Connecting the lifecycle's loose ends

Direct and indirect effects of land use on decomposition – can green leaf traits and functional composition predict decomposition in lowland Bolivian land use types?

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Preface

'En un planeta minúsculo, que corre hacia la nada desde millones de años, nacemos en medio de dolores, crecemos, luchamos, nos enfermamos, sufrimos, hacemos sufrir, gritamos, morimos, mueren y otros están naciendo para volver a empezar la comedia inútil.'

Ernesto Sábato*, El túnel* (1948)

This sentence I found in a book, which was present in the only bookshop of Ascensión de Guarayos, the village where I carried out part of my practical work. I read it swinging in a hangmat, having a headache because of working without a hat in secondary forests the day before. As I came across the sentence above, it reminded me of decomposition – my main study subject. Of course, the principal book character, Juan Pablo Castel, an obsessive tunnel-thinking painter, did not mean to expand on the life and death of plants – but I was struck by the similarities of the lifes of all living creatures, although the point of view expressed here might be somewhat too pessimistic.

The phrase illustrates that we are all part of the same (chemical?) project on earth. The events described are true for every living being – and this showed me at once that that is what makes us humans related to the smallest green leaf that is popping up from the ground, struggling for life (and sometimes having a good time). It shows how I am related to formerly unknown Bolivian people at the other end of the world – eating the seam pineapples and the same rice, even though I did not recognize the *arroz* on my plate as rice at first.

It is no negative expression, the one that struck me on that afternoon in my hangmat. I realized that decomposition is actually the composition of a new world. And that I was contributing my tiny part by investigating how this circle of life is going round and round.

I thought about how the things that happened during my stay in Bolivia, things that do now belong to the past, are going to live their own life, as memories. To keep these valuable memories alive, I would like to use this preface to remember and thank those who at the least helped me and at the most incredibly enriched my life during my time at the other end of the world.

I would like to thank Lourens, for his enthusiasm and criticism both in real life, in Bolivia, and in written life, by commenting and supporting me in actually writing this thesis. I thank Geovana, because of enduring me day in day out during fieldwork, and the funny moments we had, which became more and more abundant as the end of my internship came closer. I thank all the people of IBIF, for offering a safe place in the chaos of Santa Cruz, the parties, and the practical support. Also, I would like to thank Laura Pla for helping me with the functional diversity analyses and for programming the f-Diversity software.

I thank Don Ricardo, for his jokes and his machete and watering skills, and Don Wicho, for all the litter leaves he gathered and the fish he managed to catch in the small river near La Chonta camp – and both of them for soothing loneliness in the jungle. I am thankful to José Chuviña for carrying me safely through the fields on the back seat of his motor, helping me with measuring leaf traits and feeding me with pineapple, sugar cane and oranges. And to all farmers, for letting me work on their parcels, even though I could hardly explain what I was doing.

I would like to remember Elena, who made my stay in Santa Cruz much more fun, who was so patient with my Spanish and who introduced me in IBIF, the La Chonta forest, as well as in Bolivian life, together with Claudia, who kept on dragging me to parties – *brasileño*, university or *chiquitanía*. Thank you for being my friends!

Finally, I would like to thank Nienke, for her professional scanning skills, for being adventurous with me in Bolivia – and for her friendship. I thank Twan, for being the best litter washing and leaf weighing companion in the world, for joining me on this journey and, hopefully, the many journeys we hope to make together – and for his love.

I could have been telling many stories on my time and experiences in Bolivia. About the nature of the Bolivian people – the Bolivian spirit, on which it is much harder to gain knowledge than on decomposition. This research report, however, should be a scientific expression of what I learned on the part of the ecology of a tropical moist forest. I hope I managed not to go off this path too far, and that you will enjoy it.

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Maartje,
19 July 2009

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Abstract

1. Land use is the major form of global change, affecting changes in plant community composition and the on-going of important ecosystem processes, and ultimately determining which ecosystem services can sustainably be provided.

2. Here, I investigated the direct and indirect effects of land use on decomposition. My study was carried out in seven land use types in lowland Bolivia: tropical moist control, normally logged, light and intenstive silviculture forest; the shifting cultivation areas of secondary forests and agricultural fields; and pastures. I tested the relationship between fresh leaf physiological traits and decomposition of leaf litter for 24 plant species in order to determine which leaf traits could be used to predict decomposition in species derived from a broad range of land use types. Furthermore, I investigated how species number and diversity and functional diversity and composition changed as an effect of land use. Finally, I evaluated the effects of the environment in the different land use types on decomposition rate.

3. Leaf traits were good predictors of decomposition rate. Decomposition rate was correlated with specific leaf area (SLA), leaf dry matter content (LDMC), leaf density, leaf resistance, leaf nitrogen content (LNC) and leaf phosphorus content (LPC). Multiple regressions resulted in two models that best predicted litter decomposition rate: the first with LNC (r^2=0,53), the second with both SLA and chlorophyll concentration (r^2=0,66).

4. Functional and taxonomic diversity measures resulted into the same ranking of land use types. Diversity varied considerably among land use types, moist tropical forest systems being the most diverse, followed by agricultural fields, secondary forests and pastures respectively. As functional diversity measures, functional attribute diversity (FAD) and functional diversity (FD) were concluded to be more useful for comparing different kinds of land use types, because measures including species abundances (Rao's Q, extended FD) did not give appropriate results.

5. Community-level weighted mean of trait values (CWM) was calculated. The community of agricultural fields can be placed at the fast end of the plant economics spectrum, followed by all moist tropical forest systems, secondary forest and pastures respectively. The plant economics spectrum is the trade-off between high growth rates and cheap, short-lived, and physiologically active leaves at the one hand, and high survival due to long-lived, well-protected leaves.

6. Paper was decomposed in several land use types. However, this material turned out not to be adequate for evaluating environmental circumstances for decomposition, for it was largely eaten by macro-organisms.

7. The results indicate that fresh leaf characteristics can be used as predictors for decomposition across a range of different land use types. Based on functional composition, agricultural fields have the fastest decomposition rate, followed by moist tropical forest systems, secondary forest and pasture. Thus, characteristics of living leaves persist in litter, so that leaves lead influential afterlifes: decomposing leaves connect both ends of the plant life cycle, releasing nutrients in the environment that can be reused by seedlings. Furthermore, land use has a strong influence on functional diversity – it remains to be tested whether functional diversity of litter *per se* has an effect on decomposition rate.

1. Justification. Diversity and decomposition in a changing world

Wood for construction and warmth, fruits and vegetables for food: without plants, humanity would not be able to survive (Díaz *et al*., 2006). At the same time, humans threaten the survival of many plant (and animal) species. This is mainly caused by 'global change': the way we alter the environment – that is, climate and the composition of atmosphere, water and soil. Many scientists argue that the big impact of humanity on the earth is about to result in or has already resulted in the sixth mass extinction. With biodiversity, 'ecosystem services' get lost: the services provided by ecosystems, granted by the diversity of organisms we encounter in nature, and on which humanity is heavily dependent. As Díaz *et al.* (2006) state, biodiversity loss threatens human well-being.
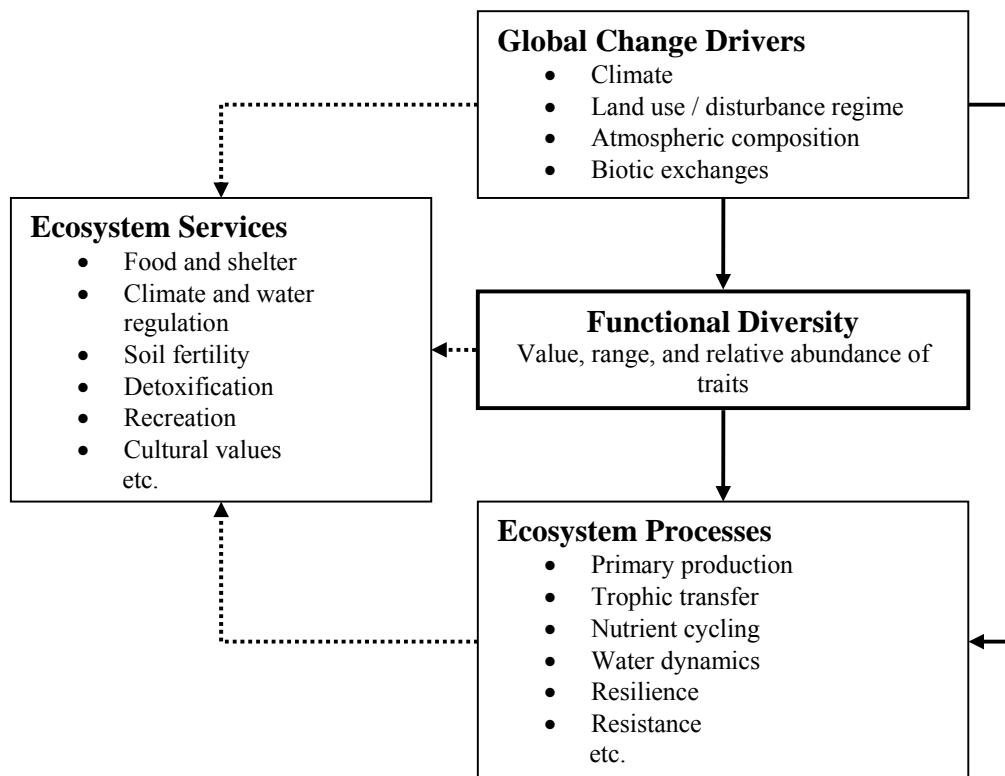

Figure 1.1 Interaction between global change, (functional) diversity, ecosystem processes and ecosystem services, along with some examples.Global change affects ecosystem processes directly, but also through its regulation of (functional) diversity that in turn influences ecosystem processes. My focus is on the links indicated by black bold arrows (modified from Díaz).

Global change, biodiversity and ecosystem services are all part of a complex web of interactions (figure 1.1). In order to preserve ecosystem services, which are so heavily relied upon, it is necessary to know what the precise causes of the threat of these ecosystem services are. Direct and indirect influences can be distinguished. Global change is assumed to have a direct effect on ecosystem services. Among global change drivers, land use change is believed to have the

greatest potential to affect biodiversity, ecosystem processes and services in the short run (Díaz unpublished, Scholes & Van Breemen 1997). Indirectly, global change exerts its influence on ecosystem processes and services via a change in plant (functional) diversity. The interaction of functional diversity, climate variability, and land use can lead to irreversible changes in ecosystem functioning, with often dramatic consequences for ecosystem services. Some examples of ecosystem processes are primary production, trophic transfer and nutrient cycling, of which decomposition forms a major step. A decrease in soil fertility, for example, when intensive agriculture is applied, can lead to a reduced harvest – which means a decrease in ecosystem services provided by the system.

People who rely most directly on ecosystem services are subsistence farmers, the rural poor, and traditional societies; they face the most serious and immediate risks from biodiversity loss. The loss of biodiversity-dependent ecosystem services is likely to accentuate inequality and marginalization of the most vulnerable sectors of society, by decreasing access to basic materials (Díaz *et al*., 2006). Thus, the regions in the world in which it is most urgent to understand the altering of ecosystems and its consequences for the services they provide, are Third World countries. Therefore, my study took place in eastern Bolivia, one of South America's countries with the lowest Gross National Product per capita (after Guyana and Paraguay).

In order to sustain ecosystems and their services for future generations, politicians should devote themselves to making the right decisions on, for example, nature conservation, land use and the environment. Indeed, one of the eight Millennium Development Goals, that the United Nations aims to achieve before 2015, wishes to assure environmental sustainability. In Bolivia, this is particularly relevant because of the forestry law, stemming from 1996, which prescribes research on sustainable exploitation of tropical forests. One important decision is whether policy makers should choose to focus on conservation of plant species richness, species diversity, dominant functional species or functional diversity. However, not only policy makers are responsible for a change in how we deal with the earth. Farmers, for instance, should also strive for maintaining diversity and ecosystem processes while gaining profits.

To obtain a solid idea of the factors endangering ecosystem services, a scientific research project is carried out across the Americas focused on global change, functional diversity and ecosystem processes. My thesis forms part of this project; I discuss the direct and indirect influence of land use on decomposition as an ecosystem process involved in nutrient cycling. Therefore, I will relate land use to (functional) diversity, (functional) diversity to decomposition, and direct effects of land use to decomposition. Doing so, I hope I will able to start and sketch a scenario of the consequences of land use on ecosystem services, such as food and wood availability and soil fertility, particularly in the systems where I carried out my practical work.

2. Introduction

2.1 THE ECOSYSTEM PROCESS OF DECOMPOSITION

Decomposition is a key ecosystem process, because it connects all trophic levels. Through the activity of decomposers, chemical elements like nitrogen and phosphorus are made available to producers. Decomposer organisms break down the organic material and recycle chemical elements to the abiotic soil, water and air reservoirs. Plants and other producers can then reassimilate these elements into organic matter (Campbell & Reece 2002).

The rates at which nutrients cycle in ecosystems are extremely variable around the world, making up an important characterization of an ecosystem. Efficient nutrient cycling within ecosystems means that most of the nutrients released from trees are rapidly taken up by roots, mycorrhizae, and decomposers, and retained within the system. This 'tight' nutrient cycling is often assumed to be typical for tropical forests (Vitousek 1984). As tropical forests generally exist on highly leached, nutrient-poor soils with relatively low soil organic matter sinks, plants rely on the process of litter decomposition for continued plant and forest productivity (Parsons & Congdon 2008). Litter decomposition is controlled by three main factors: environmental conditions, soil organisms, and substrate quality (Pérez-Harguindeguy *et al.* 2000, Toledo Castanho & Adalardo de Oliveira 2008).

Environmental conditions include both climate and soil characteristics. Climate has a direct effect on litter decomposition due to the positive effects of moisture and temperature on the metabolism of soil organisms (several authors in Toledo Castanho & Adalardo de Oliveira 2008). In the tropics, temperature and moisture conditions are near the optimum for biological activity most of the time (Toledo Castanho & Adalardo de Oliveira 2008). One measure for climate, that describes both temperature and precipitation, is actual evotranspiration (AET). At a global scale, AET is shown to be the best predictor for decomposition of litter (Aerts 1997). There is also evidence that intensity and distribution of precipitation are in itself important predictors of decomposition rates (Toledo Castanho & Adalardo de Oliveira 2008). This means that moisture conditions are slightly favoured over temperature as predictors of decomposition rates. However, on a smaller scale, climate is known not always to be the most influential determinant. Experiments have shown that in England, the season (summer or winter) does not affect decomposition rate (Cornelissen & Thompson 1997).

Given the importance of climate for the process, it is easy to imagine that climate change has lead to renewed attention for decomposition. Due to the strong climatic control of litter decomposition, climate change may significantly alter the global carbon budget (Aerts 1997). However, this is not necessarily the case, because nutrients can be the limiting factors of decomposition as well (Cleveland *et al.* 2002). A potential shift in the identity and traits of dominant plant species is another factor that can seriously affect the carbon cycle (several authors in Cornwell *et al.* 2008).

Next to climate, interactions between decomposers and plants might play an essential role in decomposition processes. Elmer *et al.* (2004, in Toledo Castanho & Adalardo de Oliveira 2008) and Scheu *et al.* (2003, in Toledo Castanho & Adalardo de Oliveira 2008) found changes in the

trophic structure and biomass of soil fauna community in response to replacement of tree species in monocultures. A Brazilian study indicated a decomposer's adaptation to specific substrates in a tropical forest (Toledo Castanho & Adalardo de Oliveira 2008). Certain plant species may even select the soil biota that facilitate decomposition of their own residue (several authors in Toledo Castanho & Adalardo de Oliveira 2008). The adaptation of a decomposer community to a particular substrate can be measured as the interaction between ecosystem and substrate quality. In other words, mutualisms between producer and decomposer subsystems may be the case. (Toledo Castanho & Adalardo de Oliveira 2008).

2.2 LEAF TRAITS AND DECOMPOSITION

In their analysis of litter decomposition within biomes worldwide, Cornwell *et al.* (2008) showed that plant species traits are the dominant control of decomposition (and climate is not). The relationship between litter quality and decay rate is consistent across higher plant species and life forms, and repeated in the floras of geographically and climatically distinct areas (Cornelissen *et al.* 1999, Cornwell *et al.* 2008). Both litter and fresh leaf traits have successfully been used to predict decomposition rate. Litter trait measurements permit to have closer look on the initial quality of the decomposing leaves, taking into account nutrient resorption for example, and to relate this to the decomposition process, while the advantage of using leaf traits is the closer link to the life cycle of leaves and the fact that more data are already available on green leaf traits.

Litter nitrogen concentration was found to correlate positively with decomposition rate (Kurokawa & Nakashizuka 2008, Parsons & Congdon 2008). Another positive correlate with decomposition is phosphorus concentration (Alvarez-Sánchez & Becerra Enríquez 1996, Cornwell *et al.* 2008, Parsons & Congdon 2008). Alvarez-Sánchez and Becerra Enríquez (1996) found that litter leaves with high [Mg], [K] and [Ca] decomposed faster. Furthermore, a negative correlation between molecules consisting of large carbon chains (mainly lignin and cellulose) and decomposition has been reported (Vaieretti *et al.* 2005, Kurokawa & Nakashizuka 2008, Parsons & Congdon 2008).

Taking a step further away from the decomposition process, chemical characteristics of green leaves are known to be related to the decay process. Nitrogen concentration has been proven to serve as a good predictor of decomposition rate, showing a positive relationship (Santiago 2007). In the global analysis of Cornwell *et al.* (2008), leaf [N] was found to be a better predictor for decomposition than litter [N]. Other leaf nutrient concentrations positively correlating with decomposition rate are those of Mg, K and Ca, also when they are measured together as total base content (Cornelissen & Thompson 1996, Santiago 2007, Parsons & Congdon 2008). Differences in decomposition rates of monocots and dicots can be explained by the different relative contributions of the various cations. Total base content, consisting of K, Ca en Mg, of living leaves does not differ much between monocots and dicots, but calcium dominates in dicots, while base concentration in monocots is mainly determined by potassium (Cornelissen & Thompson 1997). During senescence, K is withdrawn from the leaves, but calcium stays in, thus enhancing dicot litter decomposition rate.

There is no unambiguous answer to the question whether physical or chemical leaf traits are the best predictors of decomposition. Experiments suggest that chemical composition (either nutrients or chemical defences (inhibiting decomposition)) might be more important for

decomposability than structural features (Cornelissen & Thompson 1996). However, Cornelissen *et al.* (1999) found that the defences that acted as the most potent inhibitors of decomposition originated from the physical structure of the living leaf, rather than from chemical components that discourage damaging leaves (although, as we will see, physical and chemical factors are sometimes difficult to distinguish). Specific leaf area (SLA; ratio leaf area:leaf dry mass) shows a positive relation with decomposition rate (e.g. Cornelissen *et al.* 1999, Vaieretti *et al.* 2005, Santiago 2007, Kurokawa and Nakashizuka 2008), as does leaf dry matter content (LDMC; ratio leaf dry:fresh mass) (Kazakou *et al.* 2006, Cortez *et al.* 2007, Cornwell *et al.* 2008, Kurokawa & Nakashizuka 2008).

Leaf toughness has a negative effect on litter decomposition rate (Cornelissen & Thompson 1997, Cornelissen *et al.* 1999). Fibre and lignin content are probably the main contributors to toughness (Wright & Illius 1995, in: Cornelissen & Thompson 1997). However, a recent analysis indicates that fibre concentration explains ca. 30 % of toughness variation only (LIT Lourens). Another factor involved in toughness might be cell wall thickness. Cell walls are known to contain silicium, which plays a role in mechanical defense against fungi and herbivores (Epstein 1994, in: Cornelissen & Thompson 1997).

A tougher leaf is more resistant to herbivores, pathogens and physical damage (several authors in Cornelissen & Thompson 1997). As these structural defenses form effective barriers against soil decomposers, too, it can be concluded that living leaf traits persist in litter (Pérez-Harguindeguy *et* al. 1999). Leaf palatability and decomposition rates are positively correlated indeed (Grime *et al*. 1996). Now, we are gradually moving towards the leaf economics spectrum, which states that leaf traits are part of certain plant strategies, connecting several phases in the leaf's life cycle.

2.3 PLANT STRATEGIES AND THEIR CONSEQUENCES FOR DECOMPOSITION

Often, choices have to be made in order to win. In times of war and threat, you should either gain power and be strong enough to defeat the enemy, or fast enough to run away before he finds you. Can you picture the men with puffed-up muscles – the strong ones? And the marathon runners having developed another type of muscles, able to run away and stay running a long time? They prove that strategical choices have a physiological counterpart. For plants, exactly the same is true, as I will show in this paragraph. Choose or lose, the motto of life.

Back to plants. In living leaves, traits are known not to be independent, but related to each other. Species can differ a lot, even when growing at the same spot, due to niche partitioning or finer-scale environmental heterogeneity in space (e.g. soil fertility and hydrology) and time (e.g. disturbance). However, differing traits of species growing close to each other can also be the result of a trade-off between strategies followed by these species. Alternate physiological strategies (several authors in Cornwell *et al.* 2008) produce roughly the same fitness levels among coexisting species. Speaking about leaves, for example, all plant species face the trade-off between producing leaves with high photosynthetic rates, low structural costs, and fast turnover, and leaves with a long lifespan (Santiago 2007).

The plant economics spectrum ranges from plants having traits that either enhance resource conservation or resource acquisition (Cornelissen *et al.* 1999, Díaz *et al.* 2004). At one side of the spectrum, there are plants that obtain a strategically slow return on carbon and nutrient invested

(i.e. maximizing residence time), in order to reach extended durability. They invest in strong leaves. This group of plants shows for example a low SLA and a low leaf nitrogen concentration (LNC). Also, they tend to invest in protective leaf traits against the biotic and abiotic environment (tough tissues and a high C-to-N ratio). They grow more slowly, in order to establish proper leaves that are able to survive for a long time.Their leaves are designed in such a way that they can withstand agents that could cause damage, like herbivores.

At the other side of the spectrum are those plants that are capable of gaining a fast return on leaf carbon (Cornwell *et al.* 2008). They have low defence, i.e. low tensile strength, and high base content leaves that optimize photosynthesis rates (several authors in Pérez-Harguindeguy *et al.* 1999; Cornelissen *et al.* 1999). Furthermore, their leaves are highly decomposable, because they are part of a productive system with rapid (leaf) turnover. Once decomposed, nutrients can be reused.

This pattern can for example be observed when comparing evergreen and deciduous species. In comparison with deciduous species, evergreens have innately slow growth, corresponding with longer-lived leaves of lower specific leaf area and higher tensile strength. Their leaves are characterized by a low base content, largely made up by potassium, which is withdrawn during leaf senescence. This makes a leaf less appealing to decomposers, which prefer bases as they provide an important resource and make litter less acid (several authors in (Cornelissen & Thompson 1997). Indeed, the specific combination of evergreen leaf traits results in more resistant leaf litter (Cornelissen *et al.* 1999). This allows evergreens to maintain their position in infertile ecosystems, not allowing potentially fast-growing deciduous species to outcompete them (Cornelissen *et al.* 1999): there are not enough nutrients available in the environment.

In tropical forests, the several plant strategies can all be observed, ranging from shade tolerant to pioneer species, i.e. species either showing high growth rate or high competitive ability by allocating resources to sustainable tissues (r- versus K-strategy) (Poorter & Bongers 2006). However, there also exists evidence on pioneer species producing leaves of high quality (i.e., sustainable leaves; Parsons & Congdon 2008).

Selection for a suite of structural and chemical leaf traits has eventual nutrient cycling consequences (Santiago 2007). Many of the physiological and protective features of green leaves persist through senescence; resorption of nutrients by the plant is incomplete. This means that leaf 'economic' traits lead influential afterlifes. Beyond the plant's control or not, the decomposability of a species' litter is consistently correlated with that species' ecological strategy within different ecosystems globally. So, there is a connection between plant strategies and biogeochemical cycling (Cornwell *et al.* 2008).

Considering the key role that decomposition plays in an ecosystem's nutrient cycling route, the lack of published results on this subject in neotropical moist tropical forests is notable. Although there has been done some work on the influence of environmental conditions (like soil conditions, climate, water availability, decomposer community (a.o. Rueda-Delgado 2006, Sherman 2003), there is scarce information available about the relation between leaf traits in a broad range of species and decomposition in this part of the world (but see Santiago 2007). To the best of my knowledge, no study with species from a variety of land use types, including logged and undisturbed forest and several agricultural uses, has been carried out at all so far.

2.4 Indirect Effects of Land Use on Decomposition – The Role of Functional Diversity and Composition

Until now, we saw a rather theoretical overview of leaf traits influencing decomposition. However, an interesting question to address would be in which setting species with different leaf traits occur in several types of land use, and how this affects decomposition in reality. In other words, what are the consequences of farmer's and forester's practices of land use for decomposition? Several concepts of plant diversity are used to assess the change in plant communities as a result from land use and to be able to speculate on the effects for nutrient cycling caused by a shift in botanic composition. As we will see, the key concept that is able to link land use (and its consequent selection for plant leaf traits) and decomposition is functional composition and diversity: land use should be related to composition and diversity of leaf traits, and diversity in its turn can be related to decomposition.

Lavorel & Garnier (2002) strongly suggest that one should distinguish *responses* of plants to environmental factors such as resources and disturbances (response traits), and the traits that determine *effects* of plants on ecosystem functions (effect traits), such as biogeochemical cycling or propensity to disturbance. If disturbance selects species according to traits that are unconnected with functional effects, then biogeochemical cycles will be maintained (Lavorel & Garnier 2002). Thus, a shift in functional diversity or composition does not necessarily affect the ecosystem process of interest. My research focuses on traits that are relevant for decomposition. However, even if this process is not influenced by land use through a change in diversity, this could be different for other processes that are beyond the scope of my work.

In the following, the monitoring of changes due to land use and their effects will be distinguished. So, I will first go through what is sometimes called the jungle of biological diversity (Ricotta 2004). Secondly, I will discuss which tool is available for predicting ecosystem processes by means of (functional) diversity in my research. Before start a few words on why diversity is seen as beneficial for ecosystem processes such as biomass accumulation and decomposition. The idea is that complementary resource use could occur if plant species differ in the ways they harvest nutrients, light, and water. Complementarity could happen in space, for example, because of differences in rooting depth; in time, for example, due to differences in phenology of plant resource demand; or in nutrient preference, for example, nitrate versus ammonium versus dissolved organic N (Hooper & Vitousek 1997). It could be an advantage of living in a diverse community instead of a poor, because a community with a range of different plant species not all being vulnerable to the same event is more likely to be resilient in a changing environment – the community as a whole is, in such a case, more likely to persist, conserving the right circumstances for the survival of each species.

Species richness is the number of species present at a given location. It has typically low explanatory power when related to functional processes such as biomass accumulation, because it implicitly assumes that all species are equally different (increase of any species to a community will increase diversity by one unit). A more advanced methodology of calculating diversity is the measuring of species relative abundances. Well-known measures are Shannon entropy:

$$H = -\sum_{i=1}^{N} p_i \log p_i$$

and Simpson diversity $1/D$, where D is Simpson's dominance

$$D = \sum_{i=1}^{N} p_i{}^2$$

in which N is the total number of species, i is a species and p is the relative proportion of each species in the community.

Species richness can be an important measure for diversity, because of the saturating response of ecosystem properties that is commonly assumed. The reasoning behind this is that the more species there are present, the more 'complete' the ecosystem, and, most likely, the more diverse. Complementarity, facilitation, and sampling effects are all expected to show a similar saturating average response as species richness increases (Hooper *et al.* 2005).

Both of the above measures are based on taxonomic diversity. These measures were criticized because the number of species *per se* does not necessarily affect ecosystem processes; any effect arises from functional differences between species (Díaz and Cabido 2001). It has, for example, been suggested that ecosystems with a greater diversity of functional traits will operate more efficiently in terms of productivity (Tilman 1999, in Ricotta 2005), resilience (Elmqvist *et al.* 2003; Nystrom & Folke 2001, in Ricotta 2005) and resistance to invaders (several authors in Ricotta 2005).

Functional diversity, using species traits to characterize ecosystems, is widely regarded as a more proper tool for catching mechanisms such as resource use complementarity. As opposed to species diversity, functional diversity can address questions of determination of ecosystem level processes (Petchey and Gaston 2006). It can be used for predicting the functional consequences of biotic change caused by humans (see authors in Petchey and Gaston 2006).
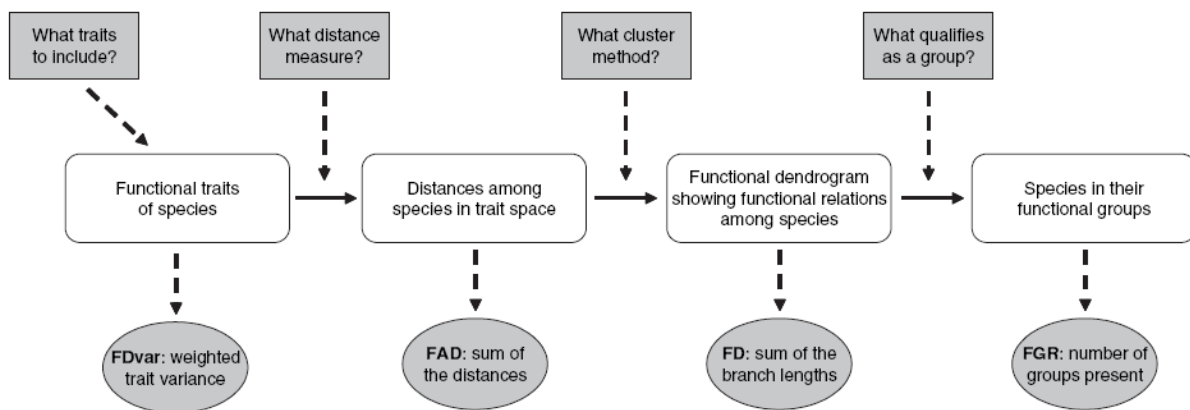

Figure 2.1 The process of producing a functional classification (unshaded objects) and estimating different measures of functional diversity (shaded ellipses). FDvar (Mason et al. *2003); FAD (Walker* et al. *1999); FD (Petchey and Gaston 2002); and FGR, functional group richness. The shaded rectangular boxes represent decisions in the process of making a classification, so that the number of decisions required for each measure increases from left to right. (Petchey and Gaston, 2006).*

Some measures available for measuring *functional* diversity are represented in figure 2.1. Going from left to right, each next box represents a decision to be made to order information about

species traits. The questions on which one should decide are pictured at the top of figure 2.1. The measures included in the figure are FDvar, FAD, FD, and FGR. A first decision involves which traits should be included. FDvar is not commonly used and will not be addressed in this thesis. Functional Attribute Diversity (FAD) is the sum of the distances among species when they are ordered in a trait space. When a functional dendrogram is drawn (including the decision on cluster method), Functional Diversity (FD) is the result, being the sum of the branch lengths between traits of the species of the ecosystem. When species are first clustered into functional groups, for example based on taxonomic criteria, the result is Functional Group Richness (FGR). With a larger number of decisions, the risk of influencing the result by means of the method is greater, which is a disadvantage. Put another way: by the ordering of the information, some information gets lost.

Fuctional composition can be quantified by calculating an average of the leaf traits occurring in a certain community.

$$CWM = \sum_{i=1}^{n} p_i * trait_i$$

This tool leans on the idea that dominant organisms contribute the most to functional processes. Community-level weighted means of trait values (CWM), defined as the mean of trait values present in a community weighted by the relative abundance of taxa bearing each value (Lavorel *et al.* 2008), can serve as a predictor for certain ecosystem processes. CWM has been shown to be useful to assess community dynamics and ecosystem properties (several authors in Lavorel *et al.* 2008).

The relative power of different measures of functional diversity for predicting ecosystem processes has only recently been started to be measured. The first experimental test results were published in August 1997, when a wave of articles appeared in *Science*, presenting the results of several studies on the effects of biodiversity on ecosystem processes. Although the concept of functional diversity had already been invented years ago, what was new in 1997 was experimental evidence on the importance of functional diversity for the functioning of ecosystem processes. This theme was chosen to be investigated in order to be able to enhance policy towards choosing priorities in the conservation of species – an urgent need, for diversity is rapidly lost all over the planet. 'The debate deepens', as Grime (1997) put it.

Functional measures are usually found as better indicators of responses to global change and predictors for ecosystem processes than taxonomic ones. The most widely tested measure is FGR. At the response side, functional composition and functional diversity (measured as CWM and FGR respectively) are proven to be useful in predicting the altering of ecosystems as a consequence of climate change in a study on plant dynamics in the field (Díaz & Cabido 1997) and different land-use regimes (Díaz *et al.* 1999). For example, in the case of xerophytic woodlands, there was a good discrimination of sites under different land-use regimes. The main trend of variation separated sites not disturbed at present, with predominance of woody, long-lived, spiny plants, highly ramified at the ground level, and with specialized animal pollination and no obvious dispersal mechanisms, from sites under severe disturbance (recent abandonment after cultivation and, to a lesser extent, heavy logging + grazing), in which short life span, high leaf weight ratio, high SLA, wind pollination and long-distance seed dispersal (wind or highly-mobile animals) were the most predominant traits. Díaz *et al.* (1999) concluded that an advantage

of using plant traits to evaluate ecosystem function is the stronger power to detect differences between ecosystems, even when floristic composition is largely the same.

Pakeman & Quested (2007) demonstrated that considering only the most dominant species did not affect the calculation of community aggregated means for adult traits associated with biogeochemistry, thereby confirming the finding by Garnier *et al.* (2004) that is was possible to capture changes in major ecosystem properties along a successional gradient even using the traits of the two most dominant species (Lepš *et al.* 2006). The same conclusion was drawn by MacGillivray *et al.* (1995) who showed that differences between five adjacent ecosystems in northern England in their responses to frost, drought, and burning ware predictable from the functional traits of the dominant plants, but were independent of plant diversity (Grime 1997). Finally, in a review by Hooper *et al.* (2005), evidence is presented that biological characteristics of dominant plants rather than species number control ecosystem productivity and biogeochemistry.

Speaking about effects of functional diversity on ecosystem processes, a study with legume and non-legume herbs and grasses, in which several diversity measures were compared in order to predict decomposition, showed that FGR increased decomposition rate of a standard material, while species richness *per se* did not affect decomposition. Also, litter decomposition increased linearly with FGR of species present in the litter mix, and again species richness did not show a relationship. An increase of decomposition rate of both standard materials and plant litter with increasing functional diversity is also observed if a continuous measure of trait dissimilarities is used (functional diversity Q) (Scherer-Lorenzen 2008). Comparison of FAD and FD for predicting biomass across sites reveals that FD is the measure with the greatest explanatory power (Petchey *et al.* 2004).

However, there is quite a lot of evidence that qualifies functional composition as a useful measure. Tilman *et al.* (1997) carried out a field experiment with plots that had either 0, 1, 2, 4, 8, 16, or 32 perennial savanna-grassland species – classified into functional groups on the basis of physiological and morphological differences, which influence differences in resource requirements, seasonality of growth, and life history. Species number, functional diversity (defined as the number of functional groups present) and functional composition (i.e. which functional groups were present) were each experimentally varied. Although each factor by itself had significant effects on many ecosystem processes, functional composition and functional diversity were the principal factors explaining plant productivity, plant percent nitrogen, and light penetration (Tilman *et al.* 1997). Likewise, Hooper and Vitousek (1997) found plant composition (the identity of plant functional groups) as a better predictor of production and nitrogen dynamics than plant richness (number of functional groups present). Work on the effects of the quality of mixed litters on decomposition and N mineralization rates (Wardle *et al.*, 1997a, in Cornelissen *et al.*, 1999) indicated that the functional types to which the litter species belonged, rather than their number, were essential.

To differ between the effects of plant composition and plant functional diversity, Hooper and Vitousek (1997) examined productivity in a serpentine grassland in California. Differences in plant composition (dominants) explained more of the variation in productivity than did the number of functional groups present (FGR). This means that in this study increased nutrient

retention results from the presence of only one (or a few) species rather than from niche differentiation and complementary resource use among many (Hooper and Vitousek 1997).

As stated, functional diversity can both be used to evaluate the response to environmental gradients and the effects of diversity on ecosystem function (Lepš *et al.* 2006). In this research, I tested the response to land use as an example of an (unquantified) disturbance gradient. The effects of functional diversity on ecosystem functioning, however, will remain speculative, because ecosystem functioning was not measured directly. Within the scope of my research, functional composition (CWM) is the only tool available for monitoring changes in ecosystem processes resulting from global change. Above we have seen evidence that CWM indeed is the most useful method for relating plant composition to ecosystem processes. Impacts of invasions, for example, clearly demonstrate that that a single species that becomes dominant can strongly influence ecosystem properties (Hooper *et al.* 2005).

3. Conceptual design: research objectives, questions and hypotheses

The main objective is to evaluate the direct and indirect effects of land use change on nutrient cycling. Direct effects of land use stem from changes in abiotic conditions, indirect effects are caused by changes in species and functional diversity. An indication of the direct, abiotic effects of land use on decomposition is obtained by measuring decomposition of a standard material (paper). Indirect effects are monitored by relating land use to functional diversity, and community-level weighted means of fresh leaf traits to decomposition. In combination with data on functional composition and diversity of the ecosystems, a model can be proposed on the cycling of nutrients in ecosystems with human interference. These systems are all common in lowland Bolivia and are henceforth referred to as land use types: undisturbed forest, three types of logged forest, shifting cultivation areas (including young forests and cultivated lands) and pastures used for cattle ranging.

Research objectives
The objectives of this research are the following:

1) to investigate which leaf traits are the main determinants of decomposition rate;

2) to identify how species richness and diversity and functional composition and diversity change with types of land use and what the consequence of the shift in functional composition is for potential decomposition rate;

3) to determine how the environment (abiotics, microbial and faunal life) contribute to decomposition in different types of land use.

Research questions
These objectives result in the following research questions:

1) Which functional traits of green leaves are good predictors of decomposition rate?

2) How are plant species richness and diversity and functional composition and diversity affected by land use?

3) How is decomposition of a standard material (paper) affected by land use?

Hypotheses
According to these questions, a number of *hypotheses* could be formulated.

1) Functional leaf traits and litter decomposition
The following leaf traits predict decomposability. Generally speaking, the influence on decomposition is negative when a characteristic leads to decreased accessibility, creating a tougher barrier for (microbial) decomposers. Whether the characteristics are expected to have a positive or negative influence on decomposition, is indicated by + and – respectively. Two symbols indicate a stronger expected relation.

- Leaf area (LA) (-). Larger leaves are more difficult to enter by decomposers – only a small part of the leaf is located at the surface – so that decomposition is negatively influenced by leaf size.
- Leaf thickness (LTH) (-). Thicker leaves are more difficult to enter by decomposers – only a small part of the leaf is located at the surface – so that decomposition is negatively influenced by leaf thickness.
- Specific Leaf Area (SLA, the leaf blade area per unit leaf mass; in cm^2 g^{-1}) (++). As a measure for leaf density, low SLA (thus dense) leaves are relatively slowly decomposed, because per unit area, more dry biomass is to be processed.
- Leaf Dry Matter Content (LDMC, leaf oven-dry mass divided by its water-saturated fresh mass; g g^{-1}) (--). A high water content (or a low dry matter content) makes that the leaf part that should actually be decomposed is relatively small, leading to a high over-all decomposition rate. Furthermore, the water itself could be attractive to decomposers (although this effect is not expected to be very strong in a tropical moist forest where conditions are humid anyway).
- Leaf volume (LV, in cm^3) (-). A leaf with a bigger volume is decomposed more slowly, because a larger part of the material to process is located inside the leaf, and difficult to access.
- Leaf density (LD, in g cm^{-3}) (-). As a denser leaf contains a larger amount of material to process per leaf, its decomposition will take longer.
- Leaf resistance (LRES) (--). High resistance could arise from the abundance of long carbon chains, like lignin. Decomposers need to make an effort to break them down to short, ready-to-use molecules, thereby slowing decomposition. Physically stronger leaves are better protected against abiotic (e.g. wind, hail) and biotic (e.g. herbivory) mechanical damage, contributing to longer leaf lifespans.
- Chlorophyll concentration (CHL) (+). High chlorophyll content is supposed to be related to fast growth and low-quality leaves, easy to process by decomposers and therefore leading to high decomposition rate.
- Leaf Nitrogen Concentration (LNC) (++). Nitrogen serves as a nutrient for the decomposer community; because nutrients are usually more limiting to decomposers than carbon, decomposers are expected to select for high LNC leaves. High LNC or LPC is generally associated with high nutritional quality to the consumers in food webs.
- Leaf Phosphorus Concentration (LPC) (++). See LNC. Since phosphorus is known to be the limiting element for biological processes in most moist tropical forests, a strong correlation between LPC and decomposability is expected, even though this correlation has never been found before for fresh leaves.

Also, N-, P- and C-content is measured in litter leaves for the same species to check whether green leaf traits are good predictors of litter traits, and whether initial litter quality predicts decomposition.

- LitterNC (++).The influence of nutrient concentrations will be the same in litter as in fresh leaves. So, high contents lead to fast decomposition, because they are advantageous to decomposer organisms. There is a correlation expected between traits of fresh and litter leaves.

- LitterPC (++). See LitterNC.
- Carbon Concentration (-). See LDMC above. Carbon impedes decomposition, because of the difficult digestion of large molecules – i.e., carbon chains.
- Litter C:N and C:P (--). As a ratio which combines data on nutrient and carbon concentrations, this parameter is regularly found as a good predictor for decomposition, because it tells about the concentration of nutrients, attracting decomposers when high, and carbon concentration, which rejects decomposers because it represents large carbon molecules which are difficult to digest. So, high ratios will result in a slow decomposition rate.

Based on literature, SLA, LDMC, leaf resistance, N- and P-concentrations of fresh and litter leaves, and litter C:N and C:P ratios are all good candidates for having the biggest influence on decomposability. These leaf traits are most likely to be selected for by decomposers. It is not possible to point out one favourite based on the wide body of literature that exists.

2) Diversity and composition

The effects of land use on species richness, diversity and functional diversity and composition are expected to be the following. For the functional parameters, the leaf traits that turned out to be the best predictors of decomposition will be used.
- Irrespective of measurement method, diversity is lower in more disturbed ecosystems: control forest > normally logged forest > light silviculture forest > intensive silviculture forest > secondary forest > cultivated lands and pasturelands. Land use leads to selection for some groups of species in the case of agricultural fields and pasture, thereby lowering the number of species present in the system. In addition, a disturbed ecosystem (as is the case for all land use except the control forest) tends to be incomplete, thereby reducing diversity and richness – as for functional diversity measures, the chance that a high variety of leaf characteristics is present is low in highly disturbed systems.
- Community-level Weighted Means of trait values relevant for decomposition will change in the following way:
   - Leaf Nitrogen Content (LNC) (+). Consistent with a rapid growth strategy, LNC will be on average high in highly disturbed ecosystems to realize rapid photosynthesis and growth.
   - Specific Leaf Area (SLA) (+). With increasing disturbance, SLA will be higher. Plants under high disturbance regimes tend to invest in rapid growth to outcompete other species. One way to realize rapid growth leads is through high SLA leaves.
   - Chlorophyll concentration (+). With increasing disturbance, chlorophyll concentration will be higher. This is the case because environments rich of nutrients and light favour plants exposing rapid growth (so-called ruderal species) and photosynthesis over slow-growing plants. In order to realize fast growth and photosynthesis, a high chlorophyll concentration is needed.

3) Environmental influences

Variation in decomposition rate of standardized plant material such as filter paper (cf. Cornelissen 1996) between land use types is determined by abiotic conditions and

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decomposer community present. The following predictions, based on the abiotic conditions of each land use type, can be made:

- In primary forest land use types, the relatively cold (due to shaded conditions) but stable temperatures, combined with high moisture, lead to a high decomposition rate. In undisturbed forest, long-term stability could have resulted in a rich microbial life, enhancing decomposition rates.
- In secondary forest, the intermediate temperatures and intermediate moisture will cause an intermediate decomposition rate.
- In cultivated lands and pasturelands, the fluctuating temperatures (due to differences in irradiation during night and day) and low moisture will have a negative influence on decomposition rate. The small humus layer provides a habitat for only a small number of decomposer organisms. Cattle excrements could further lower decomposition rate, because the need for nutrients is not as urgent as in land use types that are mainly dependent on decomposition for nutrient input. Altogether, these land use types are characterised by a relatively low decomposition rate. However, leaves are subject to rupture by mechanical effects, such as rain drops that reach the soil without being slowed down by a large protective vegetation layer, and treading by cattle (pastures) or humans (fields); this could enlarge decomposition rate a bit.

4. Methodology

4.1 SITE DESCRIPTION

Fieldwork has been carried out in farming land and a moist tropical forest in northern Bolivia (province Guarayos). Altogether, my work took place in seven land use types, which are summarized in table 4.1.

Ecosystem	Land use type	Characteristics
Moist tropical forest	Control forest (CF)	No logging or silvicultural treatment
	Normally logged forest (NF)	• Harvest of merchantable trees (10 m³/ha) • Lianas cut off merchantable trees 6 months before logging
	Light silviculture forest (LSF)	As NF, but with additional silvicultural treatment: • Lianas cut off future crop trees (FCT) 2-5 montths before harvest • Post-harvest liberation of FCTs from overtopping non-commercial trees by girdling
	Intensive silviculture forest (ISF)	As LSF, but: • Double harvest intensity (20 m³/ha) • Double liana cutting intensity 2-5 months before harvest • Double intensity pf post-harvest liberation of FCTs from overtopping non-commercial trees by girdling • Soil scarification of felling gaps during logging
Agricultural systems	Secondary forest (SF)	Aged 5-15 years, abandoned by farmers after use as cultivated land
	Agricultural fields (AF)	Crops: vegetables, rice, potatoes, etc.
Pasture	Pastures (P)	Mainly grass vegetation; used for cattle ranging

Table 4.1. Land use types and some characteristics of land use and data on intensity. Land use ntensity is increasing downwards. Forest data are based on Verwer et al. *(2008).*

The moist tropical forest is the 100 000 ha timber concession of La Chonta, 30 km east of the town of Ascensión de Guarayos (15° 47'S, 62° 55'W). As a lowland moist tropical forest, it forms a transition between the tropical dry forest of the Chiquitanía and the Amazonian wet forest. The forest has an average canopy height of 25 m and counts 59 species per hectare.

Mean annual temperature is 25,3 °C. Annual precipitation in the region is 1,580 mm (range 1 269 – 1 871 mm, data collected at La Chonta sawmill from 1994 to 2006), with five months receiving <100 mm precipitation (May through September) and one month (July) during which potential evapotranspiration exceeds rainfall. About 30 percent of the canopy trees can be classified as deciduous during the dry season.

The forest has an altitude of approximately 400 m. The area is situated on the southwestern border of the Brazilian Shield, characterized by rolling hills with thin soil mostly derived from gneiss, granitic, and metamorphic rocks (Crochane 1973; Navarro & Maldonado 2004, both in Peña-Claros *et al.*, 2008). Soils have been described as inceptisols with 10–15 percent of the area being covered by anthropogenic soils (Paz 2003). Inceptisols are soils of relatively new origin and are usually arable and fertile.

This site is part of the Long-Term Silvicultural Research Program (LTSRP) of the Instituto Boliviano de Investigación Forestal (IBIF). Plots of the LTSRP are large (27 ha for this moist forest), replicated (12 plots in the moist forest in this case), and received one of four treatments varying in managing intensity.

The farming land is located close to the small town of Ascensión de Guarayos (13.360 inhabitants, Instituto Nacional de Estadística (INE) de Bolivia 2001). Half of the inhabitants are farmers (Gobierno Municipal de Ascensión de Guarayos 2007). The main part is subsistence farmer, producing agricultural products only for own use. My research took place on agricultural fields and pastures of these subsistence farmers. Popular crop species in the department of Santa Cruz are sugar cane, soya, corn, rice, cassava, banana and sun flower (INE 2000).

New plots were established in agricultural systems and pastures, measuring 100 * 50 m each. They are designed with the wish in mind to use them in a long-term research program. Of each land use type, three plots have been established so far. Secondary forests are all aged between 5 and 15 years. Cultivated lands differ in crop species. Pasturelands are being grazed by either cows or sheep.

4.2 Experimental design: measuring leaf traits and litter decomposition

4.2.1 *Functional leaf traits and litter decomposition*

Fieldwork was conducted during the dry season from May until July 2008. A total of 24 species was selected based on dominance in their land use type on the one hand and abundance of leaves in litter collections (see below) on the other. Among these species, there were four total shade-tolerant (ST) species, six partial shade-tolerant (PST) species, four long-lived pioneers (LLP), four pioneers (P), three palms (PA), two herbs (H) and one graminoid species (G). Sun-exposed plants were selected; seedlings were avoided.

Leaf traits had already been measured for most of the species obtained from the forest land use type (Rozendaal *et al.* 2006), and I used the same method as in the previous measurements. The following variables were tested on their relation to decomposition: leaf size and thickness, SLA, leaf resistance, LDMC, chlorophyll content, nitrogen concentration and phosphorus concentration. To complete the database on tree species, some additional parameters were measured as well; I will not report about these.

For most of the species, five individuals and 4-5 leaves per individual were measured. A minimum of five individuals and two leaves per individual was used. For palms, due to their large leaves and small total number of leaves, a minimum of three individuals, with two leaves per individual, were measured. These numbers of leaves are in accordance with suggestions by Cornelissen *et al.* (2003), as are methods used for measurement.

Collecting leaves
I collected whole twig sections with the leaves still attached and not removed the leaves until just before measurement. For herbaceous and small woody species, whole leaves from plants in full-light situations were taken (under minimal tree cover) in order to measure leaves under

conditions that were optimal and the most equal possible. For tall woody species, leaves from plant parts most exposed to direct sunlight during the sample period ('outer canopy' leaves) were selected. Leaves of true shade species, never found in full sunlight, were collected from the least shady places found.

I have chosen relatively young (presumably photosynthetically more productive) but fully expanded and hardened leaves from adult plants, if possible without obvious symptoms of pathogen and herbivore attack and without substantial cover of epiphylls. Opposed to the suggestions of Cornelissen *et al.* (2003), the petiole was not considered part of the leaf for size and SLA measurement, nor for the determination of dry weight, because in large part of the data I used this was the case, and because petiole characteristics could distort traits of the leaf laminae, especially in the case of the heavy woody petioles of palms. For compound leaves, the rachis was usually included, with the exception of palms.

Storing and processing of fresh leaves
The samples (twigs with leaves attached) were put in sealed plastic bags in which I breathed some air, so that leaves would close their stomata because of the high CO_2-concentration and remain water-saturated. If they could not be handled immediately, they were stored inside their bags filled with air, carefully placed in the shadow. Measurements took place as soon as possible after collecting, certainly within a few days.
For determining fresh mass, leaves were rehydrated during the night in plastic bags filled with moist tissue. Following the rehydration procedure, the leaves were cut from the stem and gently blotted dry with tissue paper to remove any surface water before measuring water-saturated fresh mass. Next, the other measurements were carried out. Each leaf sample was then dried in the oven (see under SLA) and its dry mass was subsequently determined.

Leaf trait measurement
- *Leaf size*, measured as the one-sided projected surface area of a single leaf or an average of leaf laminae, expressed in cm^2. Leaf size is measured per individual leaf lamina or as the total of leaflets plus rachis in compound leaves, without petiole for the majority of the data. In some cases, petiole is included in size measurements (because no other data were available). Leaf area was determined by scanning the leaves with a flatbed scanner and analyzing the pictures with pixel-counting software (ImageJ).
- *Leaf thickness*. Leaf thickness is the vertical distance between both leaf sides, expressed in mm. It was measured as close as possible to the middle of the leaf. Veins were avoided during the measurement.
- *Specific leaf area (SLA)*, the one-sided area of a fresh leaf divided by its oven-dry mass, expressed in $cm^2\,g^{-1}$. After area measurement, each leaf sample was dried in the oven at 60 ˚C for at least 72 h, and subsequently dry mass was determined.
- *Leaf resistance (punch force)*, a way to measure the physical strength of leaves: the force needed to perforate a leaf (fragment), expressed in N/mm^2. It is a good indicator of the relative carbon investment in structural protection of the photosynthetic tissues. It was measured with a penetrometer. The leaves were penetrated between the veins with the head of a nail; weight was put on the leaf until the nail penetrated the leaf. Punch force was calculated using the formula $F = (m_{water} + 0,0466) * 9,81 / (\pi * r^2)$, in which m_{water} is expressed in kg and r represents the radius of the head of the nail, which is 0,181 cm.

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- *Leaf tensile strength,* a measure related to leaf resistance, but for which not vertical strength, but force needed to tear the leaf horizontally apart is determined, divided by width of the leaf fragment (= length of the crack). Some researchers argue that what is mainly measured in that case, is the strength of the bond between leaf and vein. In the case of tensile strength, the length of the fragment runs parallel to the longitudinal axis (direction of main veins). The width of the leaf fragment depends on the tensile strength and varies between 1 mm (extremely tough species) and 15 mm (delicate species). The exact width of the leaf sample was measured. Then, both ends of the sample were fixed in a 'tearing apparatus'. Next step was to pull slowly, with increasing force, until it tore. (I tried to email S. Díaz in order to obtain the formula that should be used to quantify tearing force, with no response. In the results, # lines/ width (cm) is used.)
- *Leaf dry matter content (LDMC)* is the oven-dry mass (g) of a leaf divided by its fresh mass (g), expressed in g g^{-1}. Leaf dry matter content is related to the average density of the leaf tissues and tends to scale with 1/SLA.
- *Chlorophyll content.* Chlorophyll contents per unit area (CHL, in SPAD-units) were determined with a chlorophyll meter (SPAD-502, Konica Minolta, Osaka, Japan). Correspondence between SPAD values and independent measurements of chlorophyll concentrations is very good according to Anten & Hirose (1999), so that SPAD can be used as a reliable measure of chlorophyll content.
- *Nitrogen and phosphorus concentration of the leaves*. Leaf nitrogen concentration (LNC; N_{mass}) and leaf phosphorus concentration (LPC; P_{mass}) are the total amounts of N and P, respectively, per unit of dry leaf mass, expressed in %. Concentrations were measured using a elemental analyzer for a pooled sample of the leaves per species.
- *Litter nitrogen and phosphorus concentration* were measured in the same way as concentrations of living leaves. Pooled samples were used, also to determine litter dry matter content.
- *Litter carbon concentration (LitterCC).* Total amount of C per unit leaf dry mass, expressed in %. Concentrations were measured for a pooled sample of leaves per species.

Decomposition

Litter decomposition rate per unit time is defined as the dry weight loss as a percentage of initial dry weight after one and two months respectively. Decomposition was determined using the litter bag technique.

From the forest ecosystems, litter of a broad variety of species was gathered in all forest land use types during September 2007 – April 2008 and stored in IBIF's office in Santa Cruz. Traps were emptied every month. Litter was sorted per species and the most abundant species were chosen to be used in the experiment. Apart from these species, I gathered, prior to the experiment, freshly shed, senesced, undecomposed leaf litter of cultivated plants, grasses, palms and some pioneer species from the soil surface. Each species contributed 8 replicates of 1 g dry material each. Two harvests were conducted, one and two months after the start of the experiment. In total 25 spp * 2 harvests * 8 replicates = 400 litter bags were used.

Litter was air-dried, weighted, and sealed in bags measuring 10 * 15 cm, mesh size 2,5 mm. This mesh prevents the loss of litter fragments and allows the access of mesofauna (Swift *et al.* 1979, in Toledo Castanho & Adalardo de Oliveira 2008). Mesh size affects absolute decomposition

rates, but it does not affect significantly the ranking of the species with regard to litter weight loss (Cornelissen & Thompson 1997). Each bag contained leaves from only one plant species. A 5 g subsample per species was dried to establish the relationship between air-dry and oven-dry leaf mass.

Bags were brought to IBIF's investigation camp in La Chonta. On 24 and 25 May 2008, at the beginning of the dry season, they were buried at approximately 40-50 mm depth in a purpose-built outdoor leaf-mould bed that hosts a naturally developed decomposer community. A randomized block design was used. There were sixteen blocks, each measuring 0,5 per 0,75 m^2 (see figure 4.1).

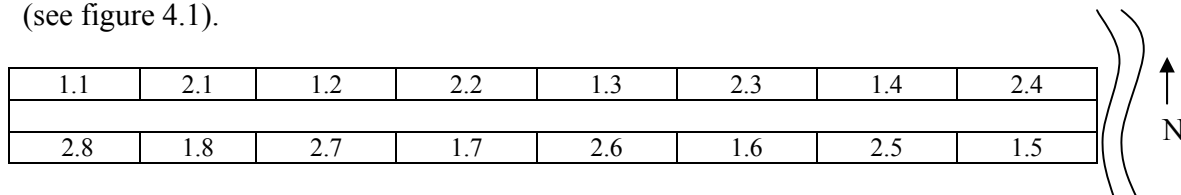| 1.1	2.1	1.2	2.2	1.3	2.3	1.4	2.4
2.8	1.8	2.7	1.7	2.6	1.6	2.5	1.5

N ↑

Figure 4.1. Randomized block design. First number indicates harvest, second number repetition.

Every day, alternating in the morning or afternoon, the leaf decomposition bed was watered, approximately 5 L per m^2 (30 L in total for the entire decomposition bed). The amount of water is in accordance with the average precipitation per day in La Chonta, averaged over a year (annual precipitation being 1580 mm). This is necessary, because the experiment took place during the dry season (which would have slowed down decomposition rate if no humid conditions were artificially provided).

After one and two months, half of the blocks was harvested. The content of the litterbags were gently brushed clean, the litter was oven-dried (65 °C) during 48 h and dry weight was measured. Mass losses were corrected for moisture content of air-dried samples.

4.2.2 *Plot establishment, dominance calculation and measuring diversity*

In cultivated lands and pastures, three plots were established in both land use types. In cultivated lands, parcels with different crop species were chosen. Pastures differed in terms of grazing regimes that were being applied. Plots measured 50*100 meter. To assess total cover of each species as calculated from relative abundance, line transects in combination with point quadrats were used (Mostacedo & Killeen 1997). Five transects, at 5, 15, ..., 45 meter – to avoid border effects – were drawn. Every 10 meter, species touching the transect or closer than 10 cm to the transect were noted. Thus, fifty point measurements were obtained for each plot. In pasturelands, trees were noted separately. To be able to compare tree cover with the grass mat beneath, crown widths were estimated by four independent observers and crown surface was obtained.

Relative abundance of each species was converted into cover for the entire plot. Groups of species, that were noted by their group name, e.g. 'herbs' and 'lianas', were excluded from the analysis, because these groups consist of a mix of different, unidentified species. Together with tree cover estimates, the plant species making up the 80 percent of the total plot cover could be determined. Only species belonging to the 80 percent most abundant were used in diversity calculations, because it was impossible to measure plant characteristics of all species within the time available. Moreover, it is generally found that the most dominant species contribute most to

ecosystem processes (MacGillivray *et al.* 1995, Díaz & Cabido 1997, Hooper & Vitousek 1997, Díaz *et al.* 1999, Garnier *et al.* 2004, Pakeman & Quested 2006). In this way it was possible to compare undisturbed moist forest with ecosystems heavily changed by land use, such as cultivated lands and pasture.

In forest ecosystems, it was assumed that herbaceous plant contribution to total plant cover was negligible. In secondary forests, tree height and DBH of all trees with DBH > 10 were measured In four sub-parcels measuring 10 * 10 m trees with 5 < DBH < 10 were measured (including their height). If trees had no stems at breast height, like many palms, height was measured at a lower point, the highest possible if some kind of stem could be observed. With DBH, basal area could be calculated, using the following formula: basal area = DBH^2 *0,78. Basal area per species was used to obtain species belonging to the 80 percent dominant in terms of basal area, which is a good measure for the species biomass. Of the 80 percent dominant species, leaf traits were measured in order to be able to calculate functional diversity.

As said before, the moist tropical forest concession of La Chonta consists of three blocks, in each of which four plots have been established that received one of the following treatments. The treatments represent a gradient in management intensity: an unharvested control plot, hereafter referred to as 'control' (C); a plot logged following practices stipulated by the Bolivian forestry law, hereafter referred to as 'normal' (N); a plot harvested as in the normal treatment but with application of silvicultural treatments at low intensity, hereafter referred to as 'light silviculture' (LS); and a plot harvested at twice the intensity of the normal treatment and with application of more intensive silvicultural treatments, herafter referred to as ' intensive silviculture' (IS) (Peña-Claros *et al.* unpublished). The more intensive treatments aimed to enhance the growth and regeneration of commercial individuals. Within these plots are four parcels of each 1 ha in which all trees > 10 DBH have been registered since 2001. DBH and height have regularly been measured. Since my newly established plots measured only 50*100 m, because cultivated lands are usually not as large as one hectare, 0,5 ha subplots had to be selected in La Chonta's database. Because there have only been measured three plots of cultivated lands and pastures, only the first parcel within each plot was used in my calculations. To guarantee random selection of species, I always took the left half of vertical subplots. By calculating basal area, I was able to see which species entered into the 80 percent dominance threshold in terms of biomass. Of these species, functional leaf traits were measured as described above.

Plant diversity and composition values were calculated per repetition; there are three repetitions per land use type. The following measures will be used to compare land use types in terms of species and functional composition and diversity; I will now provide definitions for each of these measures.
- *Species richness.* Number of species.
- *Species diversity.* Shannon's entropy will be used as a measure for species diversity, calculated as

$$H = -\sum_{i=1}^{N} p_i \log p_i$$

in which *p* is (number of individuals per species)/(total number of individuals), *i* is a species and *N* is the total number of species.

In the above species diversity measures, clustering takes place based on taxonomic classification on the species level. Another way of clustering is the identification of plant functional types (PFTs) according to vegetative and regenerative traits, leading to the possibility to calculate Functional Group Richness (FGR). One limitation is that FGR relies on an arbitrary decision about the level at which interspecific differences are functionally significant. FGR incorrectly assumes that species within groups are functionally identical, that is, species within groups are entirely redundant (Petchey *et al.* 2004). It also assumes that all pairs of species drawn from different functional groups are equally different. In other words, adding a species from a novel functional group to a community adds a unity to functional group richness, regardless of the identity of group(s) that are present and the identity of the novel group (Petchey *et al.* 2004). These disadvantages make that I will not use FGR as a measure for functional diversity.

The problems outlined were avoided by using traits of species as a foundation for estimating some component of the dispersion of species in trait space. Soft traits were chosen based on their correlation with decomposition. In plants, soft traits can be used to decrease the amount of effort required to compile functional information, so that a large data set can be obtained. This approach was chosen in my study. Soft traits, such as tissue density, leaf size and specific leaf area, provide indirect information on functionally important traits, like relative growth rate. Intuitively, you would say that the more traits are included, the better the results you obtain. However, Lepš *et al.* (2006) argue that diversity measured by using a single trait gives often the most ecologically relevant information, because (soft) traits tend to be correlated with each other.

Another point of attention is the weighing of traits, so that the biological variation within each trait is equally important (Petchey & Gaston 2006). Apart from log score, the most frequently used variable to standardize each variable is its Z-score, i.e. each variable would be transformed by

$$Z = (x - \bar{x}) / s_x$$

in which x is a trait value and s_x is standard deviation. I used Z-scores of relevant traits to calculate functional diversity when more than one trait was selected to determine the decomposition process.

When traits are considered, one should take into account that both trait range, trait number (together called functional richness), abundance evenness and regularity (together functional regularity) in trait distribution contribute to functional richness (see fig.3). I will only consider functional richness. Several measures exist that each capture one or more parts of functional richness. Functional attribute diversity (FAD) and functional diversity (FD) are two measures that comprehend the range of traits. Unlike FGR, FAD and FD require no arbitrary decision about the functional significance of interspecific differences among species, because they do not assign species to groups.

- *Functional Attribute Diversity (FAD)*. Estimated as the sum of distances between species in trait space (Walker *et al.*, in Petchey *et al.* 2004).
- *Functional Diversity (FD)*. Total branch length of the functional dendrogram that results from clustering the species in trait space (Petchey and Gaston 2002b), in Petchey *et al.* 2004).

Higher functional richness

Higher range of traits

Higher trait number

Higher abundance evenness

Higher regularity of trait distribution
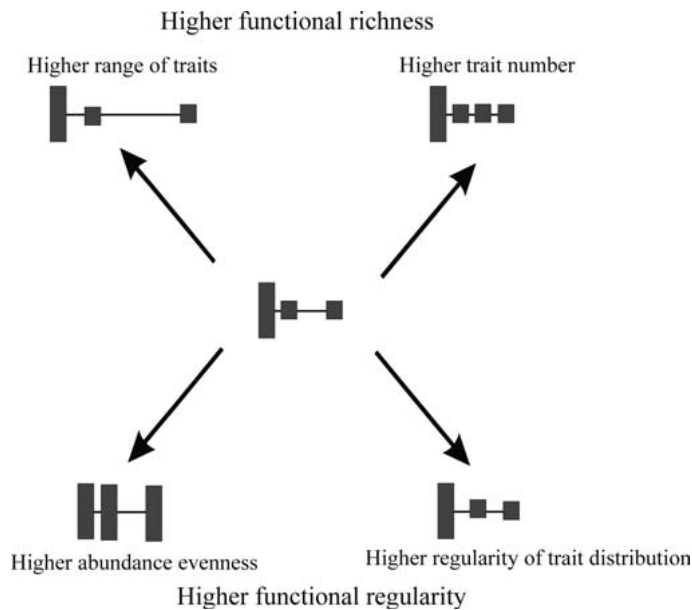
Higher functional regularity

Fig. 4.2. Influence of four functional diversity aspects on functional richness and functional regularity from a three species community (centre of the scheme). For each species, abundances are proportional to the size of the grey rectangles *and the functional traits are marked on a single axis corresponding to the functional traits. From Mouillot* et al. *(2005). (N.B. Functional regularity, as another aspect of functional diversity, is not part of the scope of my research, and was therefore not measured.)*

Difference between them is that FAD is sensitive to trait number, while FD is not (compare 'higher trait number' in fig. 3). This can be understood by considering species as points in n-dimensional trait space. Here, FD is a measure of the volume of space occupied by these points. Adding a species that lies at exactly the same point as an existing species causes no increase in the total volume occupied. In contrast, FAD is a measure of the total distance between all pairs of points. Here, adding a new species that coincides exactly with an existing species adds all the new pair-wise distances. Consequently, FAD is a function of both trait differences among species and the total number of species present, while FD is only a function of trait differences among species (Petchey *et al.* 2004). Analyses have shown that the qualitative behaviour of FAD and FD are not sensitive to a range of distance measures and cluster methods (Petchey and Gaston 2002b, in Petchey *et al.* 2004).

- *Extended FD.* Similar to FD, but now each entry of the dissimilarity matrix is loaded with a relative measure of abundance (e.g. frequency) before performing a dendrogram. If d_{ij} denotes the dissimilarity measurement between species i and j and p_i and p_j denote the relative abundance of each species, the extended FD is computed from a matrix with entries $d'_{ij} = d_i\,p_i\,p_j$. Like FD, the extended FD is computed as the total branch length of the functional dendrogram (Casanoves *et al.* 2008).

A measure that also holds both species relative abundances and a measure of the (taxonomic or functional) pairwise species distances is the diversity index termed quadratic entropy (Q), proposed by Rao (1982).
- *Rao's Q.*

$$Q = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij}\, p_i\, p_j$$

in which *p* is the relative abundance of each species, *i* and *j* are species and *S* is the total number of species; *d* is the trait distance between two species *i* and *j*.

The Rao coefficient is gaining currency as a good, efficient candidate as a functional diversity index, because it is a generalization of the Simpson's index of diversity, it is easy intuitively understandable, and it can be used with various measures of dissimilarity between species (both those based on a single trait, and those based on many traits) (several authors in Lepš *et al.* 2006). A disadvantage of Rao's Q, though, is that it may happen that Q is maximized at a reduced number of species, so that the disappearance of some species increases overall quadratic entropy (Shimatani 2001, in Ricotta 2005), because it takes into account relative abundances. Rao's Q is said not to satisfy set monotonicity, the requirement that diversity does not decrease when a new species is added to a given species set.

One problem that can not be overcome by any of the functional diversity measures is the sampling effect. The 'classical' sampling effect is based on the fact that the higher the species number in the assemblage, the higher the probability that a key species (a species that by its presence or absence drives the output of ecosystem functioning) is included. This is not only true for species number, but including the 'extreme' type usually also enhances functional diversity (Lepš *et al.* 2006). This means that one should be aware that the occurrence a large effect of high functional diversity actually can just be attributed to the presence of a key species.

As a last measure, representing functional composition, community-level weighted means of traits values (CWM) was used.

- *CWM*. Measured as

$$\text{CWM} = \sum_{i=1}^{N} p_i * trait_i$$

in which *p* is (number of individuals per species)/(total number of individuals), *trait* is the average trait value of a species, *i* is species and *N* is the total number of species.

4.2.3 Environmental influences

An additional experiment with a standard material – filter paper – was carried out to evaluate abiotic differences and differences in decomposer community between five land use types (undisturbed forest, intensively logged forest, secondary forest, cultivated lands and pastures). One gram of filter paper was sealed in bags of the same type and mesh size as in the litter decomposition experiment and attached to a 3 m long rope on equal distances. Bags were left in a representative spot on the soil in the five selected land use types. After a month (June-July 2008), the paper was collected and air-dried for over a week. Air-dried mass was determined.

Figure 4.3. The paper decomposition experiment. Litter bags with filter paper inside were left behind in five land use types for a month. Here: the experimental setting in pasture.

4.3 STATISTICAL ANALYSES

SPSS 15.0 was used to carry out the statistical analyses. When data were not normally distributed, a logtransformation was used. If a more normal distribution was obtained, logtransformed values were used.

Leaf traits and decomposition
To evaluate how leaf traits of species were associated, a Principal Component Analysis was applied using species as data points. Next, a correlation analysis was carried out, to test how individual traits were correlated with decomposition. Finally, to quantify which traits were the best predictors of decomposition, both forward and backward regression was done. Rice could not be used, because no plants were grown in the season during which I worked and therefore no green leaf traits could be measured. Braquirion, being at the end of its growth season and therefore showing an extraordinary low LNC, was also excluded from the analyses. Furthermore, I left some individual data points out of the analyses. The LDMC data point of *Ficus eximia* has been removed, because it showed an unrealistic low value. As for litter mass loss, there are arguments to exclude *Hura crepitans* (ochóo) and *Heliocarpus americanus* (baboso) from the analysis, because they were further decomposed than the other species at the start of the experiment. However, for the sake of higher reliability promoted by a higher species number, I decided to keep them.

Diversity
To calculate functional diversity indices (FAD, FD, Rao's Q and extended FD), the software application f-Diversity was used (Di Rienzo *et al.* 2008, version 21 February 2009). Species of which leaf traits had not been measured, were not used in these analyses. Diversity was compared among land use types using ANOVA or a Kruskal-Wallis test. Values were logtransformed if a more normal distribution was obtained (i.e., in the case of Rao's Q and extended FD). Because logtransformation was not possible for two out of three pasture plots – they had values of 0 – the value of third repetition was used for them as well.

Environmental influences
Differences in decomposition rates among land use types were evaluated using the non-parametric Kruskall Wallis test. To identify which land use types differed from each other, pair-wise comparisons were carried out using Mann-Whitney U.

5. Results

5.1 LEAF TRAITS AND DECOMPOSITION

Decomposition rates were measured for 24 plant species – both trees, palms, crops and a grass. After one month, average weight loss across species was 24 %, ranging from 7,6 % for *Pourouma cecropiifolia* (ambaivauva) to 76,1 % in the case of *Manihot sculenta* (yuca). After two months, plants lost an average 41,3 % in weight, with *Pourouma cecropiifolia* still being the least decomposed (12,6 %) and the peanut, *Arachis hypogea*, the most decomposed species (87,6 %). Figure 5.1 shows the percentage weight loss per species, grouped per land use type.
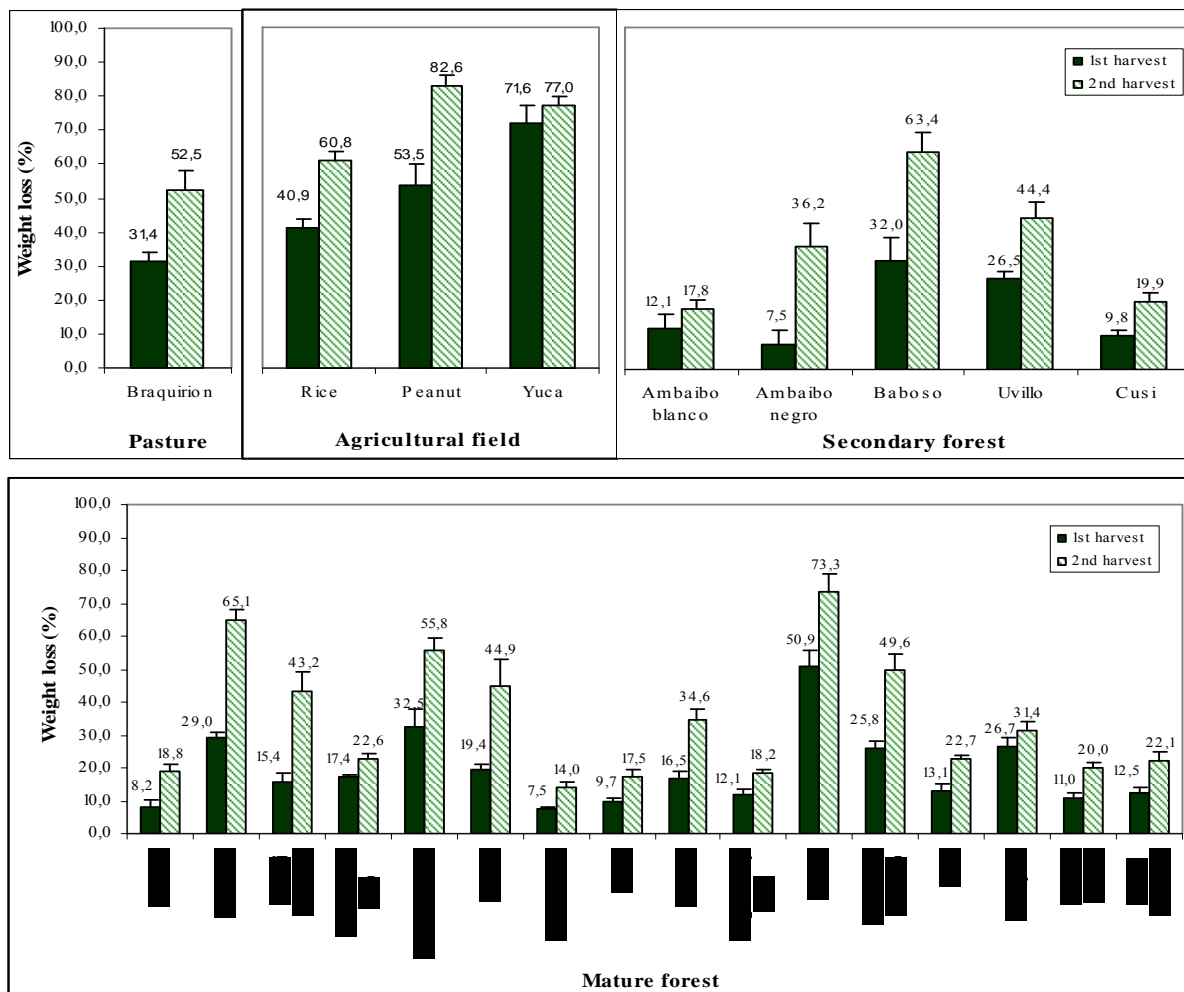
Figure 5.1. Weight loss (%) per species at harvests after one (filled bars) and two (hatched bars) months (N=8) . Species are grouped according to the land use type in which they are most common (pasture, agricultural field, secondary forest, mature forest). Species are part of different ecological guilds: the pasture species is a grass, agricultural species are a grass (rice) and herbs, secondary forest species are pioneers, apart from cusi, which is a palm, as are motacu and sumuqué. Apart from these, mature forest consists of long-lived pioneer, partial shade tolerant and shade tolerant species. Error bars indicate + SE.

Weight loss was always larger after two months than after one month. Across species, the percentage weight loss after one and two months was strongly correlated (r=0.89, n=24, P<0.001). In none of the bags, maximum weight loss was reached after two months. The ranking of the species was generally the same at both harvests, although there were some exceptions, the major being *Cecropia concolor* (ambaibo negro), which decomposition rate increased a lot in the second month compared to other species. Hereafter, I will use the weight losses as measured during second harvest, because interspecific differences were larger after two months, thus giving a better resolution.

If a mean decomposition rate per land use type is calculated based on the typical habitat of the species, then land use types are found to differ from each other almost significantly (ANOVA; F=3,2; P=0,06). A post-hoc Tukey tests shows that agricultural fields contain plant species that decompose faster than species from mature tropical forest (Tukey HSD=0,43; P=0,051) (see figure 5.2). Mature and secondary forest do not significantly differ from each other in terms of decomposition rate (Tukey HSD=0,04; P=0,95). Pastures could not be used in this analysis, because only one pasture species was included in the decomposition experiment.
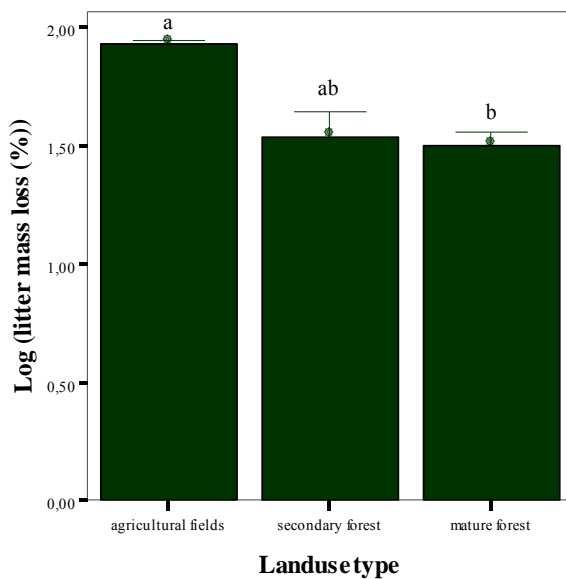

Figure 5.2. Decomposition rates of species belonging to three land use types: agricultural fields (N=3), secondary forests (N=5), and mature forest (N=16). Bars accompanied by a different letter are almost significantly different from each other (Tukey HSD=0,43; P=0,051). Bars indicate + SE.

A multivariate analysis (Principal Component Analysis, PCA) was carried out to explore the relations between leaf traits and decomposition rate (figure 5.3). Variance explained by the first component is 50,2 %, while the second component explains 13,8 % of the variance. Decomposition was added to the figure afterwards. Leaf resistance and tensile strength were found to be positively correlated (r^2=0,60; n=51; P<0,001. Figure 5.4). Because of a more complete dataset, leaf resistance was used in all analyses.

PCA shows that decomposition is likely to be most strongly and positively correlated with leaf and litter nitrogen and phosphorus concentrations and SLA. Furthermore, a negative correlation between decomposition and leaf resistance, density, volume, area, thickness, chlorophyll content, litter carbon concentration, and LDMC is shown. Leaf traits are also correlated among each other,

the traits last mentioned grouping at the other end of the main principal component axis than the group correlating with decomposition. Regarding weight loss for different ecological groups, figure 5.5 shows that some plant life forms are being grouped together based on their leaf traits. This is the case for palms, cultivated plants, shade tolerant and pioneer tree species.
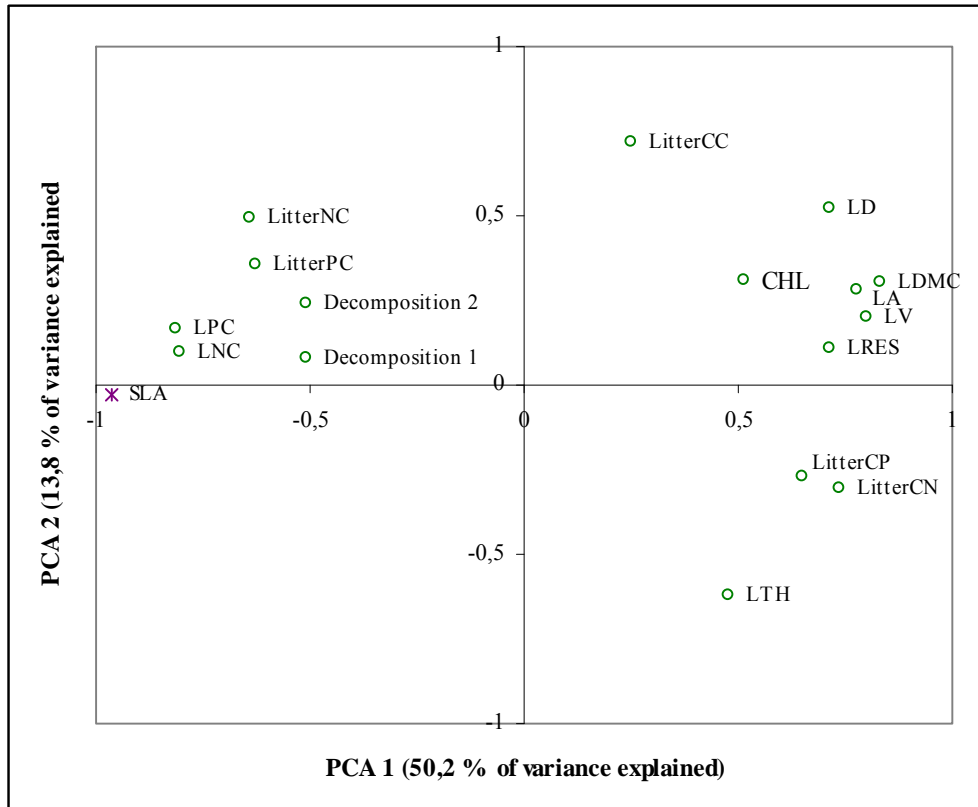

Figure 5.3. Principal Component Analysis of the 15 traits of 23 species (average of leaf traits of at least 2 leaves from 3 individuals). Decomposition after one month (1) and after two months (2) has been added to the figure afterwards. Abbreviations mean the following: LA = leaf area; LTH = leaf thickness; SLA = specific leaf area; LDMC = leaf dry matter content; LV = leaf volume; LD = leaf density; LRES = leaf resistance; CHL = chlorophyll concentration; LNC = leaf nitrogen concentration; LPC = leaf phosphorus concentration; LitterNC = litter nitrogen concentration; LitterPC = litter phosphorus concentration; LitterCC = litter carbon concentration; LitterCN = litter C:N ratio; LitterCP = litter C:P ratio.

Next, a correlation analysis was done between leaf traits and decomposition rates of the species (see table 5.1). One thing to note is the correlation between litter and leaf nutrient (nitrogen and phosphorus) concentrations. This means that the ranking of the species in terms of these nutrient concentration remains the same before or after leaf senescing and shedding. This is also shown by a regression of leaf and litter N and P concentrations (N: $r^2=0,32$; n=22; P<0,01. P: $r^2=0,39$; n=22; P<0,01; see figure 5.6).
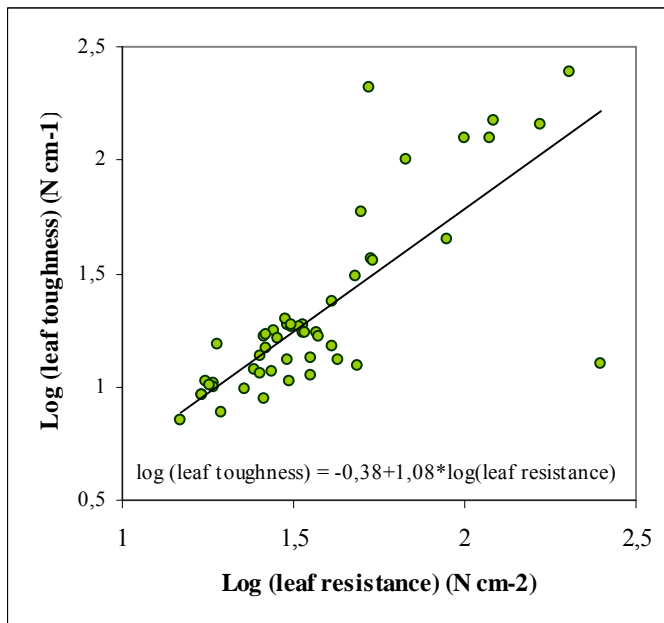
Figure 5.4. The relation between leaf resistance and leaf tensile strength for 51 plant species from seven different land use types (tropical undisturbed forest, tropical forest with three logging intensities, secondary forest, cultivated lands and pastures). $R^2=0,60$, $P<0,001$. Regression formula is shown in the figure. At least two leaves from three different individuals were used to measure leaf traits.
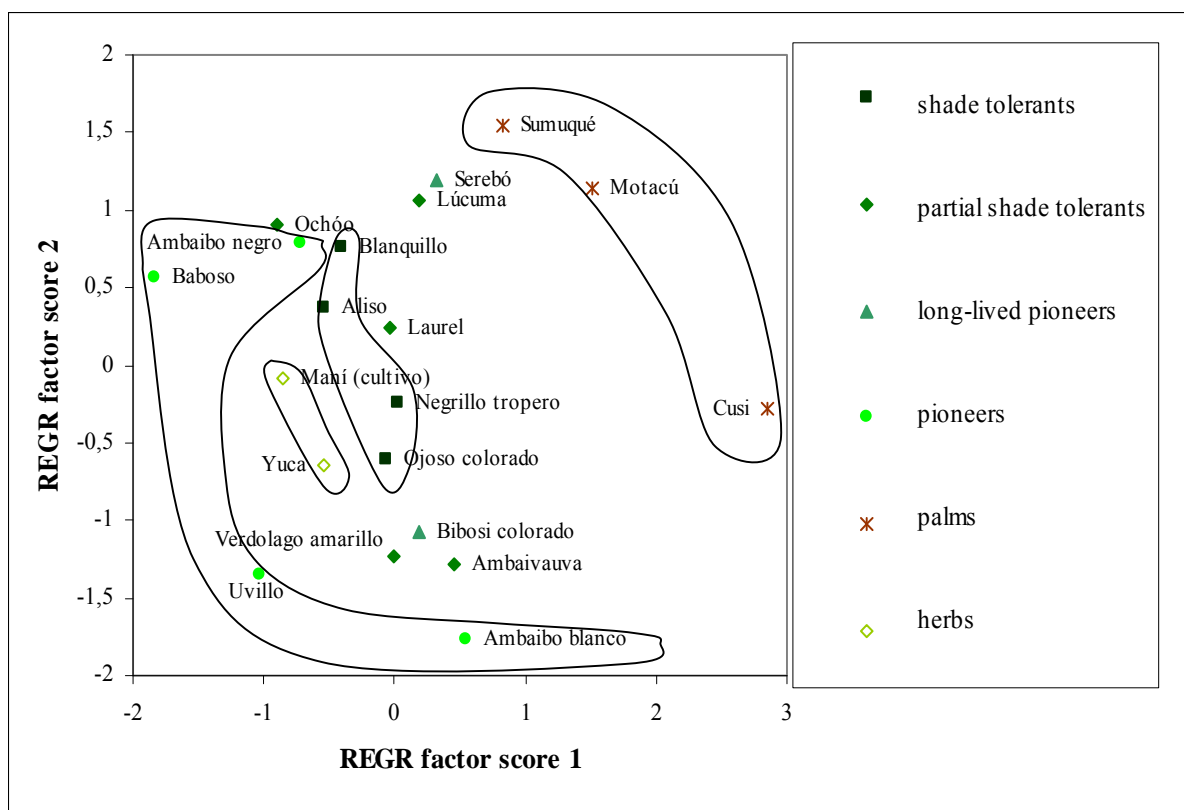
log (leaf toughness) = -0,38+1,08*log(leaf resistance)

Figure 5.5. Regression scores of 20 species, based on a PCA with 15 leaf traits. (Three species – Ficus eximia (bibosi matapalo), Ocotea sp. (negrillo negrillo), and Zanthoxylum sprucei (sauco amarillo) – were excluded, because leaf volume of these species was unknown.) Different shade tolerance classes and life forms are depicted by different symbols (see box on the right). Palms, herbs, pioneers, and shade tolerants are circled, because their regression scores are situated close together, thus featuring similar leaf traits.

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	LTH[*]	SLA[*]	LDMC	LV[*]	LD[*]	LRES[*]	CHL[*]	LNC[*]	LPC[*]	LitterNC[*]	LitterPC[*]	LitterCC	LitterCN[*]	LitterCP[*]	Decomposition1[*]	Decomposition2[*]
LA[*]	0,25	*-0,60*	**0,59**	<u>*0,99*</u>	**0,50**	**0,52**	0,38	-0,41	**-0,46**	-0,32	-0,32	0,27	0,40	0,35	-0,30	-0,14
LTH[*]		*-0,55*	0,04	0,40	-0,16	0,31	0,29	-0,41	**-0,47**	-0,32	-0,36	-0,20	0,28	0,33	-0,20	-0,31
SLA[*]			<u>*-0,81*</u>	<u>*-0,77*</u>	<u>*-0,74*</u>	*-0,55*	*-0,54*	<u>*0,82*</u>	<u>*0,76*</u>	**0,45**	**0,43**	-0,18	**-0,51**	**-0,44**	**0,52**	*0,55*
LDMC				*0,59*	*0,90*	*0,55*	0,36	<u>*-0,70*</u>	*-0,58*	**-0,42**	-0,34	0,27	**0,51**	0,36	**-0,45**	**-0,45**
LV[*]					**0,56**	**0,56**	**0,46**	**-0,50**	*-0,57*	-0,37	-0,37	0,27	**0,46**	0,40	-0,37	-0,25
LD[*]						0,40	0,38	*-0,64*	**-0,52**	-0,26	-0,21	0,37	0,37	0,25	**-0,46**	-0,40
LRES[*]							0,30	*-0,61*	**-0,46**	**-0,42**	-0,30	0,31	**0,51**	0,33	**-0,42**	-0,37
CHL[*]								-0,16	*-0,54*	0,03	-0,26	0,37	0,07	0,30	0,19	0,17
LNC[*]									<u>*0,66*</u>	0,56	0,38	-0,08	*-0,61*	-0,38	<u>*0,72*</u>	<u>*0,72*</u>
LPC[*]										**0,44**	*0,63*	0,04	**-0,44**	*-0,61*	**0,44**	0,39
LitterNC[*]											0,35	0,21	<u>*-0,96*</u>	-0,32	0,28	0,37
LitterPC[*]												-0,09	-0,38	<u>*-0,99*</u>	0,26	0,34
LitterCC													0,06	0,21	0,00	-0,01
LitterCN[*]														0,38	-0,29	-0,38
LitterCP[*]															-0,25	-0,34
Decomposition1[*]																<u>*0,89*</u>

Table 5.1. Pearson correlations between 15 leaf traits and leaf decomposition (after one (1) and two (2) months) for 23 plant species from a variety of land use types. Significant correlations are indicated in **bold** *(P<0,05),* ***bold and italics*** *(P<0,01), or* <u>***bold, italics and underlined***</u>*. Parameters flagged with * have been logtransformed before the analysis.*
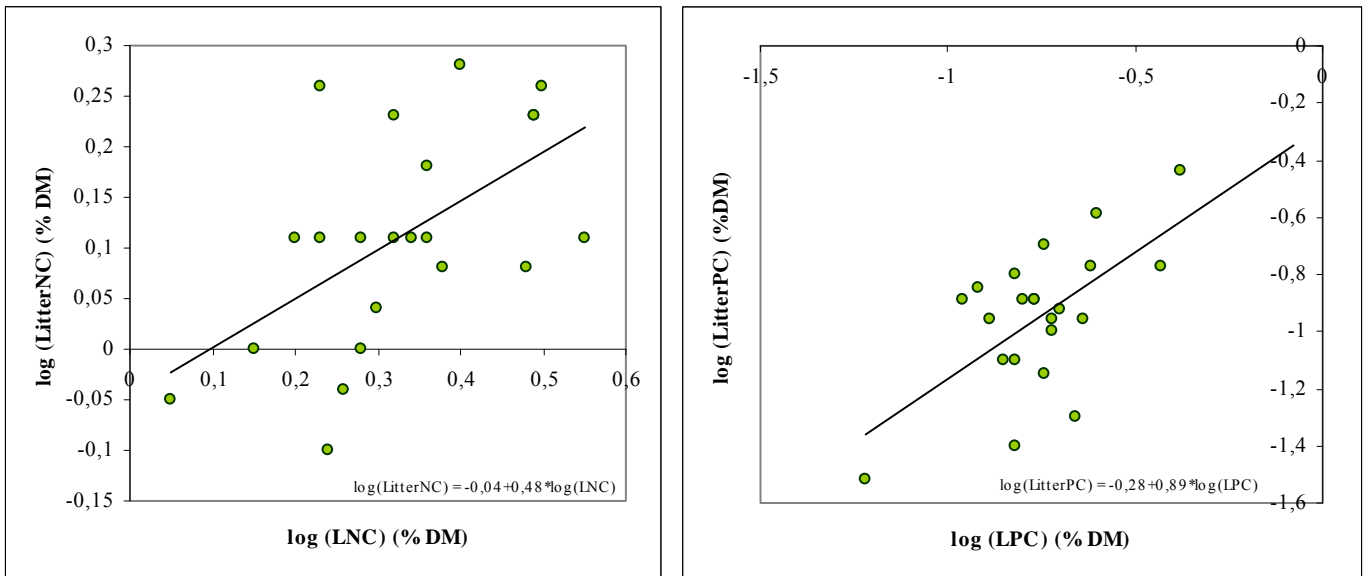
Figure 5.6. Correlation between nitrogen and phosphorus concentrations in fresh and litter leaves of 22 species belonging to seven different land use types. Regression shows that leaf and litter nitrogen and phosphurus concentrations are significantly correlated. Regression formulas are shown in the figure. Nitrogen: $r^2=0,32$; P<0,01; phosphorus: 0,39; P<0,01.

Decomposition rate is significantly associated with the quality of fresh leaves. Leaf nitrogen concentration (LNC: r=0,72; n=22; P<0,001) turned out to be strongest correlate, followed by specific leaf area (SLA: r=0,55; n=23; P<0,01) and leaf dry matter content (LDMC: r=-0,45; n=22; P<0,05). At first harvest, a significant correlation between leaf density (r^2=-0,46; n=23; P<0,05) and leaf resistance and decomposition (r=-0,42, n=24, P<0,05) is found, too, but these disappeared at second harvest (LD: r=-0,37; n=23; P=0,08; LRES: r=-0,40; n=23; P=0,06). Also, many leaf traits are mutually correlated (table 5.1).

With a multiple forward regression, I evaluated the effects leaf traits of a large variety of plant functional types have on decomposition, designing a model that can be used to predict decomposition rates in a wide range of Bolivian lowland plant species. Forward regression resulted in selection of only LNC as the leaf characteristic explaining most variation in decomposition rate (r^2=0,53; n=20; P<0,001; log(litter mass loss) = 1,07 + 1,45 log(LNC)). See figure 5.7). Things change when a backward regression is carried out: SLA and chlorophyll concentration are the variables that now are selected together as the best predictors of leaf decomposition (r^2=0,66; P<0,001; log(litter mass loss) = -3,96 + 1,26 log(SLA) + 1,67 log(CHL)).

There can be obtained other significant models though, which are able to explain decomposition more precisely. The most complete model obtained by backward regression which, as a model, is still significant at the 0,05 level includes the following parameters: leaf thickness, SLA, LDMC, leaf volume, leaf density, chlorophyll concentration, litterNC, LitterCC, and litter C:N ratio (r^2= 0,86; P<0,05). However, this model cannot be used to predict decomposition in practice, because it includes several litter parameters which are unknown for the major part of the species.
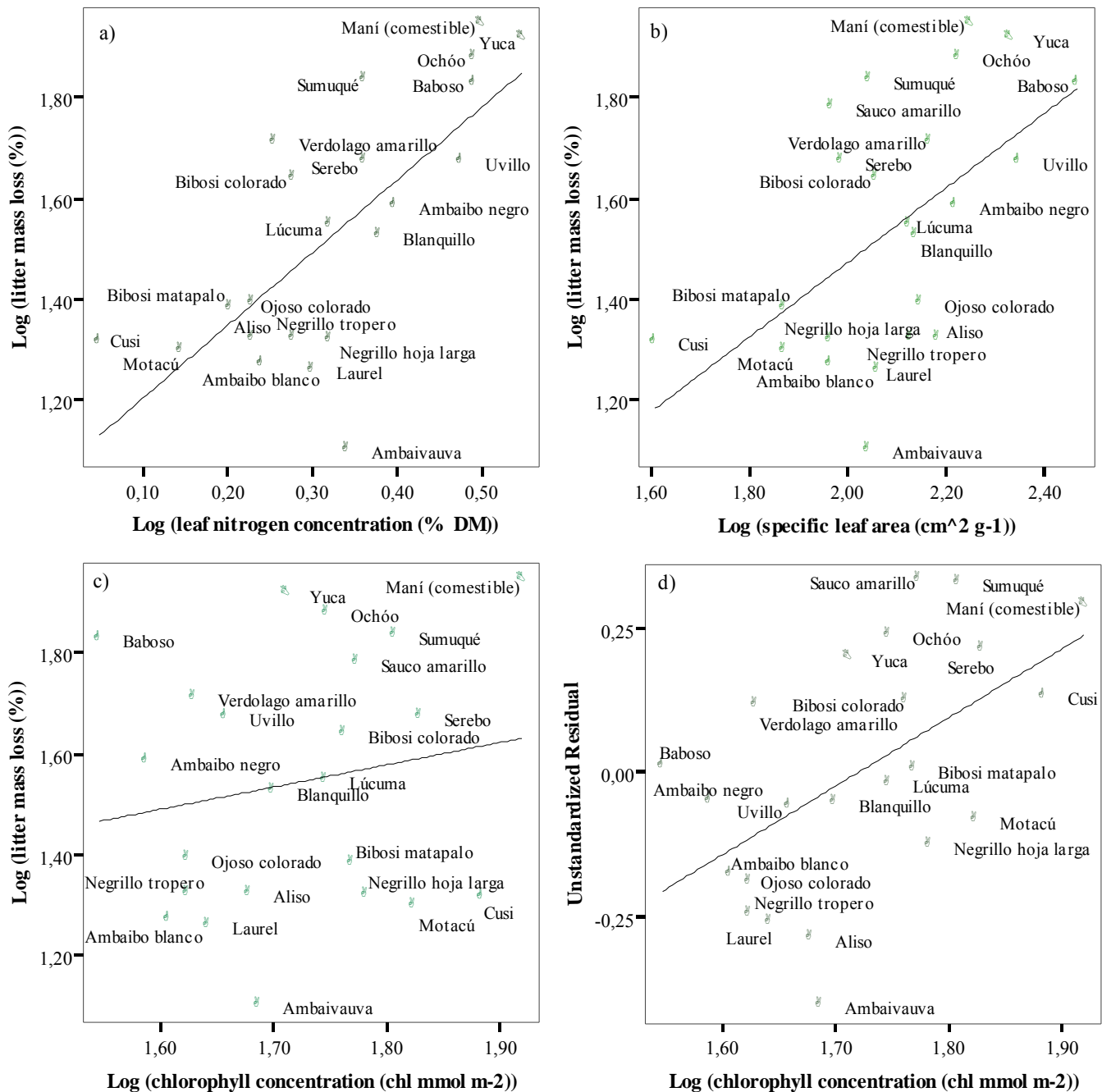
Figure 5.7. Percentage leaf litter mass loss after two months of incubation of 23 species as a function of the following traits of fresh leaves: (a) leaf nitrogen concentration (r^2=0,53; P<0,001); (b) specific leaf area (r^2=0,30; P<0,01);and (c) chlorophyll concentration (r^2 =0,03; P=0,43). The graph in (d) illustrates a regression between chlorophyll concentration and the residuals of (b) (r^2=0,31;P< 0,01). Linear regressions on the means were performed. Species that are dominant in different land use types, are indicated with a different symbol: circle = mature forest, square = secondary forest, triangle = cultivated land.

Individually, SLA still gives a significant relationship when a regression with decomposition rate is done (r^2=0,30; P<0,01). On the contrary, chlorophyll concentration turns out to be a rather poor predictor of decomposition (r^2=0,03; P=0,43) (see figure 5.7). However, when a regression is

performed using chlorophyll concentration and the residuals of the regression of SLA and decomposition rate, a significant positive relation is identied (r^2=0,31; n=23; P<0,01).

5.2 DIVERSITY

Based on the 80 percent dominant species, diversity could be calculated for every land use type, using a series of diversity measures.

Species richness and Shannon's diversity
The seven land use types are different in terms of species number (ANOVA F=13,0; P<0,001). The four mature forest land use types show a similar high species richness, followed by agricultural fields, secondary forest, and pasture (see figure 5.8). Shannon's diversity index differed also between land use types (ANOVA F=12,3; P<0,001). Pasture is the least diverse land use type. Also, secondary forest is less diverse than mature forest land use types. Diversity in agricultural fields is suprisingly high, larger than in secondary forest and not significantly differing from some of the mature forest land use types.
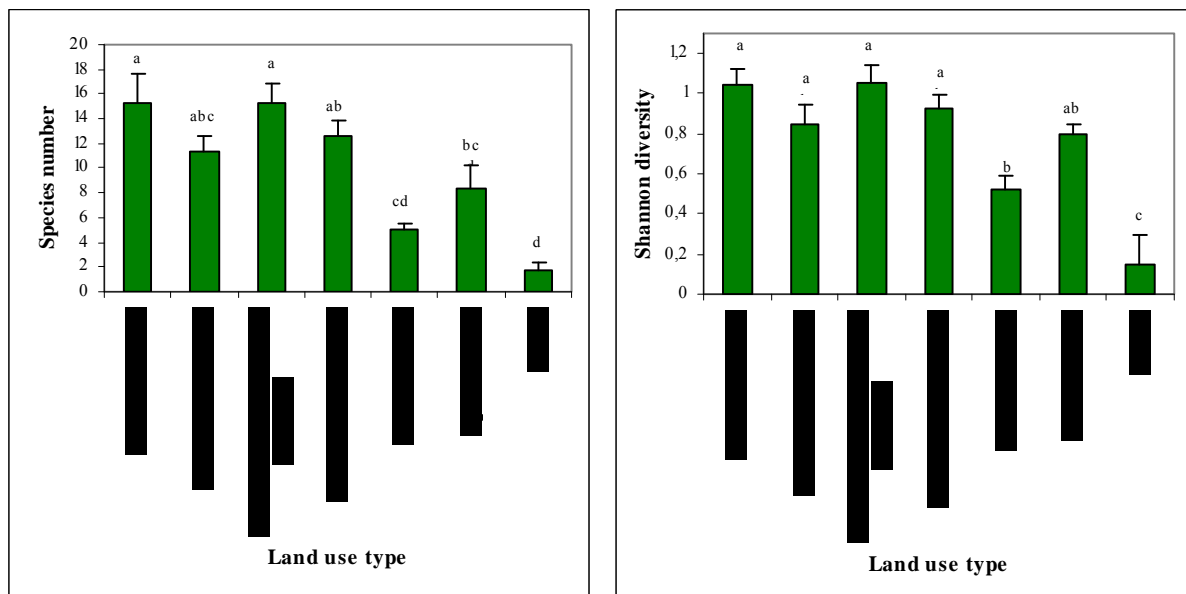

Figure 5.8. Mean species number (left graph) and Shannon's diversity (right graph) of plant communities of seven different land use types, each having 3 replicate plots measuring 50*100 meter each. The data are based on the 80 % most dominant species in each land use type. Different letters represent significant differences. Bars indicate + SE.

Functional diversity of LNC
First, functional diversity in LNC has been determined. To be able to compare between the different functional diversity measures, and to see whether some scarcely tested measures give useful and comprehensible output, I used four functional diversity measures: FAD, FD, Rao's Q and extended FD; the two last ones take abundances into account. For LNC, FAD differs between land use types (Kruskal-Wallis test; K=16,63; P<0,05). Forest plots have the highest FAD, followed by secondary forest and agricultural field. Pasture, with an FAD of zero, clearly has the lowest FAD (figure 5.9). FD tended to be different among land use types (Kruskal-Wallis test;

K=11,09; P=0,09). Pasture has another zero value on FD, because it only has one species for two repetitions, and only one species of which LNC is known for the third. There were neither significant differences of Rao's Q among the seven land use types (ANOVA; F=0,50; P=0,78). However, extended FD gives a significant result (ANOVA; F=20,75; P<0,001). All mature forest land use type have a lower extended FD than secondary forest and agricultural fields (Post Hoc Tukey HSD) (see figure). Pasture has not been included in this analysis, because logtransformed data were used and pasture had an initial value of 0.
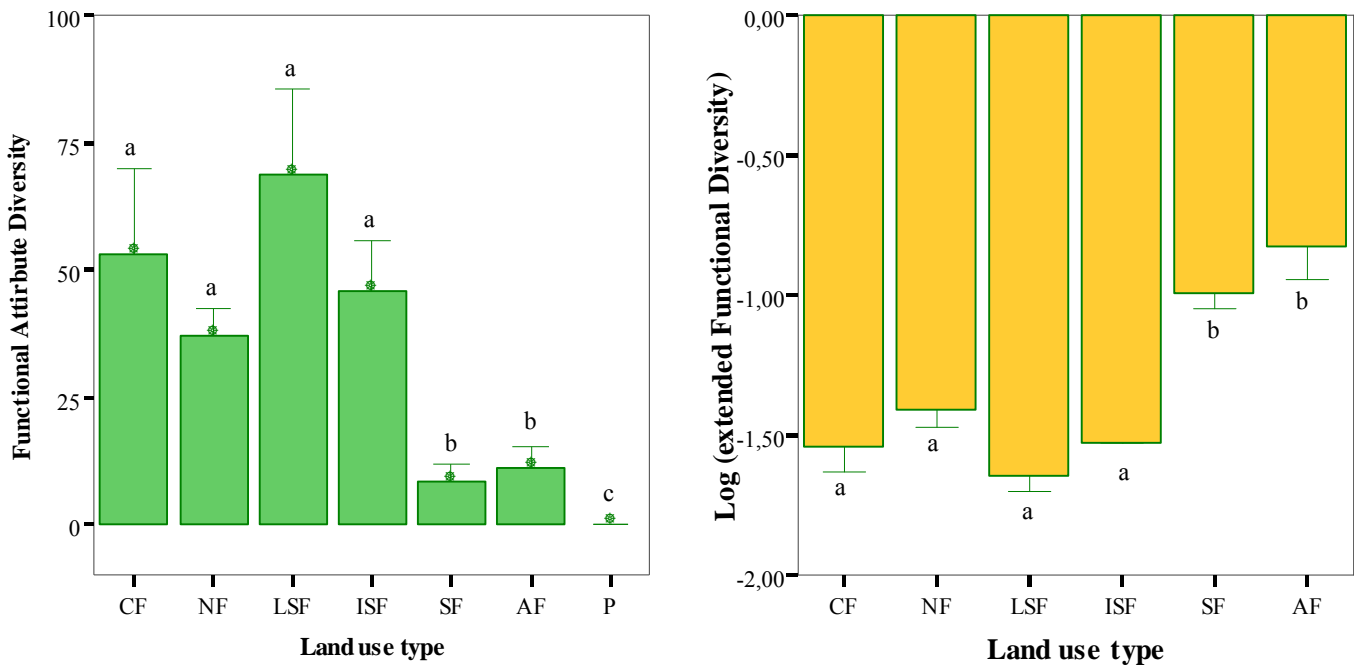

Figure 5.9. Functional attribute diversity (left) and weighted functional diversity (right) based on leaf nitrogen concentration of 80% species dominant in basal area (forest) or coverage in seven land use types (N=3). Means and + SE are shown. Letters indicate significant differences between land use types at the 0,05 level (Kruskal-Wallis and Mann-Whitney U test (left) and ANOVA and Tukey HSD (right). CF=control forest; NF=normally logged forest; LSF=light silviculture forest; ISF=intensive silviculture forest; SF=secondary forest; AF=agricultural field; P=pasture.

Functional diversity of SLA and chlorophyll
Looking at measures of functional diversity made up out of two traits – SLA and chlorophyll concentration – FAD is once again different between land use types (Kruskal-Wallis test; K=17,15; P<0,01). Normally logged forest has a lower FAD than the other forest land use types; secondary forest is less diverse than all mature forest systems. Pasture, as always, has the lowest FAD. FD differs significantly among land use types (ANOVA; F=7,87; P<0,001); pasture has a significant lower FD than all other land use type, being the only different land use type (Post Hoc Tukey HSD). Comparison of Rao's Q values results in another significant difference between the land use types (ANOVA; F=8,25; P<0,001). Secondary forest and agricultural fields have a higher diversity than pasture and mature forests (Post Hoc Tukey HSD). Finally, there has been found a significant difference between extended FD, too (ANOVA; F=49,67; P<0,001). Secondary forests, agricultural fields and pasture showed a remarkable higher diversity than the mature forest land use types (Post Hoc Tukey HSD). See figure 5.10.
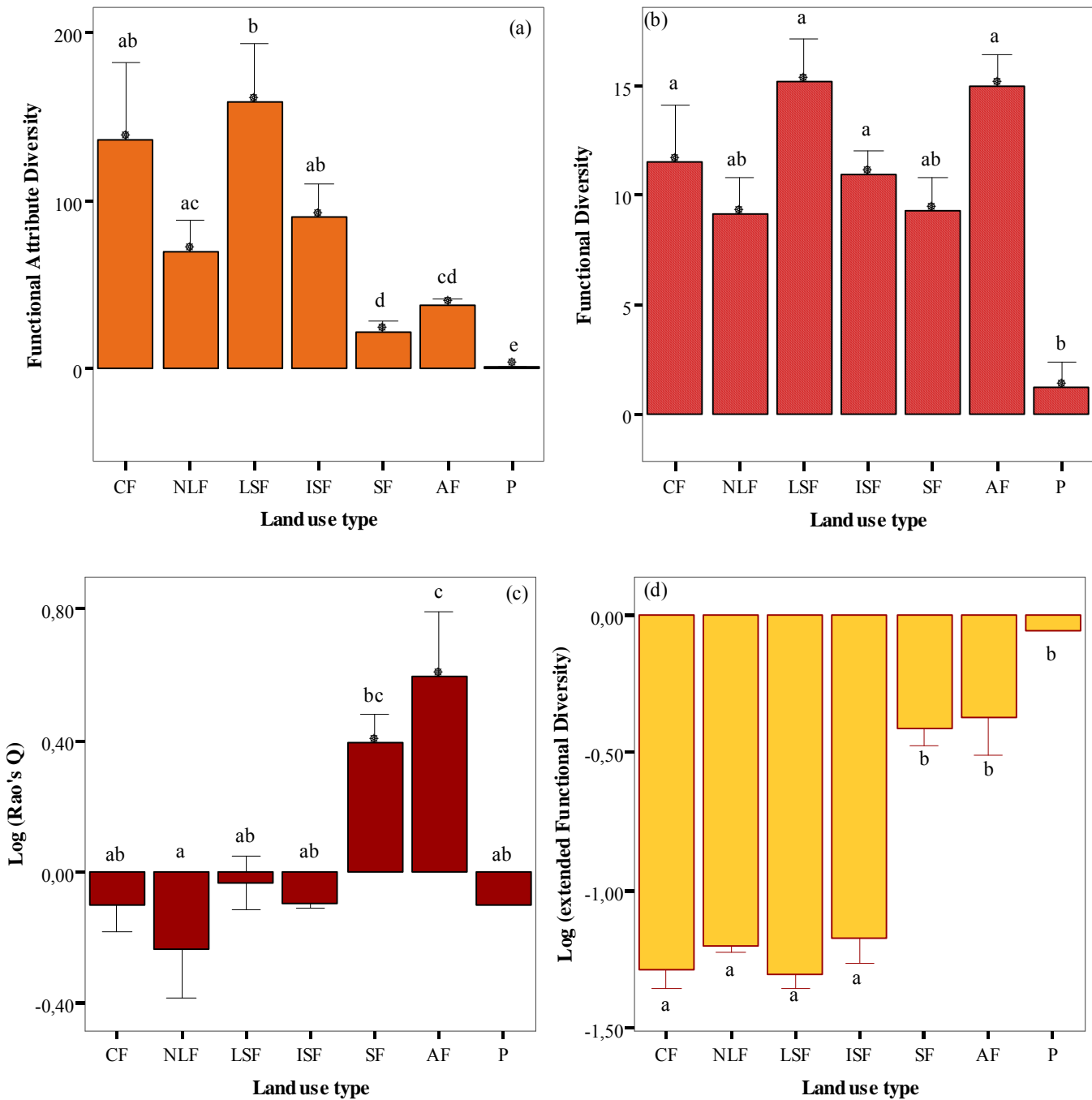
Figure 5.10. (a) FAD, (b) FD, (c) Rao's Q, and (d) extended FD of mean SLA and chlorophyll concentration (brought together in one functional diversity measure) of leaves of 80 percent dominant plants in seven land use types. Z-scores of leaf traits were used in order to obtain equal weights. Mean diversity values are shown with bars representing SE. Letters indicate significant differences ((a) Kruskal-Wallis and Mann-Whitney U test, (b-d) ANOVA and Tukey HSD. CF=control forest; NLF=normally logged forest; LSF=light silviculture forest; ISF=intensive silviculture forest; SF=secondary forest; AF=agricultural field; P=pasture.

Community-level Weighted Means of Trait Values
CWM has been calculated for LNC, SLA and chlorophyll concentration. For leaf nitrogen concentration, CWM is higher for agricultural fields and moist tropical forests than for secondary forests and pastures (Kruskal-Wallis; K=14,12; P<0,05). CWM of SLA is highest in pastures and agricultural fields, followed by the mature forest land use types and lowest in secondary forest (Kruskal-Wallis; K=17,81; P<0,01). In the case of chlorophyll concentration, secondary forest has the community with the highest mean, pasture the lowest (Kruskal-Wallis; K=13,97; P<0,05). For neither of these traits a difference has been identified among mature forest land use types. See figure 5.11.
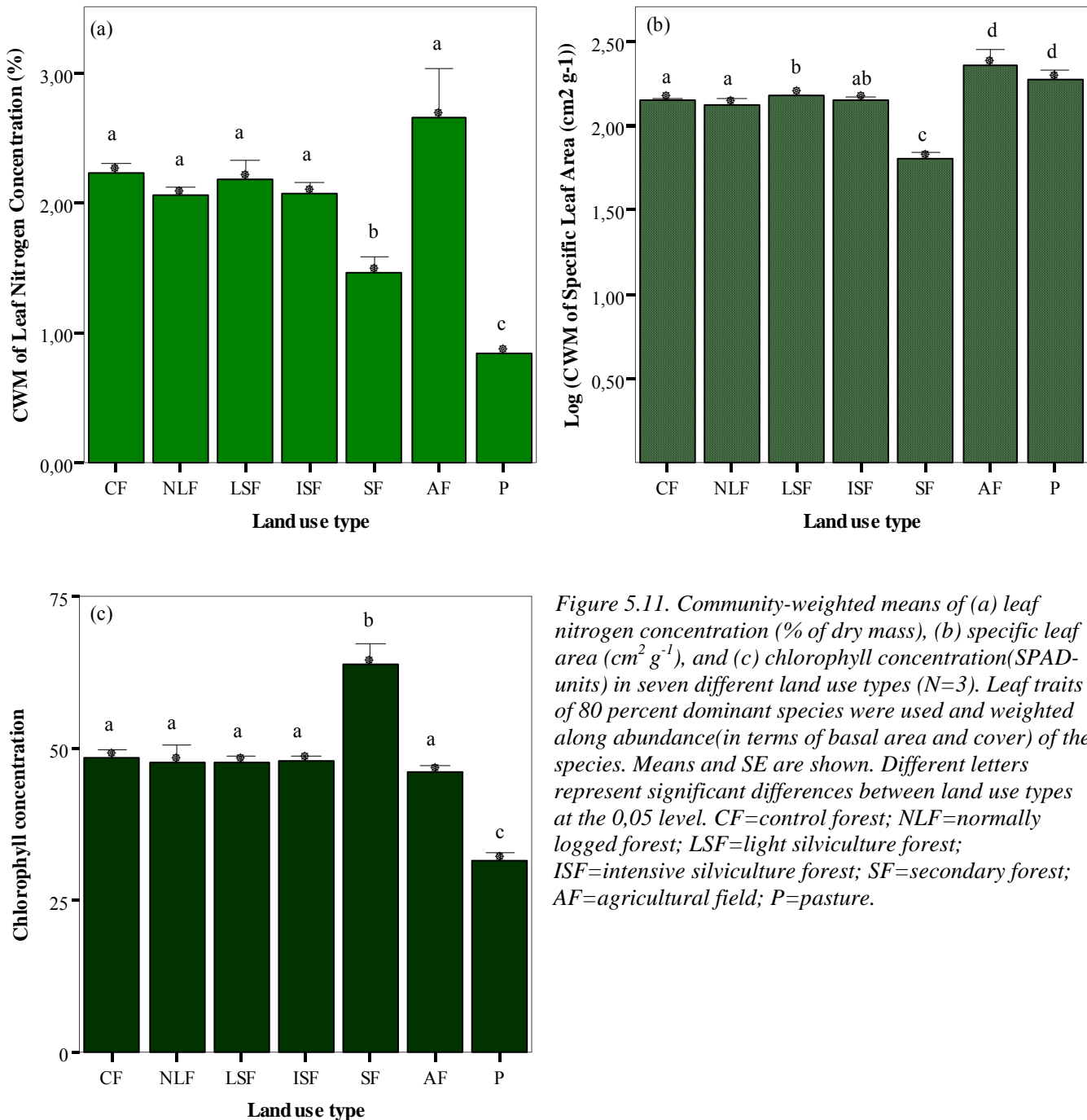

Figure 5.11. Community-weighted means of (a) leaf nitrogen concentration (% of dry mass), (b) specific leaf area (cm² g⁻¹), and (c) chlorophyll concentration(SPAD-units) in seven different land use types (N=3). Leaf traits of 80 percent dominant species were used and weighted along abundance(in terms of basal area and cover) of the species. Means and SE are shown. Different letters represent significant differences between land use types at the 0,05 level. CF=control forest; NLF=normally logged forest; LSF=light silviculture forest; ISF=intensive silviculture forest; SF=secondary forest; AF=agricultural field; P=pasture.

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Calculated decomposition rates among land use types
Among land use types, there are differences in decomposition rate as predicted by LNC
(Kruskall-Wallis Test, K=14,1; P<0,05). The plant community decomposing most slowly is
found in pasturelands (see figure 5.9). Pair-wise comparisons indicate that secondary forest,
which is dominated by the extremely low-N palm species *Attalea speciosa* (cusi), has a slower
decomposition rate as calculated based on LNC than mature forest land use types and agricultural
fields. Based on SLA and chlorophyll concentration, secondary forest turns out to be the
community with lowest decomposition rate, followed by normally logged forest and then by
forest with intensive silvicultural treatments, and agricultural fields having the fastest
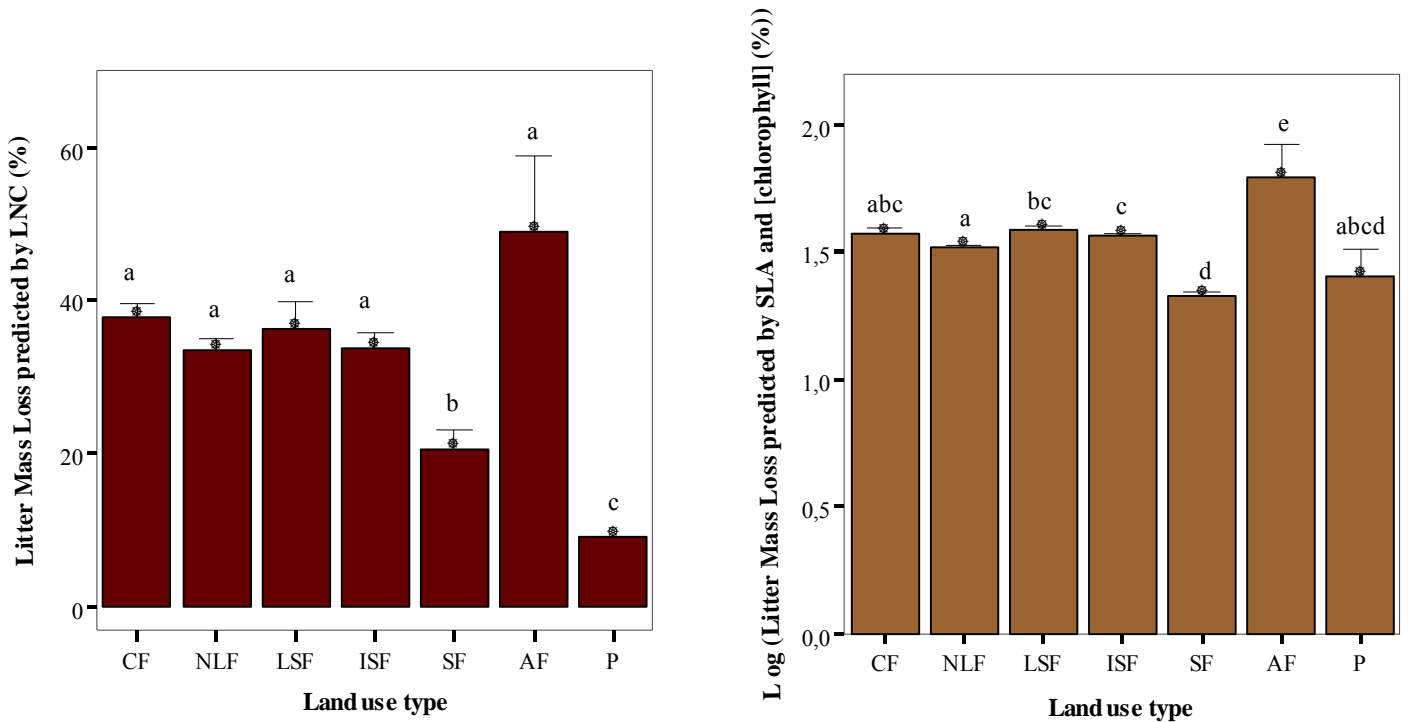decomposing community (Kruskal-Wallis; K=14,30; P<0,05) (figure 5.12).

Figure 5.12. Predicted litter mass loss (%) by either Leaf Nitrogen Concentration (LNC) (left) or SLA and chlorophyll (right). Regression coefficients that were used to calculate decomposition rate were previously determined in a decomposition experiment with 23 plant species from the same land use types as the ones that are compared here. Community-weighted means of trait values were used to calculate decomposition rates, of which N=3 repetitions per land use type were used. Means and SE are shown. Letters mark significant differences at the 0,05 level (Kruskal-Wallis and Mann-Whitney U test). CF=control forest; NLF=normally logged forest; LSF=light silviculture forest; ISF=intensive silviculture forest; SF=secondary forest; AF=agricultural field; P=pasture.

5.3 ENVIRONMENTAL INFLUENCES PER LAND USE TYPE

The rate of paper weight loss differed significantly amongst land use types (Kruskall Wallis test,
K = 10,35; P <0,05). Subsequent Mann-Whitney U tests indicates that a standard material
decomposed faster in intensively logged forest and secondary forest than in cultivated lands and
pasturelands (see figure 5.13). At harvest, it could be observed that termites (secondary forest)

and rodents (intensively logged forest) were likely to have eaten most of the paper in two bags in each of these two land use types.
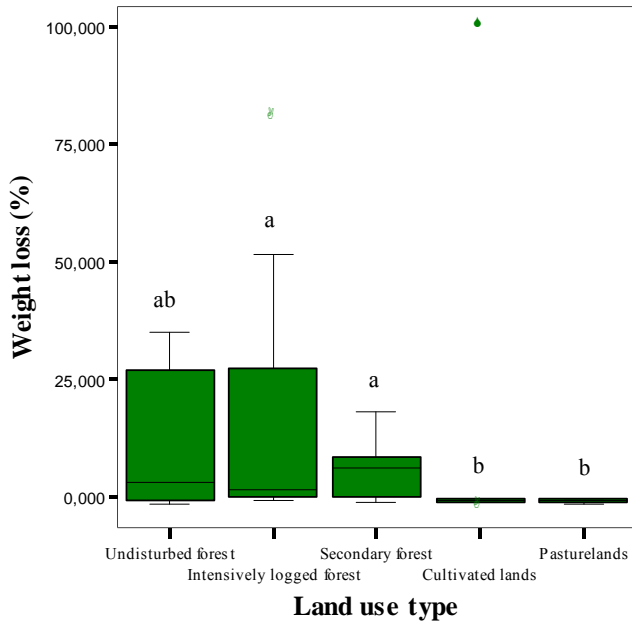

Figure 5.13. Box-plot of decomposition (weight loss in %) of paper samples incubated for one month during the dry season in five different land use types. Letters indicate significant differences between land use types. Bars represent 25 to 75% quartiles, whiskers represent ranges.

6. Discussion

Nutrient cycling is an ecosystem process playing an important role in sustainable land use. In this study, an effort is made to describe and predict nutrient cycling from plants to soil in several common tropical land use types. I aim at providing data that can incite a model showing the effect of land use on the pathway of nutrients between leaves and soil. An important step in predicting nutrient recycling is litter decomposition. It is now well established that decomposition of leaves depends on certain leaf traits, according to experiments in different parts of the world. Still, these traits have remained unknown for American tropical plant species, especially agricultural species. This experiment was designed to shed light on the relation between leaf characteristics and decomposition rate.

Methodological considerations
The relatively short incubation time (one and two months) turned out to be sufficient for ranking the species based on their decomposability. However, if I had continued the experiment longer, a better resolution at the slow end of the decomposition spectrum could have been captured. Disadvantage is that in that case, too large a portion of the litter would have reached (near-) maximum mass loss, reducing the resolution at the faster end of the species spectrum.

Another word of caution concerns the fact that for part of the species leaf traits have been measured between November 2004 and February 2005, while others have been measured during the southern-hemisphere winter (May-July) of 2008. The environmental situation could differ between these years, and especially during the different seasons. Also, since I gathered some leaves near the small town of Ascensión de Guarayos, whereas forest leaves were collected 60 kilometres away from Ascensión, soil and environmental conditions could have been different. Species traits are the combination of the expression of genotypic and environmental factors, and some leaf traits are likely to have been modified by the environment. Nevertheless, traits are probably more representative than when species were grown together in an artificial environment, because they are sampled in the species' typical habitats. One should also be aware that measurements have been carried out by three different researchers. It is impossible to guarantee that this has not had any influence on the results, even though standardized ways of measurement have always been used.

Regarding the use of a penetrometer as a measure for leaf strength, it can be concluded that a penetrometer gives an adequate measure, as it is highly correlated to previous measurements done with a tearing apparatus. This invalidates the idea that a penetrometer would merely measure strength of the leaf tissue, whereas a tearing apparatus quantifies attachment to the nerves – both measures are in fact strongly related. This means that punch force can be used as a valid measure for leaf strength. Moreover, in a world-wide meta-analysis it was found that a penetrometer gives a better measure for leaf strength than a tearing apparatus (Onada *et al.*, in prep.).

The leaves used in the decomposition experiment have been buried in the state in which they were found. This means that some composed leaves, for example peanut leaves, had their rachis

attached, while others, such as *Schizolobium parahyba* (serebó) were decomposed without rachis. Although palm leaves fall down as a whole, their woody rachae have not been included in the experiment. This could have lead to an overestimation of their decomposition rate.

For some leaves I had to tear off some parts in order to fit them into the bags. This might have influenced decomposition rate, because a damaged leaf could be more vulnerable to the breakdown by decomposers. There is, however, no evidence of a smaller leaf decomposing faster – my data did not show a significant (negative) relationship between leaf area and decomposition rate either. However, one should take into account that this might be caused by the small variation in leaf size in my experiment (because they were torn in order to fit into the bags), and because litter often does not consist of only whole leaves, influencing a species' average leaf size.

Another factor that could have influenced decomposition rate is that some species were decomposed in their own habitat (the forest species), while species belonging to cultivated lands, pastures and secondary forests were transferred to the alien habitat of mature tropical forest. The decomposition bed was even covered with litter derived from the neighbouring mature forest. Presence of the native community can both lead to positive (Toledo Castanho & Adalardo de Oliveira 2008) and negative (Parsons & Congdon 2008) influence on decay rate. This can be caused by either the presence of a species' indigenous decomposer community, or the absence of protection against the decomposer community present or unfavourable state of a species' native habitat. In future, Geovana Carreño will carry out experiments similar to mine in the other land use types in order to determine such environmental influences.

Leaf traits as predictors of decomposition
My results have provided support for the idea that the link between traits of living leaves and decomposition exists in a broad range of Neotropical plant families. In the forward multiple regression that I performed, leaf nitrogen concentration (LNC) was selected; in the backward multiple regression, specific leaf area (SLA) and chlorophyll concentration together turned out to be the best predictors of decomposition rate.

The strong relationship between decomposition rate and leaf nitrogen concentration does not come as a surprise: it has already been found in other studies (Santiago 2007, Cornwell *et al.* 2008, Fortunel *et al.* 2009). It has been suggested that nitrogen has a stimulatory effect on decomposer communities (Palm and Rowland, 1997, in Pérez-Harguindeguy *et al.*, 2000). A large number of studies report about the relationship between a ratio of N and another element (like lignin or C) and decomposition rate (Cornelissen 1996, Alvarez-Sánchez & Becerra Enríquez 1996, Pérez-Harguindeguy *et al.* 2000, Parsons & Congdon 2008, Kurokawa & Nakashizuka 2008). Such a ratio would combine concentrations of two elements that are considered relevant for decomposition. However, due to the absence of other chemical parameters, such correlations could not be verified in my experiment.

Besides, correlations between concentrations of other chemical elements (e.g. P, K, total base content, lignin, cellulose, and tannins) and decomposition are abundant in literature (Cornelissen & Thompson 1996, Alvarez-Sánchez & Becerra Enríquez 1996, Vaieretti *et al.* 2005, Cornwell *et al.* 2008, Parsons & Congdon 2008, Kurokawa & Nakashizuka 2008). The other chemical candidate measure in my research would be phosphorus concentration; however, regression did not show a significant relationship. This is quite remarkable, because P is often the most limiting

nutrient to decomposition processes in tropical forest (Cleveland et al 2002. The generalization on phosphorus as the most limiting element is based on an experiment in Costa Rica, where tropical forest are located on extremely old, highly weathered soils, as is the most common for tropical forests (Cleveland *et al*., 2002). However, the soils of the forest of La Chonta have been described as inceptisols: soils of relatively new origin and usually fertile. Like in temperate and high latitude systems, nitrogen has turned out to be the most limiting element in this tropical forest. So, these soils are an exception to the rule that tropical forest soils lack phosphorus.

To see whether N or P is limiting, N:P ratios of both fresh (13,7) and litter (12,8) leaves can be calculated. A ratio smaller than 14 indicates an N limited system, whereas leaves with N:P higher than 16 are considered P-limited (Wood *et al.* unpublished). Thus, limitation by N is once more confirmed. Moreover, a decrease in leaf N:P during senescence, as is the case in the leaves that I used, indicates greater N resorption relative to P. This points at the fact that N is more limiting than P, and therefore selected for during resorption. Indeed, N retranslocation, calculated as litter NC:LNC and averaged over all species, is above average (63,2 %) as compared to Raghubanshi (2008), who published on resorption efficiency in woody species of Indian dry tropical forests.

Finally, Santiago (2007) concluded that N seems to be most important in early stages of decomposition, whereas P is important later on. That is, decomposers first select on nitrogen concentration, but as N concentration decreases, they switch to P at a certain point. My experiment might not have lasted long enough to detect P influences on decomposition. The existence of several stages in leaf decomposition was brought to light by Vaieretti *et al.* (2005), who distinguished a (rapid) first phase in which the sum of recalcitrant components (lignin, cellulose and hemicellulose) and SLA were the best predictors for percentage remaining dry weight, and a (slow) second phase lacking a predictor among the traits measured. As the rapid phase consisted of 70 days, and my experiment did not even reach such a period of time, it could also be possible that there are different stages in decomposition within this first rapid phase, each with their own predicting leaf traits.

The ranking of leaves in terms of their LNC and LitterNC is roughly the same. Thus, LNC is a good representative of the actual nitrogen concentration at the moment of decomposition; the same is true for phosphorus. Opposed to the expected very strong relationship between litter concentrations and decomposition, no results were obtained here. One explanation for this might be the altered nutrient concentrations in the leaves at the start of the decomposition experiment; in some of them, decomposition had already slightly begun. So, LNC was a better representative than LitterNC for the overall position of a leaf in the economics (and decomposability) spectrum. Also, a higher resolution of LNC has been obtained, leading to more precise predictions of decomposition rates.

Litter carbon concentration was not found to correlate with decomposition rate. A reason could be that carbon does not have any effect on decomposers – it does not attract, neither repels them. This would mean that decomposers are guided by either nutrient concentrations or density of dry mass (as we will see below), and that carbon, which may be present in long chains, is not more difficult to process than other elements. Studies in which carbon was found to play a role in decomposition, worked with ratios indeed (Pérez-Harguindeguy *et al.* 2000, Kurokawa & Nakashizuka 2008). Still, my result is quite remarkable, given the negative relation between lignin (an element mainly consisting of carbon) and decomposition rates that has widely been

found previously (Cornelissen 1996, Vaieretti *et al.* 2005 Parsons & Congdon 2008, Kurokawa & Nakashizuka 2008). To explore the exact relationship between carbon and decomposition, it would be better to include lignin as an example of an element with long carbon chains in a next study.

A backward multiple regression leads to the selection of SLA and chlorophyll concentration as the best predictors of decomposition rate. SLA is a well-known leaf trait predicting decomposition (Cornelissen *et al.* 1999, Vaieretti *et al.* 2005, Santiago 2007). In fact, SLA is a measure for either leaf density or leaf thickness; decomposers need less time to process less material per unit area, or to process thinner leaf material that is easier to access. Apart from accessibility, SLA incorporates elements of physical toughness. Therefore, SLA successfully captures the trade-off between high levels of defence at one end of the spectrum, and high photosynthetic potential at the other. The same is true for chlorophyll concentration. It enables high photosynthetic rates and is therefore connected to growth rate; a high concentration is typical for a rapid leaf life cycle. As far as I know, the relation between chlorophyll concentration and decomposition rate has never been established, but is not very surprising for who takes into account that fast leaf growth usually goes together with poor defence.

With these two parameters that are familiar to the leaf economics spectrum, one can conclude that plant growth rate is connected to decomposition rate (Santiago 2007). Grime *et al.* (2006) suggested litter decomposability to be partly a consequence of adaptive features of living leaves affecting their palatability. Due to a high decomposition rate, nutrients are available in the environment and enable a high growth rate of especially young plants. So, decomposition makes it possible to connect both ends of the plant life cycle, connecting grown-up plants with new recruits. It seems to be true that plants lead a meaningful afterlife.

LDMC has often been associasted with decomposition (Kazakou *et al.* 2006, Cortez *et al.* 2007, Cornwell *et al.* 2008, Kurokawa & Nakashizuka 2008, Fortunel *et al.* 2009). In my experiment, this relation has been confirmed. A high percentage of dry matter makes decomposition to go slower. SLA and LDMC seem to be comparable measures, both representing leaf density in a certain way; indeed, they are highly correlated for the species in the decomposition experiment (R=-0,80; n=22; P<0,001).

The correlation at first harvest of leaf resistance and decomposition rate (r=-0,42, n=24, P<0,05) is in line with this idea, resistance partly being the result of a denser leaf. The presence of chemically resistant elements like lignin and cellulose makes decomposition even go slower (Cornelissen 1996, Vaieretti *et al.* 2005 Parsons & Congdon 2008, Kurokawa & Nakashizuka 2008). A relation between leaf strength and decomposition is consistent with other publications (Cornelissen *et al.* 1999, Pérez-Harguindeguy *et al.* 2000, Kurokawa & Nakashizuka 2008).

The difference in results in the forward and backward multiple regression indicates that leaf traits are not standing apart, but intimitaly correlated. In other words, nitrogen at the one hand and SLA and chlorophyll concentration at the other are acting as a fine summary of a whole range of traits. They are the best predictors, but not the only ones that have to do with decomposition. Correlation arises because of similarities in function in the life history of a plant. The fact that all traits are interwoven contains a message: it forms evidence for the plant strategy hypothesis as

formulated in the introduction (Cornelissen *et al.* 1999, Santiago 2007, Cornwell *et al.* 2008). Plant strategy, thus, involves decomposition.

6.2 LAND USE AND DIVERSITY

Methodological considerations

Comments regarding the measurement of functional leaf traits have already been mentioned above. Here, I will concentrate on plot establishment, dominance calculation and the measurement of functional diversity. It would have been advisable to establish a higher number of plots in secondary forest, pasture and cultivated lands, so that differences between land use types could better be proven. In the pasture plots, two out of three plots consisted of only one dominant species, which might not be representative for the pasture vegetation in the area. In cultivated plots, a larger number of plots could have captured more variation in crop species – for example, no rice was encountered, which nevertheless is a frequent crop species in the investigated area.

For agricultural fields and pastures, the point quadrat method was used. Plants that touched a 3 meter high stake were registered; this made that the trees and palms were omitted. Afterwards, crown widths of the most abundant tree and palm species have been estimated by four researchers, to include these higher species in the calculations that would determine cover of each species. These estimates are likely not to be very precise. It is preferable to use a method that includes tree species at once. Another recommendation is not to note functional groups only (like 'herb', 'fern'), but to identify each plant on the species level. Now, species belonging to functional groups were excluded altogether, because these groups were assumed to contain a variety of species.

I used cover as an estimate of abundance in agricultural fields and pastures, which appears appropriate when aspects of plant horizontal space occupation are to be related to response to environmental perturbations, such as land use (Lavorel *et al.* 2008). However, to be able to relate functional diversity and composition to ecosystem processes (like decomposition), biomass estimates might be more useful, reflecting the input for the actual process more closely (Lavorel *et al.* 2008). These methods, such as harvesting, hand-sorting and weighing of the vegetation (intenstive method), the dry-weight-rank method or BOTANAL, could be a viable, efficient alternative (Lavorel *et al.* 2008) of which I could have made use in agricultural fields and pastures – in forest systems, basal area was used, which is known to be representative for biomass.

However, comparison of cover and biomass measurement methods produce roughly the same estimates of functional diversity and composition when tested in alpine grasslands, according to Lavorel *et al.* (2008). For example, the point-quadrat method is found to produce similar ranks for the five most dominant species as the biomass methods, representing from 70% to 90% or more of cumulated abundance (Lavorel *et al.* 2008). Likewise, estimates of CWM for vegetative height, reproductive height, LDMC and LNC were consistent across the three methods estimating relative abundances. Congruency among methods was greatest for leaf traits, which means that it is not likely that the use of cover distorted results in my study. Also, fairly consistent estimates of functional divergence for leaf and height traits were obtained.

In my study, not all species that belonged to 80% dominance have been measured. In a next study, it would be wise to first calculate diversity, and then start trait measurement for the dominant species. In a next study, it would be interesting not only to take into account interspecific, but also intraspecific differences among leaf traits. Although in many cases intraspecific variability has been shown to be smaller than interspecific variability, intraspecific studies remind us that traits can vary considerably within species, due to both plasticity and genetic differences between populations (several authors in Lavorel *et al.* 2008). A solution that would capture this intraspecific variation would be to sample populations each separately to mark spatial variability. Also, data that capture annual and seasonal variablity should be gathered. Another elegant solution for the intra- vs. interspecific difference problem, regarding functional diversity measures, has been proposed by Lepš *et al.* (2006), who presented his idea as a modification for Rao's index. To capture intraspecific variation along with interspecific variation, dissimilarity among species d_{ij} is calculated as $1-O_{ij}$, where O_{ij} is the overlap between the probability density functions for the trait values of species *i* and *j*. O_{ij} is estimated using the normal approximation for each of the functions. A last option to notice within-species variations would be to use a taxon-free method, such as the trait-transect method and the trait-random method. Yet, a disadvantage of such a method is the considerable effort that is needed in vegetations with a complex vertical structure, leading to biased results (Lavorel *et al.* 2008), and the fact that data can hardly be reused.

In secondary forests, the problem arose that palms were really abundant, but lacked a proper stem, usually having a really high DBH. Because palms have a different growth form than other trees – first stretching out their leaves aboveground and later establishing a stem – the total biomass ascribed to palms might have been too high. It would be worth the effort to spend some time in discovering which 'soft' trait is related to palm total biomass. Besides, whereas other pioneer trees that are abundant in secondary forests (ambaibo, baboso, uvillo) shed their leaves every dry season, palms keep their high-economic leaves for a longer time, thus contributing less to the total amount of material available for decomposition.

The effects of land use on diversity and composition of communities
Species richness and diversity, between which no difference was found regarding the ranking of the land use types, were highest in mature moist tropical forest plots, followed by agricultural fields, then secondary forest, then pasture. This means that diversity in cultivated lands has been found to be higher than expected. A reason for this is that no monocultures are grown, but mixes of crop species (an average of 3,3 per plot), and that there is a rather large number of herbs and young trees present, whose propagules come from nearby secondary forest plots. However, different results might have been obtained when a biomass method instead of the point quadrat method would have been used, because crop species appeared to be higher and have a larger biomass than other species, thus making up a larger percentage and lowering the number of dominants.

Functional diversity measures can be split into two groups regarding the results they give: the ones including abundances (Rao's Q, extended FD) and the ones excluding them (FAD, FD). FAD is highest for mature forest plots, followed by secondary forests and agricultural fields and then by pasture; FD only differs in scaling pasture lower in terms of functional diversity than the rest of the land use types. This ranking is according to my hypothesis. Pasture repeatedly shows the lowest functional diversity, because in two out of three plots there is only one species

(braquirion) present. In agricultural fields, farmers deliberately grow a low number of species that have their place at the fast end of the growth spectrum – the faster plants grow, the sooner they can be harvested. The selection of such a characteristic – fast growth – has lead to limited diversity. Secondary forest have lower diversity than mature forest plots. While in mature forest several plant growth forms (shade-tolerant, partial shade tolerant, long-lived pioneer and pioneer species) are present, growth conditions in secondary forests favour pioneers. Tropical forest systems typically are more dynamic than other systems, with gaps being created and overgrown all the time, which leads to the manifestation of a range of different growth conditions and, therefore, plant species. Another reason for high diversity are the relatively humid, nutrient-rich circumstances that are present in mature forests.

The picture drawn by Rao's Q and extended FD is quite the reverse: lowest functional diversity has been found in mature forest plots, and secondary forest and agricultural fields have the highest diversity. As I already indicated in the method section, Q (and this seems also true for extended FD) might be maximized at a reduced number of species (Ricotta 2005). This seems to have been the case in my analyses. Although abundances in the mature forest communities are more equally distributed (because they have a higher Shannon's Diversity index), their species number is considerably higher, and this leads to overall smaller proportions and a smaller total when p_i and p_j (proportions of species) are multiplied, thus resulting into a low Rao's Q and extended FD. One solution for this problem would be to use FD and FAD separately from a species diversity index, so that functional richness and abundance evenness can be distinguished (Mouillot *et al.* 2005). Another solution is to use a more sophisticated index. As communities seldomly consist of the same number of species when they are compared, Rao's Q and extended FD have to undergo changes in order to be a mathemetical represention of what is (intuitively) regarded as functional diversity. One proposal is to calculate the maximum diversity (Q_{max}), so that a relative expression can be obtained; the expression of quadratic entropy as an absolute value is not useful when the comparisons have to be done between communities with very different numbers of species (Pavoine *et al.* (2005) in Casanoves *et al.* 2008).

Leaf nitrogen concentration (LNC), specific leaf area (SLA) and chlorophyll concentration turned out to be most relevant leaf traits in order to predict decomposition rates. For that reason I chose to evaluate these three characteristics as Community-level Weighted Means of trait values (CWM). LNC was highest in agricultural fields, intermediate in mature forest plots, lower in secondary forests, and lowest in pastures. The low value of secondary forest LNC was unexpected, because secondary forests are assumed to consist of rapid growing and photosynthesizing pioneer species with high nitrogen concentrations. However, palm species make up an average of two thirds of the 80 percent dominant species in secondary forest, the major being *Attalea speciosa* (cusi), which contributes an average 58% to the species assembly in terms of dominance. This palm especially becomes dominant if a secondary forest is frequently burned down; it is likely that the secondary forests where I conducted my practical work, have been cut down, burned and re-used for agriculture several times in the past. Palms, producing tough, long-lasting leaves, have a very low LNC.

Although pastures, as a land use type with a high disturbance regime, were expected to have a high CWM of LNC, its value might have been low due to the quality of the plant material that was gathered in order to determine LNC. The only species of which LNC was available was the dominant grass, *Brachiaria brizantha* (braquirion), and this species was at the end of its growth

season at the moment of sampling; perhaps leaves were already senescing, which means that nutrient resorption might have taken place, resulting in a lower value of LNC than is typical for this grass. Indeed, LitterNC:LNC is relatively high (71,4%) compared to other species.

SLA was highest in agricultural field and pasture communities, followed by the communities of mature forests and then by those of secondary forests. Here, a high value for pastures was noted, because the moment in the growth season does not affect SLA. It is easy to understand that agricultural fields and pastures have the highest SLA, because here, land managing is most intensive, giving way to pioneer and ruderal species. The intermediate SLA of mature forests can be explained by the variation in species occurring in these forests; species range from shade-tolerant to pioneer species. The low value for secondary forest can again be explained by the high abundance of palms.

Chlorophyll concentration was high in secondary forest, intermediate in mature forest and agricultural plots, and low in pastures. Palms, abundant in secondary forests, have a high chlorophyll concentration per unit leaf area in comparison with tree species, almost being as high as in cultivated herbs like the peanut. Reason is that palms have a very low SLA, and hence, thick leaves that stack several layers of chloroplasts. Photosynthetic rate in palms is known to decline with leaf age (Suresh & Nagamani 2006). Since we always took fully expanded and relatively young but mature leaves, a high chlorophyll concentration (per m^2) could have been necessary in order to sustain growth and fruit development in the entire plant. Chlorophyll concentration in agricultural field communities is not higher than in mature forests. This might be explained by the high light intensity that reaches the fields – even though chlorophyll concentration is not that high, photosynthesis might be going faster due to a more efficient use of the photosynthesis apparatus. Pastures show a low chlorophyll concentration, probably because leaves were harvested at the end of the season for *Brachiaria brizantha* (braquirion).

Looking at the three CWMs together, agricultural fields can be placed at the fast end of the plant economics spectrum. Secondary forests and pastures, which one would expect as immediate follow-ups, seem to be applying slower growth strategies than expected; however, this can be ascribed to the abundance of palms and the start of the dry season respectively. A re-measurement of pasture species could easily lead to different results.

Other studies have indicated a relation between disturbance intensity and functional composition in agricultural fields (e.g. Dorrough & Scroggie 2008) or grasslands (Garnier *et al.* 2007, Fortunel *et al.* 2009). Higher disturbance leads to plants with leaf characteristics at the faster end of the growth spectrum. However, in my study, disturbance intensity has not been quantified. Still, it would be interesting to see how disturbance intensity and functional composition are related in the variety of land use types where I worked. Disturbance could be quantified by disturbance intensity (percentage of biomass removed) and return interval of disturbance (year) (Fortunel *et al.* 2009).

Díaz *et al.* (1999) found a gradient in plant functional trait responses to land use. A higher logging and grazing intensity in xerophytic woodland sites lead to plants with high SLA, short life span and wind pollination. However, in my study, different logging regimes do not lead to differences in the CWM of LNC, SLA or chlorophyll concentration. A reason for this can be the low logging intensity, and the large number of species present in these forest land use types, so

that logging carries out only a minor influence on the change of functional composition of species. Also, species composition in plots was evaluated four years after logging; this time span is too short to have a significant amount of recruitment in the lower diameter class (>10 cm DBH). Results on the effects of logging on species diversity have been reported in previous publications (e.g. Verburg & Van Eijk-Bos 2003, Chen & Li 2004). However, my results indicate that low intensity logging does not affect diversity of moist tropical forest.

6.3 ENVIRONMENTAL INFLUENCE PER LAND USE TYPE ON DECOMPOSITION

Methodological considerations
Paper was used as a standard material to assess the effect of environmental conditions on decomposition, based on a successful experiment by Cornelissen (1996). However, looking back, paper seems not to be a suitable material to test the difference conditions favorable for decomposition between these South-American land use types. Paper contains cellulose, which is known to attract certain groups of animals, like termites and rodents, who digest cellulose (e.g. Pochon *et al.* 1959, Dominguezbello & Robinson 1991). These animals are likely to have destroyed part of the bags, thus influencing the results by eating all the paper in these bags. Apparently, the material that was used for the litter bags, even though synthetic, is not strong enough to keep these animals out.

In this pilot experiment, the air-dry mass of paper was used, but a more sincere comparison between land use types could be reached if dry masses would have been used. In this way, mass increases (instead of a decrease because of decomposition), which I found, are less likely to occur – these mass increases can almost certainly be ascribed to a higher water content of the paper, given that the samples were outside for over a month in sometimes rainy weather.

Furthermore, I used only one spot per land use type. It would be interesting, however, not only to use replicates within a spot, but to spread several series of samples in each land use type. Doing so, a more representative result could be obtained. Also, the experiment would be more complete if all land use types were tested instead of only five out of seven. Another correction for inequality among abiotic and decomposer community circumstances, could be obtained by an experiment in which all species are decomposed in every single land use type, so that it would be able to distinguish the effects of leaf quality and the environment statistically. In this way, it would also be possible to see the effects of the native ecosystem on decomposition of each species.

Land use and paper decomposition
Different decomposition rates are caused by abiotic conditions together with the decomposer community present. Decomposition was fastest in secondary forest and intensively logged forest, and slowest in cultivated lands and cattle ranged pastures. Secondary forest had a higher decomposition rate than expected – apparently, climatic variation among forests of different stages is rather small. Most likely is that secondary and intensively logged forest dealt with the activity of macro-organisms, which clearly ate part of the paper. This could explain the faster decomposition in logged and secondary forest than in undisturbed forest. Thus, coincidence could have played a significant role in this paper decomposition experiment. It explains why decomposition in undisturbed forest was not significantly different from neither of the other land use types – no animal signs were discovered over there. The ranking of agricultural fields and

pastures at the lower end of the decomposition spectrum points to the direction of climatic influence, the low moisture and fluctuating temperatures being unfavourable conditions for decomposition (Alvarez-Sánchez & Becerra Enríquez 1996, Aerts 1997, Toledo Castanho & Adalardo de Oliveira 2008). Furthermore, slow decomposition in pastures can partly be explained by nutrient input through cattle excrements.

This experiment does not provide enough evidence to make a correction for climate and decomposer community in the land use types I studied. However, research into better methods for a straight-forward determination of decomposition circumstances could pay off. Some suggestions to this end have been made above.

6.4 IDEAS ON DECOMPOSITION AS A TOOL FOR SUSTAINABLE LAND USE

The aim of this study was to evaluate the direct and indirect effects of land use on the ecosystem process of decomposition. There are some missing links that would be needed to have a complete picture of the influence of land use on decomposition. Firstly, direct effects of land use on decomposition – i.e., an altered climate or decomposer community – have not been clarified, due to the unsuccesful paper experiment. Secondly, although cover (pasture and agricultural fields) or biomass (forest land use types) have been estimated, it is unknown whether species are equally important in contributing litter as they are in cover or biomass. Some species are deciduous, others are not. Some species have a short life cycle; others remain upright in the same spot year after year. In short, the amount of litter that each species contributed was not known. Thirdly, functional diversity has not been directly related to decomposition – I used functional composition (CWM) instead. One way test the effects of functional diversity on decomposition is to conduct mixed litter decomposition experiments, which are likely to give the best results; another is to use near-infrared reflectance spectroscopy (NIRS), a method which allows a precise prediction of litter decomposibility of both individual species and communities (Fortunel *et al.* 2009). Without these data, it is not possible to shed light on complementarity and facilitation that might take place within a plant community during the process of decomposition.

Still, it is interesting to relate land use to ecosystem services, by means of functional composition and decomposition. Decomposition of dead plant material is a key compontent of fluxes of nitrogen and carbon in ecosystems, since it determines at which rate carbon and nutrients are mineralized from plant litter. Shifts in plant communites can thus modify litter decomposition (Fortunel *et al.* 2009). Using data of community-level weighted means of traits relevant to decomposition, I was able to predict decomposition rate per community. Pastures have the slowest decomposition. As they mainly consist of only one dominant species, this grass species is able to 'auto-engineer' its environment – creating the exact circumstances that it needs to sustain.

More complex is the switching system of agricultural fields and secondary pioneer forests, which are burned after about fifteen years to enhance soil fertility. Plant species that are cultivated are generally fast-growing and fast-decomposing – they need a nutrient-rich environment. However, after crops are harvested, their decaying material is removed from the agricultural fields and brought to secondary forests nearby, as far as I could observe. Land is cleared and prepared for a next generation of crop species. In order to retain nutrients like nitrogen and phosphorus within the system, it may be advisable to leave crop species on their plots for decomposition. Another solution for improving the quality of soils is using living plants or trees with fast-decomposing

leaves, as has been proposed by for example Mubarak *et al.* (2008) (who used mango and guava). Current practice, however, is the growth of secondary forests. Around Ascensión de Guarayos, where my study took place, these forests mainly consist of palms, which are characterized by high-quality, slowly decomposing leaves. A suggestion for improving soil fertility might be the removal of palm species from the forest, so that fast-growing, fast-decomposing pioneer tree species are favoured, and a nutrient-richer soil can be created. However, although overall decomposition rate of secondary forests is low and strongly affected by the high abundance of palms, the relatively large litter input of fast-decomposing leaves as compared to agricultural fields is still likely to enhance soil fertility. Still, a disadvantage of this system is that when these young secondary forests are burned, the main part of nutrients disappears into the air – causing major air pollution problems (L. Poorter, personal communication).

In tropical moist forests, as growth strategies of the commercial species are not known, it cannot be said which logging regime is providing the best conditions in terms of decomposition for the production of wood. Another ecosystem service, that is becoming more relevant in view of climate change, is carbon sequestration. The capture of carbon is likely to go faster in forests with silvicultural practices; there, SLA is slightly higher than in control and normally logged forests, meaning that plants are generally growing faster and, therefore, needing more carbon per unit time. However, as fast-growing plants tend to complete their life cycle fast as well, and their material is rapidly decomposed, carbon might be conserved longer within plant bodies in normally logged and control forest. Circumstances that fit carbon sequestration best are beyond the scope of my work. Intuitively, data on standing biomass would be more useful to decide on which practice favours carbon sequestration best.

Another point of attention that is relevant to mature moist tropical forests is the question of biodiversity conservation. Looking at functional diversity measures FD and FAD, light silviculture forest has the highest value, even exceeding control forest, where no logging is taking place. Thus, not only in terms of species number and diversity, but also in functional diversity, light silviculture might be the best practice to combine profit of ecosystem services with nature conservation.

7. Conclusions

Leaf nitrogen concentration (LNC), and specific leaf area (SLA) and chlorophyll concentration together, determine leaf decomposition rate in a range of plant species from several land use types in the moist tropics, showing a positive relation (fig. 5.7). These leaf traits define a species' position in the global spectrum of leaf economics, that varies from thin leaves with high nutrient concentrations and high photosynthetic rates to thick, relatively recalcitrant leaves with greater physical toughness and defenses and low photosynthetic rates (Santiago 2007). My study showed that decomposition rate is consistent with a plant's growth strategy, thus connecting living leaf traits via litter decomposition to nutrient availability for new recruits of the same species.

Species richness and diversity change with land use. Taxonomic and functional diversity measures give the same picture, with greatest diversity in moist tropical forests, especially in undisturbed and light silviculture plots, followed by agricultural fields, secondary forests and pastures. As for the functional diversity measures, only FAD (Functional Attribute Diversity) and FD (Functional Diversity), i.e. the measures that do not take relative abundances into account, generate meaningful output. High diversity can be explained by low human interference and favourable growth conditions in primary tropical forests. In agricultural fields, high diversity is likely to be caused by the mix of crop species that farmers tend to grow.

Using functional composition of the traits that predicted decomposition best, agricultural fields were calculated to show highest decomposition rates, followed by tropical moist forests, secondary forests and pastures respectively. Species of agricultural fields are typically crops that employ a fast growth strategy, being adapted to the favourable light conditions offered by the open fields. Secondary forests showed a slower predicted decomposition rate than expected, because of the abundance of a palm species, which typically has slowly decomposing leaves. This palm is known in the region to become abundant after regular burning; its dominance could change the way we regard the profitability of establishing secondary forests in order to enhance soil fertility (pointing at, for example, agroforestry). With my study it is not possible to relate environmental conditions in the different land use types to decomposability, although cultivated lands and pastures seem to be less favourable for decomposition than the other land use types.

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