# The effect of logging, microhabitat and mammalian herbivores on tree community assembly in a Bolivian moist forest 

An exclosure study in three different microhabitats and two silvicultural treatments in La Chonta, Bolivia.



> Jonna van Ulzen
> 860119-849-030
> Forest Ecology and Forest Management Group
> Wageningen University August 2012

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Supervisor:
Dr. Ir. L. Poorter

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Supervisor:
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## Summary

Sustainable Forest Management aims to log forests in a sustainable way to ensure future wood production and to protect the forest ecosystem.. Regeneration is an essential process to ensure future production, especially from the third harvest cycle onwards. However, in many tropical forests the regeneration of commercial tree species is problematic. The reasons for insufficient regeneration are unclear and are most likely caused by multiple aspects.

The questions examined in this study are: what is the effect of logging, microhabitat type (gap, (skid) trail and understory), and herbivore mammals on (a)biotic conditions, species richness, composition, structure and dynamics of the regenerating tree seedling community in a Bolivian tropical moist forest?

Logging is hypothesized to have a positive effect on light availability and, hence, seedling growth. As logged forests tend to have a high mammal density, they will also have a high browsing pressure.. Recruitment, growth and survival are expected to be highest in gaps, followed by trails and finally understory. Browsing pressure is expected to be highest in gaps and at trails. . Unfenced plots are expected to suffer more browsing damage and a decreased survival compared to fenced plots.

To address these questions, seedling growth was monitored in plots using the following design.

1) There are two logging compartments, referred to as blocks.
2) Two silvicultural treatments are applied in each block; each block contains a 27 ha plot that is unharvested (control) and traditionally harvested (logged), at an intensity of 4-6 trees per ha.
3) Three different microhabitats (gap, trail and forest understory) can be found in each treatment. Each microhabitat type is replicated three times per treatment plot.
4) Each replicate consist out of a paired exclosure (fence of 0.9 m high that excludes large mammals) and control plot of $2 \times 2 \mathrm{~m}$.
In total there are 2 blocks * 2 treatments * 3 microhabitats * 2 exclosure types * 3 replicates $=\underline{72}$ plots.
Logging took place in 2001/2002, and the seedling plots were set-up in late 2004. In 2005 and 2011 (a)biotic conditions were measured that might be important for tree regeneration; the canopy openness, cover of debris (litter, wood), and cover of competing life forms (shrubs, lianas, heliconias) and stem densities. In 2006 and 2011 all tree seedlings $>10 \mathrm{~cm}$ tall were tagged, identified, and measured for their height and survival. Based on these data the structure (seedling height and density), richness (number of species and diversity) and dynamics (recruitment rate, survival rate, growth rates) were calculated.

## (A)biotic conditions.

The environmental conditions of the plots were similar over time, with the exception of shrub cover (which explains a ,lot of the variation in 2005) and woody debris cover (which explains a lot of the variation in 2011). A 4-way ANOVA was used to test whether block, logging, microhabitat type and exclosures had a significant effect on environmental variables. Logging has the largest influence, followed by microhabitat. Total stem numbers in 2011 are higher in logged forest than in unlogged forest. Canopy openness in 2005 followed the expected order (gap>trail>understory). Differences between microhabitats disappear over time, probably because the gap plots close over time due to regrowth, whereas over the 5 year evaluation period canopy gaps have been formed above some understory plots. Overall this suggests that, at the forest level, environmental conditions oscillate around an equilibrium level.

Structure and dynamics.
Forest structure and richness in 2006 and 2011 were analysed with a four way ANOVA. For both years, average seedling height differed significantly between microhabitats and was highest in gap and trails compared to the understory. Survival was significantly higher in logged (57.8\%) than in unlogged (37.5\%) forest. Recruitment rates were highest in gap and understory microhabitats and lowest at trails. In 2005 species diversity was highest in gap and trail habitats but this difference disappears over time, because diversity decreased in both gaps and trails and increased in the understory. Exclosures had modest effects. Significant less stems were browsed in exclosures (15\%) compared to unfenced (control) plots (40\%). As a result, the
relative height growth rate of the seedlings was significantly higher in exclosures $(0.11 \mathrm{~cm} / \mathrm{cm} / \mathrm{y})$ than in control plots $(0.07 \mathrm{~cm} / \mathrm{cm} / \mathrm{y})$.

Species richness and composition
In 2006 both species richness and diversity were highest in trail microhabitats ( 7.76 ind/plot), and statistical similar in gap ( 5.37 ind/plot) and understory ( $4.37 \mathrm{ind} /$ plot) habitats. Species numbers decreased in trail habitats and increased in gaps and understories, resulting in a similar species richness and diversity in all microhabitat types in 2011.

In general logging and microhabitat type have the strongest effect on environmental conditions, and on forest composition and structure. Disturbed habitats (logged areas, gaps and trails) have an increased light availability resulting in larger average seedling heights. Microhabitats are not stable states but change over time. Areas classified as gap in 2005 have become closed in 2011 and gaps are established at sites originally marked as understory. This causes a shifting mosaic of microhabitats and corresponding environmental variables. Mammals play a smaller role than expected in the regeneration of trees. Although browsing pressure is lower and RGR higher inside exclosures animals do not influence survival and recruitment. This implicates that high mammal densities and browsing pressure are not the cause for the regeneration problem in La Chonta. It is more likely that the solution to this problem can be found in silvicultural (logging) treatments that improve light levels.

## 1. Introduction

Tropical forests play an important role in the entire world, in both an ecological and economical way. The rainforest biome around the equator is characterized by evergreen humid to wet forests, which harbour a wide range of soils, vegetations, human and geographic influences, and evolutionary histories. Biodiversity in tropical countries across the world is enormous, the total number of plant and animal species is estimated to lie between three and five million. Especially in insect and invertebrate species there is a large uncertainty about the actual number of species (Whitmore \& Sayer, 1992 in Breunig, 1996). Tropical rainforests are characterized by an extremely heterogeneous plant distribution, which is the result of a complex interaction process of many variables (Whitmore, 1991). Many tree species occur at low adult densities, often more than 100 species per ha among trees with a dbh > 10 cm (Janzen, 1970, Swaine et al., 1987), while common plants have a relative high abundance (Toledo et al., 2012). The tropical rainforest habitat fluctuates over time (e.g. gap formation, weather influences, etc.). This fluctuating habitat influences the relative abundance of seedlings and young trees, which determine changes in forest structure to a large extent (Gill, 2006). The high diversity of tree species in tropical forest communities is thought to be (partially) caused by negative densitydependent recruitment of seedlings; meaning that recruitment of a certain species is low if the density of that species is high (Harms et al., 2000). However this density-dependence hypothesis has been subject of debate, for example Silva - Matos et al. (1999) presented in a study of an edible palm tree (Euterpe edulis) that density-dependent population dynamics only occur in seedling stage. In this study the probability of a tree surviving into the next age class was dependent both on seedling density and presence of con-specific adult trees (Silva - Matos et al., 1999).
Animals, especially herbivores, are considered to have a major influence on the forest composition and forest dynamics (Dirzo \& Boege, 2008, Theimer \& Gehring, 2008 and Whitmore, 1991). Animals in general interact with plants and have interdependent relations with them in many and often complex ways, which makes them specialized to many spatial and temporal niches (Whitmore, 1991). Mammalian herbivores affect the plant community on the one hand by dispersing seeds and on the other hand by causing seed and seedling mortality due to browsing and trampling (Gill, 2006 and Theimer \& Gehring, 2008). Seedlings and young trees are the age classes most vulnerable to damage by herbivores (Gill, 2006).
The area of (primary) tropical rainforest reduced drastically over time. Before the coming up of the human species the biome consisted $>90 \%$ of primeval tropical rainforest. Development of the human race drastically reduced and modified the original vegetation in large parts of the tropics due to slash and burn techniques and logging. Tropical timber products are imported to the European market since the colonial establishments in the sixteenth century. These products where only accessible for the high classes for a long time, only after the Second World War the timber demand shifted and tropical wood became widely available. Across the world unsustainable harvesting, resulting in clear cuts and destruction of natural forests due to agricultural expansion, is responsible for more than $90 \%$ of deforestation in the tropics. (Breunig, 1996). The large demand for timber can only be satisfied in future decennia if sustainable forest management (SFM) is applied. In sustainable managed forests there is a steady flow of resources and income while at the same time forest cover, biodiversity and ecosystem integrity are left intact and preserved for future generations (Sayer et al., 1995). One of the difficulties for SFM is the limited knowledge about the extent tropical forests are capable to withstand and recover from logging (Whitmore, 1991). Forests in Bolivia are relatively undisturbed compared to other countries, especially the lack of roads keeps deforestation rates low and mammal numbers high (316 spp.) (Fredericksen, 2000), offering good chances for the implementation of SFM. However, at this moment lack or insufficient regeneration of commercial Bolivian timber species causes a large future problem for SFM, which will affect the second or third harvest (Mostacedo \& Fredericksen, 1999, Peña-Claros et al., 2008).

This study focuses on the effects of logging and microhabitat conditions on the regeneration of tree species. Next to this special attention is given to the role of herbivore mammals on the recruitment, survival and growth of seedlings in order to contribute to solving the regeneration problem in La Chonta.

This study is a continuation of the experiment set up by Tjerk de Rooij in 2004 (Rooij, 2005).

## 2. Background and problem statement

Sustainability (maintaining output and quantity over time without damaging or degrading the ecosystem) is a topic of great concern for many scientists nowadays (Barnett, 1994). Sustainable management of (commercially valuable) tree species is of upmost importance for the conservation of the tropical rainforest ecosystem and biodiversity (Gómes-Pompa \& Burley, 1991). The forest habitat is shaped by the trees, especially by the different layers in the canopy. Trees have a major influence on "the viability and functioning of forest ecosystems that determine the microclimate, the qualities and quantities of stock and flows of matter and energy, and the architectural or geometric structure of all layers of the growing stock" (Breunig, 1996).

### 2.1 Importance of regeneration for sustainable forest management

Taken the sustainable management of forests into account it is essential to ensure that the forest regenerates and that biodiversity levels are maintained after logging, in order to preserve all forest functions for future generations. Regeneration of many commercial tree species in the La Chonta forestry concession is problematic (Peña-Claros et al., 2008A). Many species have a poor regeneration, meaning that natural regeneration is low at sites were the species are found naturally as adult trees. Beside the poor regeneration often little silvicultural knowledge is present of how to enhance regeneration (Mostacedo \& Fredericksen, 1999). Furthermore silvicultural interventions in Bolivian forests are mainly focused on harvesting practices to preserve forest structure and ecological functions and not on enhancing regeneration (Peña-Claros et al., 2008). The biggest regeneration problems are found in shade intolerant and intermediate shade tolerant hardwood species. Yesquero Blanco (Cariniana ianeirensis) is one of the species that poorly regenerates at the study area. According to Nabe-Nielsen et al. (2009) the number of seeds of this species is much lower in logged than in unlogged forest due to a reduced number of seed trees and a low seed production by these trees in the logged forests (Nabe-Nielsen et al., 2009), another problem is the lo survival of seedlings. Long term experiments and observations are of upmost importance to gain insight and understanding in the (slow) ecological processes that occur in the forest. Long term observations in permanent sample plots will help to detect changes in the system and separate trends (Southwood, 1994).

### 2.2 Mammalian herbivory

Although insects seem to be the most important herbivores in tropical forests (Janzen, 1981 and Dirzo 1984B), mammalian herbivores can have large influences on plant population dynamics and distribution, particularly in limiting plant distributions, as well (Fine et al., 2004). In total over $90 \%$ of all tropical trees need some kind of animal service for their reproduction (Terborgh \& Kenneth, 2010). Animals have positive effects on plant recruitment by dispersing seeds via their faeces and coats. Together with birds mammals are considered the most important dispersers for large-seeded tree species. Mammals are particularly effective at short distance dispersal, effectively dispersing seeds into small canopy gaps close to a parent tree (Gill, 2006). In contrast to bird dispersed species which attract birds with bright colors, no specific traits known of mammal dispersed seeds but often they have large seeds and/ or fleshy fruits. Some species produce strong smells which are thought to attract mammals(Whitmore, 1990). Animals can negatively influence plant survival through browsing. Grazing and browsing causes negative effects on plant growth and survival because valuable tissues, like meristems, are removed, resulting in a loss of photosynthetic capacity (Alison et al., 2006, Dirzo,

1984B and Janzen, 1981). The influence of herbivory on the dynamics in plant populations and communities is summarized by Dirzo (1984A) (fig 1).


Figure 1 schematic overview of the consequences of herbivory on plant populations and communities. The plant's and herbivore characteristics that influence the probability that a plant will be found and eaten are described in the lower boxes (figure based on the figure in Dirzo, 1984A).

Janzen (1970) described two types of seed predators: distance and density responsive predators, both affecting seed dispersal near parent trees but in a different way. Distance responsive predators are mainly feeding on the adult trees, while density responsive predators mainly affect seedlings. The probability that a seedling is eaten by a distance responsive predator is determined by the distance between the seedling and the parent or adult tree of the same species. For density responsive predators this probability is determined by the distance between individual seedlings. Herbivore activities can belong to both categories, amongst other things depending on the environment. The effect of herbivory on the plant depends on the location and type of tissue affected as well as the plant's life stage (Alison et al., 2006, and Gill, 2006). Seedlings have a much higher vulnerability to herbivory than adult trees, especially when roots or the photosynthetic system are developing. Besides a fully grown root and photosynthetic system, adult trees have much better developed defense or compensation systems than seedlings (Whitham et al., 1991). Foraging mammals generally focus on the upper part of seedlings and saplings, foraging on growing, young leaves that contain the highest nitrogen concentrations (Alison et al., 2006 and Gill, 2006), because this is the limiting factor in their diet. The nitrogen in old leaves is converted into insoluble protein, which is much harder to digest. Eating old leaves can be unsatisfying for the animal because the energy costs of breaking down the proteins can be higher than the energy yields. Other methods used by animals to ensure or maximize nitrogen uptake are synchronising their breeding with periods that enough young leaves are present and by eating developing flowers and unripe seeds (White, 2005). Browsers are able to forage this selectively because they have, contrary to grazers, more narrow muzzles and erect incisors. This skull design and dental traits enables browsers to select very selectively, even in dense vegetation (McNaughton, 1991). Young, full sized, leaves have maximum photosynthetic capacity and export of carbohydrates, making them more important for a plant's fitness than old leaves (Dirzo, 1984A). Therefore the loss of young leaves has more severe consequences to a plant than loss of older leaves or shoots. Loss of meristematic tissues generally has more
severe consequences than loss of non-meristematic tissue due to the possible loss of apical dominance (Alison et al., 2006 and Gill, 2006). The loss of apical dominance often results in a change of tree architecture (Dirzo, 1984B and Whitham et al., 1991), which is unwanted for commercial tree species. Small seedlings are highly vulnerable to browsing, in particular if the cotyledons are lost before leaves are formed. As trees grow older their shoots become thicker and more lignified, making them harder to digest and less attractive to herbivores (Gill, 2006). In the plant's reaction to herbivory a distinction can be made between source (photosynthetic organs and storage tissues) and sink (growing meristems, flowers and fruits) mechanisms. Source mechanisms react by increasing the supply of building materials as a result of increased photosynthetic activity by undamaged leaves, the effectiveness of translocating this assimilates to damaged plant parts is small (especially in completely defoliated branches). Sink mechanisms respond to herbivory by maintaining or increasing the amount of growing points and/ or reproductive organs by activating dormant meristems or buds. The degree of compensation depends on the plant's ability to do so. In reality the response to herbivory is a combined response of source and sinks mechanisms. In general browsing negatively affects the health of a plant, making it more susceptible for pests, pathogens or fungi. Besides decreasing the plant's health, herbivory can also lower the plant's competitive ability and delay sexual maturity. Additionally to the type of tissue affected and the plant's life stage there are multiple other factors affecting plant responses to herbivory: water, light and nutrient availability, as well as intra- and interspecific competition can have major influences on plant fitness and therefore indirectly on the plant's ability to deal with losses due to herbivory. Other factors that play a role are plant size, intensity of herbivory and species, some species are much better adapted to withstand herbivory than others (Whitham et al., 1991). According to the resource availability hypothesis of Coley et al., 1985 (in Dirzo \& Boege, 2008) slow growing species suffer the highest costs from tissue loss; therefore these species should invest more in herbivore defense strategies than fast growing species. The former hypothesis is in line with the plant appearancy hypothesis which predicts that a plant's investment in defense is determined by the risk of being encountered by a herbivore (Dirzo \& Boege, 2008). ). Generally browsing is not lethal for a plant, up to a certain level plants are even able to compensate the tissue loss. Some species react to herbivory by overcompensating the biomass loss. In this situation trees that suffered from predation have a higher aboveground biomass compared to individuals of the same species not affected by herbivory. Overcompensating generally occurs in nutrient rich environments and the probability of occurrence increases when plant competition is low and when herbivory takes place early in the growing season. "Almost all cases of reported overcompensation have been due to an increase in the number of modular units when apical dominance and the hormonal suppression of dormant meristems has been removed by herbivores." The effect of overcompensation on overall plant fitness is unknown. The opposite effect of overcompensating is undercompensating, which generally occurs when insufficient nutrients are available, when herbivory takes place later in the growing season or when plant competition is high (Whitham et al., 1991). These above mentioned postherbivory effects are likely to influence growth, survival or reproductive capacity. Especially combinations of herbivory with other stress factors, like for example light or water shortage, can negatively influence plant fitness and survival. Removal of herbivores can have either positive or negative consequences for plant diversity. It turns out that this is a result of the relation between the competitive strength of plants and herbivore preferences. Removal of herbivores decreases plant diversity when strong competitive plants are the preferred food source and vice versa (Dirzo, 1984A). Although browsing reduces the height growth, most trees do not directly die because of tissue loss but indirectly because they are outcompeted by other plants and trees (Gill, 2006). The majority of trees that are killed due to browsing are seedlings or saplings, implicating that a seedling that is 'sitting' on the forest floor for multiple years has a higher susceptibility to die because of herbivory (Dirzo, 1984A). In total small mammalian herbivores kill ca 30 percent of seedlings (del Val and Armesto, 2010). There is no single process responsible for the effect herbivory has on plants, multiple factors are always interacting, affecting plant growth and the response of plants to herbivory (Whitham et al., 1991). Beside the above described processes that lead to
possible mortality, herbivory may indirectly increase mortality by providing entry for pathogens (Dirzo, 1984B and Janzen, 1981).

This study will focus on the effect of large mammalian herbivores, in literature they are generally referred to as those weighing $>2 \mathrm{~kg}$ (Ritchie \& Olff 1999, Olff et al. 2002). The number of mammalian herbivores in La Chonta is relatively high compared to other moist tropical forests because no hunting takes place. The top of the food chain is represented as well in La Chonta, amongst others by puma's and jaguars. Terborgh and Kenneth (2010) made a clear overview of the influences of carnivores (predators) on consumers (herbivores) and their influence on plants (producers). This tropical cascade is described for a neotropical dry forest in Venezuala, but the same principle counts for la Chonta (fig 2).


Figure 2 Trophic cascade of a Neotropical forest (Terborgh and Kenneth, 2010). Predators have a negative influence on the number of consumers. The main influences consumers have on producers are described in the boxes at the lowest row. Decreasing numbers of pollinators and seed dispersers result in negative effects at the producers level, while decreasing numbers of seed predators and folivores have a positive effect at plant growth.

Browsing is mainly focused on the fast growing pioneer species. Many mammals (e.g., peccaries, agoutis, pacas, coatis, deer, rats, etc.) are dependent on fallen fruits and seeds for survival, often concentrating on particular trees. The fact that they concentrate on these trees and often return after a certain amount of time creates a host-specific like effect (Janzen, 1970). Pacas, peccaries and tapirs are primarily seed predators instead of dispersers (Hallwachs, 1986 in Asquith, 1999). Dispersing species like agoutis are also predators at the same time, making the process even more complex. The main way of seed dispersal by agoutis is the burrying of seeds which they forget to eat later, in this way the seedling is able to establish. Seedling survival near a parent tree is low because these trees act as 'flags' for rodents, which act in this way as distantresponsive predators (Janzen, 1970). A disturbed or incomplete animal community can and often will result in distortions of plant recruitment resulting in changing species compositions and (bio)diversity loss (Terborg and Kenneth, 2010). The importance of an intact and complete animal community is stated by White (2005) as well. According to this author food and climate is no limiting factor for herbivores, especially in tropical
forests, making predation, intra- and interspecific competition the main limiting factors when there is no human interference (White, 2005). Without top predators the herbivory pressure on seedlings would therefore be even larger.

### 2.3 The Janzen-Connell hypothesis and gambler/struggler strategies

According to Janzen (1970) the low density of tree species in tropical forests and the more regular distribution of adults than expected are the result of two processes. First the number of seeds of a species generally decreases at increasing distance from the parent tree(s), and second seeds and seedlings are an important food source for many plant parasites and predators. Over $50 \%$ of the seeds of a majority of more than $90 \%$ of all tropical tree species is killed by predators and parasites (Janzen \& Váquez-Yanes, 1991).
The negative effect of these predators on seed and seedling survival decreases with increasing distance to the parent tree, which makes them harder to find for the predator. Figure 3 illustrates the relation between the distance from the parent tree and the probability that a seedling will mature.


Figure 3: probability that a seedling will mature as a function of the number of seeds per unit area (I) and the probability that a dispersed seed is missed by a predator ( $P$ ). The population recruitment curve (PRC) is the product of $I$ and $P$ and shows a peak at the distance where the new adult is most likely to appear (Janzen, 1970).

Although host-specificity is supposed to strongly influence the shape of the curve in figure 1, the p-curve would be horizontal without host specificity, vertebrate species show little host specificy (Janzen, 1970).
Janzen and Connell defined several processes that contribute to the high alpha-diversity and low number of individual tree species in tropical forests (Carson et al., 2008):
-plant populations are regulated by density and distance dependent natural enemies
-the community level hypothesis predicts that an area containing enemies results in a higher alpha-diversity, because these enemies prevent species from becoming highly dominant.
-keystone predation where specialist natural enemies limit the abundance of strong competitors that would otherwise outcompete other species.
-complex trade-offs between investment in competitive or establishment ability versus defense and vulnerability to enemies prevent species from dominating the entire habitat. "Connell (1971) suggested the trade-off was between lower vulnerability to predation and rapid growth."
Excluding mammalian herbivores can result in a lower species diversity because some tree species will be able to outcompete others which they would not be able to in the presence of their mammalian enemies. Despite the increased predation on seedlings and trees of the same species that are located together, these trees are
clumped together sometimes. This can be explained by the fact that not only the intensity of predation and number of predators present influences the chance that a seedling will establish and survive in a certain area, but that seedling frequency and density play a role as well in the distance from the parent tree where the seedling occurs. In this case adult offspring is most likely to occur at places where seedling frequency is maximal (Becker et al., 1985). Two main reproduction strategies can be distinguished: the gambles and the struggler strategy. Species following a gambler strategy produce large amounts of offspring to increase the chance that one seedling will survive. This strategy works best in large gaps. Species following a struggler strategy produce few, but strong seedlings which are able to suvive long periods of time in shaded environments. This strategy is most successful in (very) small canopy openings, the most extreme strugglers occur in the understory (Oldeman and van Dijk, 1991).

### 2.4 Logging and microhabitat

Logging and different microhabitat types have major influences on the dynamics and species composition in a forest. Studying the role of different microhabitat types and environmental variables on forest regeneration is important because of three reasons:

1) knowledge about plant distribution will enlarge the understanding of the complex tropical system.
2) if relations between species and environments of microhabitats are known, species can be used as indicator species.
3) the response of the forest to climate change can better be predicted when ecological niches of species are known (Toledo et al., 2012).

Light is one of the main environmental factors that differs between microhabitat types and is influenced by logging. The conceptual framework presented in figure 4 gives a simplified overview of the effects that a natural or logging gap has on the environmental, dynamic and community level of a forest. In trail microhabitats less litter is supposed to be present which has a positive effect at the regeneration of pioneer species (see APPENDIXI) for an extensive conceptual framework of the trail microhabitat). The forest trails are used by mammals as well, increasing the chance of trampling of seedlings but also increasing the change that seeds are dispersed through faeces and fur. In forest understory microhabitats (see APPENDIX II) for an extensive conceptual framework of the understory microhabitat) the light availability will be much lower, resulting in lower growth rates of both pioneer and non-pioneer species and less recruitment of pioneer species.


Figure 4: Conceptual framework about the influence of gap microhabitats on the ecosystem. Positive effects are indicated by green lines, negative effects by red lines and neutral or unknown effects by blue lines. Strong effects are indicated by a solid line, intermediate effects by a dashed line and small effects by a dotted. Gaps have a (strong positive effect) on both the light availability (due to greater canopy openness), and the number of mammals present, (they seek shelter in between the low vegetation in a gap). The litter layer has a negative effect on the recruitment of small seeded pioneer species. The increased light availability in a gap has a positive effect on recruitment, survival and growth of all species. Mammals have a negative effect on survival and growth due to herbivory and trampling. In the end all processes contribute to an increased species richness and heterogeneous structure of the forest.

### 2.4.1 Logging

Logging can have a positive effect on tree regeneration, since most species are dependent on the increased light availability of logging gaps for regeneration (Gill, 2006 and Peña-Claros et al, 2008). Light is one of the main environmental factors in a forest and is highly influenced by logging practices. Light availability and distribution in a forest is a complex process, consisting of four components described by Whitmore (1990):

1) Direct skylight: reaching the forest floor through canopy openings
2) Sun flecks: direct sunlight which is seen as flecks on the forest floor
3) Light that is transmitted through leaves
4) Reflected light: light that is reflected by leaves, trunks, and other surfaces that can be found in the forest Both transmitted and reflected light are of little to no importance for forest floor vegetation because it can be found in the green wavelengths. The orange to red wavelengths, $400-700 \mathrm{~nm}$ or photosynthetic active radiation (PAR), is already used for photosynthesis by the reflection or radiation source. The amount of radiant energy that reaches the forest floor is determined by leaf area density and leaf absorbance characteristics of the above growing vegetation (Bazzaz, 1991, Chazdon \& Pearcy, 1991 and Whitmore, 1990). Direct sunlight is only found in gaps, the larger the gap the larger the amount of direct sunlight that reaches the forest floor. The increased radiation in these gaps can cause the soil to dry out faster during prolonged dry periods (Whitmore, 1990). Sun flecks are mainly found in the forest understory, they last several seconds to minutes and are mainly caused by branches that are moved by the wind or by sun movement during the day. Although sun flecks are small and momentary they are responsible for $50-80 \%$ of the PAR that reaches the
forest floor. The PAR quality depends on the composition of the forest canopy and the position and intensity of the sun (Chazdon \& Pearcy, 1991 and Whitmore, 1990). The light environment has a large influence on the temperature of air, plants and soils in tropical forests, with high temperatures at areas which are exposed to direct sunlight (Bazzaz, 1991). Besides the increased light availability logging increases environmental heterogeneity and creates opportunities for pioneer species. Seedling densities are higher in thinned forests and a larger proportion is expected to survive browsing (Gill, 2006). On the other hand fruits and seeds may be extra visible to birds and mammals in logged forests causing increased predation rates (Nabe-Nielsen et al., 2009).

### 2.4.2 Natural or logging gaps

Light availability is known to be one of the main limiting factors for plant growth in tropical forests (NabeNielsen et al., 2009). Light availability often increases as a result of disturbances in the forest. Gaps are considered to be one of the key forms of disturbance. The light levels in gaps are significantly related to gap size, large gaps generally receive $35-40 \%$ of direct sunlight immediately after establishment. After one year the light level of a large gap is similar to a small gap, with 10-20\% of direct sunlight (Denslow et al., 1998). As a result of the increased (direct) light availability the temperature in a gap or clearing rises compared to the surrounding understory and the vapor pressure deficit is high. On average the microclimate in a gap returns to understory values two years after gap formation (Fetcher et al., 1985), but this depends on gap size as well. Especially during the first years after gap formation recruitment and growth rates are high. Schnitzer et al (2008) described three non-exclusive ways in which gaps enhance species diversity:

1) by offering a habitat for the regeneration of early successional, light demanding species
2) varying resource gradients from gap center to forest interior provide niches for species specialization and co-existence
3) gradients in gap size allow for stable species co-existence of species regenerating in small and large gaps
Gaps do not stay 'emty' or clear, especially in the tropics they are colonized rapidly by tree seedlings and other vegetation. There are three (non-exclusive) ways in which trees can colonize gaps: at first from seed regeneration by seeds that are already present in the soil seed bank or dispersed by wind (pioneer species)or animals, this seedbank is most important in large gaps. The second pathway is along advance regeneration, where seedlings and saplings (of shade-tolerant species) already present in the understory prior to gap formation rapidly grow, filling the gap. This pathway is often observed in small gaps. The third way of colonization is through vegetative reproduction of clonal shoots by vegetation present prior to gap formation or by fallen trees and lianas pulled into the gap (Bazzaz, 1991, Schnitzer et al., 2008 and Whitmore, 1991).
Especially in large gaps with limited disruption of the forest floor, pioneer and climax species can occur at the same time and grow up together. In simultaneous colonization pioneer species will establish from seeds, while climax species colonize the area with seedlings that survived gap formation or from stem or root shoots of prior vegetation. In this situation the pioneer species are expected to grow the fastest and become initially dominant (Whitmore, 1990). Gaps are assumed to follow a series of growth stages from open gap to a condition of intact forest. Gap-phase regeneration is considered to be complete when the canopy is closed by trees reaching the same height as the ones in the surrounding forest. Abundant growth of lianas slows the gap closing down due to competition for light and nutrients and mechanical interference with trees (Schnitzer et al., 2008). Compared to other microhabitats seedlings have the highest growth rates in logging gaps, due to the large light availability. Negative impacts of soil compaction due to logging machinery are not observed in La Chonta (Peña-Claros et al., 2008).

### 2.4.3 Forest understory

Compared to the gap and trail microhabitat the forest understory has the lowest light availability. Seedlings of large seeded species are the best survivors in these shaded microhabitat because of the high N reserves included in the seeds. A disadvantage of these nutrients is that it makes them favoured by seed predators (Carson et al., 2008). Lianas are generalists that even maintain positive growth rates in the shaded understory, and colonize gaps as well by growing in to them laterally (Schnitzer et al., 2008), which can make them strong competitors for tree seedlings. The thick litter layer often present in the forest understory makes it hard for small seeded species to regenerate, because they only have a limited amount of nutrient reserves. Climate in the forest understory is more stable than in gaps. The daily variation in leaf temperatures is small and leaf and air temperatures are relatively similar, except during sunflecks (Bazzaz, 1991).

### 2.4.4 Exclosures

Exclosures are a well-known tool in temperate forests to measure and investigate the role of mammals in the seed dispersal and regeneration of trees. Due to the establishment of exclosures the tree regeneration is manipulated because some trees will be set free from mammalian predation. In this way it can be proven whether or not tree recruitment in limited by mammalian herbivores. The effectiveness of exclosures is dependent on the browsing pressure and the importance of seed dispersal by mammals. If seed dispersal by mammals is low the exclosure effect is expected to be low as well, at the other hand if seed dispersal by mammals is high herbivory on seedlings is generally high as well (Theimer \& Gehring, 2008). Excluding vertebrate mammals in a study in the tropics conducted by Theimer \& Gehring (2008) resulted in a 40\% higher seedling recruitment and survival in exclosures versus open plots. On the other hand the study of Terborgh et al. (1993) on exclusion of mammals at five large-seeded tropical tree species with tree exclosure types revealed three distinct patterns, which might as well occur in this study. At first no difference was observed in seedling survival between open and exclosure plots of Calatola, the species suffered however high postestablishment mortality due to mammalian herbivory. The second pattern was shown by Astrocaryum, Bertholletia and Dypterix which showed heavy seed loss in open en semi-permeable exclosures, but not in impermeable ones. This suggests that the seeds of these tree species are mainly predated by small rodents (Oryzomys spp. and Proechimys spp.) which can enter the semi-permeable exclosures. The third pattern was observed in Hymenaea courbaril, the seeds of these species were only removed from control plots, suggesting that large animals (Myoprocta, Dasyprocta, Agouti, Tyassu spp.) are the main predators of these seeds (Terborgh et al., 1993).

### 2.4.5 Pioneer and shade tolerant species

Pioneer species are light demanding and shade intolerant, climax species on the other hand are able to survive in shaded environments for long periods of time. The main characteristics of both species groups are described by Withore (1991)(table 1).

Table 1 Summary of the main characteristics of tropical pioneer and climax species (Whitmore, 1991).

|  | Pioneer | Climax |
| :---: | :---: | :---: |
| Seeds | Small, produced early in life | Often large, produced annually or less by trees that (almost) reached full height growth |
| Seed dispersal | By wind or animals, large distances | Diverse ways (e.g. animals or gravity), sometimes small distance |
| Soil seed bank | Many species | Few species |
| Seed dormancy | Highly capable, abundant in seed bank in forest soil | Little capability, rare in soil seed bank |


| Germination | In canopy gaps with direct sunlight | Usually below canopy, soon after release |
| :---: | :---: | :---: |
| Seedlings | Cannot survive in understory | Able to survive below canopy, forming 'seedling banks' |
| Growth rate | High | Relatively low |
| Height growth | Fast | Slow(er) |
| Growth periodicity | Indeterminate, no resting buds | Determinate, with resting buds |
| Leaf life | short, high turn-over rate | Long, low turn-over rate |
| Herbivory | Susceptible leaves, little chemical defence | Sometimes less susceptible, tougher and/or toxic |

Climax species establish below a canopy of pioneers. Pioneers often have a short longevity and when they die the small climax trees in the lower forest layers grow into the canopy openings. Succession has taken place when a pioneer canopy is completely replaced by climax species. Many pioneer seeds are triggered to germinate when they are exposed "to light in which the energy of the red ( 660 nm ) wavelength exceeds the far-red ( 739 nm )", high temperature and alternating temperatures (causing a thermoblastic response) can be triggers as well. The (almost) immediate germination of climax seeds prevents them from being eaten, affected by micro-organisms or from degrading. Instead of a seed bank, like in pioneer species, seedling banks are formed, which often occur close to the parent tree. This close occurrence of seedlings to the parent trees often results in density-dependent effects, therefore seedlings with the greatest distance to the parent tree have higher survival chances (the so-called 'escape hypothesis') (Whitmore, 1990). The division between pioneer and climax species is not strict. In both functional groups the adaptation of different species to the specific environments fluctuates. Pioneer and climax species are the two 'extreme', in between them the generalists and partly-shade tolerant species can be found.

## 3. Research objectives and research questions

Regeneration of trees after logging and survival of seedlings and saplings are essential processes in a sustainable managed forest. At la Chonta regeneration and survival of juveniles of (commercial) tree species after harvesting is problematic. The objective of this study therefore is to examine the effect of logging, microhabitat types and mammalian herbivory on species composition and structure and dynamics of the seedling community.

### 3.1 Research questions

The main question if this research is divided in three parts:
What is the effect of: 1. logging, 2. microhabitat conditions (natural or logging gap, trail, forest understory), and 3. herbivore mammals on abiotic conditions, species richness, composition, structure and dynamics of the seedling community in a tropical moist forest.

Besides this main research question an additional question is formulated to gain insight in the role seed trees have on seedling composition:
Is the density of seed trees lower in logged forest and what is the correlation between seed trees and seedlings at species level?

### 3.2 Hypotheses

For each question the following corresponding hypotheses are formulated:

1) What is the effect of logging on species richness, composition, structure and dynamics ?

Logging is expected to increase light availability and therefore increasing seedling growth and survival, especially favouring light-demanding species. Herbivory rates will be higher in logged than in unlogged forest and in gaps because these habitats provide more shelter for the animals due to denser understory growth.
2) What is the effect of microhabitat on species richness, composition, structure and dynamics ?

The higher light availability in gaps will stimulate plant growth, resulting in pioneer species outcompeting shade-tolerant species. At trails the increased light availability will increase plant growth and the absence of litter will favour small-seeded tree species. In the shaded forest understory recruitment, growth and survival will be lower compared to the other microhabitat types and shade-tolerant species will be more abundant. Mammals often use trails because they facilitate their movement, which will increase the herbivory rate and seed dispersal along trails compared to forest understory.
3) What is the effect of mammals on species richness, composition, structure and dynamics ?

Disturbed areas generally contain more low vegetation which provides shelter to mammals, therefore seedlings are expected to suffer most from herbivory and trampling in trail and gap microhabitats. Especially light-demanding species with palatable leaves and less-protected leaves and stems will suffer from herbivory. Seed predation by some mammals may reduce recruitment, whereas other mammals may increase seed dispersal and therefore recruitment of, especially, large-seeded species.

Is the density of seed trees lower in logged forest and what is the correlation between seed trees and seedlings at species level?
Recruitment of new seedlings of logged tree species will be higher in unlogged forest because of the higher number of remaining seed trees. However, in logged forests $20 \%$ of the seed trees $>50 \mathrm{~cm}$ dbh are retained and trees $<50 \mathrm{~cm}$ dbh often carry seeds as well. Recruitment of all species together might therefore be larger in logged compared to unlogged forest, due to higher light availability, higher carbon availability, larger seed
crops and less diseases (damping off) due to dryer conditions in gaps compared to forest understory. These dryer conditions limit the abundance of seedling affecting pathogens. The diversity of new recruits in a plot will be dependent on the surrounding seed trees.

## 4. Research methods

This research is an experimental field study in which the seedling and sapling community in a tropical moist forest is monitored for seven years. The field experiment consists out of 72 plots of $2 \times 2 \mathrm{~m}$, it is a paired plot design with 36 exclosures (fenced with chicken wire) and 36 control plots next to them. Data is collected in the forestry concession Agroindustria Forestal in La Chonta, situated in the Guarayos province in the department of Santa Cruz, Bolivia.

### 4.1 Description of study site

The Agroindustria Forestal concession comprises a total area of 100,000 ha and is located at $15^{\circ} 47^{\prime} \mathrm{S}, 62^{\circ} 55^{\prime} \mathrm{W}$. The La Chonta forestry concession is situated at the transition zone between the Chiquitano dry forest and the moist Amazon forests. Mean annual precipitation in the area is 1580 mm , mean temperature is $25.3^{\circ} \mathrm{C}$ and the soil is characterized by a nutrient rich sandy-loam structure. The forest concession at La Chonta harbours 160 identified tree species, of which 24 are considered commercially valuable. The average density of trees with a DBH $>10 \mathrm{~cm}$ is 367 stems/ha. Average basal area is $19.3 \mathrm{~m}^{2} /$ ha and species diversity is about 59 species/ha (Peña-Claros et al., 2012). Besides the large variety of tree species the forest harbours 116 mammal species (www.ibifbolivia.org.bo).

### 4.2 Experimental design

The experiment is originally set up by Tjerk de Rooij in 2004 (Rooij, 2005) and is designed as a four layered nested design. The four layers consist of the following elements:
5) There are two logging compartments, further referred to as blocks.
6) Two silvicultural treatments are applied in each block. Each block harbours a plot of 27 ha that is unharvested (control) and one that is harvested in the traditional way.
7) Three different microhabitats (natural or logging gap, trail and forest understory)can be found in each treatment. Each microhabitat type is replicated three times per treatment plot.
8) Each replicate consist out of a paired exclosure and control plot of $2 \times 2 \mathrm{~m}$.

In total there are 2 blocks * 2 treatments * 3 microhabitats * 2 exclosure types * 3 replicates $=\underline{72}$ plots in this study. Figure 5 gives a simplified illustration of the experimental design.


Figure 5: schematic design of experimental setup, each block has a size of approximately $\mathbf{2 9}$ ha ( $\mathbf{4 5 0 * 6 5 0} \mathbf{~ m}$ ). In each block four silvicultural treatments are applied (Normal, Testigo, Intensivo and Mejorado). In this figure only two treatments; harvested (normal) and unharvested (testigo) are presented because the other treatments are not included in this study. In each treatment three different habitat types are selected; forest understory (black dots), gaps (white dots) and trails (lines). In each habitat three exclosures and control plots are set up.

### 4.2.1 Silvicultural treatments

The two different silvicultural treatments in this study consist of unharvested forest and traditionally harvested forest. Except for the removal of some lianas on commercially interesting trees during forest inventories no silvicultural treatments are used in the unharvested 'control' plots. In traditionally harvested plots the following treatments are applied (Peña-Claros et al., 2008):
-six months before logging lianas are cut back on merchantable trees
-planning of skid trails
-20\% of commercially merchantable trees are retained as seed trees
-directional felling
-only trees with a diameter above $50-70 \mathrm{~cm}$ dbh are harvested.
The number of harvested trees is low at a harvest density of 4-6 trees/ha. In block one harvesting took place in 2001 and block three was harvested in 2002.

### 4.2.2 Microhabitats

The distinction between the three different microhabitat types was made at the start of the plot experiment in 2004, three years after logging had started. When the field study started gaps with a minimum size of 10 x 10 m were selected. The trail microhabitat is slightly different between both logging treatments, but this is not expected to influence the results because microhabitat conditions were equal at the start of the experiment. In the traditional harvested forest skid trails are established 150 m apart from each other. In the unharvested 'control' forest no skid trails are present and therefore the forest paths are taken which are used for forest inventories, these trails are situated closer together at a distance of 50 m apart from each other and have a smaller width compared to the skid trails. Forest understory microhabitats are characterized by a crown structure that totally covers the understory, creating a relatively dark environment.

### 4.2.3 Exclosures

Exclosures offer the opportunity to examine the effect of mammals on the regeneration, survival and growth of trees. In this study exclosures of $2 \times 2 \mathrm{~m}$ are set up in each microhabitat type. Exclosures are made from chicken wire (mesh size $<2 \mathrm{~cm}$ ), are approximately 1 m tall and are open at the top. In October 2011 the chicken wire of all exclosures is replaced. Next to each exclosure, approximately 5-10 m apart, a control plot is established. Control plots measure $2 \times 2 \mathrm{~m}$ as well and the borders are indicated by red colored tubes.
All plots are measured by Tjerk de Rooij in December 2005 and re-measured by Peter van Buuren in February 2006, Martijn Slot and Don Eugenio Mercado in April 2007, by Lourens Poorter and Juan Carlos Licona (only block 1) in May 2009 and in September and October 2011 by Jonna van Ulzen.

### 4.2.4 Community assembly

Community assembly is examined at two levels. First the entire seedling and sapling community is taken into account and second an in-depth analysis is conducted at the species level for seven abundant species. These seven species (table 2) are selected based on their level of occurrence and their distribution among different functional groups. Cariniana ianeirensis is selected because this species is experimentally planted in the original study of Tjerk van Rooij (Rooij, 2005). The fact that the species was planted in all plots allows for a more controlled and experimental evaluation of the research questions.

Table 2: the seven most abundant species in 2006 that are analysed up to species level. In the columns $\mathbf{N}$ Gap, $\mathbf{N}$ Trail and $\mathbf{N}$ Understory the number of seedlings that is found in each of these three habitats is given per species. The Column $\mathbf{N}$ Total adds up these three numbers. In the column $\mathbf{N}$ Exclosure the number of seedlings per species that grows inside the exclosures is mentioned.

|  | Guild | N <br> Total | N <br> Gap | N <br> Trail | N <br> underst. | N <br> excl. | Occurence |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :--- |

### 4.3 Data collection

For each plot both data about the microhabitat, tree characteristics, herbivory rates and presence of seed trees is collected. For the environmental data canopy openness and soil cover are taken into account.
For all trees with $>10 \mathrm{~cm}$ height in a plot, the species is identified (if this has not been done before) and the height, dbh (for trees > 3m tall) and condition (death, alive or new recruit) are measured.
Height is measured vertically from the forest floor to the apex (leaf basis) of the stem. Height growth can be negative due to physical damage. For each tree it is noted down if height loss has occurred, height loss is divided in the following categories:
0) no past dieback

1) dieback due to pathogens/ disease
2) height loss due to browsing
3) height loss due to snapping by falling debris
4) height loss because tree is bent over (by falling debris, lianas, etc.)
5) height loss due to unknown reason.

Data of re-measured plants is compared with earlier measurement data in the field, to check for abnormal height growth or dieback. New seedlings ( $>10 \mathrm{~cm}$ height) ware tagged and numbered with an ascending number within a plot. New seedlings are identified at species level, the species names of most seedlings that were marked as unknown species during earlier measurements are determined as well. The survival of trees is divided in four classes:
0 ) dead (tag found)

1) missing (tree nor tag found)
2) alive
3) new recruit

For the environmental data the following aspects are measured:

- Canopy openness $\rightarrow$ \% light availability is measured with a spherical densitometer Model-A(convex. ) In each plot four readings are done ( $\mathrm{N}, \mathrm{E}, \mathrm{S}$ and W direction)from plot centre, which are averaged and multiplied by 1.04 to obtain the percent of canopy openness.
- aspects measured in both 2005 (February) and 2011 (October):
fern cover (\%), shrub cover (\%), woody debris cover (\%), litter cover (\%), cover of lianas up to 1.5 m (\%), Heliconia cover (\%) and seedling cover (< 0.3 m height)(\%) $\rightarrow$ all estimated sapling ( $0.3-1.5 \mathrm{~m}$ height) number, juvenile (height $>1.5 \mathrm{~m}, \mathrm{dbh}<10 \mathrm{~cm}$ ) number and small tree ( dbh $10-20 \mathrm{~cm}$ ) number $\rightarrow$ all counted.
- additional aspects measured in 2011:

Average litter thickness ( cm ) $\rightarrow$ the average of three measurements
litter weight (g) $\rightarrow$ all litter in an area of $0.25 \mathrm{~m}^{2}$ is put in a plastic bag and weighed. This number is multiplied by 8 to obtain litter weight in the entire plot. Woody debris is weighed separately if abundantly present.
palm cover (\%) and \% of leaves per tree affected by insect herbivory $\rightarrow$ estimated seedling number and number of stems browsed $\rightarrow$ counted
Litter thickness and weight are additionally measured because this is expected to have more influence on seedling recruitment, survival and growth than litter cover alone. Palm cover is measured separately because this group was missing. Seedling numbers are counted because this gives a better insight in the amount of seedlings present in a plot than the percentages they cover, since these are often very low. The number of stems browsed per plot are counted to give an insight in browsing pressure.

All data is measured inside plot borders.

The abundance of seed trees is measured in a radius of 20 m from the centre between a pair of plots (exclosure and control). Trees are included if at least $50 \%$ of their crown cover lies within the radius and if dbh is minimal 20 cm . For each tree that fulfills these requirements the species name, dbh and crown position index (fig 6) is noted down. Crown position values are derived from Clark and Clark (1992) (table 3).

Table 3 Crown position index values according to Clark and Clark (1992).

| Index <br> value | Definition |
| :---: | :--- |
|  | Crown completely |
| 5 | exposed <br> 4 |
| Full overhead light <br> (>90\%) <br> some overhead light (10- <br> 3 | $90 \%$ ) <br> 2.5 |
| 2 | high natural light |
| medium lateral light |  |
| 1.5 | low lateral light |
|  | no direct light |



Figure 6 crown position index as described by Clark and Clark (1992) (Jennings et al., 1999).

### 4.4. Data analysis

### 4.4.1 Factors and response variables

Many factors are influencing the establishment, growth and survival of seedlings in tropical forests. The factors of influence in this experiment are divided in three groups. At first treatment (harvested or unharvested), second microhabitat (natural/logging gap, trail and forest understory) and third plot type (exclosure and control). The factors mentioned above result in many responses of the forest conditions. Response variables are divided in three groups, environment, composition \& structure and dynamics. The aspects of each group taken into account in this research are listed in table 4 below.

Table 4: Response variables. In the column environment the biotic an abiotic variables are listed that are used to determine the environmental conditions in the period 2005-2011. In the column composition $\&$ structure the response variables that determine the tree formation are listed. Finally the response variables that describe the tree dynamics in the forest are listed in the third column.

| Environment | Composition \& structure | Dynamics |
| :--- | :--- | :--- |
| Abiotic <br> -light <br> Biotic <br> Cover by: <br> -litter <br> -woody debris <br> -herbs | Species richness | Recruitment |
| -ferns <br> -shrubs <br> -heliconia <br> -lianas | Species composition | Survival |

A four way ANOVA is used to test for significant differences between treatments, microhabitats and exclosures on recruitment, survival and growth of trees in the La Chonta forest. The data is analyzed at two levels:

1) At the entire community level in order to gain insight in the functioning of the forest as a whole, and because many species are present in very low numbers which makes it impossible to analyze them statistically.
2) The seven most abundant species (table 2) are analyzed at individual level in order to gain insight in the individual responses of trees.
Before each analysis the plot averages are calculated, those averages are used in the statistical analysis.

Height growth is analyzed by calculating both the relative growth rate (RGR) and absolute growth rate (AGR). Absolute growth rates are calculated to gain insight in the maximum growth over time. Since seedlings did not have the same height at the start of the experiments relative growth rates are calculated to gain insight in the growth as a function from the original height.


Lend $=$ length at last measurement (cm)
Lstart = length at first measurement (cm)
$y=$ number of years between first and last measurement ( 5.644 years in the period 2006-2011)

When significant differences in response variables between silvicultural treatments, microhabitats and exclosure types occurred in the General Linear Model, these are analyzed using an ANOVA or Kruskal-Wallis test and a multiple comparison (LSD, TUkey, Scheffe or Gabriel) post hoc test to unravel the exact differences. Besides the height, number of species and species diversity at the begin and the end of the experiment the change over time is measured as well. This change is measured to provide insight in the development of the forest over time. Change is measured by subtracting the values measured in 2006 from the values measured in 2011. In the analysis only plots with 2 or more seedlings are taken into account, resulting in 53 plots.

Seedling survival is recorded as dead or alive which makes the data categorical and therefore a log-linear analysis is conducted.

Species composition is analyzed using a correspondence or principal component analysis in CANOCO. The ordination diagram calculated gives insight in the structure of the tree community and the relation between the tree community and the different research factors. The factors (treatment, microhabitat en exclosure type) are included as dots. The dependent variables (see table 4) are included as vectors.
A separate CA is conducted with the species data of 2006 and 2011 in order to examine temporal shifts in species composition. The data is log+1 transformed, the selection criteria used is that species have to occur in at least $10 \%$ of the plots and plots need to have at least 2 species. The species composition at community level is first examined with an indirect gradient analysis, in order to get a first insight in the structure of the data and the distribution of species. This analysis is conducted on a reduced dataset, only species that occur in $10 \%$ or more of the plots are included. Plot B3TT1C is excluded because of the unrepresentative high number of Laurel seedlings in this plot. After a log transformation the data is normally distributed. A DCA is conducted in order to investigate the length of gradient and the species composition is examined with a CA. Environmental variables are log+1.1 transformed. The 1.1 is added to avoid 0 values because zero's are not taken into account in the analysis done by Canoco. In small datasets (I considered this to be a small dataset) the data can be considered to have a lognormal distribution when the standard deviation is larger than the mean, or when the highest value is more than 20 times higher than the smallest value (van Katwijk and ter Braak, 2008). This is the case for all variables, except litter cover. If there is a log normal distribution the log transformed data should follow a normal distribution. I did this log transformation for all data including litter cover, because this does not cause an outlier or have a major influence on the overall image. The importance of environmental variables in the CA is tested with a permutation test consisting of 499 permutations in a CCA.

The importance of individual environmental variables is derived from the inflation factors produced by an ordination analysis in Canoco. These are variance inflation factors (V.I.F.), which is a measure for the correlation of each individual variable with all other variables together. Variables with a V.I.F. > 20are almost completely correlated with other variables and therefore do not contribute to the explanation of the variance in species composition (ter Braak, 1987a in van Katwijk and ter Braak, 2008).

For tree species of which both seedlings and seed trees are present the correlation between seed tree density and the number of seedlings present in a plot is calculated using Spearman $r$ test because the data is not normally distributed.

Besides Canoco and Canodraw, which are used to analyze species composition, all statistical analyzes are done with IBM SPSS Statistics 19 and Microsoft Office Excel 2007 and 2010. One pair of plots (in the understory of the unlogged forest of block 3 ) is left out of the analysis because it is completely destroyed by a large stromfall of trees. The exclosure was not found back in 2011 and the control plot was almost entirely covered by a large fallen stem.

## 5. Results

### 5.1 Correlation between environment and response variables

A principal component analysis reveals that most environmental variables show the same distribution in the ordination diagram in both 2005 and 2011 (fig 7). Exemptions to this trend are seedling cover, which is negatively correlated with the first
 axis in 2005 and with the second axis in 2011. Woody debris cover in 2011 is the main variable determining the first ordination axis, while woody debris cover in 2005 is less strong correlated with this axis. The second ordination axis is mainly determined by the data of shrub cover in 2005. Canopy openness, liana cover, fern cover and litter cover do not play a large role in the determination of the axes. The distribution of environmental variables at the first ordination axis differs between logging treatments and microhabitats (table 4). A Gabriel post-hoc test yields two homogeneous subsets of microhabitat types. The distribution of environmental variables at the first axis is similar at trails and in gaps ( $p=0.500$ ) and in gaps and understories ( $p=0.224$ ). At the second axis a difference between the blocks is found.

Figure 7 ordination diagram presenting the distribution of environmental variables in 2005 and 2011.
A shift in species composition and abundance is observed over time (fig 8.A+B). The length of gradient of the first axis of the ordination diagram consisting of the data of 2006 is a bit shorter compared to the one of 2011, indicating that the variation in species composition increases over time. The second axis has the same length of gradient in both years, but is determined by different species. In 2006 the main species determining the second axis are Ochoo, Lucuma, Negrillo Tropero and Amarguillo. In 2011 the second axis is mainly determined by Ajo and to a lesser extent by Negrillo hoja larga, Pica pica Colorado and Ojos Colorado. The abundance of Ochoo drops to below 10\% over time. Negrillo hoja larga is only present in 1 plot in 2006, but has a lot of new recruits in 2011. The number of species present in at least $10 \%$ of the plots increased from 15 species in 2006 to 18 species in 2012, of which 12 species were present in both years (table 5). The absolute abundance of seven out of these 12 species decreased, the abundance of the other species increased over time. Only three species significantly differ in abundance between the years. The diversity of abundant species increases over time, as well as the variation is species composition (fig8 $A+B$ ). Logging and microhabitat type have a significant influence on the species composition of the first axis in 2006 (table 5). A Gabriel post hoc test indicates that the distribution of species at the first axis is different in all three microhabitat types. No influence is found on the species distribution on the second axis. Block, logging and microhabitat have a significant influence on the species composition of the first axis in 2011. A Gabriel post-hoc test indicates that there are
two homogeneous subsets in the microhabitat types. Species composition is similar in gap and understory microhabitats ( $p=0.904$ ) and in gaps and trails ( $p=0.077$ ). No significant effects are found for the second axis.


Figure 8 A and B biplots of first and second axis of CA's of species composition in 2006 (A) and 2011 (B). The abbreviations of the plot names should be read as follows: B indicates the block number (1 or 3 ), T or N indicates the logging treatment (testigo (unlogged) and normal (logged)), G, T, S or U represent the microhabitats (gap, trail, skid trail and understory) and $E$ and $C$ represent exclosure and control. Tree species are indicated by a triangular symbol in the figure.

Table 4 outcome of GLM on the main effects of the regression values of the environmental variables and species composition in 2006 and 2011. F values indicate to what extent group means differ more than expected within group variances. P values represent the level of significance. In this test a confidence level of $95 \%$ is used, meaning that test results with a p value below 0.05 are significantly different. The significantly different results are highlighted in green.

|  |  | Block |  |  | Logging |  |  | Microhabitat |  |  | Exclosure |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :---: | :---: | :---: |
|  |  | F | p | F | p | F | p | F | p |  |  |  |
| PCA |  |  |  |  |  |  |  |  |  |  |  |  |
| environment | axis 1 | 2.98 | 0.089 | 4.46 | 0.039 | 4.86 | 0.011 | 1.07 | 0.306 |  |  |  |
| CA species 2006 | axis 2 | 5.72 | 0.020 | 0.89 | 0.350 | 0.73 | 0.487 | 0.26 | 0.609 |  |  |  |
|  | axis 1 | 1.63 | 0.207 | 4.30 | 0.043 | 17.93 | $<0.001$ | 0.48 | 0.490 |  |  |  |
|  | axis 2 | 0.03 | 0.866 | 0.35 | 0.557 | 0.51 | 0.606 | 0.17 | 0.685 |  |  |  |
| CA species 2011 | axis 1 | 4.96 | 0.030 | 10.11 | 0.030 | 4.45 | 0.016 | 0.29 | 0.590 |  |  |  |
|  | axis 2 | 1.13 | 0.293 | 0.89 | 0.351 | 1.07 | 0.351 | 0.87 | 0.354 |  |  |  |

Table 5 Summary table of species composition in 2006 and 2011. Species that are present in both years are listed in the first column, in descending order of abundance. The second column indicates if the abundance of these species increased or decreased over time. The third column indicates whether the abundance in 2006 and 2011 are significantly different. The fourth and fifth column list the species that are only present in minimal $10 \%$ of the plots in one of the studied years.

|  | p |  |  | 2006 |
| :--- | :---: | :--- | :--- | :--- |
| Both years | Change | (Wilcoxon) | only | 2011 only |
| Blanquillo | - | 0.364 | Ochoo | Laurel |


| Ojoso colorado | + | 0.076 | Paychané | Ajo |
| :--- | :--- | :---: | :--- | :--- |
| Pica pica colorado | - | 0.001 | Coco | Pacay hoja peluda |
| Coquino | + | $<0.001$ |  | Negrillo hoja larga |
| Verdolago | - | 0.340 |  | Cari cari colorado |
| Sauco negro | - | 0.021 |  | Sapaymo colorado |
| Aliso | + | 0.068 |  |  |
| Negrillo tropero | + | 0.348 |  |  |
| Paychané blanco | - | 0.249 |  |  |
| Lucuma | + | 0.058 |  |  |
| Amarguillo | - | 0.564 |  |  |
| Mururé | - | 0.891 |  |  |

A selection criteria where only species that occur in at least $15 \%$ of the plots are taken into account results into a cumulative percentage of explained variance of $54.2 \%$ (only $39.7 \%$ at $10 \%$ occurrence selection criteria). The first two axes explain $32.8 \%$ of the variance in species composition (fig. 9), because axes three and four explain another $21.4 \%$ of the variance in species composition they are plotted as well (fig. 10). The remaining $45.8 \%$ of the variance is explained by other axes that are not reported here.


Figure 9: ordination diagram of CA species data axis 1 plotted against axis 2. Tree species are indicated by triangular symbols and plots by circles.


Figure 10: ordination diagram of CA species data axis 3 plotted against axis 4
Paychane blanco is not only positively correlated with the first axis, but also has a negative correlation with the third axis. Ohoo has a strong positive correlation with both the second and third axis. The strongest correlation on the fourth axis is the positive one with Yesquero blanco (fig 10). A clustering of different microhabitat types can be observed in figure 9 . Plots in understory microhabitats are all found on the left side of the figure, while trail microhabitats are mainly found at the right side and gap microhabitats in the centre. When the third and fourth axes are plotted against each other (fig.10) this clustering is gone and the different microhabitats are spread heterogeneously. Paychane blanco and the plots in trail microhabitats are strongly positive correlated with the first axis and Blanquillo has a negative correlation with this axis as well as the plots situated in understory microhabitat types. In ascending order of strength Ochoo, Aliso and Ojoso Colorado are positive correlated with the second axis (fig. 9).


When all factors are taken into account (plots, species and environmental variables), the strongest correlation between the species data and environmental variables is found between the species that meet the $15 \%$ selection criteria and the environmental variables measured in 2005. In total $60.1 \%$ of the variance is explained by the first four ordination axes, of

Figure 11 correlation between environmental variables, species and plots (triplot of first and second axis).
wich the first two axes explain $45.8 \%$ (fig 11). Canopy openness is the main factor determining the ordination of the first species axis (explained variance is $24 \%$ ), followed by woody debris and shrub cover, which are all negatively correlated with this axis. There is no environmental variable that has a strong correlation (at least $10 \%$ explained variance) with the second species axis. The strongest correlation between species and environmental variables at this axis is with seedling cover (almost $6 \%$ explained variance). Most variables correlate strongest with the first ordination axis. Plots located in understory microhabitats are concentrated at the bottom left side of the figure as well, indicating that canopy openness is lowest in this plots, and that woody debris and shrub cover are low as well, compared to other plots in other microhabitat types. Blanquillo, Coquino, Laurel and Pacay hoja peluda are related to the negative side of the first axis as well Seedling cover is the main environmental factor determining the second axis and is negatively correlated with it.

|  | \% of total <br> variance |
| :--- | ---: | ---: |
| variance |  |

> The low correlation of the environmental variables with the second axis indicates that this axis is mainly determined by (an) environmental factor(s) not measured in this research. A CCA permutation test also proves that canopy openness is the most important factor for the explanation of the variance in the weighed correlation between species and environmental variables (table 6).
> Table 6 result of permutation test. The variance column gives an overview of the part of the total variance of the selected variables that is explained by each single variable.

The mutual correlation of the environmental variables is examined both with a CA (table 7) and a PCA (fig 7) of environmental variables only. In the CA a threshold value of $10 \%$ explained variance is used to select the correlations of importance. The two strongest correlations are the negative correlation between woody debris and litter cover (the more woody debris the less space for litter cover, or there might be more woody debris in gaps and less litter in gaps because there are less trees), and the positive correlation between canopy openness and woody debris cover (indeed indicating that woody debris is higher in gaps). These assumptions are illustrated by the PCA biplot. The explanatory power of the PCA with only environmental variables is high. In total $98.2 \%$ of the variance is explained by the first four axes, and $91.5 \%$ by the first two axes. The first axis is mainly determined by shrub cover, which has a negative correlation with heliconia cover, indicating a tradeoff between the two of them. Shrub cover also has a positive effect on seedling cover, it probably offers protection to the seedlings. Besides woody debris canopy openness in positively correlated with liana cover as well and negatively correlated with fern cover (indicating a higher amount of ferns in the forest understory).

Table 7 weighed correlation matrix environmental variables. Factors explaining $\geq 10 \%$ of the variance are marked yellow.

| canopen | 1.0000 |  |  |  |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| ferncov | -0.4232 | 1.0000 |  |  |  |  |  |  |  |
| shrubcov | 0.1795 | -0.1869 | 1.0000 |  |  |  |  |  |  |
| wooddebc | 0.6803 | -0.0980 | 0.1551 | 1.0000 |  |  |  |  |  |
| litterco | -0.4895 | 0.1518 | -0.1575 | -0.7807 | 1.0000 |  |  |  |  |
| seedlcov | 0.0524 | 0.0887 | 0.3471 | 0.2756 | -0.2069 | 1.0000 |  |  |  |
| lianacov | 0.2677 | -0.0885 | -0.0377 | 0.3507 | -0.2644 | 0.2575 | 1.0000 |  |  |
| helicocov | 0.0139 | -0.1810 | -0.3218 | -0.0515 | 0.1250 | -0.4793 | -0.2899 | 1.0000 |  |
|  | canopen | ferncov | shrubcov | wooddebc | litterco | seedlcov | lianacov | Helicoco |  |

The inflation factors indicate that each environmental variable contributes to the explanation of the variance independently.

### 5.2 Differences betwee environmental variables and interaction effects

Test results for all environmental variables can be found in appendix V . When the main effects are examined block number is of no influence on the environmental values, meaning that both blocks have a comparable environment. Logging has influence on the most factors, namely canopy openness, litter cover, total cover, number of juvenile and small trees and the total stem number. The litter cover increased in both logged and unlogged forest, respectively with 6.9 and $2.9 \%$. Total cover of the forest floor does not significantly differ in 2005, but in 2011 it does. In 2011 the average total cover per plot is $61 \%$ in logged forest and $75 \%$ in unlogged forest. Small tree numbers are low in all plots, but in 2005 twice as many can be found in unlogged (mean 0.15 per plot) than in logged (mean 0.07 per plot) forest. In 2011 this difference has disappeared. The main effects of canopy openness, juvenile numbers and total stem numbers cannot be safely interpret due to interaction effects. Change in fern cover is the only main effect that differs between the microhabitat types and does not have an interaction with other factors. In gap and trail habitats the fern cover increased over time with respectively 2 and $4 \%$. In understory microhabitats fern cover decreased with 17\%. The total cover in 2005 is the only environmental variable that is significantly different between exclosures and control plots. In exclosure the total cover was $75 \%$, while in control plots a total cover of $97 \%$ was found.
Most effects can be found in the interactions between Logging and Microhabitat and Block and Logging, except shrub cover, each environmental variable has a significant interaction effect. The most interesting interactions are displayed in figure 12 and figure 13. In 2005 there is a significant difference in canopy openness between the different microhabitats. As expected canopy openness is highest in gaps and lowest in understory habitats. An interaction with logging treatments is observed as well, with canopy openness percentages being lower in unlogged than in logged forest. The differences in canopy openness became smaller over time. In 2005 the woody debris cover significantly differed between blocks and logging treatments. Most woody debris was found in logged forest parts and in block 1, in the logged forest gaps contained the highest amount of woody debris. Differences in heliconia cover are large, both over time and between blocks and logging treatments. In both 2005 and 2011 by far the most Heliconias are found in block 3. In both years and both blocks the majority is found in unlogged forest. The heliconia cover in block 3 increased over time, while it decreased to almost zero in block 1. Changes in total plot cover over time varies between logging treatments and microhabitat types. The variation in these data is enormous, indicating that there are large differences between the plots. Interaction effects in stem density numbers are mainly found in the amounts of saplings and juveniles and in total stem density. Both sapling and juvenile numbers decreased over time in a similar pattern. In 2005 the highest numbers are found in the unlogged parts of block 1 and the logged parts of block 3, in 2011 the highest numbers were found in the logged parts of both blocks. Total stem numbers decrease as well, in both years the highest numbers are found in trail habitats in logged forest.

 $x$-axis, microhabitats with the same symbol belong to the same homogeneous subset Test results can be found in appendix $V$.

 microhabitats with the same symbol belong to the same homogeneous subset Test results can be found in appendix $V$.

### 5.3 Effects at community level

In this section the results are presented for the analysis at community level.
First the influence of the different blocks, logging treatments and microhabitats on growth, number of seedlings and species, recruitment and survival rates is presented. The outcome of the four way ANOVA (table 8) shows that microhabitat type has the largest influence on the factors mentioned above.

Table 8 outcome of four way ANOVA for response variables at community level. F values indicate to what extent group means differ more than expected within group variances. P values represent the level of significance. In this test a confidence level of $95 \%$ is used, meaning that test results with a p value below 0.05 are significantly different. Exclosures are not presented in this table because no significant effects are found. The significantly different results are highlighted in green.

|  | Block |  | Logging |  |  | Microhabitat |  |
| :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- |
|  | F | p | F | p | F | p |  |
| Dynamics |  |  |  |  |  |  |  |
| Recruitment | 0.796 | 0.378 | 0.291 | 0.593 | 5,244 | 0.010 |  |
| Arcsinsurvival | 0.976 | 0.330 | 8,717 | 0.005 | 1,273 | 0.292 |  |
| Absolute Growth Rate (AGR) | 5,688 | 0.021 | 0.013 | 0.911 | 3,163 | 0.051 |  |
| Relative Growth Rate (RGR) | 0.030 | 0.864 | 0.001 | 0.970 | 1,527 | 0.231 |  |
| \% stems browsed | 0.381 | 0.540 | 0.384 | 0.539 | 0.516 | 0.601 |  |
| Height loss | 0.467 | 0.498 | 0.622 | 0.434 | 2,160 | 0.127 |  |
| Structure |  |  |  |  |  |  |  |
| Log stem density 06 | 1,671 | 0.204 | 4.23 | 0.047 | 5,034 | 0.012 |  |
| Log stem density 11 | 0.001 | 0.979 | 0.046 | 0.831 | 2,242 | 0.120 |  |
| Stem density change | 2,192 | 0.147 | 4,048 | 0.052 | 5,878 | 0.006 |  |
| Log average height 06 | 3,961 | 0.054 | 2,258 | 0.141 | 8,282 | 0.001 |  |
| Log average height 11 | 2,294 | 0.138 | 0.009 | 0.925 | 12,353 | $<0,001$ |  |
| Height change | 0.787 | 0.380 | 0.267 | 0.608 | 3,193 | 0.050 |  |
| Richness |  |  |  |  |  |  |  |
| Log N species 06 | 0.342 | 0.562 | 0.978 | 0.329 | 8,509 | 0.001 |  |
| Log N species 11 | 0.103 | 0.750 | 0.871 | 0.357 | 0.093 | 0.912 |  |
| N species change | 1,841 | 0.183 | 0.147 | 0.704 | 9,469 | $<0.001$ |  |
| Shannon-Wiener div. 06 | 0.292 | 0.592 | 2,759 | 0.105 | 3,955 | 0.028 |  |
| Shannon-Wiener div. 11 | 0.097 | 0.757 | 0.457 | 0.503 | 0.007 | 0.993 |  |
| Shannon-Wiener div. change | 0.037 | 0.849 | 0.891 | 0.351 | 4,369 | 0.020 |  |
| Total nr significant interactions | $\mathbf{1}$ |  | $\mathbf{2}$ |  | 9 |  |  |
| df block = 1, logging = 1, and microhabitat =2 |  |  |  |  |  |  |  |

### 5.3.1 Influence of blocks, logging treatments and microhabitats

The abundance of stems and species densities per microhabitat type can be found in figure 14 . Stem density at the beginning of the experiment (2006) is significantly different between the two logging treatments. In unlogged forest the average stem density per plot is 14,5 , in logged forest an average of 11.2 seedlings per plot was found. In 2011 no significant differences between logging treatments and microhabitat types are found, indicating that the different forest parts have become more similar. The change in stem density from 2006 to 2011 differs significantly between the different microhabitats. Stem density declined in gap and trail microhabitats with on average 0.63 and 5.29 stems per plot. The large whiskers in the figure indicate a large variation in the data set and show that plots with positive stem density changes occur as well. In understory microhabitats stem density increased on average with 4.62 stems per plot. Next to stem density, the number of species present per plot provides valuable information about forest composition. In 2006 the number of species found differed significantly between the different microhabitat types. The average number of species found was the lowest in gap and understory microhabitats, respectively 5.37 and 4.37 species per plot. Species number was more than $30 \%$ higher in trail habitats with averagely 7.76 species per plot. As well as found for stem density this differences disappeared over time. The change of species density over time is significant. With the results of 2011 in mind the species density in trail microhabitats decreased as expected, on average with 1.29
species per plot. Species density in gap and understory microhabitats increased, on average with 0.63 and 2.23 species per plot.


Figure 14 boxplot representing the stem density and species numbers in 2006, 2011 and the change over time. The black squares in the boxplots indicate the mean values. Homogeneous subsets (according to a Gabriel test) are marked at the x-axis, microhabitats with the same symbol belong to the same homogeneous subset. The stem density in 2006 is divided in logged and unlogged forest because of the significant difference between them. This division is not made for the other parameters because logging is of no influence there.


Shannon-Wiener diversity indexes (fig 15) provide similar results as the number of species. In 2006 the Shannon-Wiener diversity was highest in trail microhabitats (1.78), followed by gap microhabitats (1.43) and understory's (1.24). The largest variation in diversity was found in trail habitats. The differences in Shannon-Wiener diversity have vanished over time, no significant differences are found in 2011 anymore. In the period from 2006 to 2011 the diversity index increased in gap (0.15) and understory (0.32) microhabitats. The Shannon-Wiener diversity decreased with 0.18 in trail habitats. In 2006 Blanquillo was the most abundant species in trail microhabitats, but in 2011 this position was taken over by Laurél.

Figure 15 boxplot representing the Shannon-Wiener diversity scores in 2006, 2011 and the change over time. The black squares in the boxplots indicate the mean values.
Homogeneous subsets (according to a Gabriel test) are marked at the $x$-axis.

The average heights per microhabitat type (fig 16) show large variations. With a mean value of 95.5 cm , the average height in 2006 was highest in trail microhabitats, followed by gaps ( 69.2 cm ) and understory microhabitats (34.7). Although quite some seedlings suffered height losses, the average heights have increased in all microhabitats in 2011. The largest seedlings are still found at trails, with a mean height of 158.5
cm , again followed by gaps ( 114.8 cm ). The lowest heights are, as expected, found in the understory with a mean height of 44.7 cm . No significant results are found in height change over time. Height losses are examined as well, but no significant differences in height loss between any of the experimental parameters are found. The mean height losses are much lower in understory microhabitats (5\%) than in gap microhabitats ( $14.8 \%$ ). Mean height loss at trails is $13.2 \%$, which makes it comparable to gaps.


Figure 16 boxplot representing average heights in 2006, 2011 and the change over time per microhabitat type. The black squares in the boxplots indicate the mean values. Homogeneous subsets (according to a Gabriel test) are marked at the x-axis.

Absolute Growth Rate (AGR) is the only factor that is significantly different between the two blocks.
The AGR in Block 1 is much higher (mean is 19.6 cm ) than in Block 3 (mean is 10 cm ). For all other factors the block number is of no significant influence.


Figure 17 boxplot representing survival and recruitment values. The black squares in the boxplots indicate the mean values. Homogeneous subsets (according to a Gabriel test) are marked at the $x$-axis.

Survival percentages over time significantly differ between logged and unlogged forest parts. With a survival rate of $57.75 \%$ the survival in logged forest is much higher than in unlogged forest (37.5\%). No significant differences in survival percentages are found between microhabitat types. In fig 17 it can be seen that in logged forest the mean survival is highest in gaps, while gaps are the microhabitat type with lowest mean survival in unlogged forest. The large variation in the data indicate that the survival rates between plots in the same microhabitat type differ greatly. Recruitment rates are similar between the different logging treatments, but differ significantly between microhabitat types. The highest recruitment is found in the understory microhabitat, on average 14.54 seedling per plot over a period of 5.6 years. Gaps have the second highest recruitment rates of 8.44 seedlings on average per plot. The lowest recruitment rates is found at trails with a mean of 6.21 seedlings per plot.
Neither Block, Logging treatment or Microhabitat type has a significant influence on the percentage of stems browsed (table 8). Browsing percentages range from zero to 100 percent.

### 5.3.2 Exclosure effect

The effect of exclosures on the response variables is much smaller than expected beforehand. All test results of the exclosures on both response and environmental variables can be found in appendix III and IV, significant results are presented here. Relative growth rate (fig 18) is higher in exclosures than in control plots, and explanation can be found in the \% of stems browsed (fig 19). In exclosures on average $15 \%$ of the plants suffers height loss, while plants in control plots suffer $40 \%$ height loss.


Figure 18 relative growth rates in exclosures and control Plots. Mean values are indicated by black squares.


Figure 19 \% of stems browsed in exclosures and control plots. Mean values are indicated by black squares.

Exclosures have a significant effect on a number of environmental variables (table 9) as well, this affect is in particular observed in 2005.

Table 9 significantly different environmental variables between exclosures and control plots. Mean values are back-transformed where needed.

|  |  |  |  | $\begin{array}{l}\text { mean } \\ \text { exclosure }\end{array}$ |  |
| :--- | :--- | :--- | :--- | :--- | :--- |
|  | mean |  |  |  |  |
| control |  |  |  |  |  |$]$



Canopy openness (fig 20) is slightly larger in exclosures, but with $15 \%$ in exclosures and $13.5 \%$ in exclosures this does not seem to be crucial. In 2005 forest floor cover with ferns, shrubs, litter and total cover is always lower in exclosures than in control plots.

Sapling ( $0.3-1.5 \mathrm{~m}$ height) and total stem numbers are both higher in control plot in 2005 (fig 21). Sapling numbers are relative low in both plot types; on average 0.9 in exclosures and 1.8 in control plots. Total stem numbers are much higher; on average 15.4 in exclosures and 22.5 in control plots. The biggest contribution to the total amount of stem numbers is made by seedlings. Differences in environmental variables between plot types have disappeared in 2011, indicating that plots have become more similar over time.


Figure 21 Average stem numbers per plot in 2006. Black squares represent mean values.

### 5.4 Seed trees

As expected the number of seed trees per plot area is slightly lower in logged (mean is 53.39) than in unlogged (mean is 54.76) forest (fig 22). Although the difference is small, it is significant ( t -test, $\mathrm{df}=17, \mathrm{t}=12.480$, $\mathrm{p}<0.001$ ). Although the number of seed trees differs per logging treatment, no difference between seedling abundance in logged versus unlogged forest is found.


Figure 22 Average number of seedlings per plot in logged and unlogged forest. In 2006 all seedlings present are taken into account, in 2007 and 2011 only new recruits are presented. The last two bars represent the number of seed trees. Mean values are indicated by a black square.

### 5.5 Results individual species

A General Linear Model is conducted for Blanquillo, Laurél and Ojoso Colorado, there are too little individuals of the other species to conduct reliable statistics.

### 5.5.1 Blanquillo

With 138 individuals Blanquillo is by far the most abundant species in 2006. Almost half of these plants (49\%) is still alive in 2011. The Blanquillo population is declining over time, but the recruitment rate is increasing from $9 \%$ in 2007 till $21 \%$ in 2012 regarding to the population size in 2006. This recruitment rate is low compared to other species, but actual population numbers remain high because the Blanquillo population is large (Appendix
VI). The GLM model only results in a significant effect for the average height in 2006 (table 10). According to these data Blanquillo behaves like a generalist.

Table 10 outcome of GLM response variables for Blanquillo. $F$ values indicate to what extent group means differ more than expected within group variances. $P$ values represent the level of significance. In this test a confidence level of $95 \%$ is used. Significant effects are highlighted in green.

|  | Block |  |  |  |  |  |  | Logging |  |  |  | Microhabitat |  | Exclosure |  |
| :--- | ---: | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :--- | :---: | :---: | :---: | :---: | :---: | :---: |
|  | F | p | F | p | F | p | F | p |  |  |  |  |  |  |  |
| Dynamics |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Recruitment | 0.0664 | 0.421 | 0.079 | 0.780 | 0.464 | 0.632 | 0.015 | 0.903 |  |  |  |  |  |  |  |
| Survival | 1.740 | 0.201 | 0.845 | 0.368 | 0 | 1 | 0.089 | 0.768 |  |  |  |  |  |  |  |
| Absolute Growth Rate | 0.081 | 0.779 | 0.916 | 0.351 | 0.297 | 0.746 | 0.280 | 0.603 |  |  |  |  |  |  |  |
| Relative Growth Rate | 0.336 | 0.569 | 0.058 | 0.812 | 0.438 | 0.652 | 0.711 | 0.410 |  |  |  |  |  |  |  |
| Structure |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| Stem density 06 | 0.018 | 0.894 | 0.014 | 0.906 | 0.993 | 0.381 | 1.321 | 0.258 |  |  |  |  |  |  |  |
| Stem density 11 | 1.189 | 0.283 | 0.641 | 0.429 | 0.683 | 0.512 | 0.715 | 0.403 |  |  |  |  |  |  |  |
| Stem density change | 0.852 | 0.362 | 0.408 | 0.527 | 1.036 | 0.366 | 1.622 | 0.211 |  |  |  |  |  |  |  |
| Average height 06 | 3.878 | 0.059 | 6.925 | 0.013 | 4.926 | 0.014 | 0.262 | 0.613 |  |  |  |  |  |  |  |
| Average height 11 | 2.140 | 0.155 | 0.009 | 0.924 | 2.466 | 0.105 | 1.448 | 0.240 |  |  |  |  |  |  |  |
| Average height change | 2.209 | 0.146 | 0.899 | 0.350 | 2.214 | 0.124 | 3.785 | 0.060 |  |  |  |  |  |  |  |

The differences in average height are presented in figure 23. Average height is much higher in logged than unlogged forests. The average heights in the different microhabitat types correspond to the hypothesis that seedlings in gaps have the largest heights and in understory microhabitats the lowest.


There is a negative correlation between the number of individuals in 2006 and the number of seed trees (table 12). The lesser seed trees there are, the more seedlings are present in the plots at the start of the experiment.


This negative correlation is strongest witch large seed trees (dbh $\geq 20 \mathrm{~cm}$ ). Seed trees with crown position index 4 or 5 are found in each plot, indicating that Blanquillo is a dominant species in the forest canopy. A relation between the basal area of seed trees and the number of seedlings is not found (fig 24). There is no difference in seedling abundance between plots with the presence of a seed tree an plots without (Mann Whitney-U, $\mathrm{p}=0.189$ ).

Figure 24 Relation between the basal area of the seed trees and the number of seedlings present.

### 5.5.2 Laurél

The Laurél population has a relative low initial population size but is increasing fast due to a high recruitment rate. In the period 2006-2007 the survival of the species is $100 \%$, but declines to $57 \%$ in 2011 (Apendix VI). There are only six plots with Laurel seedlings in 2006, a number too low to conduct reliable statistics. In 2011 the number of plots containing Laurél seedlings increased to 30 . No significant differences in average height, stem density or recruitment were found with a GLM testing for main effects (table 11). Implying that Laurél is a generalist species.

Table 11 outcome of GLM response variables for Laurél. $F$ values indicate to what extent group means differ more than expected within group variances. $P$ values represent the level of significance. In this test a confidence level of $95 \%$ is used.

|  | block |  | logging |  | habitat |  | exclosure |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | F | p | F | $p$ | F | p | F | p |
| average height 11 | 1.54 | 0.226 | 0.71 | 0.407 | 1.72 | 0.2 | 0 | 0.989 |
| stem density 11 | 0.78 | 0.081 | 1.11 | 0.303 | 1.41 | 0.264 | 2.14 | 0.156 |
| recruitment | 1.06 | 0.314 | 1.12 | 0.3 | 1.39 | 0.268 | 1.39 | 0.252 |

Although Laurél is one of the most abundant species in La Chonta (101 seed trees and 126 seedlings in 2011),no significant correlations are found between Laurél seed trees and the occurrence and recruitment of seedlings of this species (table


Figure 25 Relation between the basal area of the seed trees and the number of seedlings present.
13). Basal area of seed trees does not have an influence on the number of seedlings present (fig 25). There is no difference of plots with a seed tree present and without (Mann Whitney U, $\mathrm{p}=0.570$ ).

### 5.5.3 Ojoso Colorado

From 2007 onwards the population shows a large increase due to a high recruitment rate, the species has an excellent survival rate with $100 \%$ plants present in 2006 surviving (Appendix VI). Two variables have a significant difference between blocks or logging treatments. At first the stem density in 2006 is much higher ( 8.8 individuals) in unlogged than in logged forest where the average stem density is only 2.14 (GLM, df=1, $\mathrm{F}=5.577, \mathrm{p}=0.030$ ). Recruitment rates differ between blocks. In block 1 the average recruitment is 1.33 seedling per plot, while this is 3.94 seedling per plot in block 3 ( $G L M, d f=1, F=6.006, p=0.024$ ).

A significant correlation between seed trees of Ojoso colorado and recruitment of the species is found in 2011 (table 12). The correlation is positive, meaning that more seedlings are found at higher seed tree densities. Seed trees with crown position index 4 or 5 are found in each plot, indicating that Ojoso colorado is a dominant species in the forest canopy. Numbers of adult trees are high, with up to 40 individuals surrounding a plot. The species is shade-tolerant, it occurs in both blocks, both logging treatments and all three microhabitat types.

### 5.5.4 Pica pica colorada

Pica pica colorada starts with a population size of 52 individuals in 2006 , which is quite large compared to other tree species in the experiment. The survival of these plants is however marked by a steep decline from 2006 onwards, to only $19 \%$ in 2011. The low recruitment rate of $6 \%$ in 2007 and $0 \%$ in 2011 (Appendix VI) together with the low survival rate makes that the abundance of these species in the plots is declining fast. The species is only present in six plots in 2011, a number too low to conduct reliable statistics. A GLM for the stem density and average height in 2006 does not yield any significant results.

A strong, negative, correlation is found between the seedlings present in 2006 and the larger seed trees (table 12), meaning that seedling density is highest where seed tree density is low. In the experiment there is no adult pica pica colorada with a fully exposed crown (CPI 5), CPI's of the seed trees range from $2.5-4$, with the majority found in class 3 (even the tree with the largest diameter of $30,3 \mathrm{~cm}$ only has a CPI of 3 ).

### 5.5.5 Coquino

The population size of Coquino is increasing over time, this growth is mainly caused by the large recruitment rate, respectively $107 \%$ in 2007 and $280 \%$ in 2011. The survival of the initial population shows a gradual but not dramatic decrease of $87 \%$ in 2007 and $73 \%$ in 2011 (Appendix VI). There are too little plots containing Coquino seedlings to conduct reliable statistics for height growth, stem densities, growth and survival rates.

There is a strong negative significant correlation between the seedlings present in 2006 and all seed trees of the species present (table 12). The absence of this significant correlation with the larger seed trees (dbh $\geq$ 20 cm ) indicates that the number of seedlings is particular low at plots with little 'small' seed trees. All trees with a dbh $\geq 20 \mathrm{~cm}$ have a crown position index of three or higher. The smaller trees have CPI's of 1.5 till 3 , making it unlikely that they (actively) contribute to seed production and dispersal.

### 5.5.6 Verdolago

The population of Verdolago is slowly decreasing over time, 60\% of the originals seedlings is still alive in 2011 and they are all found in block 3. Recruitment rate is decreasing as well, from $17 \%$ in 2007 to $7 \%$ in 2011. The recruitment rate is too low to compensate for the decreasing survival rate. There are too little plots containing these species to conduct reliable statistics.

There are multiple, negative, correlations between seed trees and seedlings of Verdolago (table 12). In 2006 and 2007 these correlations are the strongest between seedlings and large ( $\mathrm{dbh} \geq 20 \mathrm{~cm}$ ) seed trees, meaning that seed density is low near adult trees. Most large trees have a CPI of 3 or 4, but there are individuals with a fully exposed crown as well. These trees with a CPI of 5 are often real giants, with dbh's up to 120 cm . The little difference in correlation when all seed trees taken into account and only the seed trees with dbh $\geq 20 \mathrm{~cm}$ is most likely explained by the fact that 31 out of the 43 seed trees in the experiment belong to the latter size class.

### 5.5.7 Yesquero blanco

The initial survival of the transplanted Yesquero blanco seedlings was relatively low. Two and a half month after transplantation the highest survival rate of $47 \%$ was found in exclosures situated in trail microhabitats. The lowest survival rate, $25 \%$, was found in control plots in both gap and trail microhabitats (van Rooij, 2005).

Seven living seedlings of Yesquero blanco are found in 2011, a number too low to conduct reliable statistics. The remaining seedlings occur in both blocks, logged and unlogged forest, all microhabitat types, and both exclosures and control plots. Only one of these seven seedlings, located in a control plot situated in a gap microhabitat in the normal logged part of block 1, is a certain survivor of the original experimental plants planted in December 2004 by Tjerk van Rooij (van Rooij, 2005). The future survival chance of this plant is uncertain regarding the fact that it already suffered height loss twice. In 2007 the seedling is reported as broken, in the period between 2009 and 2011 the seedling suffered major dieback, but resprouted to half of its original length, measuring 35 cm in 2011 . Two seedlings are likely to have survived the entire study period as well, but this is not entirely clear in the data. One of them, growing in an exclosure, in a trail microhabitat in the unlogged part of block 1, is first measured in 2009, but marked as an old experimental plant overseen before. Compared to
the other Yesquero blanco seedlings this plant has a low absolute growth rate of only 4 cm in 2.4 year. The second seedling that might be present since the start of the study is located in an exclosure situated in a gap microhabitat in the unlogged part of block 1 . This seedling is first measured in 2007, but the remarkably large height ( 117 cm , while all other seedlings measure between 12 and 43 cm at first encounter) suggests that this seedling might be overlooked during earlier inventories. This seedling appears to be healthy and did not suffer from dieback or (insect) herbivory. It is the largest Yesquero blanco seedling in the study, measuring 192 cm in 2011. The highest natural regeneration of this species is found in 2007, when 10 new plants established in nine different plots, seedlings are found in all blocks, logging treatments and microhabitat types, but nine of the seedlings grow in exclosures. The majority of these seedlings ( 7 individuals) is found in block 3, but the survival is low. All three seedlings that established in block 1 in 2007 are still alive in 2011, in block 3 only one seedling survived. Three of these four surviving seedlings are found in gap microhabitats and all four grow in exclosures. Seed trees of the Yesquero blanco are only found in block 1, 7 individuals with diameters ranging from 13.2 till 41.5 cm dbh. Only three 'matches' between seed trees and seedlings at a site are found. Generally this are the plots located near the larger Yesquero blanco's, but there is one exception where a seedling is found in the neighbourhood of a Yesquero blanco measuring only 13.2 cm at dbh. Two of the four seedlings that established in 2007 and are still alive in 2011 grow in an exclosure next to a seed tree, both seedlings show a positive growth. The other two seedlings do not have a seed tree in their surrounding, only one of them has a positive growth, the other one suffered dieback and resprouted.

Table 12 Spearman rho values for the correlation between seed trees and the number of seedlings. 2006 is set as reference year, meaning all seedlings present are correlated to the seed trees. In 2007 and 2011 the newly recruited seedlings relative to the previous measurement are correlated to the seed trees. First the correlation with all seed trees of the species is presented ( $\mathbf{m i n} . \mathrm{dbh} 10 \mathrm{~cm}$ ) and second the correlation between seedlings and seed trees with a min. dbh Of 20 cm . Significant correlations at a plevel of 0.05 are highlighted in green. There were no new recruits of both Pica pica colorado and Yesquero blanco in 2011.

|  | 2006 all seedlings |  |  | $\mathbf{2 0 0 7}$ new recruits |  |  |  | $\mathbf{2 0 1 1}$ new recruits |  |  |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
|  | N | All | $\geq \mathbf{2 0} \mathbf{d b h}$ | $\mathbf{N}$ | All | $\geq \mathbf{2 0} \mathbf{d b h}$ | $\mathbf{N}$ | All | $\geq \mathbf{2 0}$ dbh |  |
| Blanquillo | 138 | -0.25 | -0.39 | 12 | 0.09 | 0.13 | 29 | -0.01 | 0.01 |  |
| Laurél | 14 | 0.29 | 0.12 | 52 | -0.06 | 0.14 | 91 | 0.07 | -0.02 |  |
| Ojoso colorado | 33 | 0.004 | 0.16 | 14 | 0.16 | 0.22 | 66 | 0.33 | 0.39 |  |
| Pica pica colorado | 52 | 0.18 | -0.61 | 3 | -0.07 | -0.35 | 0 | - | - |  |
| Coquino | 15 | -0.5 | -0.3 | 16 | 0.16 | 0.01 | 42 | 0.05 | 0.3 |  |
| Verdolago | 30 | -0.47 | -0.52 | 5 | -0.25 | -0.48 | 2 | -0.44 | -0.41 |  |
| Yesquero blanco | 6 | -0.37 | -0.29 | 10 | -0.01 | -0.19 | 0 | - | - |  |

## 6. Discussion

The overall aim of this study was to gain insight in the effects logging, microhabitat and mammals have on the regeneration in order to gain insight in the processes underlying the low regeneration of many commercial tree species.

### 6.1 Blocks

In the experimental set-up the blocks are supposed to be equal since they act as experimental duplicates. In a field study like this the blocks are chosen because of their similarity, but they will never be the same like a in an experiment in a controlled environment. Environmental variables were supposed to be similar in both blocks, but many significant two-way interactions are found with logging and microhabitat (appendix V). In combination with logging many significant difference is stem densities are found (fig. 13). The most remarkable effect in biotic conditions is found in heliconia cover. Heliconas play a large role in determining the environmental conditions in block 3, while they are almost absent in Block 1. An explanation for this enormous difference in heliconia cover between the blocks is not found in this study. At forest structure and dynamics level a significant effect is found for absolute growth rate. It is unclear what they underlying cause is. Canopy openness values are similar in both blocks, ruling out the possibility that the difference is caused by a greater light availability in block 1. As expected before the blocks do not have significant influences on other variables determining forest structure and dynamics nor on species richness and composition. On the individual species level block number has a significant influence on the survival rates of Blanquillo. This effect can either be caused by a variable that is not measured in this study but that differs between the blocks. Another, more likely, explanation is that it is caused by the fact that many plots contain only 1 individual. During the fieldwork mammal densities appeared to be higher in block 3, based on sightings and tracks. But no evidence for greater mammal influence in this block is found in the data.

### 6.2 Logging

The research question to be answered was: what is the effect of logging on abiotic conditions, species richness, composition, structure and dynamics of the seedling community? It was hypothesized that logging would increase light availability and therefore increase seedling growth and survival, especially favouring lightdemanding species. Herbivory rates were expected to be higher in logged than in unlogged forest and in gaps because these habitats provide more shelter for the animals due to denser understory growth.
At the (a)biotic level many significant effects of logging on the environment are found (appendix V). As expected canopy openness is higher in logged than in unlogged forest at the start of the experiment. Over time the forest develops and the difference in canopy openness between logged and unlogged forest disappears (fig 12). The decreasing effects of logging over time are also described by Toledo et al., (2011) who found that the effects of logging in la Chonta disappear after ca. seven years. Considering the low logging rates in La Chonta, the influence on the environment is larger than expected. In 2011 there are still many environmental variables that respond to the logging treatment, indicating that it takes quite some time for the forest to recover, even when harvest rates are very low. At forest community and structure level logging has a significant influence on the stem density in 2006 and survival. Stem density (of seedlings and a sporadic sapling or small tree) was higher in unlogged forest (14.5), average stem density in logged forest was 11.2. This effect disappears over time, when stem densities become equal in logged and unlogged forest. Logged forests have a survival percentage of $57.8 \%$, which is much higher than the $37.5 \%$ in unlogged forest. This is in
line with the hypothesis and the higher canopy openness in logged forest at the start of the experiment. Average height and growth rates are not influenced by logging, which is unexpected. A possible explanation might be that logging in the normal logged plots in la Chonta does not create enough disturbance to enhance growth conditions over a longer period of time. Peña-Claros et al. (2008A) examined the effects of all four logging treatments applied in the Long Term Silvicultural Research Plots (LTSRP) of la Chonta. They found that growth rates increased with the intensity of silvicultural methods applied. Since no additional silvicultural measures are applied in the normal logged forest this might be an explanation for the lack of difference between growth rates in logged and unlogged forest. Logging does not influence the number of species or species diversity. A positive influence of logging on average height is found in Blanquillo (fig 23), corresponding to the larger canopy openness in 2005. The fact that these larger average height in logged forest is not observed in other species might be caused by the fact that many species only have few individuals.

### 6.3 Microhabitat

The research question to be answered was: what is the effect of microhabitat conditions (natural or logging gap, trail, forest understory) on abiotic conditions, species richness, composition, structure and dynamics of the seedling community? It was hypothesized that the higher light availability in gaps will stimulate plant growth, resulting in pioneer species outcompeting shade-tolerant species. At trails the increased light availability will increase plant growth and the absence of litter will favour small-seeded tree species. In the shaded forest understory recruitment, growth and survival will be lower compared to the other microhabitat types and shade-tolerant species will be more abundant. Mammals often use trails because they facilitate their movement, which will increase the herbivory rate and seed dispersal along trails compared to forest understory. Microhabitat types has much influence, both on the environmental or (a)biotic factors as on structur, dynamics and richness. The environment at trails is more moderate compared to gaps and understory's. Both gaps an trails have an increased light availability compared to understory, but less direct light passes through the smaller canopy openings above trails ensuring a more stable climate near the forest soil and less risk of heath stress. Extreme pioneer species might suffer in trail habitats, but other species might benefit from this more stable climate. Microhabitat is the factor with the largest influence on forest structure and richness (table 7). Highest growth rates and average heights were expected to be found in gaps, due to the high light availability there. Largest average heights are found in gaps and at trails and there is no influence of microhabitat on growth rates. In 2011 height growth is largest in both trail and gap microhabitats, but canopy openness has become less in gaps over time. Stem density, number of species and ShannonWiener diversity, measured in 2006 have the highest values in trail microhabitats. Hardly any significant responses are found in 2011, indicating that the microhabitat types have become more similar over time. Herbivory rates were expected to be higher at trail habitats because animals use these trails as well. The results prove otherwise, there is no difference in the percentage of stems browsed between the different microhabitats. Possible explanations for this result are that animals forage less when they are walking at the trails or that they use the trails less often than hypothesised. Recruitment rates are highest in gap and trail microhabitats. This was expected because gaps offer a new space in the forest that can be colonized and trails offer both an opening in the vegetation and seed dispersal is expected to be high near trails due to the animals using them. There is however little evidence for the role of mammals as effective pollinators (Bawa and Krugman, 1991).The average height of Blanquillo seedlings in 2006 is as expected, with highest values found in gaps and lowest heights found in the understory plots.

### 6.4 Mammals

The effect of mammals is studied by excluding them for plots through exclosures. The research question to be answered was: What is the effect of herbivore mammals on abiotic conditions, species richness, composition, structure and dynamics of the seedling community? It was hypothesized that disturbed areas generally contain more low vegetation which provides shelter to mammals, therefore seedlings are expected to suffer most from herbivory and trampling in trail and gap microhabitats. Especially light-demanding species with palatable leaves and less-protected leaves and stems will suffer from herbivory. Seed predation by some mammals may reduce recruitment, whereas other mammals may increase seed dispersal and recruitment, especially of large-seeded species. The large difference in forest floor covers between exclosures and control plots in 2005 (fig 20 ) is remarkable. The exclosures are set up in 2005, so no difference in soil cover was to be expected. The differences in forest floor cover may be caused by unconscious choices for easy spots during exclosure establishment or by human trampling and soil disturbance during the establishment of the exclosures. This idea is supported by the fact that no differences in total cover between exclosures and control plots are found in 2011. The effect mammals have on seedlings is smaller than expected. Exclosures do not have an effect on the average height or stem densities. There are several possible explanation for the absence of these exclosure effects. It could be that mammalian herbivores are not the limiting factor in tree reproduction. The higher relative growth rates (fig 18)and lower percentages of stems browsed (fig 19) in exclosures however suggests that mammals certainly do affect forest dynamics. . In order to gain insight in the use of the forest by mammalian herbivores and the browsing pressure at and near plots is would be interesting to place camera traps. The low effect large herbivore mammals seem to have on forest reproduction and composition in this study is not in line with the results found in other studies, like Ickes et al., 2001. Ickes et al. conducted an exclosure study in Malaysia in an area with a high density of wild pigs, which are comparable with the peccaries in La Chonta. In the study of Ickes et al. the pigs significantly influence growth and survival of woody plants in the understory. They found a 3 times higher recruitment rate inside exclosures and a highly increased stem and species density and. The different study results might be explained by the density of animals in the area or by the fact that Ickes et al. used much larger exclosures of $49 \mathrm{~m}^{2}$. DelVal and Armesto (2010) conducted an exclosure study in two forests (in the subtropical forest of Fray Jorge national Park, Chile and in the temperate forest of Guabún, Chiloé Island), where they studied the effect of herbivory on Olivillo (Aextoxicon punctatum) seedlings. They used the same experimental design as used in this study, with the half of each plot fenced with chicken wire to exclude (small) mammals. Their research pointed out that seedling mortality was significantly higher in tropical than in temperate forests ant that herbivore mammals contributed significantly to seedling mortality. Their exclosures decreased seedling mortality, but there was no significant difference. Mammalian herbivores are not the only species consuming plants. Invertebrate species can have major influences as well (Marquis, 2010), a process observed in La Chonta as well. The influence of invertebrate herbivory is pointed out by Dirzo and Miranda (1991) as well, in an observation of seedlings in permanent sample plots at Los Tuxtlas, Mexico. Reasons for the smaller influence of mammals than expected might be that La Chonta has an intact and complete animal population, including large carnivores. Large carnivores can play a major role in keeping herbivore pressure in control because exclusion of carnivores generally results in a large increase of herbivory (Marquis, 2010). Other possible explanations for the absence of more exclosure effects might be that that size of the fence is inaccurate. Since the fence is less than 1 m high deer species can forage on plants that grow above the fence. The small size of $2 * 2 \mathrm{~m}$ also cause a large edge effects. Since the fence is made out of chicken wire plants sometimes grow through it, making them come into the reach of foraging mammals. Another possibility is that the exclosure is entered by small mammals like mousses, or from above by monkeys. The fence of some exclosures was damaged or broken, but this did not seem to have a large influence

### 6.5 The effect of seed trees on regeneration

The question to be answered was: Is the density of seed trees lower in logged forest and what is the correlation between seed trees and seedlings at species level? It was hypothesized that recruitment of new seedlings of logged tree species will be higher in unlogged forest because of the higher number of remaining seed trees. However, in logged forests $20 \%$ of the seed trees $>50 \mathrm{~cm}$ dbh are retained and trees $<50 \mathrm{~cm}$ dbh often carry seeds as well. Recruitment of all species together might therefore be larger in logged compared to unlogged forest, due to higher light availability, higher carbon availability, larger seed crops and less diseases (damping off) due to dryer conditions in gaps compared to forest understory. These dryer conditions limit the abundance of seedling affecting pathogens. The diversity of new recruits in a plot will be dependent on the surrounding seed trees. In la Chonta the number of seed trees at community level in logged forest is slightly lower than in unlogged forest (fig 22). Beforehand it was uncertain whether the number of seedlings would be higher in unlogged or in logged forest. On the one hand it was expected to be higher in unlogged forest due to the higher amount of seed trees present. On the other hand recruitment numbers were expected to be higher in logged forest due to higher light and nutrient availability. It turned out that recruitment rates in this experiment did not differ between logging treatments, presumably due to the low logging rates in La Chonta. Except for Laurél and Yesquero Blanco, significant correlations between the number of seed treed and seedlings are found for the individual species examined. For Blanquillo, Ojoso Colorado, Coquino and Verdolago these correlations are negative, meaning that the number of seedlings is high where the number of seed trees is low. This could be a confirmation of the distance density dependent Janzen-Connel hypothesis, but it could also be caused by over-shading adult trees. Pica pica colorada is the only species behaving opposed, with higher seedling densities at spots with many seed trees.

### 6.6 Environment

In the correlation diagram of species and environmental factors (fig 11) it can be seen that canopy openness is the main factor determining species composition. Light is also the most limiting factor according to several authors (Bunker and Carson, 2005). In figure 11 there is no strong correlation of an environmental variable with the second axis, indicating that this axis is probably explained by a variable not measured. This variable might be moisture availability, according to Bunker and Carson (2005) is the second most limiting factor after light availability. Baraloto et al (2005) on the other hand state that soil moisture plays a subordinate role in seedling survival.

### 6.7 Yesquero blanco

Yesquero blanco was one of the reasons for the start of this study. It was thought that the relative high abundance of mammals in the La Chonta forest caused the regeneration problems. It has turned out that Yesquero blanco seedlings have very low survival rates in either exclosures and control plots. This information makes it unlikely that mammals are the main reason for the low survival of Yesquero Blanco seedlings. When the results of this study on community level are taken in to account it can be expected that Logging treatments and subsequently microhabitat conditions have a greater influence on regeneration of the species than mammals.

### 6.8 Scope en limitations of the study

The scope of this experimental study was to gain insight in the effect of several factors, but most of all mammals, on the regeneration and dynamics of the forest. This has succeeded, but some limitations have raised as well. A big limitation is formed by the exlosure types, their small size makes that many edge effects occur. Chicken wire is a cheap and easy manner to build an exclosure, but large animals like tapirs can push them aside. Another big limitation in this study is the large species heterogeneity of the forest. When the species structure, composition and dynamics are measured at community level the different traits of species
are not taken into account. When species are analyzed at species level the $N$ is often too low to come up with a reliable result. A limitation of the Yesquero blanco experiment was that only one individual was planted in each plot. When more individuals were planted per plot the change of survival would have been higher.

### 6.9 Recommendations for future research

The problematic regeneration of commercial tree species is not solved by this study. Since logging and microhabitat treatments turned out to be the main factors determining forest structure, dynamics and composition it is worthwhile to keep investing in a better understanding of the effect of these processes on regeneration. When looking at the interactions between environmental variables and logging and microhabitat conditions it is recommended to take water availability and soil nutrient availability into account since these parameters are missing in this study. It is highly recommended to investigate the moisture availability and climatic change effects in future research because this might be a very important environmental factor as well. Knowledge about the effects of climate change are essential to secure a sustainable forest management in the future.

## 7. Conclusions

Not all expected interactions and influences of treatments are found in this experiment. Nevertheless, logging and microhabitat have the largest influences on environmental variables as well as on forest composition, structure and dynamics. In general it can be concluded that increased disturbance of the forest increased canopy openness and subsequently average height of seedlings. Of the environmental variables measured canopy openness in the most important variable in determining species composition and distribution. The forest has developed and changed since the plots are established in 2005. For example some gaps are closed and forest understory receives more light at some plots than during experiment set-up. As a result of this development the different microhabitats over which the plots are divided will change and the differences will disappear, indicating that forests patches oscillate around an equilibrium. The influence of exclosures is much lower than expected, indicating that mammalian herbivores are not the main reason for the lack of regeneration of commercially interesting species.
At this moment the ecosystem of La Chonta seems to be, largely, intact. It is essential to keep it this way in the future to ensure a sustainable wood production.

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## 8. References

Alison et al., 2006. Impacts of large herbivores on plant community structure and dynamics. Large herbivore ecology, ecosystem dynamics and conservation Danell, K. 2006. Cambridge University Press. Conservation Biology (11).

Baraloto, C. and Forget, P.M. 2005. Seed size, seedling morphology, and response to deep shade and damage in neotropical rain forest trees. American Journal of Botany (94),pp901-911.

Barnett, V. 1994. Statistics and the long-term Experiments: Past Achievements and Future Challenges. In Leigh, R.A. and Johnston, A.E. (eds.) Long-term Experiments in Agricultural and Ecological Sciences, pp. 165183. CAB International, UK.

Bawa, K.S. and Krugman, S.L. 1991. Reproductive biology and genetics of tropical trees in relation to conservation and management. In Gómez-Pompa, A., Whitmore, T.C., and Hadley, M. (eds.) Rain Forest Regeneration and Management, Man and the Biosphere series, vol. 6, pp. 119-136. UNESCO/The Parthenon Publishing Group, Paris/UK.

Bazzaz, F.A. 1991. Regeneration of tropical forests: physiological responses of pioneer and secondary species. In Gómez-Pompa, A., Whitmore, T.C., and Hadley, M. (eds.) Rain Forest Regeneration and Management, Man and the Biosphere series, vol. 6, pp. 91-118. UNESCO/The Parthenon Publishing Group, Paris/UK.

Becker, P., Lee, L.W., Rothman, E.D. and Hamilton, W.D. 1985. Seed Predation and the Coexistence of Tree Species: Hubbell's Models Revisited. Oikos, vol.44, No.3, pp.382-390.

Breunig, E.F., 1996. Conservation and Management of Tropical Rainforests. An integrated approach to sustainability. Wallingford: CAB International.

Bunker, D.E. and Carson, W.P. 2005. Drought stress and tropical forest woody seedlings: effect on community structure and composition. Journal of Ecology( 93), pp 794-806.

Carson, W.P., Anderson, J.T., Leigh Jr. E.G. \& Schnitzer, S.A. 2008. Challenges associated with testing and falsifying the Janzen-Connell hypothesis: a review and critique. Tropical forest community ecology 2008. Chpter 13, p 210-241.

Chazdon, R. L. and Pearcy, R. W. 1991. The Importance of Sunflecks for Forest Understory Plants. BioScience 41 (11): 760-766.

Clark, D.A. and Clark, D.B. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. Ecological monographs. 62 (3), pp315-344.

Del Val, E. and Armesto, J.J. 2010. Seedling mortality and herbivory damage in subtropical and temperate populations: Testing the hypothesis of higher herbivore pressure toward the tropics. Biotropica 42 (2), pp 174179.

Denslow, J.S., Ellison, A.M. and Sanford R.E. 1998. Treefall gap size effects on above- and below-ground processes in a tropical wet forest. Journal of Ecology 86 (4), pp 597-609.

Dirzo, R. 1984A. Herbivory: A Phytocentric Overview. In Dirzo, R. and Sarukhán, J. (ed.) Perspectives on Plant Population Ecology, pp. 141-165. Sinauer associates inc., Massachusetts.

Dirzo, R. 1984B. Insect-plant interactions: some ecophysiological consequences of herbivory. In Medina, E., Mooney, H.A. and Vázquez-Yanes, C. (eds.) Physiological Ecology of Plants of the Wet Tropics, pp.209-224. Dr. W. Junk Publishers, The Hague.

Dirzo, R. \& Boege, K. 2008. Patterns of herbivory and defense in tropical dry and rain forests. Tropical forest community ecology 2008. Chapter 5, p.63-78.

Dirzo, R. and Miranda, A. 1991. Altered Patterns of Herbivory and Diversity in the Forest Understorey: A Case Study of the Possible Consequences of Contemporary Defaunation. In Price, P.W., Lewinsohn, T.M., Wilson

Fetcher, N., Oberbauer, S.F. and Strain, B.R. 1985. Vegetation Effects on Microclimate in Lowland Tropical Forest in Costa Rica. International Journal of Biometeorology. Vol. 9 (2), pp 145-155.

Fredericksen, T.S. 2000. Logging and conservation of tropical forests in Bolivia. International Forestry Review. 2 (4), p. 271-278.

Gill, R. 2006. The influence of large herbivores on tree recruitment and forest dynamics. Large herbivore ecology, ecosystem dynamics and conservation Danell, K. 2006. Cambridge University Press. Conservation Biology (11).

Harms, K.E., Wright, E.J., Calderón, O. \& Hernández, A. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature (404), pp 493-495.

Ickes, K., Dewalt, S.J. and Appanah, S. 2001. Effects of native pigs (Sus scrofa) on woody understorey vegetation in a Malaysian lowland rain forest. Journal of Tropical Ecology 17 (2), pp 191-206.

Janzen, D. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104, 501528.

Janzen, D.H. 1981. Patterns of herbivory in a tropical deciduous forest. Biotropica 13(4), pp 271-282.

Janzen, D.H. and Vázquez-Yanes, C. 1991. Aspects of tropical seed ecology of relevance to management of tropical forested wildlands. In Gómez-Pompa, A., Whitmore, T.C., and Hadley, M. (eds.) Rain Forest Regeneration and Management, Man and the Biosphere series, vol. 6, pp. 137-157. UNESCO/The Parthenon Publishing Group, Paris/UK.

Jennings, S.B., Brown, N.D. and Sheil, D. 1999. Assessing forest canopies and understorey illumination: canopy closure, canopy cover and other measures. Forestry 72 (1), pp 59-73.

Marquis, R.J. 2010. The role of herbivores in Terrestrial trophic cascades. In Terborgh, J. and Estes, J.A. (ed.) Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature, pp. 109-123. Island Press, Washington.

McNaughton, S.J. 1991. Evolutionary Ecology of Large Tropical Herbivores. In Price, P.W., Lewinsohn, T.M., Wilson Fernandes, G., and Benson, W.W. (ed.) Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions, pp. 509-522. John Wiley \& Sons, Inc.

Mostacedo, B. \& Fredericksen, T.S. 1999. Regeneration status of important tropical forest tree species in Bolivia: assessment and recommendations. Forest Ecology and Management. 124, p.263-273.

Nabe-Nielsen, J., Kollmann, J. \& Peña-Claros, M, 2009. Effects of liana load, tree diameter and distances between conspecifics and seed production in tropical timber trees. Forest Ecology and

Oldeman, R.A.A., and van Dijk, J. 1991. Diagnosis of the temperament of tropical rain forest trees. In GómezPompa, A., Whitmore, T.C., and Hadley, M. (eds.) Rain Forest Regeneration and Management, Man and the Biosphere series, vol. 6, pp. 21-65. UNESCO/The Parthenon Publishing Group, Paris/UK.

Peña-Claros, M., Fredericksen, T.S., Alarcón, A., Blate, G.M., Choque, U., Leaño, C., Licona, J.C., Mostacedo, B., Pariona, W., Villegas, Z. \& Putz, F.E. 2008A. Beyond reduced-impact logging: Silvicultural treatments to increase growth rates of tropical trees. Forest Ecology and Management 256, p. 1458-1467.

Peña-Claros, M., Peters, E.M., Justiniano, M.J., Bongers, F., Blate, G.M., Fredericksen, T.S. \& Putz, F.E. 2008B. Regeneration of commercial tree species following silvicultural treatments in a moist tropical forest. Forest Ecology and Management. Volume 255, Issue 3-4, p.1283-1293.

Peña-Claros, M., Poorter, L., Alcarcón, A., Blate, G., Choque, U., Fredericksen, T.S., Justiniano. M.J., Leaño, C., Licona, J.C., Pariona, W., Putz, F.E., Quevedo, L. and Toledo, M. 2012. Soil Effects on Forest Structure and Diversity in a Moist and a Dry Tropical Forest. BIOTROPICA 44 (3), p. 276-283.

Rooij, T.M.R. van. 2005. Why don't Cariniana ianeirensis and Spondias mombin regenerate in the humid forest of La Chonta, Bolivia? Master thesis, Wageningen Univeristy and IBIF.

Sayer, J.A., Zuidema, P.A. \& Rijks, M.H. 1995. Managing for biodiversity in humid tropical forests, Commonwealth Forest. Rev. 74. p. 282-287.

Schnitzer, S.A., Mascaro, J. \& Carson, W.P. 2008. Treefall Gaps and the Maintenance of Plant Species Diversity in Tropical Forests. Tropical forest community ecology 2008. Chapter 12, p196-209.
Silva Matos, D.M., Freckleton, R.P. \& Watkinson, A.R. 1999. The role of density dependence in the population dynamics of a tropical palm. Ecology 80, 2635-2650.

Southwood, T.R.E. 1994. The importance of Long-term Experimentation. In Leigh, R.A. and Johnston, A.E. (eds.) Long-term Experiments in Agricultural and Ecological Sciences, pp.3-8. CAB International, UK.

Swaine, M.D., Lieberman, D., and Putz, F.E. 1987. The dynamics of tree populations in tropical forest: a review. Journal of Tropical Ecology. Vol. 3. Issue 4. Pp 359-366.

Terborgh, J., and Kenneth, F. 2010. Propagation of Trophic Cascades via Multiple Pathways in Tropical Forests. In Terborgh, J. and Estes, J.A. (ed.) Trophic Cascades: Predators, Prey, and the Changing Dynamics of Nature, pp. 125-140. Island Press, Washington.

Terborgh, J., Losos, E., Riley, M.P. \& Bolaños Riley, M. 1993. Predation by vertebrates and invertebrates on the seeds of five canopy tree species of Amazonian forest. Plant Ecology 107-108, 375-386.

Theimer , T.C. \& Gehring, C.A. 2008. Variation in Tree Seedling and Arbuscular Mycorrhizal Fungal Spore Responses to the Exclusion of Terrestrial Vertebrates: Implications for How Vertebrates Structure Tropical Communities. Tropical forest community ecology 2008. Chapter 17, p 294-307.

Toledo, M., Peña-Claros, M., Bongers, F., Alarcón, A., Balázar, J., Chuviña., J., Leaño, C., Licona, J.C., and Poorter, L. 2012. Distribution patterns of tropical woody species in response to climatic and edaphic gradients. Journal of Ecology, 100, pp253-263.

Toledo, M., poorter, I., Peña-Claros, M., Alarcón, A., Balázar, J., Leaño, C., Licona, J.C., Llanque, O., Vroomans, V., Zuidema, P. \& Bongers, F. 2011. Climate is a stronger driver of tree and forest growth rates than soil and disturbance. Journal of Ecology. 99, pp254-264.
van Katwijk M.M., and ter Braak, C.J.F. 2008. Handleiding voor het gebruik van multivariate analysetechnieken in de ecologie. Ecoscience, Universiteit Nijmegen (versie 1.1).

White, T.C.R. 2005. Why does the world stay green?: Nutrition and survival of plant-eaters. CSIRO Publishing, Australia.

Whitham, T.G., Maschinski, J., Larson, K.C., and Paige, K.N. 1991. Plant Responses to Herbivory: The Continuum From Negative to Positive and Underlying Physiological Mechanisms. In Price, P.W., Lewinsohn, Whitmore, T.C. 1990. An introduction to tropical rainforests. Clarendon press, Oxford.

Whitmore, T.C. 1991. Tropical rain forest dynamics and its implications for management. In Gómez-Pompa, A., Whitmore, T.C., and Hadley, M. (eds.) Rain Forest Regeneration and Management, Man and the Biosphere series, vol. 6, pp. 67-89. UNESCO/The Parthenon Publishing Group, Paris/UK.
www.ibifbolivia.org.bo, visited on August 31, 2011.

## Appendix I



Conceptual framework about the influence of trail microhabitats on the ecosystem. Positive effects are indicated by green lines, negative effects by red lines and neutral or unknown effects by blue lines. Strong effects are indicated by a solid line, intermediate effects by a dashed line and small effects by a dotted. The amount of light that reaches the forest floor in the trail microhabitat depends on the width of the trail. Skid trails in the logged forest are often wider than forest paths in the unlogged forest. Above skid trails there is a greater change that the canopy layer is affected, resulting in a greater light availability at the forest floor. Mammals use the trails as roads, increasing the risk of trampling the seedlings, but also contributing to seed dispersal. The amount of litter is often reduced at trails, especially when they are used frequently by either humans or animals.


Conceptual framework about the influence of understory microhabitat on the ecosystem. Positive effects are indicated by green lines, negative effects by red lines and neutral or unknown effects by blue lines. Strong effects are indicated by a solid line, intermediate effects by a dashed line and small effects by a dotted. The close canopy in the understory microhabitat has a strong negative effect on the light availability for seedlings, the amount of litter is supposed to be high due to the closed canopy. The number of ground dwelling is supposed to be lower in a dark understory microhabitat, because less vegetation and food can be found on the forest floor. An exception can occur if large trees are flowering and their seeds are falling to the forest floor. The lower light availability is expected to have negative consequences for the recruitment, growth and survival of both pioneer and non-pioneer species. Although these negative effects are expected to be larger for pioneer species. A thick litter layer will negatively influence the recruitment of pioneer species. Generally, non-pioneer species are better adapted to grow through a thick litter layers due to the greater reserves in the seeds, but there are limits. Mammals are not expected to have a large influence on the recruitment of pioneer species because these are often wind dispersed.

## Appendix III

Exclosure effect on response variables

|  |  |  |  | mean <br> exclosure |  |  | mean <br> control |
| :--- | :--- | :--- | :--- | ---: | ---: | :---: | :---: |
| Stem density 06 (\#) | test | t | pilcoxon |  | 0.537 |  |  |
| Stem density 11 (\#) | paired t | -0.228 | 0.821 | 10.88 | 12 |  |  |
| Stem density change (\#) | wilcoxon |  | 0.812 | 0.78 | 12.19 |  |  |
| N species 06 | wilcoxon |  | 0.889 | 5.25 | 5.09 |  |  |
| N species 11 | wilcoxon |  | 0.896 | 5.63 | 5.88 |  |  |
| N species change | wilcoxon |  | 0.456 | 0.38 | 0.78 |  |  |
| Shannon-Wiener div. 06 | paired t | 0.271 | 0.788 | 1.2881 | 1.3169 |  |  |
| Shannon-Wiener div.11 | paired t | -0.221 | 0.826 | 1.4553 | 1.4263 |  |  |
| Shannon-Wiener div. change | paired t | 0.918 | 0.366 | 1.7844 | 1.0375 |  |  |
| Log average height 06 (cm) | paired t | 0.620 | 0.540 | 78.96 | 73.06 |  |  |
| Average height 11 (cm) | wilcoxon |  | 0.432 | 108.91 | 109.03 |  |  |
| Height change (cm) | wilcoxon |  | 0.513 | 29.96 | 35.97 |  |  |
| Height loss (\%) | wilcoxon |  | 0.293 | 8 | 14 |  |  |
| AGR (cm/y) | wilcoxon |  | 0.084 | 18.22 | 9.53 |  |  |
| RGR (cm/cm/y) | wilcoxon |  | 0.032 | 0.11 | 0.07 |  |  |
| Log recruitment (\#) | paired t | 1.330 | 0.193 | 9.69 | 8.78 |  |  |
| ASINsurvival (\%) | wilcoxon |  | 0.489 | 37.93 | 45.84 |  |  |
| Stems browsed (\%) | wilcoxon |  | 0.026 | 15 | 40 |  |  |
| df =31 |  |  |  |  |  |  |  |

## Appendix IV

Exclosure effect on environmental variables

|  | test | t | p | mean exclosure | mean control |
| :---: | :---: | :---: | :---: | :---: | :---: |
| ASIN canopy openness 05 | wilcoxon |  | 0.481 | 0.14 | 0.14 |
| Sqrt ASIN canopy openness 11 | paired t | -2.116 | 0.042 | 0.15 | 0.13 |
| fern cover 05 | paired t | -3.445 | 0.002 | 0.32 | 0.42 |
| fern cover 11 | paired t | -1.3 | 0.202 | 0.31 | 0.35 |
| shrub cover 05 | wilcoxon |  | 0.018 | 0.14 | 0.2 |
| shrub cover 11 | wilcoxon |  | 0.431 | 0.07 | 0.06 |
| woody debris cover 05 | wilcoxon |  | 0.273 | 0.12 | 0.13 |
| woody debris cover 11 | wilcoxon |  | 0.698 | 0.1 | 0.1 |
| litter cover 05 | wilcoxon |  | 0.032 | 0.79 | 0.84 |
| litter cover 11 | wilcoxon |  | 0.554 | 0.86 | 0.86 |
| seedling cover 05 | wilcoxon |  | 0.092 | 0.08 | 0.11 |
| seedling cover 11 | wilcoxon |  | 0.337 | 0.06 | 0.05 |
| liana cover 05 | wilcoxon |  | 0.109 | 0.07 | 0.1 |
| liana cover 11 | wilcoxon |  | 0.557 | 0.08 | 0.08 |
| heliconia cover 05 | wilcoxon |  | 0.258 | 0.15 | 0.14 |
| heliconia cover 11 | wilcoxon |  | 0.494 | 0.15 | 0.12 |
| Sqrt total cover 05 | paired t | 5.848 | <0.001 | 0.73 | 0.95 |
| total cover 11 | paired t | 0.463 | 0.646 | 0.68 | 0.66 |
| sapling nr 05 | wilcoxon |  | 0.004 | 0.98 | 1.82 |
| sapling nr 11 | wilcoxon |  | 0.573 | 3.63 | 4.49 |
| juvenile nr 05 | wilcoxon |  | 0.474 | 1.09 | 1.23 |
| juvenile nr 11 | wilcoxon |  | 0.563 | 1.8 | 1.6 |
| total stem nr 05 | wilcoxon |  | 0.006 | 2.17 | 3.17 |
| log+1 total stem nr 11 | paired t | -0.405 | 0.688 | 4.26 | 4.59 |
| Sqrt litter thickness 11 (cm) | paired t | 1.745 | 0.09 | 2.45 | 2.8 |
| log litter weight 11 (gr) | paired t | 0.636 | 0.529 | 229.35 | 217.07 |
| seedling nr 11 | wilcoxon |  | 0.709 | 5.69 | 6.4 |
| nr stems browsed 11 | wilcoxon |  | 0.002 | 0.83 | 2.23 |
| $\mathrm{df}=34$ |  |  |  |  |  |

## Appendix V

Outcome of GLM on environmental variables with main and two way interactions. Significant results are highlighted in green.

|  | Normality of unstandardized residuals | Block | Logging | Microhabitat | Exclosure | Block* <br> Logging |  | $\begin{aligned} & \text { Block* } \\ & \text { Exclo- } \\ & \text { sure } \\ & \hline \end{aligned}$ | Logging* <br> Microhabitat | Logging* <br> Exclosure | Microhabitat* Exclosure |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| ARCSINcan.opennes11 | 0,683 | 0,476 | 0,1484 | 0,909 | 0,282 | 0,199 | 0,003 | 0,429 | 0,339 | 0,146 | 0,352 |
| ARCSINcan.opennes05 | 0,006 | 0,162 | 0,002 | <0,001 | 0,948 | 0,147 | <0,001 | 0,809 | 0,029 | 0,109 | 0,659 |
| canopenchange | 0,07 | 0,949 | 0,472 | 0,169 | 0,206 | 0,016 | 0 | 0,604 | 0,097 | 0,014 | 0,504 |
| ARCSINferncover11 | 0,955 | 0,405 | 0,293 | 0,918 | 0,556 | 0,183 | 0,165 | 0,353 | 0,013 | 0,257 | 0,397 |
| ARCSINferncover05 | 0,51 | 0,357 | 0,285 | 0,209 | 0,308 | 0,097 | 0,177 | 0,301 | 0,013 | 0,516 | 0,907 |
| ferncoverchange | 0,672 | 0,75 | 0,243 | 0,009 | 0,608 | 0,562 | 0,913 | 0,05 | 0,558 | 0,717 | 0,4 |
| ARCSINshrubcover11 | 0,534 | 0,347 | 0,088 | 0,514 | 0,731 | 0,772 | 0,232 | 0,193 | 0,644 | 0,924 | 0,189 |
| LogARCSINshrubcov 05 | 0,378 | 0,565 | 0,424 | 0,102 | 0,336 | 0,08 | 0,63 | 0,613 | 0,359 | 0,798 | 0,621 |
| LogASINwoodebcover11 | 0.776 |  | 0.577 | 0,504 | 0,695 |  |  |  | 0,011 | 0,057 | 0,018 |
| ASIN wooddeb cover 05 | 0,483 | 0,292 | 0,673 | 0,11 | 0,827 | 0,02 | 0,006 | 0,036 | 0,102 | 0,126 | 0,831 |
| wooddebcovchange | 0,105 | 0,44 | 0,908 | 0,115 | 0,911 | 0,028 | 0,078 | 0,048 | 0,567 | 0,595 | 0,291 |
| ARCSIN litter cover 2011 | 0,89 | 0,93 | 0,819 | 0,366 | 0,789 | 0,387 | 0,303 | 0,64 | 0,087 | 0,758 | 0,707 |
| ARCSIN litter cover 2005 | 0,531 | 0,52 | 0,136 | 0,354 | 0,437 | 0,648 | 0,001 | 0,074 | 0,484 | 0,466 | 0,303 |
| Littercover change | 0,113 | 0,379 | 0,029 | 0,198 | 0,439 | 0,659 | 0,068 | 0,262 | 0,468 | 0,864 | 0,923 |
| ARCSIN seedling cover 2011 | 0,679 | 0,247 | 0,337 | 0,937 | 0,613 | 0,484 | 0,032 | 0,294 | 0,503 | 0,271 | 0,374 |
| ARCSIN seedling cover 2005 | 0,068 |  | 0,116 | 0,007 | 0,304 |  |  |  | 0,046 | 0,564 | 0,674 |
| Seedligcover change | <0,001 | 0,644 | 0,197 | 0,08 | 0,203 | 0,644 | 0,822 | 0,166 | 0,57 | 0,614 | 0,514 |
| ARCSIN liana cover 2011 | 0,413 | 0,681 | 0,613 | 0,533 | 0,921 | 0,001 | 0,135 | 0,454 | 0,005 | 0,581 | 0,419 |
| ARCSIN liana cover 2005 | 0,305 | 0,718 | 0,207 | 0,277 | 0,652 | 0,316 | 0,273 | 0,055 | 0,558 | 0,396 | 0,035 |
| ARCSIN helicocov 2011 | 0,138 | 0,237 | 0,507 | 0,682 | 0,654 | 0,003 | 0,284 | 0,254 | 0,391 | 0,263 | 0,032 |
| ARCSIn helicocov 2005 | 0,302 | 0,358 | 0,725 | 0,69 | 0,575 | <0,001 | 0,006 | 0,347 | 0,005 | 0,113 | 0,312 |
| helicocov change | 0,226 | 0,999 | 0,869 | 0,045 | 0,749 | 0,081 | 0,915 | 0,094 | 0,019 | 0,03 | 0,355 |
| Totalcov05 | <0,001 | 0,44 | 0,404 | 0,561 | 0,017 | 0,404 | 0,505 | 0,436 | 0,075 | 0,436 | 0,999 |
| Totalcov11 | 0,15 |  | 0,043 | 0,239 | 0,713 |  |  |  | 0,061 | 0,909 | 0,164 |
| Total cover change | 0,093 | 0,347 | 0,972 | 0,902 | 0,322 | 0,664 | 0,21 | 0,093 | 0,028 | 0,943 | 0,159 |


| Logsaplingnr 11 | 0,307 | 0,76 | 0,446 | 0,526 | 0,608 | 0,032 | 0,463 | 0,358 | 0,053 | 0,194 | 0,98 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Log2adapsaplingnr 05 | 0,485 | 0,818 | 0,811 | 0,796 | 0,192 | <0,001 | 0,047 | 0,368 | 0,011 | 0,473 | 0,337 |
| Sapling nr change | <0,001 | 0,563 | 0,854 | 0,482 | 0,02 | <0,001 | 0,023 | 0,466 | 0,168 | 0,33 | 0,528 |
| Log adapted juvenile nr 05 | 0,185 | 0,799 | 0,821 | 0,402 | 0,932 | <0,001 | 0,379 | 0,777 | 0,015 | 0,343 | 847 |
| Juvenile nr 11 | 0,014 | 0,52 | 0,001 | 0,001 | 0,608 | 0,014 | 0,368 | 0,077 | <0,001 | 0,22 | 0,696 |
| Juvenile nr change | 0,114 | 0,934 | 0,037 | 0,067 | 0,74 | 0,867 | 0,683 | 0,055 | 0,004 | 0,125 | 0,637 |
| adepted small tree nr 05 | 0,327 | 0,913 | 0,003 | 0,284 | 0,335 | 0,913 | 0,442 | 0,335 | 0,179 | 0,114 | 0,131 |
| Small tree nr 11 | <0,001 | 0,411 | 0,749 | 0,13 | 0,8 | 0,071 | 0,268 | 0,08 | 0,023 | 0,08 | 0,289 |
| change small tree nr | <0,001 | 0,411 | 0,749 | 0,13 | 0,8 | 0,071 | 0,268 | 0,08 | 0,023 | 0,08 | 0,289 |
| Total stem nr 05 | 0,192 | 0,8 | 0,812 | 0,676 | 0,137 | <0,001 | 0,019 | 0,577 | 0,006 | 0,177 | 0,647 |
| Total stem nr 11 | <0,001 | 0,307 | 0,001 | 0,057 | 0,566 | 0,414 | 0,866 | 0,601 | 0,001 | 0,05 | 0,755 |
| Change total stem nr | 0,006 | 0,542 | 0,003 | 0,192 | 0,729 | 0,006 | 0,362 | 0,408 | 0,019 | 0,028 | 0,903 |


|  | Normality of unstandardized residuals | Block | Logging | Microhabitat | Exclosure | Block* <br> Logging | Block* <br> Micro- <br> habitat | Block* <br> Exclo- <br> sure | Logging* <br> Micro- <br> habitat | Logging*Exclosure | Micro- <br> habitat* <br> Exclosure |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| ARCSINcan.opennes11 | 0,683 | 0,476 | 0,1484 | 0,909 | 0,282 | 0,199 | 0,003 | 0,429 | 0,339 | 0,146 | 0,352 |
| ARCSINcan.opennes05 | 0,006 | 0,162 | 0,002 | <0,001 | 0,948 | 0,147 | <0,001 | 0,809 | 0,029 | 0,109 | 0,659 |
| canopenchange | 0,07 | 0,949 | 0,472 | 0,169 | 0,206 | 0,016 | 0 | 0,604 | 0,097 | 0,014 | 0,504 |
| ARCSINferncover11 | 0,955 | 0,405 | 0,293 | 0,918 | 0,556 | 0,183 | 0,165 | 0,353 | 0,013 | 0,257 | 0,397 |
| ARCSINferncover05 | 0,51 | 0,357 | 0,285 | 0,209 | 0,308 | 0,097 | 0,177 | 0,301 | 0,013 | 0,516 | 0,907 |
| ferncoverchange | 0,672 | 0,75 | 0,243 | 0,009 | 0,608 | 0,562 | 0,913 | 0,05 | 0,558 | 0,717 | 0,4 |
| ARCSINshrubcover11 | 0,534 | 0,347 | 0,088 | 0,514 | 0,731 | 0,772 | 0,232 | 0,193 | 0,644 | 0,924 | 0,189 |
| LogARCSINshrubcov 05 | 0,378 | 0,565 | 0,424 | 0,102 | 0,336 | 0,08 | 0,63 | 0,613 | 0,359 | 0,798 | 0,621 |
| LogASINwoodebcover11 | 0.776 |  | 0.577 | 0,504 | 0,695 |  |  |  | 0,011 | 0,057 | 0,018 |
| ASIN wooddeb cover 05 | 0,483 | 0,292 | 0,673 | 0,11 | 0,827 | 0,02 | 0,006 | 0,036 | 0,102 | 0,126 | 0,831 |
| wooddebcovchange | 0,105 | 0,44 | 0,908 | 0,115 | 0,911 | 0,028 | 0,078 | 0,048 | 0,567 | 0,595 | 0,291 |
| ARCSIN litter cover 2011 | 0,89 | 0,93 | 0,819 | 0,366 | 0,789 | 0,387 | 0,303 | 0,64 | 0,087 | 0,758 | 0,707 |
| ARCSIN litter cover 2005 | 0,531 | 0,52 | 0,136 | 0,354 | 0,437 | 0,648 | 0,001 | 0,074 | 0,484 | 0,466 | 0,303 |
| Littercover change | 0,113 | 0,379 | 0,029 | 0,198 | 0,439 | 0,659 | 0,068 | 0,262 | 0,468 | 0,864 | 0,923 |
| ARCSIN seedling cover 2011 | 0,679 | 0,247 | 0,337 | 0,937 | 0,613 | 0,484 | 0,032 | 0,294 | 0,503 | 0,271 | 0,374 |
| ARCSIN seedling cover 2005 | 0,068 |  | 0,116 | 0,007 | 0,304 |  |  |  | 0,046 | 0,564 | 0,674 |
| Seedligcover change | <0,001 | 0,644 | 0,197 | 0,08 | 0,203 | 0,644 | 0,822 | 0,166 | 0,57 | 0,614 | 0,514 |
| ARCSIN liana cover 2011 | 0,413 | 0,681 | 0,613 | 0,533 | 0,921 | 0,001 | 0,135 | 0,454 | 0,005 | 0,581 | 0,419 |
| ARCSIN liana cover 2005 | 0,305 | 0,718 | 0,207 | 0,277 | 0,652 | 0,316 | 0,273 | 0,055 | 0,558 | 0,396 | 0,035 |
| ARCSIN helicocov 2011 | 0,138 | 0,237 | 0,507 | 0,682 | 0,654 | 0,003 | 0,284 | 0,254 | 0,391 | 0,263 | 0,032 |
| ARCSIn helicocov 2005 | 0,302 | 0,358 | 0,725 | 0,69 | 0,575 | <0,001 | 0,006 | 0,347 | 0,005 | 0,113 | 0,312 |
| helicocov change | 0,226 | 0,999 | 0,869 | 0,045 | 0,749 | 0,081 | 0,915 | 0,094 | 0,019 | 0,03 | 0,355 |
| Totalcov05 | <0,001 | 0,44 | 0,404 | 0,561 | 0,017 | 0,404 | 0,505 | 0,436 | 0,075 | 0,436 | 0,999 |
| Totalcov11 | 0,15 |  | 0,043 | 0,239 | 0,713 |  |  |  | 0,061 | 0,909 | 0,164 |
| Total cover change | 0,093 | 0,347 | 0,972 | 0,902 | 0,322 | 0,664 | 0,21 | 0,093 | 0,028 | 0,943 | 0,159 |
| Logsaplingnr 11 | 0,307 | 0,76 | 0,446 | 0,526 | 0,608 | 0,032 | 0,463 | 0,358 | 0,053 | 0,194 | 0,98 |
| Log2adapsaplingnr 05 | 0,485 | 0,818 | 0,811 | 0,796 | 0,192 | <0,001 | 0,047 | 0,368 | 0,011 | 0,473 | 0,337 |
| Sapling nr change | <0,001 | 0,563 | 0,854 | 0,482 | 0,02 | <0,001 | 0,023 | 0,466 | 0,168 | 0,33 | 0,528 |


| Log adapted juvenile nr 05 | 0,185 | 0,799 | 0,821 | 0,402 | 0,932 | <0,001 | 0,379 | 0,777 | 0,015 | 0,343 | 847 |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Juvenile nr 11 | 0,014 | 0,52 | 0,001 | 0,001 | 0,608 | 0,014 | 0,368 | 0,077 | <0,001 | 0,22 | 0,696 |
| Juvenile nr change | 0,114 | 0,934 | 0,037 | 0,067 | 0,74 | 0,867 | 0,683 | 0,055 | 0,004 | 0,125 | 0,637 |
| adepted small tree nr 05 | 0,327 | 0,913 | 0,003 | 0,284 | 0,335 | 0,913 | 0,442 | 0,335 | 0,179 | 0,114 | 0,131 |
| Small tree nr 11 | <0,001 | 0,411 | 0,749 | 0,13 | 0,8 | 0,071 | 0,268 | 0,08 | 0,023 | 0,08 | 0,289 |
| change small tree nr | <0,001 | 0,411 | 0,749 | 0,13 | 0,8 | 0,071 | 0,268 | 0,08 | 0,023 | 0,08 | 0,289 |
| Total stem nr 05 | 0,192 | 0,8 | 0,812 | 0,676 | 0,137 | <0,001 | 0,019 | 0,577 | 0,006 | 0,177 | 0,647 |
| Total stem nr 11 | <0,001 | 0,307 | 0,001 | 0,057 | 0,566 | 0,414 | 0,866 | 0,601 | 0,001 | 0,05 | 0,755 |
| Change total stem nr | 0,006 | 0,542 | 0,003 | 0,192 | 0,729 | 0,006 | 0,362 | 0,408 | 0,019 | 0,028 | 0,903 |

Appendix VI


A: total population number per species over time. B: Survival per species over time, as a percentage of the plants present in 2006 C : recruitment of individual species over time, displayed a percentage of the total population in the reference year 2006.


