopy tree
	Quercus ocoteaefolia Liebm.	Canopy tree
	Quercus rugosa Née	Canopy tree
	Quercus segoviensis Liebm.	Canopy tree
	Quercus skutchii Trel.	Canopy tree
GARRYACEAE	*Garrya laurifolia* Hartw. ex Benth.	Understory tree
LAMIACEAE	*Salvia karwinskii* Benth.	Shrub or small tree
LAURACEAE	*Litsea glaucescens* Kunth	Shrub or small tree and understory tree
	Persea americana Mill.	Understory tree and canopy tree
MALVACEAE	*Malvaviscus arboreus* Cav.	Shrub or small tree
	Triumfetta columnaris Hochr.	Shrub
MELASTOMATACEAE	*Miconia glaberrima* (Schltdl.) Naudin	Shrub or small tree
MYRICACEAE	*Morella cerifera* (L.) Small	Understory tree
MYRSINACEAE	*Myrsine juergensenii* (Mez) Ricketson & Pipoly	Understory tree
	Synardisia venosa (Mast.) Lundell	Understory tree
	Myrsinaceae sp.	
MYRTACEAE	*Ugni montana* (Kunth) O. Berg	Shrub or small tree
OLEACEAE	*Forestiera reticulata* Torr.	Understory tree
ONAGRACEAE	*Fuchsia microphylla* Kunth	Shrub or small tree
	Fuchsia paniculata Lindl.	Shrub or small tree
	Fuchsia splendens Zucc.	Shrub or small tree
	Fuchsia thymifolia Kunth	Shrub or small tree
PENTAPHYLACACEAE	*Cleyera theoides* (Sw.) Choisy	Understory tree
	Ternstroemia lineata DC.	Understory tree

CLASS / FAMILY	Scientific name	Life form
POLYGALACEAE	*Monnina xalapensis* Kunth	Shrub or small tree
PRIMULACEAE	*Parathesis chiapensis* Fernald	Shrub or understory
	Parathesis leptopa Lundell	Shrub or small tree
RHAMNACEAE	*Rhamnus mcvaughii* L.A. Johnst. & M.C. Johnst.	Shrub
	Rhamnus sharpii M.C. Johnst. & L.A. Johnst.	Understory tree
	Ceanothus coeruleus Lag.	Small tree or shrub
ROSACEAE	*Crataegus pubescens* (C. Presl.) C. Presl.	Understory tree
	Holodiscus argenteus (L. f.) Maxim.	Shrub or small tree
	Photinia microcarpa Standl.	Small tree
	Prunus brachybotrya Zucc.	Understory tree
	Prunus lundelliana Standl.	Understory tree
	Prunus rhamnoides Koehne	Understory tree
	Prunus serotina Ehrenb. subsp. *capuli* (Cav.) McVaugh	Understory tree
	Rubus trilobus Moc. & Sessé ex Ser.	Shrub
	Rubus sp.	Shrub
RUBIACEAE	*Deppea grandiflora* Schltdl.	Shrub or small tree
	Rubiaceae sp.	
RUTACEAE	*Zanthoxylum melanostictum* Schltdl. & Cham.	Understory tree
	Zanthoxylum foliolosum Donn. Sm.	Shrub or small tree and vine
SABIACEAE	*Meliosma dentata* (Liebm.) Urb.	Understory tree
SALICACEAE	*Xylosma chiapensis* Lundell	Shrub
SOLANACEAE	*Cestrum aurantiacum* Lindl.	Shrub or small tree
	Cestrum guatemalense C.V. Morton	Shrub or small tree
	Lycianthes purpusii (Brandegee) Bitter	Shrub or small tree
	Lycianthes ciliolata (M. Martens & Galeotti) Bitter	annual herb
	Solanum aligerum Schltdl.	Shrub or small tree
	Solanum hispidum Pers.	Shrub or small tree
	Solanum nigricans M. Martens & Galeotti	Shrub or small tree
STYRACACEAE	*Styrax magnus* Lundell	Understory tree
SYMPLOCACEAE	*Symplocos breedlovei* Lundell	Understory tree
THYMELAEACEAE	*Daphnopsis radiata* Donn. Sm.	Shrub
VERBENACEAE	*Lantana hispida* Kunth	Shrub or small tree
	Lippia umbellata Cav.	Shrub
	Verbenaceae sp1	

CLASS / FAMILY	Scientific name	Life form
	Verbenaceae sp2	
WINTERACEAE	*Drimys granadensis* var. *mexicana* (DC.) A.C. Sm.	Understory tree
ANGIOSPERMAE monocotiledonaceae		
POACEAE	*Chusquea nubicola* Soderstr. ex Breedlove	Herbaceous

Appendix 3.3 Structural attributes of adults (≥ 5 cm DBH) and saplings (< 5 cm DBH, ≥ 30 cm height) of 77 species fully identified. Data for adults come from the study in Chapter 2. Data of saplings are divided in open (31-60% of canopy cover) and closed (61-90% of canopy cover) plots. Data corresponding to the 26 dominant species are denoted in bold. RIV = relative importance value.

Species	Adults				Saplings							Saplings: adult ratio
	Basal area (m^2 ha^{-1})	Density (ind ha^{-1})	Frequency (%)	RIV (%)	Density (ind ha^{-1})			Frequency (%)			RIV (%)	
					open	closed	Total	open	closed	Total		
Alnus acuminata	10.17	220	12.50	4.44	200	40	240	8.33	2.08	5.21	2.62	0.08
Arbutus xalapensis	**40.95**	**750**	**54.17**	**19.08**	**1360**	**500**	**1860**	**29.17**	**16.67**	**22.92**	**11.57**	**0.18**
Baccharis vaccinioides	0.12	20	2.08	0.71	2160	580	2740	18.75	4.17	11.46	5.89	10.00
Buddleja cordata	**13.42**	**850**	**56.25**	**19.42**	**2000**	**1140**	**3140**	**39.58**	**45.83**	**42.71**	**21.54**	**0.27**
Buddleja nitida	4.76	330	14.58	5.11	300	20	320	10.42	2.08	6.25	3.14	0.07
Celastrus vulcanicola	0.06	10	2.08	0.70	240	6020	6260	10.42	16.67	13.54	7.15	45.70
Cestrum aurantiacum	0.09	20	4.17	1.40	4780	2240	7020	31.25	20.83	26.04	13.44	25.63
Cestrum guatemalense	0.03	10	2.08	0.70	10140	4940	15080	43.75	37.50	40.63	21.22	110.10
Chiranthodendron pentadactylon	**26.17**	**50**	**6.25**	**2.51**	**0**	**0**	**0**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Clethra macrophylla	**22.22**	**820**	**12.50**	**4.95**	**800**	**9840**	**10640**	**14.58**	**14.58**	**14.58**	**7.93**	**0.95**
Clethra mexicana	1.08	30	2.08	0.73	120	0	120	4.17	0.00	2.08	1.05	0.29
Clethra oleoides	**10.74**	**320**	**12.50**	**4.50**	**180**	**640**	**820**	**6.25**	**8.33**	**7.29**	**3.69**	**0.19**
Cleyera theoides	4.60	250	14.58	5.07	340	680	1020	12.50	16.67	14.58	7.35	0.30
Cornus disciflora	**28.32**	**860**	**12.50**	**5.06**	**940**	**840**	**1780**	**12.50**	**10.42**	**11.46**	**5.84**	**0.15**
Cornus excelsa	1.25	150	10.42	3.57	1640	620	2260	12.50	12.50	12.50	6.39	1.10
Crataegus pubescens	5.19	490	22.92	7.99	1620	1460	3080	37.50	22.92	30.21	15.29	0.46
Critoniadelphus nubigenus	3.55	260	10.42	3.67	5300	1800	7100	18.75	22.92	20.83	10.84	1.99
Daphnopsis radiata	2.95	600	8.33	3.15	1840	4180	6020	12.50	18.75	15.63	8.17	0.73
Deppea grandiflora	2.38	310	6.25	2.29	4420	6000	10420	8.33	6.25	7.29	4.27	2.45
Drimys granadensis	4.43	300	12.50	4.40	540	2360	2900	12.50	12.50	12.50	6.42	0.71
Eupatorium ligustrinum	0.88	140	8.33	2.87	17620	12920	30540	56.25	54.17	55.21	29.43	15.93
Eupatorium pycnocephalum	0.06	20	2.08	0.71	1300	2640	3940	12.50	16.67	14.58	7.53	14.38
Forestiera reticulata	0.47	20	2.08	0.71	0	280	280	0.00	6.25	3.13	1.58	1.02
Garrya laurifolia	9.19	930	39.58	13.84	12860	13420	26280	56.25	58.33	57.29	30.22	2.06
Holodiscus argenteus	0.77	140	12.50	4.25	220	240	460	10.42	10.42	10.42	5.24	0.24
Lippia umbellata	0.78	250	10.42	3.62	20860	16160	37020	25.00	25.00	25.00	14.72	10.81
Litsea glaucescens	0.77	150	20.83	7.04	8020	7020	15040	64.58	64.58	64.58	33.19	7.32

Species	Adults				Saplings							Saplings: adult ratio
	Basal area (m^2 ha^{-1})	Density (ind ha^{-1})	Frequency (%)	RIV (%)	Density (ind ha^{-1})			Frequency (%)			RIV (%)	
					open	closed	Total	open	closed	Total		
Malvaviscus arboreus	0.02	10	2.08	0.70	1360	8620	9980	14.58	16.67	15.63	8.41	72.86
Meliosma dentata	1.36	120	8.33	2.86	60	300	360	2.08	4.17	3.13	1.58	0.22
Miconia glaberrima	**8.13**	**1110**	**12.50**	**4.90**	**5720**	**13300**	**19020**	**10.42**	**18.75**	**14.58**	**8.43**	**1.25**
Morella cerifera	4.70	840	14.58	5.39	4500	700	5200	14.58	12.50	13.54	7.08	0.45
Myrsine juergensenii	13.25	2000	43.75	15.88	12580	19080	31660	41.67	56.25	48.96	26.37	1.16
Oreopanax arcanus	0.98	70	10.42	3.53	140	80	220	4.17	6.25	5.21	2.62	0.23
Oreopanax peltatus	0.19	30	4.17	1.41	660	1600	2260	6.25	8.33	7.29	3.78	5.50
Oreopanax xalapensis	**23.21**	**1530**	**45.83**	**16.46**	**19220**	**27860**	**47080**	**50.00**	**56.25**	**53.13**	**29.38**	**2.25**
Ostrya virginiana	7.10	360	14.58	5.17	340	420	760	10.42	8.33	9.38	4.73	0.15
Parathesis chiapensis	0.02	10	2.08	0.70	40	20	60	2.08	2.08	2.08	1.05	0.44
Parathesis leptopa	0.73	60	4.17	1.43	80	1780	1860	2.08	10.42	6.25	3.24	2.26
Persea americana	**107.54**	**1180**	**20.83**	**9.21**	**7260**	**22840**	**30100**	**22.92**	**29.17**	**26.04**	**14.82**	**1.86**
Photinia microcarpa	0.14	40	4.17	1.41	0	300	300	0.00	4.17	2.08	1.06	0.55
Pinus ayacahuite	**38.72**	**340**	**22.92**	**8.41**	**300**	**120**	**420**	**6.25**	**6.25**	**6.25**	**3.15**	**0.09**
Pinus montezumae	**309.99**	**5150**	**33.33**	**18.60**	**1560**	**2140**	**3700**	**14.58**	**16.67**	**15.63**	**8.03**	**0.05**
Pinus pseudostrobus* var. *apulsensis	**35.56**	**690**	**14.58**	**5.77**	**0**	**0**	**0**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Pinus pseudostrobus* var. *pseudostrobus	**10.98**	**50**	**6.25**	**2.28**	**0**	**0**	**0**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Pinus tecunumanii	**301.19**	**5030**	**43.75**	**21.87**	**7400**	**1140**	**8540**	**31.25**	**10.42**	**20.83**	**10.93**	**0.12**
Prunus brachybotrya	0.88	30	6.25	2.11	440	820	1260	10.42	10.42	10.42	5.28	3.07
Prunus lundelliana	1.96	290	12.50	4.35	2480	4860	7340	14.58	14.58	14.58	7.73	1.85
Prunus rhamnoides	**15.40**	**480**	**16.67**	**6.05**	**1920**	**4400**	**6320**	**14.58**	**27.08**	**20.83**	**10.80**	**0.96**
Prunus serotina	5.30	110	16.67	5.70	3140	2220	5360	50.00	33.33	41.67	21.15	3.56
Quercus candicans	5.33	50	6.25	2.19	0	40	40	0.00	2.08	1.04	0.52	0.06
Quercus crassifolia	**117.01**	**3060**	**35.42**	**15.24**	**4380**	**2680**	**7060**	**35.42**	**33.33**	**34.38**	**17.61**	**0.17**
Quercus crispipilis	**66.49**	**2860**	**31.25**	**12.98**	**2400**	**2660**	**5060**	**37.50**	**29.17**	**33.33**	**16.97**	**0.13**
Quercus laurina	**253.06**	**3070**	**47.92**	**21.47**	**8120**	**3820**	**11940**	**50.00**	**33.33**	**41.67**	**21.55**	**0.28**
Quercus ocoteaefolia	**148.93**	**5220**	**14.58**	**9.96**	**2000**	**1300**	**3300**	**12.50**	**12.50**	**12.50**	**6.45**	**0.05**
Quercus rugosa	**339.55**	**6300**	**64.58**	**30.09**	**9200**	**8280**	**17480**	**66.67**	**56.25**	**61.46**	**31.78**	**0.20**
Quercus segoviensis	**79.19**	**4570**	**18.75**	**9.94**	**2520**	**1480**	**4000**	**27.08**	**20.83**	**23.96**	**12.22**	**0.06**
Quercus skutchii	1.88	110	8.33	2.87	880	520	1400	25.00	18.75	21.88	11.02	0.93
Quetzalia contracta	**18.39**	**700**	**14.58**	**5.52**	**240**	**5400**	**5640**	**12.50**	**22.92**	**17.71**	**9.19**	**0.59**
Rhacoma tonduzii	0.18	30	4.17	1.41	0	520	520	0.00	6.25	3.13	1.59	1.27

Species	Adults				Saplings							Saplings: adult ratio
	Basal area (m^2 ha^{-1})	Density (ind ha^{-1})	Frequency (%)	RIV (%)	Density (ind ha^{-1})			Frequency (%)			RIV (%)	
					open	closed	Total	open	closed	Total		
Rhamnus mcvaughii	0.03	10	2.08	0.70	7400	7060	14460	35.42	27.08	31.25	16.49	105.57
Rhamnus sharpii	1.77	130	10.42	3.57	2640	1400	4040	18.75	16.67	17.71	9.10	2.27
Roldana acutangula	0.02	10	2.08	0.70	11220	5240	16460	35.42	31.25	33.33	17.65	120.18
Senecio uspantanensis	0.05	10	2.08	0.70	0	720	720	0.00	6.25	3.13	1.61	5.26
Solanum aligerum	0.41	60	4.17	1.43	1040	760	1800	12.50	18.75	15.63	7.92	2.19
Solanum nigricans	0.04	10	2.08	0.70	6420	6180	12600	39.58	27.08	33.33	17.42	91.99
Styrax magnus	**8.38**	**880**	**10.42**	**4.08**	**3260**	**4020**	**7280**	**20.83**	**16.67**	**18.75**	**9.81**	**0.60**
Symplocos breedlovei	**19.45**	**1310**	**14.58**	**5.87**	**380**	**2260**	**2640**	**6.25**	**14.58**	**10.42**	**5.37**	**0.15**
Synardisia venosa	0.08	20	4.17	1.40	0	20	20	0.00	2.08	1.04	0.52	0.07
Ternstroemia lineata	**14.22**	**890**	**16.67**	**6.26**	**1460**	**2820**	**4280**	**14.58**	**22.92**	**18.75**	**9.63**	**0.35**
Verbesina perymenioides	0.12	40	6.25	2.11	620	560	1180	10.42	12.50	11.46	5.80	2.15
Vernonia leiocarpa	0.29	80	6.25	2.13	1380	1820	3200	8.33	10.42	9.38	4.88	2.92
Viburnum acutifolium	0.24	60	4.17	1.43	16180	2440	18620	16.67	20.83	18.75	10.49	22.66
Viburnum elatum	0.54	80	8.33	2.83	520	280	800	8.33	10.42	9.38	4.74	0.73
Viburnum jucundum	21.98	2250	47.92	17.53	9840	12640	22480	52.08	54.17	53.13	27.91	0.73
Viburnum obtusatum	0.34	60	2.08	0.73	0	600	600	0.00	8.33	4.17	2.12	0.73
Weinmannia pinnata	**19.54**	**860**	**6.25**	**2.85**	**0**	**140**	**140**	**0.00**	**4.17**	**2.08**	**1.05**	**0.01**
Zanthoxylum melanostictum	5.07	230	10.42	3.67	0	1280	1280	0.00	12.50	6.25	3.20	0.41

Appendix 3.4 Results for ANOVA to test for effects of canopy condition on densities of saplings of 84 species found in ten or more plots (at least in five open and five close plots). Results of *Quercus* spp. and *Pinus* spp. are denoted with an asterisk (*). Means with different letters are significantly different (Fisher LSD test; P < 0.05) and are denoted in bold.

Species	Total number of plots analysed	Mean of density in open plots		SE	Mean of density in closed plots		SE	F value	P
Ageratina mairetiana	53	996.92	A	177.79	723.08	A	177.79	1.2	0.2813
Arbutus xalapensis	**36**	**75.56**	**A**	**15.33**	**27.78**	**B**	**15.33**	**4.9**	**0.0344**
Asteraceae sp3	12	213.33	A	97.75	0.00	A	0.00	2.4	0.1538
Baccharis vaccinioides	18	240.00	A	88.03	64.44	A	88.03	1.2	0.1776
Bartlettina sordida	16	697.50	A	273.30	47.50	A	273.30	2.8	0.1148
Buddleja cordata	60	66.67	A	14.52	38.00	A	14.52	2.0	0.1681
Buddleja nitida	12	50.00	A	19.03	3.33	A	19.03	3.0	0.1136
Celastrus vulcanicola	**20**	**24.00**	**B**	**163.87**	**602.00**	**A**	**163.87**	**6.2**	**0.0226**
Cestrum aurantiacum	34	281.18	A	66.47	131.76	A	66.47	2.5	0.1218
Cestrum guatemalense	54	375.56	A	79.32	182.96	A	79.32	3.0	0.0919
Clethra macrophylla	**18**	**88.89**	**B**	**315.39**	**1093.33**	**A**	**315.39**	**5.1**	**0.0387**
Clethra oleoides	10	36.00	A	54.59	128.00	A	54.59	1.4	0.2675
Cleyera theoides	24	28.33	A	22.38	56.67	A	22.38	0.8	0.3804
Cornus disciflora	14	134.29	A	60.92	120.00	A	60.92	0.0	0.8711
Cornus excelsa	20	164.00	A	88.80	62.00	A	88.80	0.7	0.4273
Crataegus pubescens	40	81.00	A	21.85	73.00	A	21.85	0.1	0.7972
Critoniadelphus nubigenus	30	353.33	A	123.69	120.00	A	123.69	1.8	0.193
Daphnopsis radiata	20	184.00	A	143.25	418.00	A	143.25	1.3	0.2632
Drimys granadensis	**16**	**67.50**	**B**	**73.57**	**295.00**	**A**	**73.57**	**4.8**	**0.0462**
Eupatorium areolare	**16**	**302.50**	**A**	**89.56**	**17.50**	**B**	**89.56**	**5.1**	**0.041**
Eupatorium ligustrinum	68	518.24	A	126.67	380.00	A	126.67	0.6	0.4431
Eupatorium pycnocephalum	16	162.50	A	134.23	330.00	A	134.23	0.8	0.3925
Fabaceae sp.	20	592.00	A	203.94	492.00	A	203.94	0.1	0.7328
Fuchsia microphylla	62	722.58	A	182.06	469.68	A	182.06	1.0	0.3299
Fuchsia paniculata	**12**	**480.00**	**A**	**107.58**	**0.00**	**B**	**0.00**	**10.0**	**0.0102**
Fuchsia splendens	40	243.00	A	64.23	88.00	A	64.23	2.9	0.0961
Fuchsia thymifolia	38	473.68	A	97.11	281.05	A	97.11	2.0	0.1693

Species	Total number of plots analysed	Mean of density in open plots		SE	Mean of density in closed plots		SE	F value	P
Garrya laurifolia	64	401.88	A	92.10	419.38	A	92.10	0.0	0.8936
Gaultheria chiapensis	20	2196.00	A	690.30	780.00	A	690.30	2.1	0.1641
Holodiscus argenteus	18	24.44	A	11.73	26.67	A	11.73	0.0	0.8951
Lantana hispida	22	212.73	A	75.64	207.27	A	75.64	0.0	0.9598
Lippia umbellata	30	1390.67	A	343.72	1077.33	A	343.72	0.4	0.5244
Litsea glaucescens	70	229.14	A	38.89	200.57	A	38.89	0.3	0.6051
Lycianthes purpusii	14	80.00	A	80.29	148.57	A	80.29	0.4	0.5571
Malvaviscus arboreus	20	136.00	A	298.25	862.00	A	298.25	3.0	0.1023
Miconia glaberrima	18	635.56	A	349.20	1477.78	A	349.20	2.9	0.1074
Monnina xalapensis	60	252.00	A	53.20	122.00	A	53.20	3.0	0.0893
Morella cerifera	20	450.00	A	133.94	70.00	A	133.94	4.0	0.0601
Myrsine juergensenii	56	449.29	A	111.45	681.43	A	111.45	2.2	0.1466
Oreopanax xalapensis	56	686.43	A	226.94	995.00	A	226.94	0.9	0.3406
Ostrya virginiana	16	42.50	A	27.95	52.50	A	27.95	0.1	0.804
Parathesis leptopa	12	13.33	A	100.67	296.67	A	100.67	4.0	0.0746
Persea americana	**34**	**427.06**	**B**	**307.80**	**1343.53**	**A**	**307.80**	**4.4**	**0.0432**
Perymenium ghiesbreghtii	30	464.00	A	157.89	209.33	A	157.89	1.3	0.2637
Pinus ayacahuite	10	60.00	A	31.11	24.00	A	31.11	0.7	0.4369
Pinus montezumae	16	195.00	A	119.33	267.50	A	119.33	0.2	0.6740
Pinus tecunumanii	32	462.50	A	187.34	71.25	A	187.34	2.2	0.1502
Prunus brachybotrya	12	73.33	A	40.18	136.67	A	40.18	1.2	0.2911
Prunus lundelliana	16	310.00	A	295.78	607.50	A	295.78	0.5	0.4886
Prunus rhamnoides	28	137.14	A	98.78	314.29	A	98.78	1.6	0.2160
Prunus serotina	52	120.77	A	30.93	85.38	A	30.93	0.7	0.4224
Quercus crassifolia	50	175.20	A	46.28	107.20	A	46.28	1.1	0.3040
Quercus crispipilis	36	147.78	A	30.17	133.33	A	30.17	0.1	0.7370
Quercus laurina	52	312.31	A	66.68	146.92	A	66.68	3.1	0.0856
Quercus ocoteaefolia	14	285.71	A	84.76	185.71	A	84.76	0.7	0.4205
Quercus rugosa	70	262.86	A	35.57	236.57	A	35.57	0.1	0.7492
Quercus segoviensis	28	180.00	A	41.97	105.71	A	41.97	1.6	0.2219
Quercus skutchii	36	48.89	A	15.49	28.89	A	15.49	0.8	0.3675
Quetzalia contracta	24	20.00	A	150.24	450.00	A	150.24	4.1	0.0553

Species	Total number of plots analysed	Mean of density in open plots		SE	Mean of density in closed plots		SE	F value	P
Rhamnus mcvaughii	40	370.00	A	133.56	353.00	A	133.56	0.0	0.9288
Rhamnus sharpii	22	240.00	A	75.90	127.27	A	75.90	1.1	0.3062
Rhus terebinthifolia	20	226.00	A	118.29	314.00	A	118.29	0.3	0.6053
Roldana acutangula	44	510.00	A	162.34	238.18	A	162.34	1.4	0.2431
Roldana barba-johannis	**20**	**30.00**	**B**	**10.24**	**132.00**	**A**	**10.24**	**8.5**	**0.0094**
Rubus sp.	24	93.33	A	34.15	68.33	A	34.15	0.3	0.6098
Rubus trilobus	24	168.33	A	54.21	46.67	A	54.21	2.5	0.1268
Salvia karwinskii	16	1227.50	A	593.23	1615.00	A	593.23	0.2	0.6513
Saurauia oreophila	12	33.33	A	140.06	433.33	A	140.06	4.1	0.0711
Smallanthus maculatus	10	216.00	A	71.61	0.00	A	0.00	4.6	0.0655
Solanum aligerum	26	80.00	A	30.49	58.46	A	30.49	0.3	0.6219
Solanum nigricans	48	267.50	A	89.80	257.50	A	89.80	0.0	0.9376
Styrax magnus	22	296.36	A	166.77	365.45	A	166.77	0.1	0.7726
Symplocos breedlovei	16	47.50	A	104.55	282.50	A	104.55	2.5	0.1343
Ternstroemia lineata	32	91.25	A	50.57	176.25	A	50.57	1.4	0.2439
Triumfetta columnaris	16	165.00	A	84.49	85.00	A	84.49	0.5	0.5141
Ugni montana	16	252.50	A	492.43	1152.50	A	492.43	1.7	0.2172
Verbesina perymenioides	18	68.89	A	30.87	62.22	A	30.87	0.0	0.8805
Vernonia leiocarpa	10	276.00	A	157.91	364.00	A	157.91	0.2	0.7038
Viburnum acutifolium	30	1078.67	A	336.10	162.67	A	336.10	3.7	0.0642
Viburnum elatum	16	65.00	A	26.39	35.00	A	26.39	0.7	0.4349
Viburnum jucundum	56	351.43	A	77.79	451.43	A	77.79	0.8	0.3674
Xylosma chiapensis	34	368.24	A	122.43	557.65	A	122.43	1.2	0.2821
Zanthoxylum foliolosum	20	122.00	A	104.71	402.00	A	104.71	3.6	0.0749
Zanthoxylum melanostictum	**12**	**0.00**	**B**	**0.00**	**213.33**	**A**	**57.12**	**7.0**	**0.0247**
*** *Pinus* spp.**	64	516.88	**A**	120.23	145.63	**B**	120.23	4.7	0.0328
* *Quercus* spp.	90	655.56	A	88.32	461.78	A	88.32	2.4	0.1244

Appendix 3.5 Complementary results of the variation partitioning analysis on floristic composition (Table 3.9). Adjusted R^2 statistics (R^2_{adj}) and F statistics are presented for all measured predictors. The effect of predictors controlling for any combinations of other predictor is denoted by symbol │.

Kind of analysis	Variables controlled	Predictor	Adj R^2	F	P
Including canopy openness	Controlling 1 variable	Spatial variables │ Climate	0.07	5.10	0.005
		Spatial variables │ Altitude	0.12	7.91	0.005
		Spatial variables │ Canopy openness	0.11	6.74	0.005
		Climate │ Spatial variables	0.20	4.26	0.005
		Climate │ Altitude	0.16	3.50	0.005
		Climate │ Canopy openness	0.23	4.60	0.005
		Altitude │ Spatial variables	0.10	13.01	0.005
		Altitude │ Climate	0.02	2.77	0.010
		Altitude │ Canopy openness	0.09	10.36	0.005
		Canopy openness │ Spatial variables	0.02	2.71	0.005
		Canopy openness │ Climate	0.01	2.16	0.005
		Canopy openness │ Altitude	0.01	2.28	0.015
	Controlling 2 variables	Spatial variables │ Altitude, Canopy openness	0.11	5.33	0.005
		Spatial variables │ Climate, Canopy openness	0.06	4.68	0.005
		Spatial variables │ Climate, Altitude	0.07	7.80	0.005
		Climate │ Altitude, Canopy openness	0.16	2.88	0.005
		Climate │ Spatial variables, Canopy openness	0.18	4.04	0.005
		Climate │ Spatial variables, Altitude	0.11	3.49	0.005
		Altitude │ Spatial variables, Canopy openness	0.10	3.23	0.005
		Altitude │ Climate, Canopy openness	0.02	12.33	0.005
		Altitude │ Spatial variables, Climate	0.02	2.85	0.005
		Canopy openness │ Climate, Altitude	0.01	1.45	0.130
		Canopy openness │ Spatial variables, Altitude	0.01	2.19	0.005
		Canopy openness │ Spatial variables, Climate	0.004	2.24	0.005
Including disturbance level	Controlling 1 variable	Spatial variables │ Climate	0.07	5.10	0.001
		Spatial variables │ Altitude	0.12	7.91	0.001
		Spatial variables │ Disturbance level	0.10	6.61	0.001
		Climate │ Spatial variables	0.20	4.26	0.001
		Climate │ Altitude	0.16	3.50	0.001
		Climate │ Disturbance level	0.21	4.33	0.001
		Altitude │ Spatial variables	0.10	13.01	0.001
		Altitude │ Climate	0.02	2.77	0.001
		Altitude │ Disturbance level	0.08	9.33	0.001
		Disturbance level │ Spatial variables	0.04	5.58	0.001
		Disturbance level │ Climate	0.02	3.47	0.001
		Disturbance level │ Altitude	0.03	4.43	0.011
	Controlling 2 variables	Spatial variables │ Altitude, Disturbance level	0.10	5.33	0.001
		Spatial variables │ Climate, Disturbance level	0.05	4.43	0.001
		Spatial variables │ Climate, Altitude	0.07	6.97	0.001
		Climate │ Altitude, Disturbance level	0.15	2.88	0.001
		Climate │ Spatial variables, Disturbance level	0.16	3.74	0.001
		Climate │ Spatial variables, Altitude	0.11	3.39	0.001
		Altitude │ Spatial variables, Disturbance level	0.08	3.23	0.001
		Altitude │ Climate, Disturbance level	0.02	9.95	0.001
		Altitude │ Spatial variables, Climate	0.02	2.89	0.001
		Disturbance level │ Climate, Altitude	0.02	2.25	0.003
		Disturbance level │ Spatial variables, Altitude	0.02	2.81	0.001
		Disturbance level │ Spatial variables, Climate	0.01	3.58	0.001

CHAPTER 4. TESTING FOR THE EFFECTS OF LEAF QUALITIES AND FOREST TYPE ON LEAF-LITTER DECOMPOSITION IN MOUNTAINS OF THE CENTRAL HIGHLANDS OF CHIAPAS, MEXICO

4.1. ABSTRACT

Leaf-litter decomposition rates may be determined by the structural and biochemical components of litter and by the forest understory environments and soil substrate conditions under which decomposition takes place; it is highly likely that these two sets of factors interact. The relationships between functional traits and growth, recruitment and mortality in plant species are now quite well known, but trait effects on ecosystem processes like litter decomposition are much less well-known, and it is not known whether the functional characteristics of forest stands are related to decomposition rates *in situ*. Research in this area can make a valuable contribution to the development of functional ecology. For tropical montane forests of the Central Highlands, state of Chiapas, Mexico, this study evaluated the effect of functional leaf traits of individual tree species and forest environments on leaf-litter decomposition. For this, two complementary experiments were conducted. In a greenhouse experiment, the direct and indirect associations of litter decomposition rates with 10 functional traits were assessed in 20 dominant tree species. Six of these traits were measured on fresh leaves (leaf area, LA; specific leaf area, SLA; leaf dry matter content, LDMC; leaf tensile strength, LTS; leaf phosphorous concentration, LPC and leaf nitrogen concentration, LNC), and four on dry leaf-litter (lignin, cellulose and hemicellulose concentrations -carbon fractions). We hypothesised that leaf litter decomposition rates would be lower in conservative species such as some *Quercus* spp. which have low SLA, LNC and LPC and high LDMC and carbon fractions, and higher in tree species of the understorey and sub-canopy of the forest, which have higher SLA, LNC and LPC and lower LDMC and carbon fractions. In a field experiment we assessed the effect of four different forest association (mixed broad-leaved, pine-oak, oak and pine dominated) on the decomposition of six litter types (four combinations of field-collected leaf litter, one for each forest association, and two reference species) tested in all four forest associations. Because of the exploratory nature of the field experiment, we tested a simple hypothesis that decomposition rates would differ between forest associations. Hypotheses were met in the greenhouse experiment. Conservative *Quercus* spp. with high LTS, LDMC and lignin had slow decomposition, though so did *Pinus* spp. which have low SLA and high LTS. Sub-canopy and understorey species with more acquisitive leaves had high decomposition rates. In contrast, in the field experiment, decomposition rates were similar between the four different forest types, supporting the hypothesis that leaf characteristics of species that persist after senescence, rather than forest stand characteristics, are the most important drivers of decomposition processes. Nevertheless, there was evidence of “home-field advantage” with oak litter decomposing fastest in the oak forest and pine litter in the pine forest, indicating that the interaction between forest association and litter type is also an important driver of decomposition. This interaction may depend on the characteristics of leaf-litter substrates determined by forest functional composition. Overall, the results of this study support the emerging principle of functional ecology that traits of living plants and their leaves, and possibly also the soil surface conditions of the stands they dominate, can drive leaf litter decomposition rates, with important implications for understanding of ecosystem functioning and ecosystem service provision.

Key words: Functional traits, leaf quality, tree species, montane forests.

4.2. INTRODUCTION

Leaf-litter decomposition is an important ecological phenomenon in forest ecosystems that links above- and below-ground processes, providing a major source of nutrients for plant growth. Despite its importance, and its tight link with plant performance and productivity, decomposition is poorly understood since it is complex and is affected by numerous variables acting together (Eijsackers & Zehnder 1990). The interactions between abiotic (humidity and temperature) and biotic controls of decomposition (quantity, quality and heterogeneity of litter, as well as abundance and heterogeneity of decomposers and detritivores) have been explored deeply only in recent years (Hättenschwiler, Tiunov & Scheu 2005).

Studies of decomposition processes have demonstrated that litter decomposition rate depends on the structural and biochemical components of litter (Pérez-Harguindeguy *et al.* 2000), which in turn depend on ecological characteristics of living plants and their leaves (for example, life-form and deciduous versus evergreen habit, leaf life span, foliar nutrient content, components of leaf structure and plant defences) (Grime *et al.* 1996; Cornelissen 1996; Cornelissen & Thompson 1997; Wardle *et al.* 1998; Pérez-Harguindeguy *et al.* 2000; Quested *et al.* 2003; Cornelissen *et al.* 2004; Dorrepaal *et al.* 2005; Kazakou *et al.* 2006). In general terms, fast growing and poorly defended species produce litter with high decomposability whereas slower-growing and better-defended species produce litter with low decomposition rates (Cornelissen *et al.* 1999).

There is convincing evidence that species' traits are important drivers of leaf-litter decomposition but it is necessary to verify the universality of these relationships across species, such as those that live in particular conditions like mountains (Körner 2004; Becker *et al.* 2007; Richter 2008). In addition, litter decomposition rates are also affected by micro-environment, microbial and invertebrate composition which are linked to forest structure and composition, forest floor characteristics and vegetation cover (Gholz *et al.* 2000; Vivanco & Austin 2008; Ayres *et al.* 2009; van der Putten *et al.* 2013). The effect of variation in forest conditions on litter decomposition is an important issue in the current anthropogenic context of tropical mountainous areas where land use produces major changes in composition, structure and cover of native forests; potentially producing effects on forest productivity (sensu Chave *et al.* 2008) and nutrient cycling.

This is the case for the Central Highlands of Chiapas, Mexico, in which a variety of species and community and functional assemblages coexist within a complex environment and topography, under different types and intensities of land use (see Chapters 2 and 3). A considerable amount of ecological knowledge has been obtained from and about the different montane forest associations of the region (González-Espinosa *et al.* 1991, 1997; Quintana-Ascencio & González-Espinosa 1993; Ramírez-Marcial, Camacho-Cruz & González-Espinosa 2008; Ramírez-Marcial *et al.* 1998; Ramírez-Marcial, González-Espinosa & Williams-Linera 2001; Camacho-Cruz *et al.* 2000; López-Barrera & González-Espinosa 2001; Galindo-Jaimes *et al.* 2002; Quintana-Ascencio *et al.* 2004; Cayuela, Golicher & Rey-Benayas 2006a), however only one exploratory study has assessed leaf-litter decomposition (Rocha-Loredo & Ramírez-Marcial 2009).

The complex spatial and environmental context of the Central Highlands and its particular tree species and functional associations offer a good opportunity to explore the effect of environmental and species variables on litter decomposition. For this, the objective of this study is to assess 1) the effects of tree species' functional traits on leaf-litter decomposition, and 2) the effect of different forest conditions on leaf-litter decomposition. We hypothesise that 1) variation in leaf-litter decomposition rates is largely explained by species functional traits, 2) forests with different structure, functional characteristics and composition, associated with variation in microenvironment, also explain a proportion of variation in leaf-litter decomposition rates, with a specific "home-field advantage" of higher decomposition rates within a given forest type of litter collected from that forest type, and 3) decomposition of natural litter mixtures is a function of the interaction between the properties of their constituent litter and local environmental conditions.

To test these hypotheses, we developed two experiments, one in a controlled greenhouse environment and the other in field conditions. The greenhouse experiment was designed to test the relationships between tree species' decomposition rates and both inter- and intra-specific variation in their leaf traits. The field experiment was designed to compare the relative effect of litter type versus forest environment and the interaction between the two.

4.3. METHODS

4.3.1. Study area and description of forest types

The Central Highlands is located in the state of Chiapas, southeast of Mexico, and is a topographically complex region that elevates from 600-2900 m a.s.l., mostly above 1500 m (Cayuela *et al.* 2006a; d) (Fig. 4.1). It possesses a cool and humid climate (mean annual temperature between 13-14 °C, mean annual rainfall between 1200-1800 mm. Fig. 4.2), with a rainy summer and a dry season of 5-6 months. The underlying geology is carboniferous limestone with many rocky outcroppings whereas the soils are a mixture of thin lithic rendzinas, deeper humic acrisols in forested areas, and infertile chromic luvisols (Cayuela *et al.* 2006c; ad; b).

Pine-oak, oak, pine, and broad-leaved forests are the four main tree associations defined for the region (González-Espinosa *et al.* 1997; see description in Chapter 2) and they were the source of the leaf-litter samples for both greenhouse and field experiments, as well as being the locations for the field experiment (Fig. 4.1). For this field experiment, we selected a total of eight stands distributed throughout the study area, corresponding to two replicates of each of the four forest types (Table 4.1). These replicates of each forest type were similar in structure and physiognomy. Moreover, even when they did not share exactly the same composition at the level of species, the sites of pine, oak, and pine-oak forests conserved similarities at the genus level.

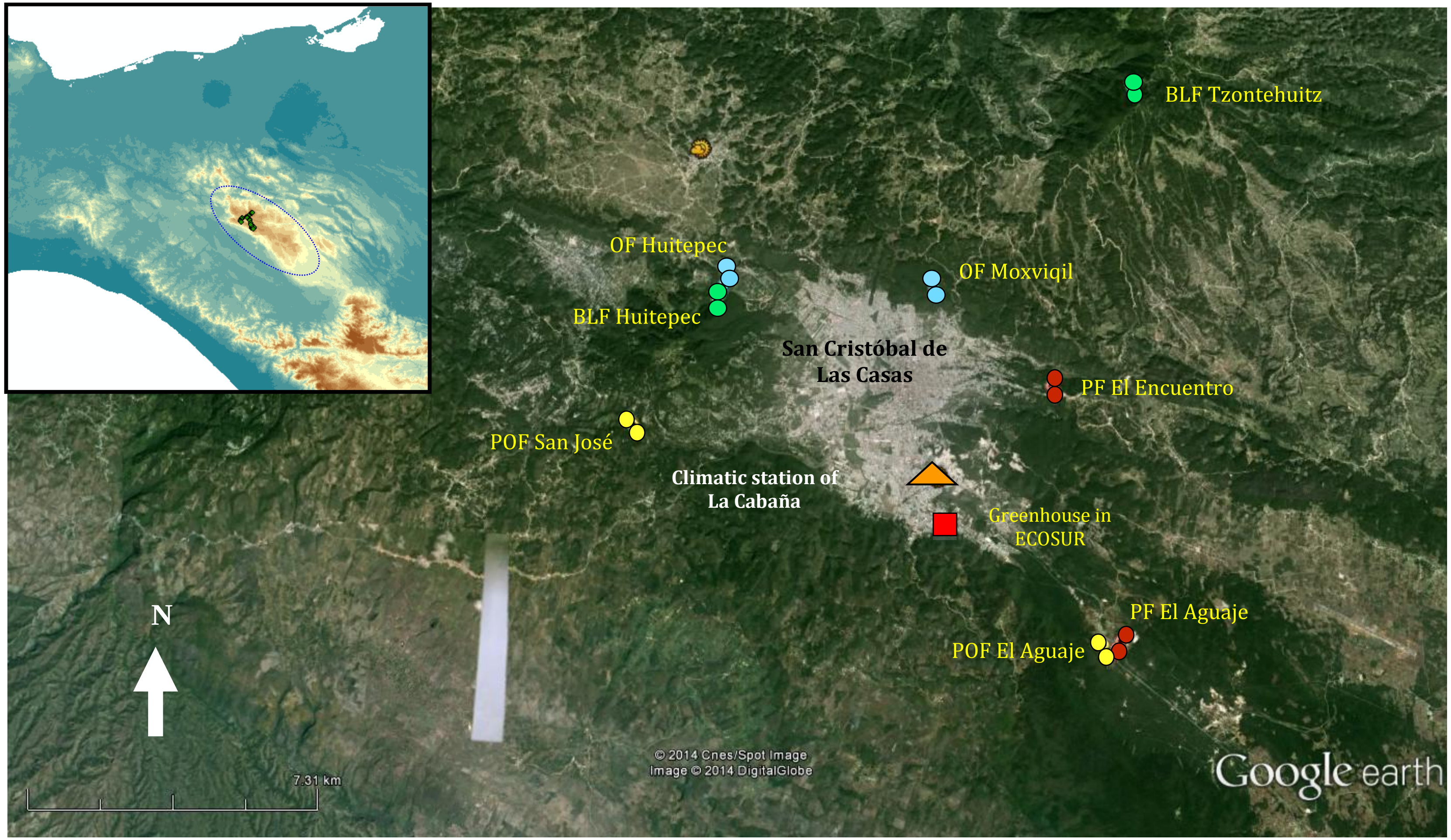

Figure 4.1 The Central Highlands (circled in blue within the box) in the state of Chiapas, Mexico, and the location of the two decomposition plots within each of the two sites corresponding to the four forest types (Compare with Table 4.1). Broad-leaved forests (BLF) are in green dots, pine-oak forests (POF) in yellow, oak forests (OF) in light blue and pine forests (PF) in red. The location of the climatic station of La Cabaña (orange triangle) and the greenhouse for the experiment in standard conditions (red square) are also shown.

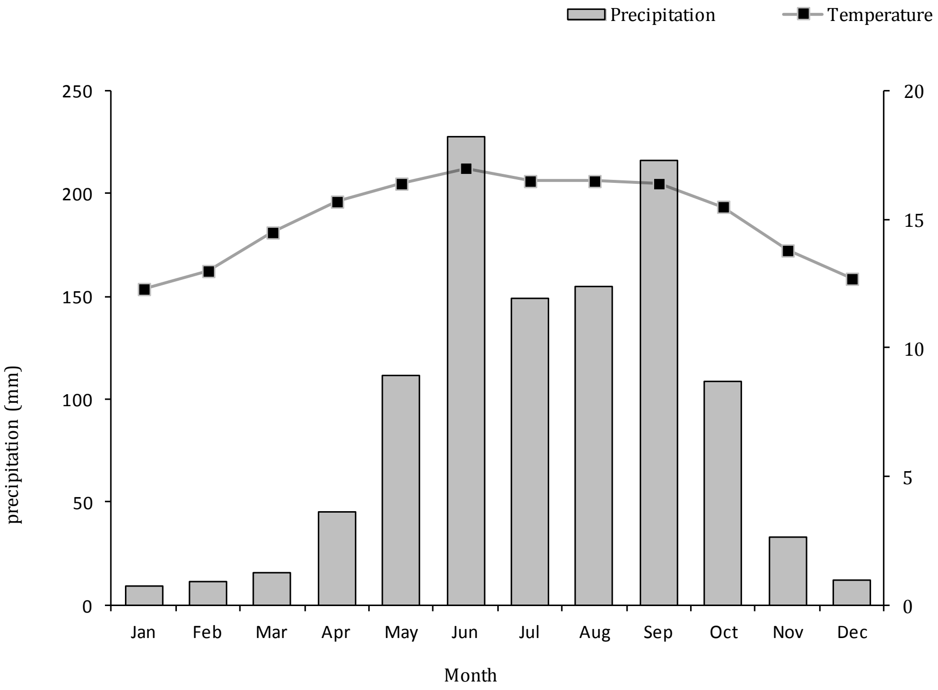

Figure 4.2 Temperatures and precipitation (monthly average) recorded between the years 1961 to 2010 in the climatic station of La Cabaña (CONAGUA 2012). See approximate location of the station in Fig. 4.1.

Table 4.1 Some structural and environmental characteristics (in ranges) of the eight forest stands where the 16 decomposition plots were placed for the experiment *in situ* conditions (See Fig. 4.1). The dominant species used for the experiment in greenhouse conditions are denoted in bold. Environmental values were obtained from WorldClim data layers (Hijmans *et al.* 2005). BLF = Broad-leaved forest, POF = Pine-oak forest, OF = Oak forest, PF = Pine forest; Hu = Huitepec, Tz = Tzontehuitz, Ag = Aguaje, Sa = San José, Mo = Moxviquil, En = Encuentro; Temp mean = mean annual temperature, Preci mean = mean annual precipitation.

Forest type	Site	Structural attributes			Altitude (m)	WorldClim data		Dominant species of the site	Locations of plots		
		Species number	Basal area ($m^2\ ha^{-1}$)	Density ($ind\ ha^{-1}$)		Temp mean (°C)	Preci mean (mm)		Plot	Altitude (m)	Latitude, longitude
BLF	Hu	16 - 24	53.78 - 67.95	1200 - 1760	2533 - 2698	12.9	1249	***Quercus laurina***, ***Q. rugosa***, ***Clethra macrophylla***, ***Styrax magnus***, *Arbutus xalapensis*, *Quetzalia contracta*	1	2505	16°44'59.3'', 92°41'00.8''
									2	2470	16°45'03.2'', 92°40'59.0''
	Tz	17 - 26	48.79 - 85.60	1570 - 3110	2651 - 2777	11.7 - 12.6	1309 - 1396	***Persea americana***, ***Q. ocoteaefolia,*** ***Symplocos breedlovei***, ***Quetzalia contracta***, ***Miconia glaberrima***, ***Prunus rhamnoides***, ***Weinmannia pinnata***, *Ternstroemia lineata*, *Clethra oleoides*, *Oreopanax xalapensis*	1	2665	16°48'26.9'', 92°35'17.7''
									2	2700	16°48'23.2'', 92°35'16.9''
POF	Ag	5 - 10	25.08 - 38.88	1240 - 1520	2363 - 2449	13.1 - 14.1	1121 - 1177	***Pinus montezumae***, ***P. tecunumanii***, ***Q. crispipilis***, ***Q. rugosa***, ***Q. segoviensis***, *Arbutus xalapensis*	1	2375	16°40'45.5'', 92°35'22.7''
									2	2380	16°40'38.6'', 92°35'18.6''
	Sa	6 - 15	31.28 - 51.64	1060 - 1680	2314 - 2399	13.8 - 14.0	1144 - 1167	***P. tecunumanii***, ***Q. rugosa***, ***Q. crassifolia***, **Q. crispipilis**, *P. pseudostrobus var apulcensis*	1	2375	16°43'12.0'', 92°42'03.1''
									2	2390	16°43'13.0'', 92°42'04.6''
OF	Hu	8 - 15	46.56 - 52.02	870 - 1680	2317 - 2396	13.9 - 14.1	1138 - 1146	***Q. crassifolia***, ***Q. rugosa***, ***Q. laurina***	1	2345	16°45'13.8'', 92°40'55.9''
									2	2330	16°45'17.5'', 92°40'54.0''
	Mo	9 - 11	26.59 - 44.68	1100 - 2110	2213 - 2337	13.6 - 15.1	1166 - 1230	***Q. segoviensis***, ***Q. rugosa***, ***Q. crispipilis***	1	2270	16°45'28.5'', 92°37'57.7''
									2	2225	16°45'23.9'', 92°37'56.0''
PF	Ag	1 - 7	29.91 - 34.57	430 - 1200	2280 - 2370	13.8 - 14.0	1115 - 1123	***P. montezumae***	1	2330	16°40'43.7'', 92°35'12.0''
									2	2348	16°40'49.3'', 92°35'18.6''
	En	3 - 11	31.65 - 55.01	1050 - 1150	2290 - 2331	14.3	1135 - 1141	***P. tecunumanii***	1	2245	16°44'07.1'', 92°36'09.3''
									2	2245	16°44'09.6'', 92°36'12.6''

4.3.2. Preparation of materials, experimental design and data collection

The widely used litterbag technique of Bocock & Gilbert (1957) was used for both experiments. In general, the decomposition protocol of Pérez-Harguindeguy (2010) was the basis for the methods used although the methodological considerations of Cornelissen (1996), Pérez-Harguindeguy *et al.* (2000, 2008), Gurvich, Easdale & Pérez-Harguindeguy (2003), Vaieretti *et al.* (2005), and Cortez *et al.* (2007) were also taken into account. The leaf-litter for both experiments was manually collected during the dry season, at the time of the major peak of natural senescence (December 2010-March 2011). The samples were sorted, cleaned and air-dried in an open area and then stored in paper bags (Cornelissen 1996) until the beginning of the decomposition experiments.

For both experiments, leaf-litter was placed in nylon bags of 0.3 mm mesh size. Although this mesh size does not allow the invertebrate mesofauna to contribute to the decomposition process, the effect of these animals is small compared with that of bacteria, protozoa and fungi (Cornelissen 1996). The initial dry mass of each leaf-litter sample was estimated from the measured fresh weight minus the water content estimated from its concentration measured in a set of litter subsamples. For this, six sub-samples of each stored litter type were weighed, and then oven-dried at 60 °C for 72 hours and then reweighed.

A split-plot design was used for the two experiments. The details of the leaf-litter collection and the particular procedures of each experiment are presented below.

4.3.2.1. Experiment 1. Litter decomposition of tree species in greenhouse conditions

For this experiment, we define a working set of 20 species, native to the four forest types of the study area. Of these, 16 are members of the set of 21 dominant species of the eight sites used for the *in situ* experiments (section 1.3.2.2), with 5 omitted due to unavailability of leaf-litter (Table 4.1). Five other species were added to the experiment due to their abundance and leaf-litter availability either in some of the same forest-site combinations (*Persea americana*, *Ternstroemia lineata* and *Viburnum jucundum* for BLF Huitepec; *Quercus candicans* for OF Huitepec. Table 4.1) or in other forest stands (*Pinus ayacahuite* dominant in another POF forest (see Chapter 2)). In order to explore possible intraspecific differences in decomposability associated with the individual site of origin, the resulting combinations of species, site and forest type were included as separate cases resulting in a final total of 33 combinations (12 native species with collections from a single site, 5 species with collections from 2 sites, 2 species with collections from 3 sites and 1 species with collections from 5 sites) (Table 4.2); additionally, the leaf-litter of *Acalypha communis* and *Stipa eriostachya*, two species coming from Argentinean meadows with recognised rapid and slow decomposition respectively (Vaieretti *et al.* 2005), were used as decomposition references in the experiment.

Table 4.2 The 33 species-forest site combinations and the two exotic species (*Acalypha communis* and *Stipa eriostachya*, data from Vaieretti *et al.* (2005)), their collection sites, and their corresponding functional traits and carbon fractions. BLF = broad-leaved forest, POF = pine-oak forest, OF = oak forest, PF = pine forest, MA = meadow; Hui = Huitepec, Tzo = Tzontehuitz, Ag = Aguaje, Sjo = San José, Mo = Moxviquil, En = Encuentro, Arg = Argentina, LDMC = leaf dry matter content (mg g^{-1}), LA = leaf area (mm^{2}), SLA = specific leaf area (mm^{2} mg^{-1}), LTS = leaf tensile strength (N mm^{-1}), H$_{max}$ = maximum height (m), WD = wood density (g mm^{-1}), LPC = leaf phosphorous content (mg g^{-1}), LNC = leaf nitrogen content (mg g^{-1}), Lig = Lignin (mg g^{-1}), Cellu = Cellulose (mg g^{-1}), Hemi = Hemicellulose (mg g^{-1}); N.A. = Not available.

Species	Acronym	Traits								Carbon fractions		
		LDMC	LA	SLA	LTS	H$_{max}$	WD	LPC	LNC	Lig	Cellu	Hemi
Clethra macrophylla	Cmac_Blf_Hui	412.87	6898.92	10.32	0.48	22.70	0.44	0.93	21.50	489.60	66.40	47.35
Miconia glaberrima	Mgla_Blf_Tzo	284.45	3020.00	14.76	0.12	5.72	0.52	1.28	24.50	229.23	66.80	62.05
Persea americana	Pame_Blf_Hu	472.47	10057.44	8.15	0.66	20.32	0.49	0.53	22.10	568.80	63.60	29.03
Persea americana	Pame_Blf_Tzo	443.22	8616.33	7.89	0.56	23.61	0.55	1.28	24.20	525.20	88.00	38.62
Pinus ayacahuite	Paya_Pof_Mit	390.12	623.89	9.09	1.96	28.70	0.41	1.46	23.60	532.59	119.55	43.18
Pinus montezumae	Pmon_Pf_Agu	390.51	1367.22	4.67	6.53	32.39	0.47	1.48	31.30	440.00	97.60	67.02
Pinus montezumae	Pmon_Pof_Agu	427.44	1138.10	5.40	7.71	29.00	0.46	1.08	26.60	453.42	110.36	75.43
Pinus tecunumanii	Ptec_Pf_Enc	433.53	552.38	6.29	1.44	31.21	0.50	0.83	24.30	505.20	114.80	51.12
Pinus tecunumanii	Ptec_Pof_Agu	399.14	477.13	6.68	1.07	32.73	0.52	1.03	26.30	461.20	138.00	22.40
Pinus tecunumanii	Ptec_Pof_Sjo	404.64	728.05	6.13	1.04	34.06	0.54	0.78	26.30	457.60	148.20	55.27
Prunus rhamnoides	Prha_Blf_Tzo	433.38	1359.53	9.44	0.32	19.05	0.50	1.53	18.50	478.21	60.38	50.72
Quercus candicans	Qcan_Of_Hui	464.53	6796.03	10.40	0.59	21.67	0.66	1.38	24.70	637.20	52.00	55.73
Quercus crassifolia	Qcra_Of_Hui	485.03	11643.37	6.82	0.89	22.45	0.69	0.88	24.80	582.80	79.60	48.45
Quercus crassifolia	Qcra_Pof_Sjo	515.86	14847.61	6.31	1.20	22.49	0.69	0.73	24.90	519.60	94.00	48.28
Quercus crispipilis	Qcri_Of_Mox	488.97	2641.47	9.17	0.66	19.62	0.66	1.13	25.50	554.98	55.58	75.88
Quercus crispipilis	Qcri_Pof_Agu	425.30	2616.86	11.82	0.61	15.78	0.71	1.18	28.00	494.40	53.20	30.43
Quercus crispipilis	Qcri_Pof_Sjo	493.22	1905.68	10.92	0.60	22.66	0.72	1.38	26.10	598.40	118.80	10.19
Quercus laurina	Qlau_Of_Hu	461.47	1790.44	11.59	0.67	24.48	0.66	1.03	24.50	618.80	100.00	35.30
Quercus laurina	Qlau_Blf_Hui	450.30	1768.81	12.92	0.61	35.34	0.69	1.08	23.10	442.22	111.95	21.34
Quercus ocoteifolia	Qoco_Blf_Tzo	536.13	2223.99	9.28	0.78	17.52	0.70	1.03	23.00	544.40	111.20	35.39
Quercus rugosa	Qrug_Of_Hui	499.37	8623.14	8.46	0.77	20.78	0.71	1.43	23.80	454.47	110.80	14.22
Quercus rugosa	Qrug_Of_Mox	491.24	7491.87	7.36	1.01	15.22	0.78	1.43	20.20	500.80	108.80	69.60
Quercus rugosa	Qrug_Blf_Hui	469.55	11444.20	8.83	0.68	32.14	0.76	1.58	26.10	497.21	136.47	18.79
Quercus rugosa	Qrug_Pof_Agu	490.47	10748.48	6.95	0.95	15.16	0.73	1.18	23.10	514.00	159.20	18.34
Quercus rugosa	Qrug_Pof_Sjo	453.86	10552.52	8.62	0.85	18.91	0.78	1.23	24.10	586.17	123.55	28.92
Quercus segoviensis	Qseg_Of_Mox	469.37	4672.23	10.29	0.70	20.40	0.78	1.48	26.20	498.40	59.60	43.46
Quercus segoviensis	Qseg_Pof_Agu	458.91	4697.49	11.41	0.55	15.25	0.80	1.53	26.70	458.80	50.40	34.54
Quetzalia contracta	Qcon_Blf_Tzo	337.14	1250.92	12.53	0.87	12.82	0.44	1.18	20.90	451.64	31.97	29.57
Symplocos breedlovei	Sbre_Blf_Tzo	396.61	1852.83	7.72	0.86	13.84	0.69	1.28	24.90	302.60	102.80	33.76
Styrax magnus	Smag_Blf_Hui	486.93	9778.33	10.11	0.35	16.54	0.46	1.28	24.70	468.03	67.57	30.09
Ternstroemia lineata	Tlin_Blf_Hui	427.64	1520.73	6.34	1.00	10.86	0.61	0.88	27.10	303.20	96.80	89.95
Viburnum jucundum	Vjuc_Blf_Hui	375.76	11752.65	13.45	0.27	10.28	0.58	1.38	24.30	447.93	36.36	19.41
Weinmania pinnata	Wpin_Blf_Tzo	383.47	3639.27	13.11	0.60	20.14	0.57	0.88	25.50	486.40	87.20	44.51
Acalypha communis	Acal_mea_Arg	N.A.	N.A.	8.00	0.67	N.A.	N.A.	5.40	45.00	73.00	179.00	63.00
Stipa eriostachya	Styp_mea_Arg	N.A.	N.A.	4.80	13.23	N.A.	N.A.	1.50	16.60	131.00	427.00	270.00

The fresh leaf-litter of the 33 native species-forest site combinations was directly collected from at least five individuals randomly located within each forest site. For these and for the two exotic species, 12 leaf-litter samples of 10 g each were placed into mesh bags of 20 × 15 cm, to enable the harvesting of two bags at each of six times. The mean leaf size of the different species ranged between 10 × 2 mm for leaflets of *Weinmania pinnata* to 180 × 140 mm for *Quercus crassifolia* so the size of the litterbags was sufficient to contain leaves of each species with only limited cutting. The 420 litter decomposition bags prepared were split into the 210 replicate bags for each harvest time which were randomly placed on the surface of each of two blocks contained in a rectangular decomposition bed of 24.48 m^2 (3.4 × 7.2 m) (Fig. 4.3). This decomposition bed was previously filled with a 10 cm-high base of homogenized soil collected from open land, different from the original forest soil systems but with a natural decomposers community. Twenty litterbags were randomly placed on each 1 m^2 of the decomposition bed (4 × 5 bags). A final layer of 10 cm height of the same homogenized soil was then used to cover all the litterbags in order to reduce the possible environmental variability and to homogenize the samples' decomposition.

The two decomposition beds were located within a greenhouse of ECOSUR-San Cristóbal (approx. 2146 m a.s.l., Lat 1642'19'', Lon 9236'55''. Fig. 4.1). Sun exposure, temperature, and soil humidity were made as similar as possible for all the leaf-litter bags during the entire experiment. The beds were systematically and homogeneously irrigated with a watering can, two days per week (Monday and Friday) at 10:00 a.m., with known amounts of water (2000 ml per m^2, scattered in bands). The soil humidity, the soil temperature and the air temperature in the greenhouse were monitored within the first 10 days of the experiment in order to have a reference for planning the watering regime. Nevertheless, regular assessments of the environment were performed during the experiment to find and correct possible variations.

Two litterbags of each of the 33 species-forest site combinations and 2 reference species were randomly harvested in the two blocks, at 30, 60, 90, 120, 150 and finally 210 days after the start of the experiment (between August 2011 and April 2012).

4.3.2.1.1. Determination of leaf and leaf-litter quality in species

For the greenhouse experiment, eight continuous functional traits were measured and subsequently used in statistical analyses to explore their relationship with species' leaf-litter decomposition rates (Table 4.2): leaf area (LA) in mm^2, specific leaf area (SLA) in mm^2 mg^{-1}, leaf dry matter content (LDMC) in mg g^{-1}, leaf tensile strength (LTS) in N mm^{-1}, leaf phosphorous concentration (LPC) in mg g^{-1}, leaf nitrogen concentration (LNC) in mg g^{-1}, wood density (WD) in g mm^{-1}, and maximum plant (H_{max}) in m. These traits were obtained for each of the 33 native species-forest site combinations following the general procedures detailed in Chapter 2, mainly based on the protocols of Cornelissen *et al.* (2003) and Pérez-Harguindeguy *et al.* (2013). Additionally, the content of lignin, cellulose, and hemicellulose in the leaf-litter of each of the 33 combinations were determined from a composite litter sample for each combination. These carbon fractions were obtained by means of sequential digestion of fibres (Van Soest 1994).

4.3.2.2. Experiment 2. Decomposition of litter mixtures in each forest type

In the experiment conducted in forest conditions we used the leaf-litter recently fallen on the upper layer of the forest floor in each of the two replicates of the four forest types (Fig. 4.1, Table 4.1), from five random points within them in order to get representative samples. The samples corresponding to both replicates per forest type were subsequently mixed in order to get a total of four combined leaf-litters corresponding to each type. Given the different patterns of tree species dominance amongst the forest types and their replicates (Table 4.1), the set of four litter mixtures cover a range from more homogeneous (pine and oak forests respectively) to more heterogeneous (pine-oak and broad-leaved forests respectively) compositions.

Additionally, the leaf-litter of *Acalypha communis* and *Stipa eriostachya*, the two species used in the first experiment, were also used in this section as "common" reference materials. Thus, six leaf-litter types (4 mixtures and 2 reference species) were incubated in all 8 forest-sites. One sample of each of the 6 leaf litter types was placed in mesh bags of 9 × 12 cm: 1 g for *A. communis* and *S. eriostachya*, and 5 g for the 4 litter mixtures.

Two square experimental plots of 4 m^2 (2 × 2 m) were established within each of the 8 sites giving 16 in total (4 forest types × 2 replicate sites per type × 2 experimental plots per site = 16. Figs 4.1 and 4.4, Table 4.1). For each of the 16 experimental plots, 18 decomposition bags were prepared for each of the six leaf-litter types (9 litter bags × 2 replicates) in order to cover 9 dry-mass assessments distributed over 360 days of decomposition, from June 2011 to June 2012. In total, 1728 decomposition bags were prepared (16 sites × 9 sample times × 6 leaf-litter types × 2 decomposition bags per leaf-litter type = 1728). These decomposition bags were systematically placed on the forest floor within each of the 16 plots, with each subdivided into two subplots, according to the random arrangement sketched in Figure 4.4. They were then gently covered with a layer of leaf-litter of approx. 20 mm depth collected from the same site. Two decomposition bags of each of the six leaf litter types were recovered at each sample time for dry mass assessment. Therefore: 2 bags × 6 leaf-litter types × 16 experimental sites = 192 litter bags recovered per sampling.

The sample times occurred at an interval of 30 days for the first 180 days (approx. July to December 2011) and an interval of 60 days for the final 180 days (approx. January to June 2012) giving a total of 9 sampling events over 360 days (Fig. 4.4).

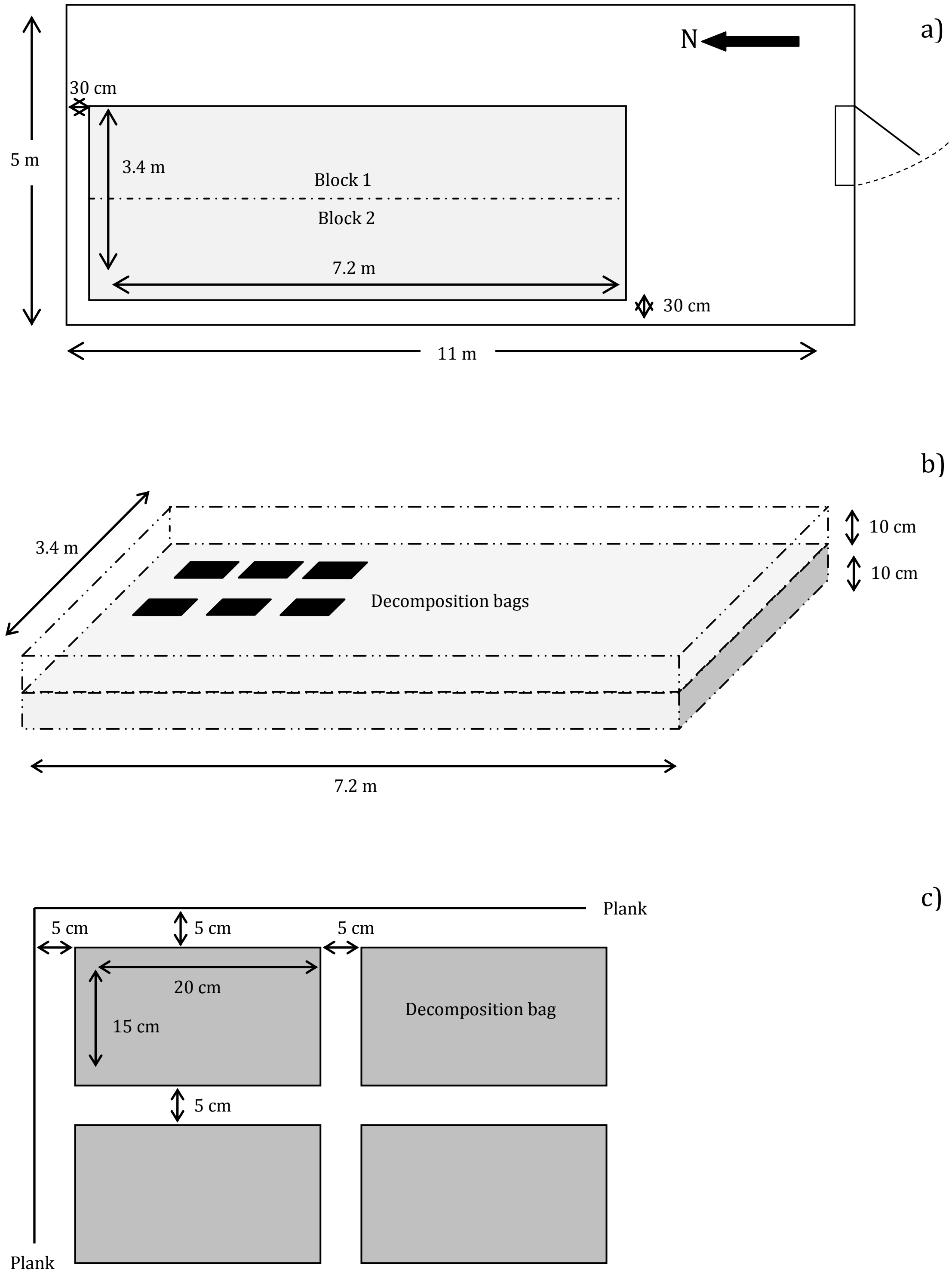

Figure 4.3 General characteristics of the experiment in greenhouse conditions. a) Layout of the greenhouse and approximate location of the decomposition bed and its two blocks. b) Layout of the 24.48 m^2 decomposition bed showing the two soil layers of 10 cm depth and the location of the decomposition bags. c) Layout of the decomposition bags (15 x 20 cm) in the decomposition bed. Bags were separated by 5 cm, with 20 bags included per square metre.

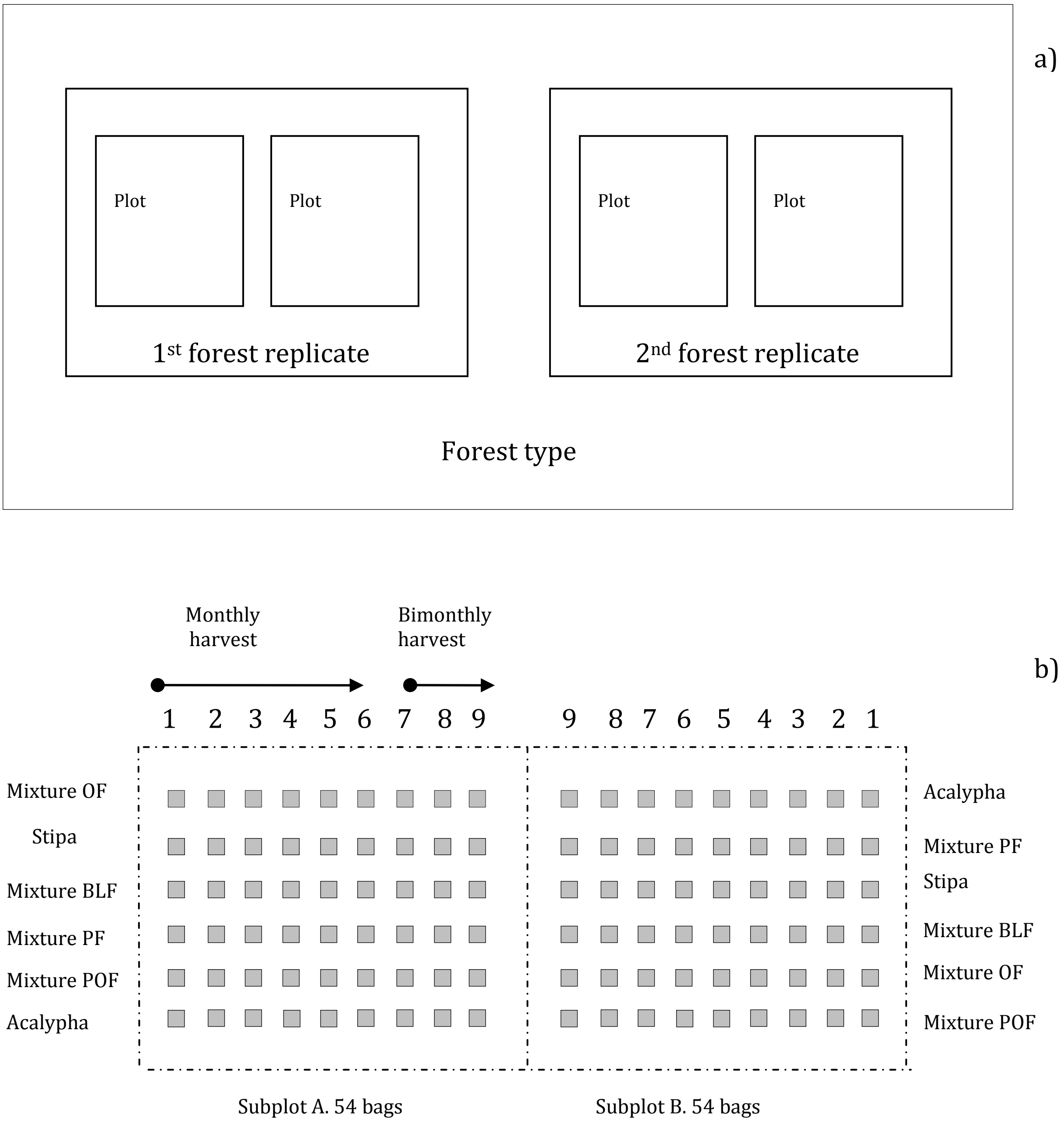

Figure 4.4 General characteristics of the experiment *in situ* conditions. a) Design the experiment. b) Layout of an experimental plot with the corresponding two sub-plots. The position of the rows of each leaf-litter type was randomly assigned.

4.3.3. Data analyses

Decomposition was measured as the proportional remaining dry weight (RDW) at each sample time. For all the RDW across all sample times calculated both for the individual species-fores site combinations in the greenhouse experiment and the leaf-litter types in experiment in forests, we used a general linear mixed model in order to consider the correlation structure because of the repeated measures over time and the heterogeneous variance of the proportion of decomposition in the different sample times. All these procedures were carried out after checking for compliance with the appropriate statistical assumptions (variance homogeneity, normality, independence). *A posteriori* Fisher's LSD tests, using a critical $\alpha = 0.05$, were used to assess individual effects. The Akaike and Bayesian Information Criteria (AIC and BIC) were used to evaluate the fit of models.

Both blocks and subplots were considered random effects. The model for the greenhouse experiment included the fixed effect of (1) each of the 33 native species-forest site combinations and 2 reference species and the 6 sample times, and (2) the interaction of each combination with the times. The response variable was the RDW of each species in the two blocks at each of the 6 times (layout in Fig. 4.3). The model for the experiment in forests considered the fixed effect of (1) leaf-litter type, forest type, and sample time, and (2) the interactions of leaf-litter type and forest type, leaf-litter type and time, forest type and time, and the three-way interaction of leaf-litter type, forest type and time. The response variable was the RDW of each leaf-litter type in the two subplots (4 forest types × 2 sites × 2 plots × 2 subplots = 32 subplots) at each of the 9 sample times (layout in Fig. 4.4).

Pearson's correlations were calculated to assess relationships ($P < 0.05$) amongst functional traits and carbon fraction concentrations, and between each of these and the decomposition rates of the 33 native species-forest site combinations, calculated as the difference between RDWs at successive harvests. In addition, a Principal component analysis (PCA) was performed to explore species-traits relationships. Finally, a triplot exploring the relationships between species, decomposition rates and significant functional traits and carbon fraction concentrations was produced by means of a partial least squares (PLS) regression.

All these statistical routines were executed with the Infostat statistical package (Di Rienzo *et al.* 2008).

4.4. RESULTS

4.4.1. Relationships amongst species' green and leaf-litter traits

Significant Pearson correlations indicated that LA was weakly correlated with LDMC (r = 0.42) whereas SLA was strongly negative related with LTS (r = −0.52) and H_{max} (r = −0.42) (Table 4.3). LTS was also positively correlated with H_{max} (r = 0.40). WD had a strong positive correlation with LDMC (r = 0.57), whereas LNC only had a strong positive relationship with LPC (r = 0.73). Regarding the carbon fractions, lignin concentration was strongly negatively correlated with both cellulose (r = −0.51) and hemicellulose (r = −0.54). Amongst the other traits, lignin was strongly positively correlated with LDMC (r = 0.61) but was negatively correlated with LTS (r = −0.39), nitrogen (r = −0.34) and especially (r = −0.57) with phosphorous concentration. Cellulose and hemicellulose concentrations were positively correlated with each other (r = 0.75) and both were similarly correlated with other traits: both were strongly negatively correlated with lignin and SLA (r = −0.51 and r = −0.54) and positively with LTS (r = 0.73 and r = 0.82). Cellulose was positively correlated with H_{max} (r = 0.53).

These correlations amongst traits and their distribution amongst species are well represented in the ordination analysis (Fig. 4.5). The first two ordination axes together explained 48% of the species variation (25% for axis 1 and 23% for axis 2, Table 4.4). Axis 1 was negatively related to SLA and LA but positively to LTS, H_{max}, hemicellulose and LNC. This axis represents a first axis of foliar specialisation of hard-leaved canopy species, from needle to broad leaves. Axis 2 showed negative association with SLA but very strong positive association with LDMC, also with lignin, cellulose, WD and Hmax. This axis represents a second axis of species variation, from those hard-leaved species to middle-storey species with low H_{max} and generally with soft leaves. *Quercus* species and their replicates form a relatively compact group associated with negative axis 1 scores and more related to high LA, WD, lignin and LDMC values. The *Pinus* species and their replicates are more widely dispersed though mostly with positive axis 1 values, associated with their high LTS and LNC, and low WD. The remaining species, mostly with high SLA, are mainly located in the negative side of axis 2 with foliar and wood qualities very different from *Quercus* and *Pinus* species (compare with Table 4.2).

Table 4.3 Pearson correlations (r-value and (P)) amongst functional traits and carbon fractions. Significant correlations ($P < 0.05$) are marked in bold, marginal significances marked in red. LDMC = Leaf dry matter content, LA = Leaf area, SLA = Specific leaf area, LTS = Leaf tensile strength, H_{max} = Maximum height, WD = Wood density, LPC = Leaf phosphorous concentration, LNC = Leaf nitrogen concentration.

	LA	SLA	LTS	H_{max}	WD	LPC	LNC	Lignin	Cellulose	Hemicellulose
LDMC	**0.42** **(0.02)**	−0.34 (0.06)	−0.12 (0.51)	0.14 (0.42)	**0.57** **(5.4E−04)**	−0.06 (0.75)	−0.09 (0.63)	**0.61** **(1.6E−04)**	0.23 (0.20)	−0.17 (0.35)
LA		−0.06 (0.74)	−0.26 (0.14)	−0.21 (0.23)	0.33 (0.06)	−0.03 (0.87)	−0.17 (0.35)	0.28 (0.11)	−0.07 (0.70)	−0.29 (0.10)
SLA			**−0.52** **(1.2E−03)**	**−0.42** **(0.01)**	0.07 (0.69)	−0.01 (0.96)	−0.08 (0.65)	0.12 (0.48)	**−0.50** **(2.1E−03)**	**−0.41** **(0.02)**
LTS				**0.40** **(0.02)**	−0.33 (0.06)	0.01 (0.94)	−0.15 (0.40)	**−0.39** **(0.02)**	**0.73** **(5.8E−07)**	**0.82** **(1.7E−09)**
H_{max}					−0.19 (0.29)	−0.14 (0.43)	0.26 (0.15)	0.33 (0.06)	**0.53** **(1.6E−03)**	−0.06 (0.76)
WD						0.25 (0.16)	0.11 (0.56)	0.22 (0.23)	0.15 (0.39)	−0.24 (0.18)
LPC							**0.73** **(6.8E−07)**	**−0.57** **(3.3E−04)**	0.23 (0.19)	0.09 (0.60)
LNC								**−0.34** **(0.05)**	−0.07 (0.68)	−0.19 (0.27)
Lignin									**−0.51** **(1.7E−03)**	**−0.54** **(7.5E−04)**
Cellulose										**0.75** **(2.6E−07)**

Table 4.4 Loadings of traits on the first two axes of the principal component analysis; see also Fig. 4.5. The most important correlations (> 0.30) are shown in bold.

	Functional traits	
	Loadings on axis 1	Loadings on axis 2
Total variation explained by axis	25%	23%
Variables		
Leaf dry matter content LDMC	−0.14	**0.53**
Leaf area LA	**−0.30**	0.27
Specific leaf area SLA	**−0.40**	**−0.32**
Leaf tensile strength LTS	**0.49**	0.02
Maximum height H_{max}	**0.36**	**0.30**
Wood density WD	−0.28	**0.31**
Leaf phosphorous content LPC	−0.14	−0.08
Leaf nitrogen content LNC	**0.30**	0.03
Lignin	−0.12	**0.43**
Cellulose	0.26	**0.35**
Hemicellulose	**0.32**	−0.18

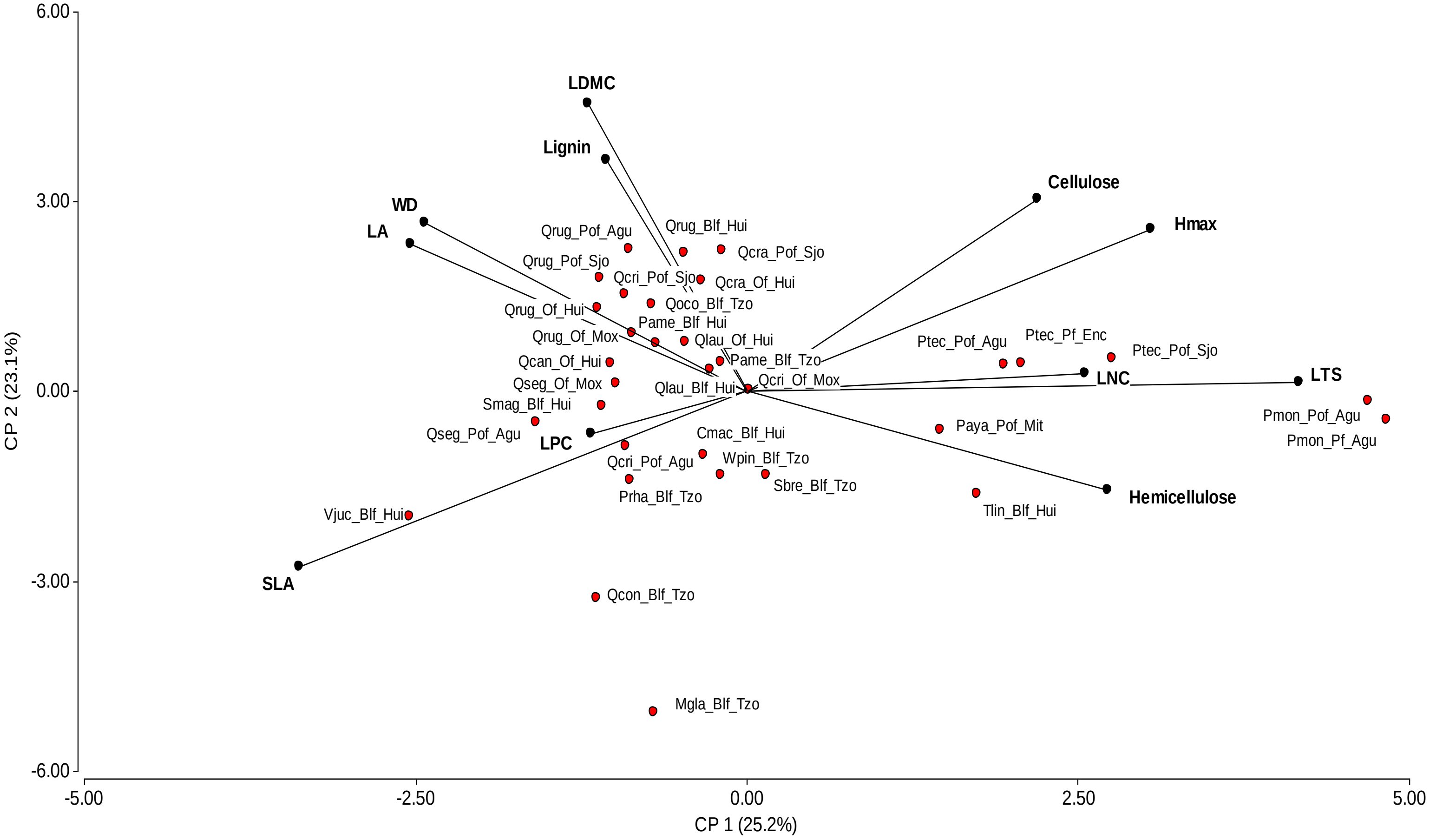

Figure 4.5 PCA biplot relating the 33 native species-forest site combinations with functional traits and carbon fraction concentrations. Compare with Table 4.4. Species/site abbreviations in Table 4.2.

4.4.2. Leaf litter decomposition in greenhouse conditions

The results of the mixed model applied to this experiment (Table 4.5) indicate that there are significant differences between the 33 native species-forest site combinations and two exotic reference species, between the six sample times, and that there are significant interactions between the species-forest site combinations and time.

The total adjusted means for each of the 35 combinations in each of the 6 times assessed are presented in Figure 4.6 (see Appendix 4.1). The 20 native species and their corresponding replicates showed different decomposition patterns over time but none of them decomposed more than the 50% of their dry-mass during the 210 days of the experiment. Fisher's LSD test indicates that there are significant differences between and within some species (Appendix 4.2). Extreme cases are a replicate of *Quercus crispipilis* of POF-San José (final RDW of 0.69) and *Miconia glaberrima* of BLF-Tzontehuitz (final RDW of 0.44) with slow and fast decomposition respectively. Of the two exotic species, *Acalypha communis* (final RDW of 0.19) displayed much more rapid decomposition than the native *M. glaberrima*, whereas *Stipa eriostachya* showed an expected slow decomposition rate (final RDW of 0.50). In general, the leaves of most individual species collected from different sites shared similar decomposition rates, however exceptions with high divergence between collection sites were *Q. crispipilis*, *Persea americana*, *Pinus tecunumanii*, *P. montezumae* and *Q. segoviensis*.

In general, the *Quercus* and *Pinus* species had lower decomposition rates although those of *Prunus rhamnoides*, *P. americana*, *Clethra macrophylla* and *Weinmania pinnata* were comparably low (Figs. 4.7, 4.8, and 4.9). On the other hand, *Quetzalia contracta*, *Viburnum jucundum*, *Ternstroemia lineata*, *Styrax magnus,* and especially *M. glaberrima* showed the highest decomposition rates amongst native species. The genus *Quercus* showed a higher inter-specific variation in decomposition than that showed by *Pinus* species (Figures 4.7 and 4.8) and in several cases, RDW at the end of the experiment was considerably lower in *Quercus* than in *Pinus* (Appendix 4.1). This was probably due to the high species number and the concomitant variety in leaf size, structure and morphology in *Quercus*; nevertheless, it is evident that differences amongst cases within the two genera were not well defined.

Table 4.5 Key statistics for the mixed models selected for each of the two experiments. DF = degree freedom, denDF = degree of freedom of experimental error.

Experiment	Source of variation	DF	denDF	F value	P value
Greenhouse	Cases (combination of species, forest type and site)	34	209	59.02	<0.0001
	Sample time	5	209	1280.12	<0.0001
	Case * Time	170	209	2.36	<0.0001
In forest	Leaf-litter type	5	1484	1437.24	<0.0001
	Forest type	3	28	2.61	0.0713
	Time	8	1484	909.76	<0.0001
	Leaf-litter type * Forest type	15	1484	4.11	<0.0001
	Leaf-litter type * Time	40	1484	7.28	<0.0001
	Forest type * Time	24	1484	2.16	0.0009
	Leaf-litter type * Forest type * Time	120	1484	0.91	0.7561

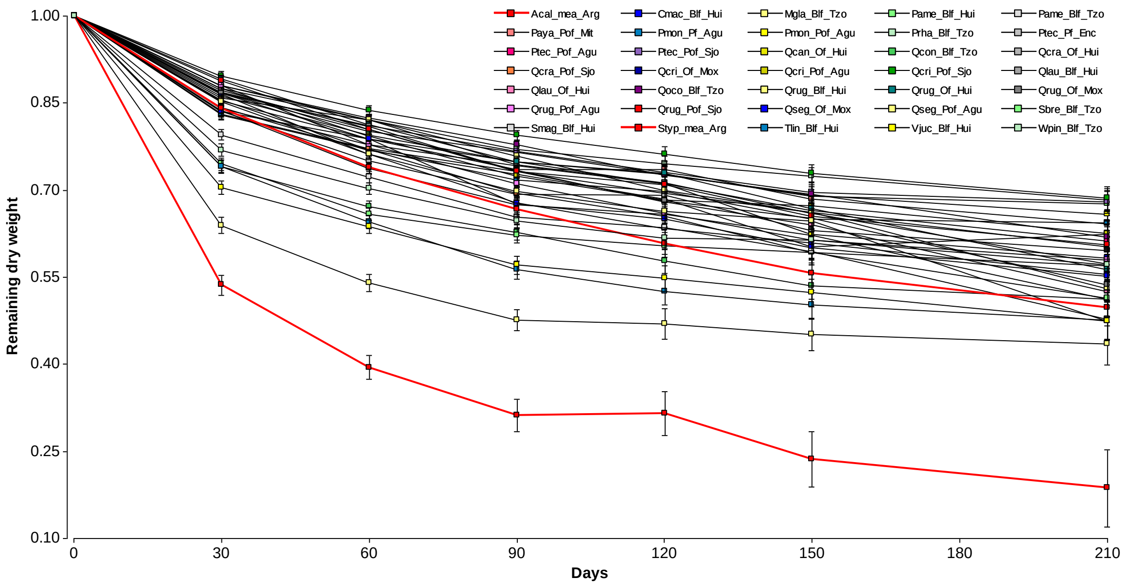

Figure 4.6 Adjusted means and standard errors of the remaining dry weight of the decomposed leaves of the 33 native species-forest site combinations and the two exotic species for the 6 sample times in the greenhouse experiment. Lines in red correspond to the two exotic reference species *Acalypha communis* and *Stipa eriostachya*. Details of group of species are in Figures 4.7, 4.8 and 4.9. Species' acronyms are given in Table 4.2.

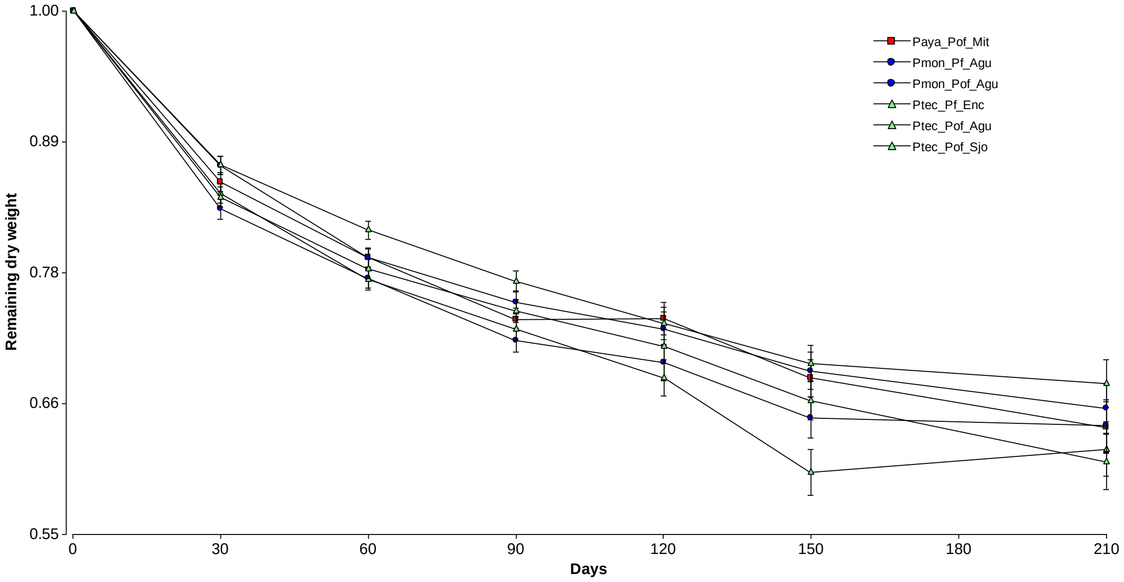

Figure 4.7 Adjusted means and standard errors of the remaining dry weight of the decomposed leaves collected from different forest sites of the three *Pinus* species for the 6 sample times in the greenhouse experiment. Species' acronyms are given in Table 4.2.

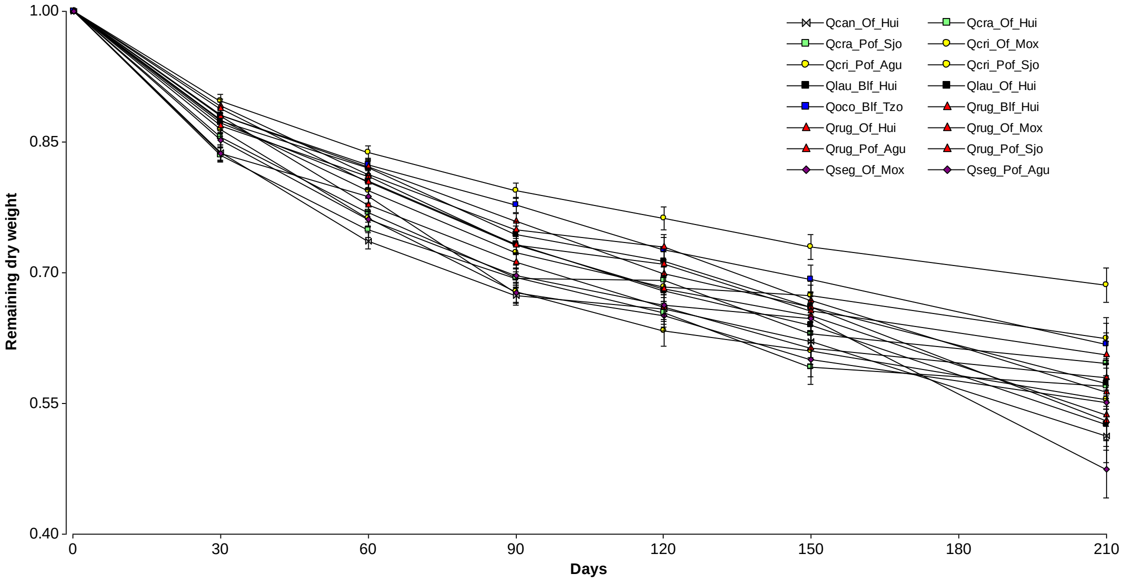

Figure 4.8 Adjusted means and standard errors of the remaining dry weight of the decomposed leaves collected from different forest sites of the seven *Quercus* species for the 6 sample times in the greenhouse experiment. Species' acronyms are given in Table 4.2.

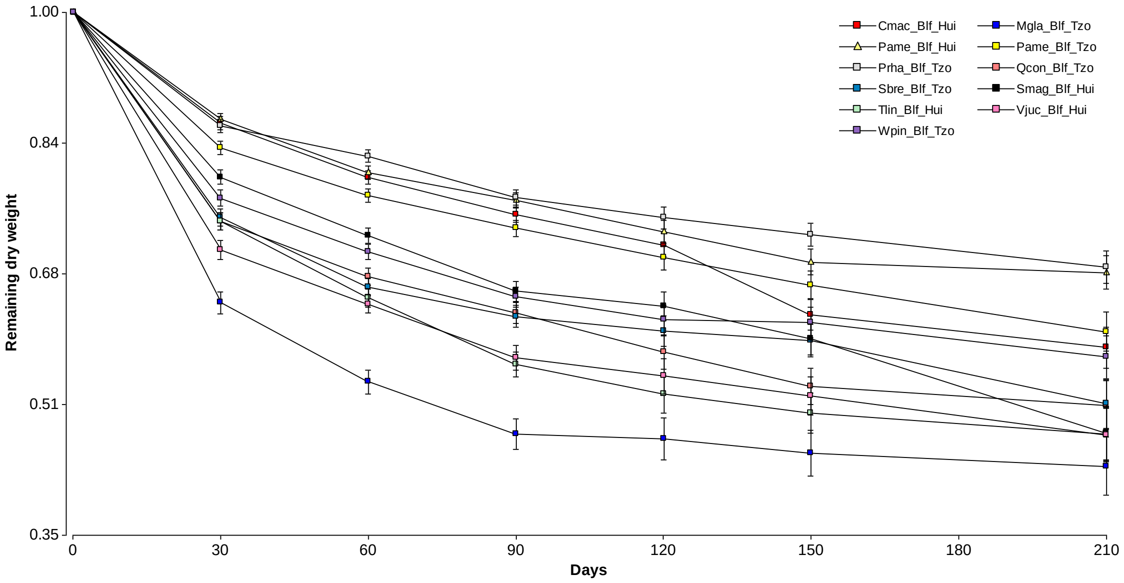

Figure 4.9 Adjusted means and standard errors of the remaining dry weight of the decomposed leaves collected from different forest sites of the remaining 11 species for the 6 sample times in the greenhouse experiment. Species' acronyms are given in Table 4.2.

4.4.2.1. Relationships between leaf decomposition rates and foliar traits

Relationships between leaf decomposition rates and fresh leaf traits and carbon fraction concentrations (collectively termed "traits") were assessed separately for each sample time (Table 4.6). Significant relationships between at least two traits and decomposition were found at all sample times except 90 days. All traits had a significant correlation with decomposition at at least one sample date except LNC and LTS. LPC was the only trait to be significantly correlated (positively) with decomposition rate to the end of the experiment (210 days) although hemicellulose was marginally negative correlated. However, the fresh leaf LDMC and lignin (and to a lesser extent, cellulose) were notable for being significantly negatively correlated with decomposition rate at the majority of earlier sample times (30-150 days). It is particularly notable that both were negatively correlated with decomposition rate at 30 and 60 days, not significantly at 90 days, and positively at 120 and 150 days. SLA was only marginally positively related to 30 days.

These fresh leaf trait-leaf decomposition rate relationships, together with the species associations, are also apparent in the tri-plot formed by the PLS regression (Fig. 4.10). The two main axes explain 71% of the total variation although the first axis explains much more than the second (51% and 20% respectively). High rates of decomposition at 30 and 60 days are associated positively with axis 1, together with SLA, while decomposition rates at 120 and 150 days and LDMC, lignin and cellulose are negatively associated. On axis 2, the final decomposition rate at 210 days (and to a lesser extent the rate at 150 days) together with LPC (and to a lesser extent SLA) are positively associated. It is possible to consider axis 1 as a broad gradient of foliar toughness that contains species with a broad spectrum of decomposition rates, which are mainly defined in terms of SLA, LDMC, and lignin and cellulose.

Along these two axes it is possible to identify groups of species and replicates with similar functional traits, carbon fractions, and decomposition characteristics (compare with biplot in Fig. 4.5). In the extreme positive part of axis 1 are scattered species with high SLA, frequently with soft leaves and with a markedly rapid decomposition in the first two periods of the experiment. These are mainly species of the lower strata of broad-leaved forests, such as *M. glaberrima*, *V. jucundum*, *W. pinnata*, *S. breedlovei*, *Q. contracta* and *T. lineata*. At the middle and the negative side of this same first axis are distributed a variety of species with intermediate and high LDMC and high lignin and cellulose concentrations, mainly related to slow decomposition. In this group are located all the *Quercus* species as well as *P. rhamnoides*, *S. magnus*, *C. macrophylla*, and the two cases of *P. americana*. However, a second group of hard-leaved species with low decomposition, mainly associated to the negative side of axis two, is formed by *Pinus* species and their replicates. They are characterised with intermediate amounts of carbon fractions, low LDMC and LPC but also with high LTS, according to the characteristics defined in Chapter 2.

Table 4.6 Pearson correlations (r−value and (P)) between leaf decomposition rates (at each sample time) and leaf functional traits and carbon fraction concentrations. Significant correlations (< 0.05) marked in bold, marginal significances marked in red. LDMC = Leaf dry matter content, SLA = Specific leaf area, LTS = Leaf tensile strength, LPC = Leaf phosphorous content, LNC = Leaf nitrogen content

Sample time (days)	Traits					Carbon fractions		
	LDMC	SLA	LTS	LPC	LNC	Lignin	Cellulose	Hemi cellulose
30	**−0.63 (9.6E−05)**	0.32 (0.07)	−0.09 (0.64)	0.04 (0.83)	0.19 (0.29)	**−0.76 (2.3E−07)**	−0.33 (0.06)	0.18 (0.32)
60	**−0.52 (1.7E−03)**	0.27 (0.13)	−0.13 (0.46)	−0.10 (0.59)	0.16 (0.36)	**−0.66 (2.8E−05)**	**−0.37 (0.04)**	0.28 (0.12)
90	0.24 (0.18)	−0.01 (0.94)	−0.18 (0.31)	−0.20 (0.26)	−0.09 (0.61)	0.20 (0.25)	−0.07 (0.71)	0.17 (0.34)
120	**0.55 (9.8E−04)**	−0.10 (0.60)	−0.16 (0.38)	−0.06 (0.74)	−0.18 (0.32)	**0.53 (1.4E−03)**	0.11 (0.54)	−0.02 (0.91)
150	**0.64 (5.2E−05)**	−0.04 (0.82)	−0.19 (0.29)	0.13 (0.48)	−0.18 (0.31)	**0.56 (7.1E−04)**	0.13 (0.47)	−0.16 (0.37)
210	**0.34 (0.05)**	0.22 (0.22)	−0.23 (0.20)	**0.49 (3.8E-03)**	−0.04 (0.81)	0.09 (0.64)	−0.02 (0.91)	−0.32 (0.07)

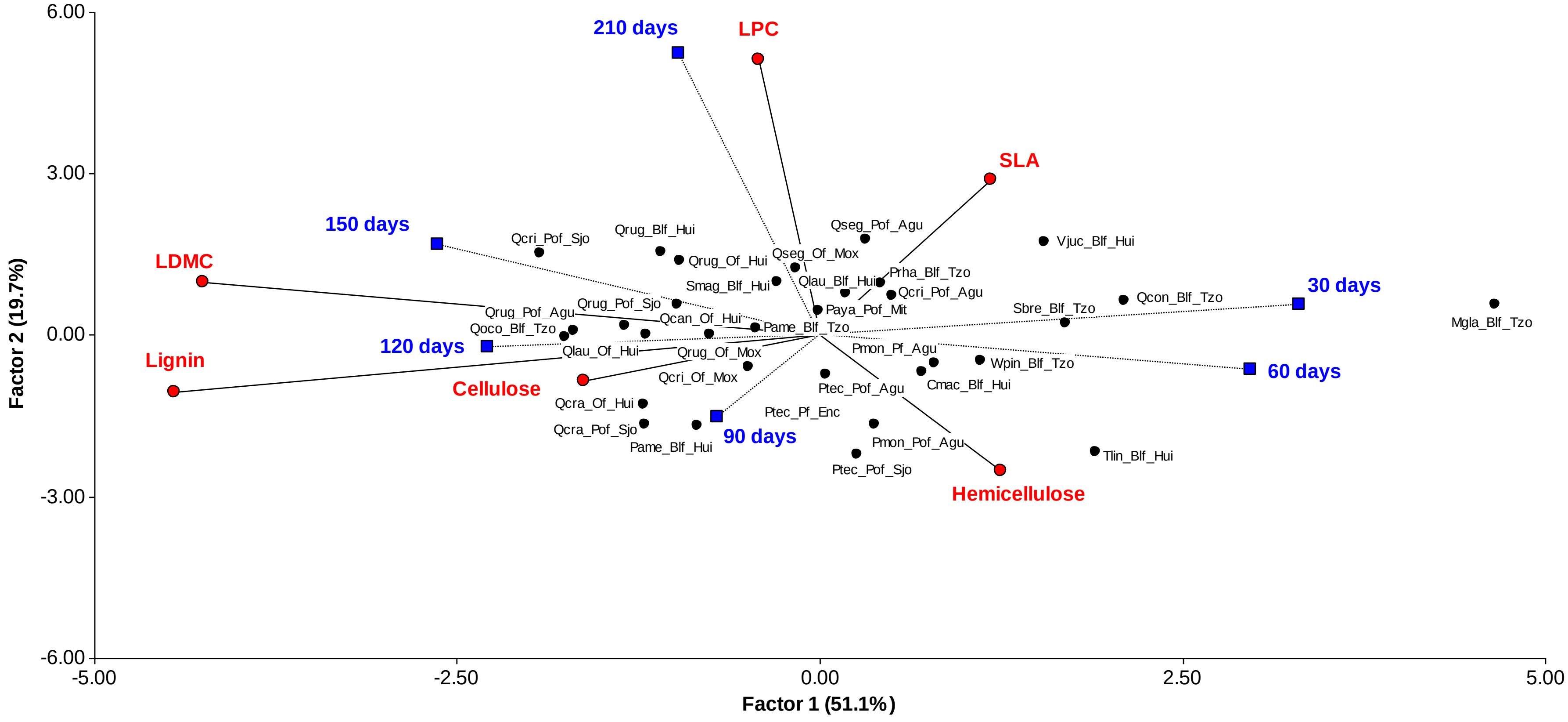

Figure 4.10 Triplot formed by the Partial least squares regression with the 33 native species-forest site combinations, the decomposition rates at the 6 sample times and the significant traits of the Pearson's correlation analyses (Table 4.6). LDMC = leaf dry matter content, SLA = specific leaf area, LTS = leaf tensile strength, LPC = leaf phosphorous content. Acronyms are given in Table 4.2.

4.4.3. Leaf-litter decomposition in the field

The selected mixed model showed that many factors contributed to variation in leaf litter decomposition rates in the experiment conducted in the four forest types. While leaf-litter type, sample time and all of the two way interactions had highly significant effects, the forest type in which the decomposition took place was marginally non-significant (Table 4.5. See Appendix 4.3). All four native leaf-litter mixtures had low decomposition rates (losing less than 45% of their initial dry weight after 360 days of decomposition), though they did differ significantly (Fisher's LSD test) (Figures 4.11, 4.12. Appendix 4.4). The pine (0.77 ± 3.7E−03 RDW) and oak (0.72 ± 4.4E−03) forest mixtures had the lowest and highest decomposition rates respectively and the broad-leaved (0.74 ± 4.0E−03) and pine-oak (0.73 ± 3.7E−03) forest mixtures were intermediate and did not differ significantly from each other. The single exotic reference species *A. communis* had the highest decomposition rate (RDW 0.30 ± 0.01) whereas *S. eriostachya* (RDW 0.72 ± 4.5E−03) had a much slower decomposition rate that was not statistically different from the oak forest mixture. These differences amongst the leaf-litter types, particularly between the pine and oak mixtures, prevailed at each sample time throughout the 360 day decomposition period (Fig. 4.11).

There was considerable variation amongst the litter types in the pattern of variation of their decomposition rates amongst the four forest types (Fig 4.12. Appendix 4.4). This shows good evidence of "home-field advantage" as reflected in the highly significant ($P < 0.0001$) litter-type forest-type interaction term in the mixed model. The home-field advantage seems evident: the oak forest litter decomposed fastest in the oak forest and second fastest in the pine-oak forest and the pine forest litter decomposed fastest in the pine forest and second fastest in the pine-oak forest. The pine-oak forest litter showed the least variation in its decomposition rate amongst the forest types but was fastest (almost equally) in the oak forest and the pine-oak forest. The one exception was the broadleaved forest litter which decomposed much the fastest in the oak forest, though it was second fastest in the broadleaved forest.

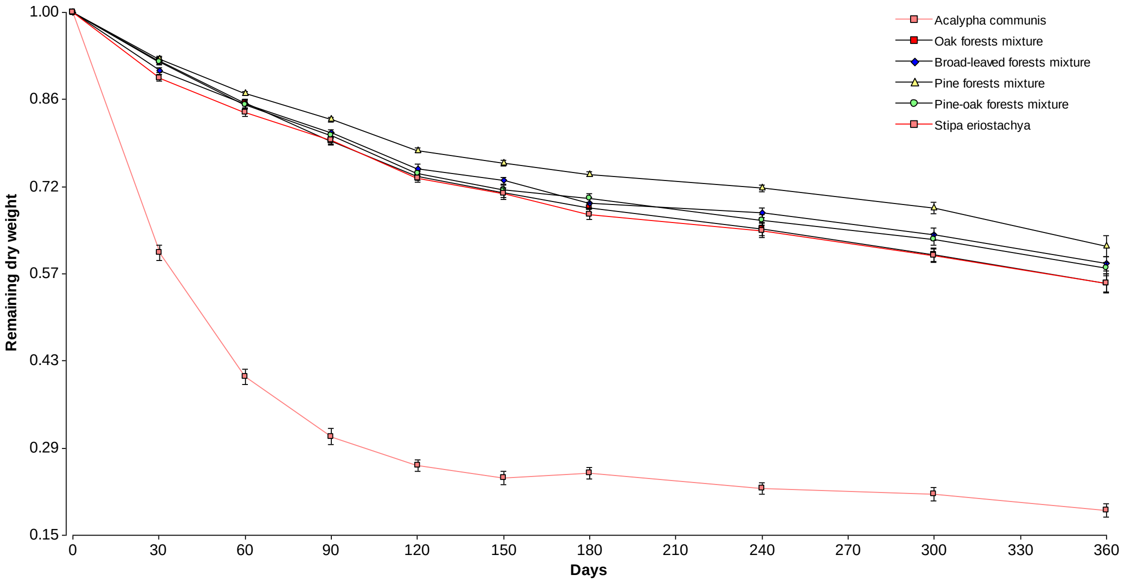

Figure 4.11 Adjusted means and standard errors of the decomposition of the leaf-litter mixtures collected from the four forest types and the two leaf-litter of the exotic reference species *Acalypha communis* and *Stipa eriostachya* (shown in red) over 360 days.

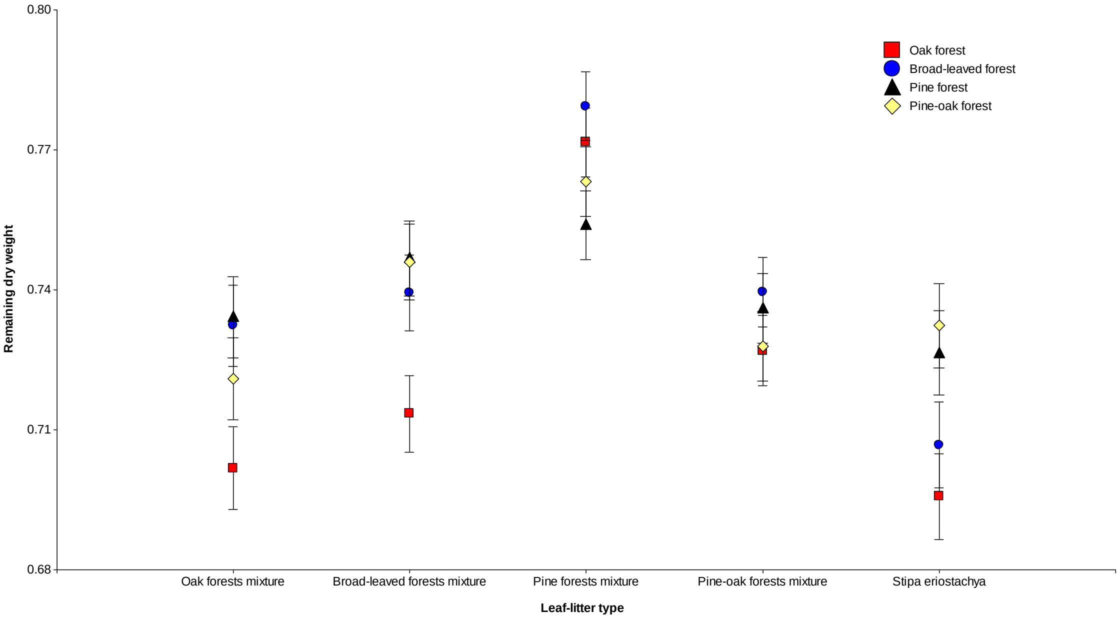

Figure 4.12 Adjusted means and standard errors of the decomposition (RDW as proportion of 1.0 after 360 days) *in situ* in each of the four forest types, of the lea-litter mixtures collected from the four forest types, including the leaf-litter of the exotic reference species *Stipa eriostachya*.

4.5. DISCUSSION

4.5.1. The plant economics spectrum of litter decomposability – general considerations

Our study found that the range of species used in the experiments have a wide variety of traits, which in turn affect the decomposition rates of the leaves of the species. This link between inter-specific variations in leaf traits with variations in leaf-litter decomposition rate has been found in many previous studies (e.g. Cornelissen 1996; Cornelissen *et al.* 1999; Pérez-Harguindeguy *et al.* 2000; Vaieretti *et al.* 2005; Cortez *et al.* 2007; Cornwell *et al.* 2008; Schindler & Gessner 2009).

Physico-chemical features of leaf-litter depend, to some extent, on features of the living plants and their leaves (Cortez *et al.* 2007), well associated with different 'economic' strategies for carbon gain and growth (acquisitive and conservative species), as outlined by Wright *et al.* (2004) and Cornwell *et al.* (2008). These features may be, for example, life-form and deciduous versus evergreen habit, leaf life span, foliar nutrient content, components of leaf structure and plant defences. This functional differentiation of species has large and consistent afterlife effects on the decomposition rate of senesced leaves (Cornwell *et al.* 2008) leading to some species having recalcitrant traits and slow decomposition (Schindler & Gessner 2009) and others having labile traits and fast decomposition. For example, the chemical and physical defences of tough leaves (related to defence against herbivores) may persist in their litter causing slower decomposition (Grime *et al.* 1996; Cornelissen *et al.* 1999; Pérez-Harguindeguy *et al.* 2000); in contrast, tender and soft leaves would decompose more quickly (Pérez-Harguindeguy *et al.* 2000). As was pointed out by Cornelissen *et al.* (1999), more generally, fast-growing, poorly-defended species produce litter with a high decomposability whereas slower-growing, better defended species produce poor-quality litter with low decomposition rates. These observations and experimental results have led to the proposal of a plant economics spectrum of litter decomposability (Freschet *et al.* 2012).

Several studies have found that carbon-rich structural compounds such as lignin (e.g. Schindler & Gessner 2009) or traits like LTS (e.g. Pérez-Harguindeguy *et al.* 2000) and LDMC (e.g. Cortez *et al.* 2007; Cornwell *et al.* 2008; Fortunel *et al.* 2009; Bakker, Carreño-Rocabado & Poorter 2011) are good indicators of leaf toughness (resistance to herbivores, pathogens, physical damage and soil decomposers) and, as a consequence, of low decomposition rates since decomposers need a range of specific enzymes to decompose this type of substrate (Wieder, Cleveland & Townsend 2009). On the other hand, high SLA, a trait related to soft leaves, is one of the best predictors of rapid decomposition rate (Cornelissen *et al.* 1999; Vaieretti *et al.* 2005; Santiago 2007) possibly because decomposers can consume soft leaf-litter more rapidly and easily, processing less leaf material per unit area or volume (Bakker *et al.* 2011). Within our study, we can distinguish two types of species with tough leaves and slow decomposition rates: *Quercus* spp. (high LTS, LDMC and lignin) and *Pinus* spp. (low LDMC and SLA; high LTS). The species studied also include middle-storey trees which in general display soft leaves (high SLA and LA; low LTS, LDMC and lignin) and rapid decomposition, with some exceptions.

4.5.2. Decomposition dynamics and traits in our experiments

The results of the present study show a clear differentiation amongst leaf traits in their correlation with decomposition rates at different stages of the process. However, the pattern shows some differences from that reported in previous studies. No traits were significantly positively associated with the early period of decomposition, the recalcitrant compound lignin was positively correlated with the middle period of decomposition, whereas the concentration of the nutrient phosphorus was only significantly positively correlated with the last phase of decomposition, and foliar nitrogen concentration not at all. In contrast Vaieretti et al. (2005) reported that in the early period the decomposition of labile fractions prevails, being controlled by nutrient concentration, and in the later period, the decomposition of lignified carbohydrates is the main process, and is controlled by the concentration of non-labile (recalcitrant) components in litter. The relationship of the concentration of slowly degradable compounds such as lignin with low decomposition in the second phase has also been documented by Aerts & de Caluwe (1997); Loranger *et al.* (2002), Meentemeyer (1978), amongst others.

4.5.3. Decomposition and forest condition

The forest types in which the field experiment was conducted varied widely in the community-weighted mean trait values of their dominant species (Chapter 2) suggesting that ecological process rates, such as decomposition, would also vary widely (see e.g. Finegan *et al.* (2015), for relationships between CWM traits and biomass production in tropical forests). Our field experiment provided a more detailed breakdown of this phenomenon. It showed that the difference in litter properties between forest types was a major factor in the variation in decomposition rates. It also showed a very strong interaction between this litter origin factor and the forest type in which decomposition takes place, which is strongly associated with "home-field advantage" (Gholz *et al.* 2000; Vivanco & Austin 2008; Ayres *et al.* 2009; van der Putten *et al.* 2013). The strength of this interaction term is a major reason why the overall main effect of forest type in which decomposition took place was not significant in this factorial experiment. This reinforces the hypothesis that after-life characteristics of species (Freschet, Aerts & Cornelissen 2012) rather than forest stand characteristics, are the most important drivers of decomposition processes, but that the interaction between the two is also very important. The interaction may be linked to the range of geographical positions of the experimental sites, with their ranges of altitude, mean annual temperature and mean annual precipitation. However, previous studies have also shown that home-field advantage is linked to the differentiation in communities of microbial decomposer species amongst sites, associated with their variation in leaf litter substrates determined by tree species composition (Gholz *et al.* 2000; Vivanco & Austin 2008; Ayres *et al.* 2009; van der Putten *et al.* 2013). Indeed, other studies have found that while climate exerts a strong influence on decomposition rates over broad gradients (e.g. Salinas *et al.* 2010), it does not have a strong direct influence at local levels (e.g. Pérez-Harguindeguy *et al.* 2000; Vaieretti *et al.* 2005; Cortez *et al.* 2007) where decomposition processes may nevertheless be strongly affected by the chemical and physical quality of the substrate.

The results of the greenhouse experiment, lead to the prediction that forests dominated by *Pinus* and *Quercus* species will have the lowest decomposition rates in the study area, whereas broadleaved forests with a higher ecological importance of species with high SLA will show higher rates (compare with CWM trait values in Chapter 2). This was the trend that was observed in the experiment conducted *in situ* in the forests.

Such decomposition differences between vegetation stands, in terms of species change and the concomitant change in functional traits, have been found by Gurvich, Easdale & Pérez-Harguindeguy (2003); Cortez *et al.* (2007) and Bakker *et al.* (2011) when comparing different land uses and successional stages. In this manner, we can infer that forest change either by natural or anthropogenic causes will have consequences not only for the decomposition process and nutrient cycling (Anderson 1991; Vitousek 1997; Schindler & Gessner 2009; Saura-Mas *et al.* 2012) but also for other components of ecosystem functioning (Chapin III *et al.* 2000; Díaz & Cabido 2001).

4.5.4. Conclusions and final reflections

The present study represents one of the first exhaustive and controlled experimental assessments in tropical montane forests to link leaf-litter decomposition of tree species with leaf functional traits and forest condition. It finds strong evidence that the foliar characteristics of species mostly drive the decomposition process both in controlled conditions and in the field, producing a spectrum from rapid to slow decomposition amongst the species.

Species associations in forests represent a range of functional composition in terms of community weighted mean trait values, with major implications for ecosystem functioning. It follows that any change in the composition of a plant assemblage, either by natural or anthropogenic causes, will impact on the decomposition processes. This scenario is particularly worrying in mountain forests such as those in the Central Highlands of Chiapas where human activities have led to highly degraded forests, with low functional diversity and functional redundancy, as in pine-dominated forests. This situation is aggravated because of the particular vulnerability of mountain ecosystems to climate change (Theurillat & Guisan 2001; Bugmann *et al.* 2007) in which changes in temperature, humidity, and drought will decisively affect decomposition processes as has been found by several authors (e.g. Cornwell *et al.* 2008; Schindler & Gessner 2009; Salinas *et al.* 2010; Saura-Mas *et al.* 2012).

This situation indicates the importance not only of investigating the different factors affecting the processes, functioning and services of forest ecosystems but also of conserving their structure and functional composition.

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4.7. APPENDICES

Appendix 4.1 Adjusted means of the remaining dry weight (± SE) produced by the mixed model for the decomposition data of the experiment in greenhouse conditions. BLF = broad-leaved forest, POF = pine-oak forest, OF = oak forest, PF = pine forest.

#	Species	Forest - Site	Mean ± SE					
			30 days	60 days	90 days	120 days	180 days	210 days
1	*Clethra macrophylla*	BLF - Huitepec	0.86 ± 0.01	0.79 ± 0.01	0.75 ± 0.01	0.71 ± 0.01	0.62 ± 0.02	0.58 ± 0.03
2	*Miconia glaberrima*	BLF - Tzontehuitz	0.64 ± 0.01	0.54 ± 0.01	0.48 ± 0.02	0.47 ± 0.03	0.45 ± 0.03	0.44 ± 0.04
3	*Persea americana*	BLF - Huitepec	0.87 ± 0.01	0.80 ± 0.01	0.77 ± 0.01	0.73 ± 0.01	0.69 ± 0.02	0.68 ± 0.02
4	*Persea americana*	BLF - Tzontehuitz	0.83 ± 0.01	0.77 ± 0.01	0.73 ± 0.01	0.69 ± 0.02	0.66 ± 0.02	0.60 ± 0.02
5	*Pinus ayacahuite*	POF - Mitziton	0.85 ± 0.01	0.79 ± 0.01	0.73 ± 0.01	0.74 ± 0.01	0.68 ± 0.02	0.64 ± 0.02
6	*Pinus montezumae*	PF - Aguaje	0.83 ± 0.01	0.77 ± 0.01	0.72 ± 0.01	0.70 ± 0.02	0.65 ± 0.02	0.64 ± 0.02
7	*Pinus montezumae*	POF -Aguaje	0.87 ± 0.01	0.79 ± 0.01	0.75 ± 0.01	0.73 ± 0.01	0.69 ± 0.02	0.66 ± 0.02
8	*Pinus tecunumanii*	PF - Encuentro	0.84 ± 0.01	0.77 ± 0.01	0.73 ± 0.01	0.68 ± 0.02	0.60 ± 0.02	0.62 ± 0.02
9	*Pinus tecunumanii*	POF - Aguaje	0.84 ± 0.01	0.78 ± 0.01	0.74 ± 0.01	0.71 ± 0.01	0.67 ± 0.02	0.61 ± 0.02
10	*Pinus tecunumanii*	POF -San José	0.87 ± 0.01	0.81 ± 0.01	0.77 ± 0.01	0.73 ± 0.01	0.70 ± 0.02	0.68 ± 0.02
11	*Prunus rhamnoides*	BLF - Tzontehuitz	0.86 ± 0.01	0.82 ± 0.01	0.77 ± 0.01	0.74 ± 0.01	0.72 ± 0.01	0.68 ± 0.02
12	*Quercus candicans*	OF- Huitepec	0.84 ± 0.01	0.74 ± 0.01	0.67 ± 0.01	0.66 ± 0.02	0.62 ± 0.02	0.51 ± 0.03
13	*Quercus crassifolia*	OF- Huitepec	0.84 ± 0.01	0.75 ± 0.01	0.69 ± 0.01	0.69 ± 0.02	0.63 ± 0.02	0.60 ± 0.03
14	*Quercus crassifolia*	POF - San José	0.86 ± 0.01	0.77 ± 0.01	0.69 ± 0.01	0.65 ± 0.02	0.59 ± 0.02	0.57 ± 0.03
15	*Quercus crispipilis*	OF - Moxviquil	0.86 ± 0.01	0.76 ± 0.01	0.68 ± 0.01	0.63 ± 0.02	0.61 ± 0.02	0.55 ± 0.03
16	*Quercus crispipilis*	POF - Aguaje	0.87 ± 0.01	0.79 ± 0.01	0.72 ± 0.01	0.68 ± 0.02	0.67 ± 0.02	0.62 ± 0.02
17	*Quercus crispipilis*	POF – San José	0.90 ± 0.01	0.84 ± 0.01	0.79 ± 0.01	0.76 ± 0.01	0.73 ± 0.01	0.69 ± 0.02
18	*Quercus laurina*	BLF - Huitepec	0.87 ± 0.01	0.82 ± 0.01	0.74 ± 0.01	0.71 ± 0.01	0.66 ± 0.02	0.57 ± 0.03
19	*Quercus laurina*	OF - Huitepec	0.87 ± 0.01	0.80 ± 0.01	0.73 ± 0.01	0.68 ± 0.02	0.64 ± 0.02	0.53 ± 0.03
20	*Quercus ocoteifolia*	BLF - Tzontehuitz	0.88 ± 0.01	0.82 ± 0.01	0.78 ± 0.01	0.73 ± 0.01	0.69 ± 0.02	0.62 ± 0.02
21	*Quercus rugosa*	BLF - Huitepec	0.88 ± 0.01	0.82 ± 0.01	0.76 ± 0.01	0.70 ± 0.02	0.66 ± 0.02	0.53 ± 0.03
22	*Quercus rugosa*	OF- Huitepec	0.89 ± 0.01	0.81 ± 0.01	0.75 ± 0.01	0.73 ± 0.01	0.67 ± 0.02	0.56 ± 0.03
23	*Quercus rugosa*	OF - Moxviquqil	0.87 ± 0.01	0.81 ± 0.01	0.73 ± 0.01	0.68 ± 0.02	0.65 ± 0.02	0.54 ± 0.03
24	*Quercus rugosa*	POF - Aguaje	0.88 ± 0.01	0.78 ± 0.01	0.71 ± 0.01	0.66 ± 0.02	0.61 ± 0.02	0.58 ± 0.03
25	*Quercus rugosa*	POF - San José	0.89 ± 0.01	0.80 ± 0.01	0.73 ± 0.01	0.71 ± 0.01	0.66 ± 0.02	0.61 ± 0.02
26	*Quercus segoviensis*	OF - Moxviquil	0.84 ± 0.01	0.79 ± 0.01	0.68 ± 0.01	0.65 ± 0.02	0.60 ± 0.02	0.55 ± 0.03
27	*Quercus segoviensis*	POF - Aguaje	0.85 ± 0.01	0.76 ± 0.01	0.70 ± 0.01	0.66 ± 0.02	0.65 ± 0.02	0.47 ± 0.03
28	*Quetzalia contracta*	BLF - Tzontehuitz	0.74 ± 0.01	0.67 ± 0.01	0.63 ± 0.01	0.58 ± 0.02	0.54 ± 0.02	0.51 ± 0.03
29	*Styrax magnus*	BLF - Huitepec	0.80 ± 0.01	0.72 ± 0.01	0.65 ± 0.01	0.63 ± 0.02	0.59 ± 0.02	0.48 ± 0.03
30	*Symplocos breedlovei*	BLF - Tzontehuitz	0.75 ± 0.01	0.66 ± 0.01	0.62 ± 0.01	0.60 ± 0.02	0.59 ± 0.02	0.51 ± 0.03
31	*Ternstroemia lineata*	BLF - Huitepec	0.74 ± 0.01	0.65 ± 0.01	0.56 ± 0.02	0.52 ± 0.02	0.50 ± 0.02	0.48 ± 0.03
32	*Viburnum jucumdum*	BLF - Huitepec	0.70 ± 0.01	0.64 ± 0.01	0.57 ± 0.01	0.55 ± 0.02	0.52 ± 0.02	0.47 ± 0.03
33	*Weinmania pinnata*	BLF - Tzontehuitz	0.77 ± 0.01	0.70 ± 0.01	0.65 ± 0.01	0.62 ± 0.02	0.61 ± 0.02	0.57 ± 0.03
34	*Acalypha communis*	Mea - Argentina	0.54 ± 0.02	0.39 ± 0.02	0.31 ± 0.03	0.32 ± 0.04	0.24 ± 0.05	0.19 ± 0.07
35	*Stipa eriostachya*	Mea - Argentina	0.84 ± 0.01	0.74 ± 0.01	0.67 ± 0.01	0.61 ± 0.02	0.56 ± 0.02	0.50 ± 0.03

Appendix 4.2 Adjusted means of the remaining dry weight (± SE) of the 35 species-forest-site combinations tested in the greenhouse experiment including Fisher's LSD tests, using a critical α = 0.05.

Species	Acronym	Means	SE	Relationship																					
Quercus crispipilis	Qcri_Pof_Sjo	0.785	0.006	A																					
Prunus rhamnoides	Prha_Blf_Tzo	0.767	0.006		B																				
Pinus tecunumanii	Ptec_Pof_Sjo	0.759	0.006		B	C																			
Persea americana	Pame_Blf_Hui	0.754	0.006		B	C	D																		
Quercus ocoteaefolia	Qoco_Blf_Tzo	0.753	0.007		B	C	D																		
Pinus montezumae	Pmon_Pof_Agu	0.747	0.007			C	D	E																	
Pinus ayacahuite	Paya_Pof_Mit	0.74	0.007				D	E	F																
Quercus rugosa	Qrug_Of_Hui	0.736	0.007				D	E	F	G															
Quercus rugosa	Qrug_Pof_Sjo	0.733	0.007					E	F	G	H														
Quercus laurina	Qlau_Blf_Hui	0.731	0.007					E	F	G	H														
Pinus tecunumanii	Ptec_Pof_Agu	0.729	0.007					E	F	G	H	I													
Quercus rugosa	Qrug_Blf_Hui	0.725	0.008						F	G	H	I	J												
Quercus crispipilis	Qcri_Pof_Agu	0.725	0.007						F	G	H	I	J												
Clethra macrophyla	Cmac_Blf_Hui	0.721	0.007						F	G	H	I	J	K											
Pinus montezumae	Pmon_Pf_Agu	0.718	0.007							G	H	I	J	K	L										
Persea americana	Pame_Blf_Tzo	0.716	0.007								H	I	J	K	L										
Quercus rugosa	Qrug_Of_Mox	0.713	0.008								H	I	J	K	L										
Quercus laurina	Qlau_Of_Hui	0.709	0.008									I	J	K	L	M									
Pinus tecunumanii	Ptec_Pf_Enc	0.708	0.007										J	K	L	M									
Quercus rugosa	Qrug_Pof_Agu	0.704	0.008											K	L	M	N								
Quercus crassifolia	Qcra_Of_Hui	0.699	0.007												L	M	N								
Quercus crassifolia	Qcra_Pof_Sjo	0.689	0.008													M	N	O							
Quercus segoviensis	Qseg_Of_Mox	0.684	0.008														N	O							
Quercus segoviensis	Qseg_Pof_Agu	0.684	0.008														N	O							
Quercus crispipilis	Qcri_Of_Mox	0.682	0.008														N	O							
Quercus Candicans	Qcan_Of_Hui	0.673	0.008															O	P						
Weinmania pinnata	Wpin_Blf_Tzo	0.654	0.008																P	Q					
Stipa eriostachya	Styp_mea_Arg	0.651	0.009																P	Q					
Styrax magnus	Smag_Blf_Hui	0.646	0.009																	Q	R				
Symplocos breedlovei	Sbre_Blf_Tzo	0.622	0.009																		R	S			
Quetzalia contracta	Qcon_Blf_Tzo	0.61	0.009																			S			
Ternstroemia lineata	Tlin_Blf_Hui	0.576	0.01																				T		
Viburnum jucundum	Vjuc_Blf_Hui	0.575	0.01																				T		
Miconia glaberrima	Mgla_Blf_Tzo	0.502	0.012																					U	
Acalypha communis	Acal_mea_Arg	0.33	0.019																						W

Appendix 4.3 Adjusted means (± SE) of the remaining dry weight produced by the mixed model for the decomposition data of the experiment in *in situ* conditions. BLF = broad-leaved forest, POF = pine-oak forest, OF = oak forest, PF = pine forest.

#	Litter type	Forest	Mean ± SE								
			30 days	60 days	90 days	120 days	150 days	180 days	240 days	300 days	360 days
1	OF mixture	OF	0.91 ± 0.01	0.83 ± 0.01	0.78 ± 0.01	0.72 ± 0.01	0.68 ± 0.02	0.66 ± 0.02	0.63 ± 0.02	0.57 ± 0.02	0.54 ± 0.03
2		BLF	0.93 ± 0.01	0.86 ± 0.01	0.82 ± 0.01	0.76 ± 0.01	0.72 ± 0.02	0.70 ± 0.02	0.64 ± 0.02	0.62 ± 0.02	0.55 ± 0.03
3		PF	0.93 ± 0.01	0.86 ± 0.01	0.78 ± 0.01	0.72 ± 0.01	0.72 ± 0.02	0.69 ± 0.02	0.67 ± 0.02	0.63 ± 0.02	0.60 ± 0.03
4		POF	0.92 ± 0.01	0.86 ± 0.01	0.79 ± 0.01	0.74 ± 0.01	0.70 ± 0.02	0.69 ± 0.02	0.65 ± 0.02	0.60 ± 0.02	0.56 ± 0.03
5	BLF mixture	OF	0.90 ± 0.01	0.84 ± 0.01	0.80 ± 0.01	0.75 ± 0.02	0.71 ± 0.01	0.69 ± 0.02	0.63 ± 0.02	0.58 ± 0.02	0.52 ± 0.02
6		BLF	0.91 ± 0.01	0.88 ± 0.01	0.80 ± 0.01	0.75 ± 0.02	0.74 ± 0.01	0.70 ± 0.02	0.67 ± 0.02	0.61 ± 0.02	0.59 ± 0.02
7		PF	0.90 ± 0.01	0.85 ± 0.01	0.80 ± 0.01	0.75 ± 0.02	0.73 ± 0.01	0.68 ± 0.02	0.70 ± 0.02	0.67 ± 0.02	0.63 ± 0.02
8		POF	0.91 ± 0.01	0.84 ± 0.01	0.81 ± 0.01	0.73 ± 0.02	0.72 ± 0.01	0.69 ± 0.02	0.70 ± 0.02	0.69 ± 0.02	0.62 ± 0.02
9	PF mixture	OF	0.93 ± 0.01	0.87 ± 0.01	0.83 ± 0.01	0.78 ± 0.01	0.76 ± 0.01	0.75 ± 0.01	0.72 ± 0.01	0.69 ± 0.02	0.61 ± 0.03
10		BLF	0.94 ± 0.01	0.89 ± 0.01	0.84 ± 0.01	0.80 ± 0.01	0.78 ± 0.01	0.75 ± 0.01	0.72 ± 0.01	0.69 ± 0.02	0.60 ± 0.03
11		PF	0.92 ± 0.01	0.86 ± 0.01	0.81 ± 0.01	0.75 ± 0.01	0.73 ± 0.01	0.71 ± 0.01	0.70 ± 0.01	0.67 ± 0.02	0.66 ± 0.03
12		POF	0.91 ± 0.01	0.86 ± 0.01	0.82 ± 0.01	0.77 ± 0.01	0.75 ± 0.01	0.74 ± 0.01	0.72 ± 0.01	0.68 ± 0.02	0.61 ± 0.03
13	POF mixture	OF	0.92 ± 0.01	0.84 ± 0.01	0.80 ± 0.01	0.73 ± 0.01	0.69 ± 0.01	0.72 ± 0.02	0.66 ± 0.02	0.62 ± 0.02	0.56 ± 0.02
14		BLF	0.93 ± 0.01	0.87 ± 0.01	0.81 ± 0.01	0.75 ± 0.01	0.73 ± 0.01	0.70 ± 0.02	0.67 ± 0.02	0.61 ± 0.02	0.58 ± 0.02
15		PF	0.92 ± 0.01	0.85 ± 0.01	0.79 ± 0.01	0.73 ± 0.01	0.72 ± 0.01	0.69 ± 0.02	0.67 ± 0.02	0.64 ± 0.02	0.61 ± 0.02
16		POF	0.91 ± 0.01	0.84 ± 0.01	0.80 ± 0.01	0.74 ± 0.01	0.71 ± 0.01	0.68 ± 0.02	0.65 ± 0.02	0.64 ± 0.02	0.58 ± 0.02
17	*Acalypha communis*	OF	0.58 ± 0.03	0.37 ± 0.03	0.31 ± 0.03	0.26 ± 0.02	0.23 ± 0.02	0.24 ± 0.02	0.23 ± 0.02	0.21 ± 0.02	0.18 ± 0.02
18		BLF	0.62 ± 0.02	0.37 ± 0.03	0.28 ± 0.03	0.25 ± 0.02	0.22 ± 0.02	0.23 ± 0.02	0.16 ± 0.02	0.18 ± 0.02	0.13 ± 0.02
19		PF	0.64 ± 0.02	0.45 ± 0.02	0.31 ± 0.03	0.26 ± 0.02	0.26 ± 0.02	0.26 ± 0.02	0.24 ± 0.02	0.21 ± 0.02	0.21 ± 0.02
20		POF	0.60 ± 0.03	0.45 ± 0.02	0.34 ± 0.03	0.29 ± 0.02	0.26 ± 0.02	0.27 ± 0.02	0.27 ± 0.02	0.27 ± 0.02	0.23 ± 0.02
21	*Stipa eriostachya*	OF	0.89 ± 0.01	0.80 ± 0.01	0.77 ± 0.01	0.70 ± 0.01	0.67 ± 0.02	0.64 ± 0.02	0.62 ± 0.02	0.59 ± 0.02	0.57 ± 0.03
22		BLF	0.89 ± 0.01	0.83 ± 0.01	0.78 ± 0.01	0.73 ± 0.01	0.70 ± 0.02	0.66 ± 0.02	0.64 ± 0.02	0.59 ± 0.02	0.53 ± 0.03
23		PF	0.90 ± 0.01	0.86 ± 0.01	0.81 ± 0.01	0.75 ± 0.01	0.71 ± 0.02	0.66 ± 0.02	0.64 ± 0.02	0.61 ± 0.02	0.59 ± 0.03
24		POF	0.89 ± 0.01	0.86 ± 0.01	0.81 ± 0.01	0.74 ± 0.01	0.74 ± 0.02	0.69 ± 0.02	0.69 ± 0.02	0.62 ± 0.02	0.55 ± 0.03

Appendix 4.4 Adjusted means of the remaining dry weight (± SE) of the four native leaf-litter mixtures and the two leaf-litter of exotic reference species tested in the four forest types of the *in situ* experiment. Fisher's LSD tests using a critical α = 0.05. BLF = broad-leaved forest, POF = pine-oak forest, OF = oak forest, PF = pine forest.

Litter type	Forest	Means	SE	Relationship
PF mixture	BLF	0.779	0.007	A
PF mixture	OF	0.772	0.007	A B
PF mixture	POF	0.763	0.007	A B C
PF mixture	PF	0.754	0.007	B C D
BLF mixture	PF	0.747	0.008	C D E
BLF mixture	POF	0.746	0.008	D E F
POF mixture	BLF	0.739	0.007	D E F G
BLF mixture	BLF	0.739	0.008	D E F G
POF mixture	PF	0.736	0.007	D E F G
OF mixture	PF	0.734	0.009	D E F G H
Stipa eriostachya	POF	0.732	0.009	D E F G H
OF mixture	BLF	0.732	0.009	D E F G H
POF mixture	POF	0.728	0.007	E F G H I
POF mixture	OF	0.727	0.008	E F G H I
Stipa eriostachya	PF	0.726	0.009	F G H I J
OF mixture	POF	0.721	0.009	G H I J
BLF mixture	OF	0.713	0.008	H I J K
Stipa eriostachya	BLF	0.707	0.009	I J K
OF mixture	OF	0.702	0.009	J K
Stipa eriostachya	OF	0.696	0.009	K
Acalypha communis	POF	0.331	0.011	L
Acalypha communis	PF	0.317	0.011	L M
Acalypha communis	OF	0.290	0.011	M N
Acalypha communis	BLF	0.271	0.011	N

CHAPTER 5. OVERALL DISCUSSION

5.1. GENERAL AIM OF THE STUDY

Using a functional ecology approach combined with floristic analysis, the present thesis aimed to contribute to the understanding of factors that determine variation of forest characteristics and ecological processes in tropical mountains of the Central Highlands, state of Chiapas, Mexico. The investigation focused on two main issues: 1) the major factors driving the floristic and functional variation, emphasising the ecological debate about the influence of either environmental (niche) or dispersal factors; and 2) the effect of leaf and litter functional traits, as well as forest conditions, on leaf-litter decomposition.

All these aspects were investigated within the context of the four forest types of the region previously classified by González-Espinosa *et al.* (1997; pine PF, oak OF, pine-oak POF, and broad-leaved forests BLF), carrying out field work at seven sites (see maps in Chapters 2 and 3): Huitepec (BLF, OF), Moxviquil (OF), El Encuentro (PF), San José (POF), Military zone (BLF, POF, PF), El Aguaje (POF, PF) and Tzontehuitz (BLF, OF). The study area encompassed a narrow altitudinal range from 2100 to 2800 m a.s.l., located on a carboniferous limestone substrate with abrupt topography and cool and humid climate. Land uses are situated in the transition between traditional and modern use exerted by indigenous and mestizo-mixed race people; forest property regimes include communal, private and governmental.

Given the mountainous and heterogeneous environmental conditions of the region, its long history of human influence and the high floristic variation documented, it was expected to find i) prevalence of environmental variables and human disturbance over spatial factors in explaining the floristic and functional variation, 3) strong influence of functional traits of species on sapling abundances and distribution, 4) strong effects of functional traits on leaf-litter decomposition, and 5) strong effects of forest condition on leaf-litter decomposition.

5.2. KEY FINDINGS

5.2.1. Relationships between floristic variation and variables

High richness of species was found in the study area and the species distribution and abundance was far from uniform (Chapters 2 and 3). As showed by NMS ordination both in adult trees and saplings, species were associated in a variety of contrasting assemblages although the most distinct floristic associations correspond to the forest stands of the Tzontehuitz site in the north of the study area.

The Mantel correlograms indicate that the floristic turnover is high even over distances of less than two kilometres (for instance, from POF to PF in sites like Military zone and Aguaje or from OF to BLF forests in Huitepec or Tzontehuitz). This phenomenon occurs over the short altitudinal range of our study area and is consistent with the vegetation mosaic described by González-Espinosa *et al.* (1991, 1997) for the Central Highlands.

Both chapters 2 and 3 indicate that forest stand characteristics range from low floristic richness, basal area and tree density – PF and some POF plots – to high species richness, basal area and density – BLF plots with most of the OF and POF plots being intermediate. Correlation analyses in Chapter 3 showed for saplings that lower species richness and stem density are associated with high human disturbance levels and a low percentage of forest canopy cover. In addition, the positive relationships of stem density and species richness with altitude and the negative relationship of these characteristics with anthropogenic disturbance indicates that, in general, altitude may well constitute a gradient of local people's access to forest resources, determining the pattern and impact of human activities: land at lower altitudes and with flat terrain is historically dedicated to productive activities, land at a higher altitude and with abrupt topography is mostly occupied by private, communal, municipal or military reserves.

For the particular case of the sapling assessment (Chapter 3), canopy openness, an indicator of disturbance level in our study, has a significant effect on the abundances of eight species, and it also has an effect on the abundance of saplings of the genus *Pinus* as a whole. Although the increased regeneration of *Pinus* spp. in open sites has previously been widely documented for the study area (González-Espinosa *et al.* 1991; Galindo-Jaimes *et al.* 2002), less robust information is available to corroborate the significant effects on the other eight species. These results must be interpreted with care since a high density of individuals in a location with particular light levels may not indicate a direct relationship of species abundance and canopy openess. This happens with *Persea americana* whose significantly higher sapling abundance under closed canopies may be more related to a corresponding abundance of adults. The large size of the fruits and seeds of this species suggests a poor dispersal capacity, which may lead to a dominant role of dispersal limitation (Hubbell 2005) rather than a preference for particular light conditions in determining its local-scale distribution. Considering the possible caveats of the sapling assessment, contrary to expectations in such a highly disturbed landscape as the study area, the number of tree species showing marked preference for a particular light condition is quite low; this suggests that most of the tree species of the Central Highlands may be generalists rather than specialists (compare with Lieberman *et al.* 1995).

Leaf area was the only tested functional trait that was associated with changes in species' sapling abundance. Regeneration of dominant species (absolute density) was more abundant for those species that have big leaves; however the possible functional explanations for this trend are limited and need further assessments (Niinemets *et al.* 2007).

The Mantel correlograms and the variation partitioning analysis indicate that there is both vertical and horizontal spatial structure in climate in the complex topography of the study area, and that floristic composition is strongly related to this variation. Nevertheless, the variation partitioning suggests that variation in floristic composition in adult trees and saplings is also associated with geographical distance. This provides further evidence that part of the variation may be explained by spatial processes such as dispersal limitation.

5.2.2. Relationships between functional variation and environmental and spatial variables

Dominant species of the forests of the study area have leaves ranging from soft (high SLA, low LDMC and LTS) to hard leaves (high LDMC and LTS, low SLA) and from needle to broad leaves, with a wide range in wood density and in maximum tree height at maturity. Nevertheless, three main groups largely defined the functional characteristics of species in the Principal Components Analysis: *Quercus* species, *Pinus* species and a third group of different species mainly with low to intermediate maximum heights. Trait values of the *Quercus* species (high WD, high LDMC, and relatively high LTS and H_{max}, with relatively low SLA and low leaf nutrient concentrations) may be indicative of high resource conservation and slow growth rates (Pérez-Harguindeguy *et al.* 2013). In contrast, those of the *Pinus* species (low WD, LDMC and SLA, but high LTS, H_{max}, LNC and LCC) may be indicative of rapid resource acquisition and growth, with a quick return on investment of nutrients, with investment of some forms of leaf tissue defence against mechanical damage suggested by high LTS. *Pinus* and *Quercus* contributed the highest number of species (5 and 7 respectively) and they constituted the canopy dominant species of the forest stands. Species of the third group have higher SLA but lower WD, H_{max}, LTS and LDMC, indicating high potential growth rates and preference for environments with less stress from heat, cold, drought, and shortage of nutrients and light (Pérez-Harguindeguy *et al.* 2013).

In contrast to the NMS ordination, the PCA with CWM groups the BLF and OF sample plots in the Tzontehuitz site with the BLF and OF plots in other sites. It also creates a clearer grouping of the PF plots and some POF plots, whose CWM trait values reflect the dominance of *Pinus* spp. This first PCA axis explains 53% of the CWM variation and suggests that the wood and leaf economics spectra scale up to the community level (Finegan *et al.* 2015), since CWM LTS, LNC and LCC are positively related to this axis and negatively related to CWM WD, SLA and LDMC. In terms of forest type, this functional axis represents a clear gradient from PF (in particular the eight plots dominated by *P. montezumae* – related to high CWM values of LTS, LNC, and LCC) to BLF and OF (related to high CWM WD, SLA and LDMC). Most of the POF plots were intermediate, except those in the Military zone where *Quercus* species were more dominant and, therefore, they were more associated with the BLF and OF plots.

In contrast to floristic composition, variation partitioning indicates that functional composition is poorly related to the variation in climate, altitude and geographical distance, which was in accordance with the results of PCA using CWMs which suggests that a floristic change does not necessarily mean a functional change. This pattern seems to work well at the landscape scale of the study but other studies have found evidence of changes in functional beta diversity along big altitudinal ranges and broad geographical areas (Swenson, Anglada-Cordero & Barone 2011; Siefert *et al.* 2013; Liu, Tang & Fang 2015), indicating vertical and horizontal functional variation along the associated environmental gradients.

Anthropogenic disturbance was the underlying factor that best explained the functional variation probably because of the large trait differences found between stands with high (mainly pine forests) and low disturbance (the remaining forest types).

5.2.3. Floristic and functional variation and leaf-litter decomposition

It is a basic assumption of functional ecology that the measurement of traits of species, and the scaling up of trait values to the community level using measures like the community weighted mean, permit inference regarding species life histories, leaf-level photosynthetic characteristics and community ecological processes, amongst others (Díaz & Cabido 2001; Easdale *et al.* 2007; Poorter *et al.* 2008; Finegan *et al.* 2015). My study of leaf litter decomposition permitted testing of this assumption at the species and community levels.

Species tested in the experiment in greenhouse conditions showed a range of foliar characteristics and their decomposition is consistent with the hypothesised link between interspecific variations in leaf traits and variations in litter decomposition rate (Chapter 4). In line with Chapter 2, two types of species with tough leaves associated with slow decomposition can be distinguished: *Quercus* spp. (high WD, LTS, LDMC and lignin) and *Pinus* spp. (low WD, LDMC and SLA; high LTS). In spite of exceptions with low decomposition (*Prunus rhamnoides*, *Styrax magnus*, *Clethra macrophyla*, *P. americana*), there are also a variety of the group of forest understorey species that display soft leaves (high SLA and LA; low LTS, LDMC, lignin and WD) and rapid decomposition (*Miconia glaberrima*, *Viburnum jucundum*, *Weinmania pinnata*, *Symplocos breedlovei*, *Quetzalia contracta* and *Ternstroemia lineata*). These results lead to the hypothesis that forests dominated by *Pinus* and *Quercus* species will have the lowest decomposition rates in the study area, whereas broadleaved forests with a higher ecological importance of species with high SLA will show higher rates (compare with CWM trait values in Chapter 2).

The results of the field experiment indicate a lack of difference in the decomposition rates amongst the different forest types, reinforcing the hypothesis that intrinsec characteristics of species (Freschet, Aerts & Cornelissen 2012) rather than the local environment mostly drive the decomposition process. Nevertheless, the forest types in which the field experiment was conducted varied widely in the community-weighted mean trait values of their dominant species (Chapter 2) suggesting that ecological process rates, such as decomposition, would also vary widely. In this sense, the field experiment showed that the difference in litter properties between forest types was a major factor in the variation in decomposition rates. It also showed a very strong interaction between the origin of litter and the forest type in which decomposition takes place, which is strongly associated with the “home-field advantage” hypothesis (Gholz *et al.* 2000; Vivanco & Austin 2008; Ayres *et al.* 2009; van der Putten *et al.* 2013).

5.3. A BRIEF ECOLOGICAL INTERPRETATION OF KEY RESULTS

The study area contains a variety of tree species with different characteristics, which are distributed amongst a variety of local assemblages, associated with both spatial and environmental variation and with different types and intensities of human disturbance. The species assemblages are far from discrete associations although the study finds three possible drivers under which species distributions and the consequent community composition may be arranged:

1. The two big groups formed in NMS analyses, species of the northern humid zone (Tzontehuitz) and drier southern zone (the rest of areas), suggest the joint action of evolutionary processes and macro-environment acting over geological time-scales at large spatial scales, generally associated with "phytogeography". Therefore, in the first instance, the species of the study area would group in two main floristic provinces, with two species source pools (*sensu* Sokol *et al.* 2011).

2. Human disturbance better explains the dominance of pines in several forest stands of the southern part of the study area (southern floristic province). This phenomenon has been well documented by other local studies (e.g. González-Espinosa *et al.* 1991; Galindo-Jaimes *et al.* 2002) indicating that human activities are the main promoter of pine expansion, as well of the rapid floristic and structural change of montane forests.

3. The analyses performed suggest the role of both climatic and spatial factors in determining the floristic variation, which implies that the presence of species in a given space of the study area is subjected to both environmental factors and dispersal limitation. The effects of climate factors on species distributions has been taken for granted in the Central Highlands and only one study suggests the operation of dispersal limitation (Zavala, Galindo-Jaimes & González-Espinosa 2007) although the present investigation is the first that is intended to quantify their relative contribution.

The set of dominant species of this study and their ranges of functional traits indicates a variety of strategies developed over evolutionary times to adapt to the conditions offered by the species interactions and the changing environment. As other previous studies have pointed out (González-Espinosa *et al.* 1991, 1997; Quintana-Ascencio & González-Espinosa 1993), the numerous species of *Quercus* and *Pinus* represent the structural basis of the forests of the Central Highlands. Our study finds that these genera encompass very different but efficient trait packages enabling species to maintain abundance in the stressful environment of the mountains. Under their cover and shelter a variety of other species may survive that are less tolerant of open conditions. The different forest associations formed present particular functional associations varying according to their species assemblages, being dynamically modified by the climate, space and anthropogenic disturbance, the drivers of species change found in this study.

In general terms, the functional approach used in this investigation provided a comprehensive tool to scale from species to communities and ecosystems (Garnier *et al.* 2004; Violle *et al.* 2007; Díaz *et al.* 2007; Lavorel *et al.* 2008), and permitted to relate important ecosystem processes, in particular, leaf-litter decomposition. Nevertheless our findings must be revised in the light of future studies.

5.4. SOME IMPLICATIONS AND APPLICATIONS OF THE STUDY

The present study is the first in the Central Highlands of Chiapas, Mexico, that explicitly uses the functional traits approach to relate species' characteristics with species' ecological performance and ecosystem processes. The results complement the findings of previous local ecological studies about the influence of environmental and anthropogenic factors on the species' assemblages (González-Espinosa *et al.* 1991; Quintana-Ascencio & González-Espinosa 1993; Ochoa-Gaona 2001; Galindo-Jaimes *et al.* 2002; Cayuela *et al.* 2006) but also give a first glimpse of the role of dispersal limitation in floristic variation, as well as the possible conservation implications of functional change in montane forest ecosystems.

The study findings lead to a variety of considerations for the conservation of ecosystem functions, processes and services of local montane forests. This study provided clear evidence of variation in inherent dispersal capacity amongst tree species. This suggests that species with very limited dispersal capacity (as well as those with low abundance of seed-parents in the landscape) will have a limited capacity to colonize sites that become available after disturbance. This will limit their capacity to recover from deforestation, fragmentation or climate change through migration, or even rapid evolution promoted by gene flow. On one hand, this would support an “ecosystem approach” to forest conservation and sustainable forest management, with integrated conservation of the regional landscape, including all the floristic and functional elements, instead of emphasising the conservation of particular species or communities. This approach should recognize the regional species pool and its phytogeography and should emphasize connectivity of tree communities and the reduction of fragmentation effects (compare with Jamoneau *et al.* 2012 and Chain-Guadarrama *et al.* 2012). On the other hand, in a scenario of climate change, dispersal limitation implies that the future distribution of species is in part determined by dispersal capacities rather than by environment alone; therefore, climate envelope models could be underestimating real distribution of species and therefore need to be amended to incorporate the uncertainty of stochastic factors, exerting more care with the predictions and the resulting conservation decisions (Anderson 1991; Dullinger, Dirnbock & Grabherr 2004).

Our study finds that disturbance is another important factor that changes not only the composition and structure but also the function of the local forests. These forests represent a variety of tree species with different functional characteristics that are directly associated with ecosystems processes as it was found in the litter decomposition study (Chapter 4). It then follows that any change in the composition of plant assemblages, either by natural or anthropogenic factors, will have impacts and consequences in ecosystem services such as nutrient cycling, water provision, carbon sequestration, soil retention (Chapin III *et al.* 2000; Hooper *et al.* 2005; Díaz *et al.* 2006, 2007).

This scenario is particularly worrying in the study area where human activities are leading to pine-dominated forests with low number of species and individuals, potentially with low functional diversity and functional redundancy as in other degraded systems (Laliberté *et al.* 2010; Carreño-Rocabado *et al.* 2012). This risk will be compounded by the fragmentation of the remaining forests due to conversion to crop agriculture, livestock farming, and settlements, affecting forest connectivity and limiting capacity for species dispersal. This situation urgently requires not only investigation of the different factors affecting the ecosystem processes, functioning and services of these montane forests but also active conservation measures targeted at the most threatened species, plant associations, and forest habitat connectivity. Research evidence should indicate the required levels of functional diversity and functional redundancy to maintain the resilience of these ecosystems in the face of climate change and future disturbance impacts. This resilience relates to the ecosystem functions required to deliver the services required by the human populations of mountains (sufficient to compensate them for the opportunity costs of loss of access to forest land for food and other resource provisioning). This is a demanding agenda for research.

5.5. SOME ADDITIONAL CONSIDERATIONS

For the assessment of the relationships of environmental factors with floristic variation, it is necessary to take into account that the mountainous topography of the study area undoubtedly creates high environmental heterogeneity. Therefore, the variables used (altitude, geographical position, aspect, and WorldClim climate data) do not give a complete picture of environment. Other studies in Neotropical forests have found evidence of the effect of a wide range of other environmental factors on floristic variation, for example, soil physics, soil chemistry, terrain inclination, relative humidity, evapotranspiration, sun and wind exposure, fog frequency and cloudiness, amongst others. In this same sense, it is also necessary to incorporate other functional types such as palms and herbs, since different groups of species may respond in different ways to environmental factors (e.g. Sesnie *et al.* 2009; Chain-Guadarrama *et al.* 2012). Additionally, in order to include the other species assemblages present in the region it would be necessary to extend both the study area and the altitudinal range, requiring a much larger project budget.

The study was limited to a number of traits that demonstrated in general strong relationships with patterns and processes. Nevertheless, for the particular case of assessments of the factors influencing sapling abundance we recommend the future inclusion of reproductive traits and those potentially linked to acquisition of below-ground resources.

The decomposition of leaves is, of course, an important process in forest ecosystems, however, as far as possible, other plant structures such as flowers, fruit, seeds, bark, stems, branches and roots must be incorporated in future experiments. They should be analysed to assess the importance of reproductive and below-ground traits such as wood density, fruit and flower sizes, fruit volume, bark thickness, nutrient and carbohydrate composition of these structures, in determining their rate of decomposition. Additionally, future studies on plant decomposition must consider including i) other different functional types such as herbs, epiphytes and ferns, ii) to extend the period of assessments in order to encompass the complete decomposition of plant organs-leaves, iii) to quantify the delivery of nutrients from the decomposition process by measurement of the rate of loss and fate of, for example, nitrogen, phosphorous and carbon from the samples, iv) to assess the direct effect of variables such as temperature, humidity and soil nutrients; and v) to assess the direct effect of the microbes, micro-fauna and macro-fauna in the decomposition process.

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