Response of amphibians to habitat changes caused by selective logging

in Bolivia

Joost van Gijn

Supervised by:
Lourens Poorter
Marielos Peña-Claros
Mayra Maldonado
Steffen Reichle

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Summary

About half of Bolivia consists of forest, and timber exploitation provides an important source of income to the people. If forestry is done in a sustainable way, future generations will be able to use this natural resource as well, and biodiversity will be preserved. To evaluate whether logging is sustainable, and does not have adverse impacts on biodiversity, I have studied the response of amphibians to logging. I have used amphibians as indicator species, because they have small home ranges and need humid conditions, and are probably the animals that are most sensitive to the opening up of the forest canopy due to logging.

Research was carried out in two tropical lowland forests in Bolivia; a moist semi-evergreen forest (La Chonta) and a dry deciduous forest (Inpa). In both forest a silvicultural experiment is being carried out by the Instituto Boliviano de Investigación Forestal (IBIF) consisting of four treatments: Control (without logging), Normal (with logging), Improved (with logging and some liberation of future crop trees) and Intensive (with logging, liberation and liana cutting). Together these treatments represent a disturbance gradient ranging from no disturbance (the control treatment) to a high disturbance intensity (the intensive treatment). In these treatments amphibian abundance, richness and composition is monitored by IBIF four years after logging, for three different trap sites per treatments. I measured the environmental conditions (litter, light, temperature, water, vegetation cover and composition) at those trap sites, and related them to the amphibian data of the monitoring study to evaluate possible mechanisms through which amphibians are affected by logging.

Logging had a positive effect on the number of seedlings and the height of the understory in both forests. The canopy openness was negatively influenced by logging, either due to a more closed canopy (wet forest) or a decrease in the number of gaps (dry forest). All these changes in environmental conditions were caused by the vegetation regrowth during the four years after logging. In the moist forest a low disturbance intensity is enough to cause changes in the environment (the control treatment differed significantly from the three other treatments in which logging occurred). This change only has an effect on the amphibian abundance.In the dry forest a high disturbance intensity is needed to cause differences in the environment (the intensively logged treatment differed significantly from the other, less intense treatments). Reason for these different treshold levels for the two forest types are the different background light levels in the forest. The dry forest has a much more open, and seasonally deciduous canopy compared to the moist forest. Hence, to go from an open (undisturbed) forest to a more open forest a bigger disturbance is required in the dry forest. In contrast, the moist forest is “opened up” a lot sooner because it had a closed canopy before.

In the moist forest only the amphibian species richness is affected by logging disturbance. Soil water content and the presence of water are the most important environmental variables and had a positive effect on amphibian abundance in both forests (r^2=0,67 in the wet forest; r^2=0,98 in the dry forest). This

is mainly due to the preference of amphibians for humid conditions and their need for breeding sites (as measurements were done in the breeding season). For species richness understory density in the moist forest, and litter mass in the dry forest were found to be most important. Both had a negative effect on species richness (r^2=0,59 in the wet forest; r^2=0,71 in the dry forest). None of these variables were affected by the logging, so logging does not have a dramatic effect on amphibian abundance and species richness in either forest. If anything, amphibians in the wet forest benefit from logging, as abundance was highest in areas with an average logging intensity (the Normal treatment). High intensities of logging (the Intensive treatment) cause a drop in abundance. By far the most important environmental variable for amphibians is water. And as logging near water is prohibited by the present Bolivian forest law, amphibian populations should not be affected.

Resumen

Próximamente la mitad de la superficie de Bolivia tiene una cubertura forestal, y el aprovechamiento forestal es una fuente de ingresos muy importante para la gente y el pais. Si el aprovechamiento forestal esta hecho en una manera sostenible, las generaciones futuras podrán utilizar este recurso natural también, y la biodiversidad será preservada. Para evaluar si el aprovechamiento es sostenible, y no tiene impactos adversos en la biodiversidad, he estudiado la respuesta de anfíbios al aprovechamiento. He utilizado anfíbios como especies indicadoras, porque ellos tienen pequeñas áreas de acción, necesitan condiciones húmedas, y son probablemente los animales que son mas sensibles a la apertura del dosel del bosque causado por el aprovechamiento.

Esta investigación se llevo al cabo en dos bosques tropicales del oriente de Bolivia; un bosque húmedo (La Chonta) y un bosque seco (Inpa). En ambos bosques el Instituto Boliviano de Investigación Forestal (IBIF) se lleva al cabo un experimento silvicultural cual consiste de cuatro tratamientos silviculturales: Testigo (sin aprovechamiento), Normal (con aprovechamiento), Mejorado (aprovechamiento y liberación de árboles futuros de cosecha) e Intensivo (la doble intensidad de aprovechamiento, liberación de árboles y el corte de bejucos). Juntos estos tratamientos representan un gradiente de perturbación que varia de ningún perturbación (el tratamiento del control) a una intensidad alta de perturbación (el tratamiento intensivo). Cuatro años después del aprovechamiento forestal, IBIF ha monitoreado en estos tratamientos la abundancia, riqueza y composición de anfíbios, usando tres sitios de trampa por tratamiento. Para mi investigación he medido las condiciones ambientales (hojarasca, la luz, la temperatura, el agua, la cobertura de vegetación y la composición de vegetación) en estos sitios, y he relacionado estos datos ambientales con los datos de los anfíbios para evaluar los mecanismos posibles por cuál los anfíbios son afectados por el aprovechamiento.

En ambos bosques el aprovechamiento tuvo un efecto positivo en el número de plantines y la altura de la vegetación en el sotobosque. Cuatro anos después del aprovechamiento forestal la apertura del dosel disminuyó con la intensidad del aprovechamiento. Todas estas respuestas pueden ser atribuidos al desarrollo de vegetación durante estos cuatro años. En el bosque húmedo una intensidad baja de perturbación es suficiente para causar cambios en el ambiente (el tratamiento Testigo difirió significativamente de los tres otros tratamientos en que se aprovechó la madera). El bosque seco requiere una intensidad alta de perturbación para causar cuatro años después del aprovechamiento diferencias en el ambiente (el tratamiento intensivo fue significativamente diferente de los otros tratamientos). La razón para estos diferentes niveles de impacto en los dos tipos de bosque son los diferentes intensidades de luz que se encuentra en los dos bosques. El bosque seco tiene un dosel mucho más abierto y temporalmente caducifolio en comparación con el bosque húmedo. Por lo tanto, para realmente abrir el dosel se necesita una perturbación más grande en el bosque seco. Al

contrario, el bosque húmedo se “abre” mucho más rápido, porque este bosque tuvo un dosel mas cerrado antes.

En el bosque húmedo sólo la riqueza de especies de anfíbios es afectada por la intensidad del aprovechamiento. La humedad del suelo y la presencia de agua son las variables ambientales más importantes para anfíbios, y tuvieron un efecto positivo en la abundancia de anfíbios en ambos bosques (r^2=0.67 en el bosque húmedo; r^2=0.98 en el bosque seco). Este se debe principalmente a la preferencia de anfíbios para condiciones húmedas y su necesidad para sitios de reproducción (las mediciones fueron tomadas en la época de reproducción). Para la riqueza de especies de anfíbios la densidad de plantines en el sotobosque fue el factor mas importante en el bosque húmedo, y la biomasa de hojarasca fue el factor mas importante en el bosque seco. Ambos variables tuvieron, sorprendentemente un efecto negativo en la riqueza de las especies (r^2=0.59 en el bosque húmedo; r^2=0,71 en el bosque seco). Ninguna de estas variables fue afectada por el intensidad de aprovechamiento, y por lo tanto el aprovechamiento no tiene un efecto dramático en la abundancia y riqueza de anfíbios en los dos bosques. Si hay algún efecto de aprovechamiento, es un efecto positivo porque en el bosque húmedo la abundancia de anfíbios fue más alta en el tratamiento con una intensidad de aprovechamiento cual es regular (el tratamiento Normal). Sin embargo, las intensidades más altas de aprovechamiento (el tratamiento Intensivo) causan una disminución de la abundancia. La variable ambiental más importante para anfíbios es agua. Mientras se respecta la ley forestal, y toma en cuenta de no aprovechar cerca de arroyos, el aprovechamiento forestal no tiene un efecto negativo en las poblaciones de anfíbios.

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1 Introduction

1.1 Bolivian forestry

At the moment Bolivia has the largest area of certified forest in the world. About 48% of the country consists of forest. Of this forest about 2 million ha is certified. Forestry is one of the most important income generating sectors of Bolivia (PLAN, 2007). If forestry is done in a sustainable way, future generations will be able to use this natural resource as well. To assure this the BOLFOR project was launched in 1993 with the goal to protect Bolivian biological diversity and keep the country's forests, soils and water healthy by promoting sustainable forestry. Because of its success a second project (BOLFOR II) was started in 2003. One of the objectives of BOLFOR II is: 'To show that sustainable forest management conserves biodiversity and assures productivity'. There are many different definitions for sustainable forest management that are used, but BOLFOR II uses the following definition: Sustainable forest management is the exploitation of forest products (wood, leaves, resins, fruits and others) with techniques that allow harmonization of ecological interests, economical interests and the social interests of Bolivia (BOLFOR, 2007).

1.2 Effects of selective logging on microclimate

With selective logging only certain valuable species, like Tarara, are harvested from the forest leaving other trees intact. Selective logging is done at such low intensities that the overall forest structure is not altered much. Only a gap is created and these occur naturally in the forest as well. Microclimates in gaps vary widely, even between gaps of similar sizes. The location and time of gap creation play an important role in changing such microclimates (Brown, 1993). Temperatures were found to be a lot higher in these gaps then in the surrounding forest. They were also higher than temperatures in natural gaps. This increase in temperature was caused by an increase in irradiance (Vitt et al, 1997). Another effect of this is that temperatures in logged forests are higher than in forests without logging (Fredericksen, 2004a). One of the effects of this increase in temperature is that relative humidity drops. Differences between logging gaps and natural tree falls are mainly caused by the removal of in understory vegetation in logging gaps due to on-site activities (Vitt et al, 1997). Species composition of the understory vegetation is also changed by selective logging (Costa, 2001). The amount of woody debris also increases (Fredericksen, 2004a)

Not only flora is affected, fauna is affected as well. Most fauna is mobile and most animals can move to the habitat with their preferred conditions so local effects like gaps can be overcome. The effect selective logging has depends on the species. Logging gaps cause population growth of heliothermic lizards, but because they prey on other lizards the community composition is altered (Vitt et al, 1997). Bird communities are changed as well, with a shift from specialists to

generalists (Woltmann, 2003). Fredericksen (2004a) found that Formidae (ants) and Blattidae (cockroaches) are less abundant in logged areas because of lower soil moisture levels, while there was an increase of Orthoptera (grasshoppers). Small mammals and reptiles were found more in logged areas because of an increase in food availability and the increase in woody debris. For amphibians the effect is unclear (Fredericksen, 2004a) and not always according to general animal theory (Gibbs, 1997). Amphibians have a strong need for a humid environment and have a small home-range which makes them more sensitive to habitat changes (Fredericksen, 2004b). They also have problems recolonizing disturbed areas because of low mobility and strong site fidelity (Blaustein, 1994).

1.3 Amphibians

One class of animals that relies on humid conditions to survive is amphibians. Named from Greek *αμφις* "both" and *βιος* "life", they need both water and land to survive. In some frog species this need for water has been replaced by need for humid conditions. Two other characteristics that all amphibians share is that they are exothermic and have cutaneous gas exchange. In other words, they are cold-blooded and can breathe with their skin. This “skinbreathing” makes them highly reliant on humid conditions since a dry skin doesn’t have much gas exchange resulting in the animal suffocating (Encyclo, 2007).

Amphibians consist of three orders with members that still exist today: frogs and toads (Anura), the newts and salamanders (Caudata) and the Caecilians (Gymnophiona) (Encyclo, 2007). Of the three orders the Anura are by far the most common in the study area (Maldonado, 2003).

Anurans are very diverse. Each species has different, living, feeding and breeding needs. They are also widely adapted to different conditions and they can be found all over the world except on Antartica and some oceanic islands ((Encyclo, 2007).

Amphibians are most diverse in the tropics where high humidity is common and found in a wide variation of habitats. Some have adapted to living in trees (Donnelly, 1994), some live on the ground and some bury themselves during periods of harsh conditions.

There is also a wide variation in their feeding behavior, some actively hunt, others hunt passively, waiting in ambush (Toft, 1980). Their diet is also highly variable. Some are specialists and eat hard-bodied insects (such as ants and mites). and others specialize on soft-bodied insects and spiders (Toft, 1980).

Amphibians usually breed in an aquatic environment. Species prefer different sizes and locations of pools to breed in (Gascon, 1991; Magnusson, 1990). Some species have managed to overcome the need for standing water. They bypass the tadpole stage and when they hatch, they are already in their adult form. Some treefrogs (Hylids) solve this problem by carrying the tadpoles on their

back or make a foam nest on a leaf which stays moist until the eggs hatch (Donnelly, 1994). Breeding of some species occurs only in the wet season, but other species breed all year round (Donnelly, 1994). Other studies show that breeding is triggered by prey availability (Watling, 2001).

The direct habitat, the forest floor, is especially important to anurans who live there. Increased litter depth and humidity of the litter cause an increase in amphibian populations (Sluys, 2007).

The effects of logging on amphibians are not very clear (Cushman, 2005). Some tree frog species and toads prefer selectively logged areas, while other species prefer undisturbed forest due to different habitat preferences and prey choices (Pearman, 1997; Fredericksen, 2004b). Because of the many species-specific needs little is yet known about the effects of logging on amphibian populations in general.

In the forests of Bolivia many species of amphibians are found. Almost 200 species have been identified in Bolivia so far (Maldonada, 2003; de la Riva, 2000).

1.4 Questions and Hypotheses

To evaluate if logging is sustainable, we want to know how animals, respond to the changes caused by logging operations. To this end I studied amphibians, which are probably the animals that are most sensitive to opening up of the forest canopy. The aim of this study is:

"To evaluate how amphibians respond to habitat changes caused by selective logging"

From this objective several questions have been raised:

1. How does selective logging change environmental conditions?

2. How do amphibian abundance and species richness change with different environmental conditions?

3. What environmental factors predict amphibian abundance and species richness best?

4. How do amphibian abundance and species richness change with selective logging?

To answer these questions the following corresponding hypotheses have been formulated:

1. With selective logging there will be an increase in gaps, temperature, and more understory growth caused by the increase in light. Basal area, humidity and soil moisture will decrease.

2. Amphibian abundance and richness will increase with humidity, temperature and amount of litter.

3. Humidity and temperature have the strongest effect on amphibian abundance, and richness, because they are fundamental for their survival and activity.

4. Amphibian abundance and species richness will decrease with selective logging because of decreasing humidity. Temperature is not important for amphibians in the tropics because it stays high all year round.

2 Material and methods

2.1 Study sites

Research has been carried out in Bolivia, in the moist semi-evergreen forest of La Chonta and the dry deciduous forest of Inpa. La Chonta (15°45'S, 62°60'W) is located 50 km south from Guarayos, in the department of Santa Cruz. It is a semi-evergreen moist forest which is used as a timber concession. The elevation at the site is 400–600 m above sea level; with undulating topography. The area has a mean annual rainfall of 1.580 mm, 77% of the annual precipitation falls between November and April. During the dry season, temperatures often drop to 5–10°C due to Antarctic fronts (Gil, 1997) and a mean annual temperature of 25.3C°. Inpa (16°6'S, 61°42'W) is a private property located at 60 km from Concepción, in the department of Santa Cruz. The forest can be classified as a dry deciduous forest. It is used as a timber production property as well. Mean annual rainfall is 1.160 mm. and it has a 5 month dry season. The mean annual temperature is 24.3°C. However, it can get as cold as 8.0 °C during the dry season because of cold southern winds coming from Patagonia.

2.2 Two studies

Two separate studies were carried out; a logging effect study and a heterogeneity study. The goal of the first study was to quantify environmental changes (on the local scale). due to different logging regimes, and look into relations between the amphibian populations and the environment. To this end the study of Mayra Maldenado (Maldonado, 2003). was used. The aim of the second study was to investigate whether amphibians also respond to small-scale environmental heterogeneity. To this end the study of Wilma Lasthuis was used (Lasthuis, 2007). The environmental differences between different sites, in which Wilma Lasthuis studied amphibians, will also be assessed.

2.2.1 Study to monitor amphibian responses to logging

The Instituto Boliviano de Investigación Forestal (IBIF) has a long-term silvicultural research program (LTSRP) going on in La Chonta and Inpa. This experiment started in La Chonta in 2000 and in Inpa in 2001 with the implementation of four treatments. The four treatments are: Testigo (control), Normal (normal), Mejorado (improved) and Intensivo (intensive). The treatments were applied in a randomized block design with three replicated blocks in La Chonta and two in Inpa. The control treatment has not been logged and only some liana cutting has been done. In the normal treatment some selected species have been logged. The improved treatment has that as well and includes liberating and

cutting lianas from future crop trees. The intensive treatment has even more liberation and liana cutting. This means that there is a gradient of disturbance going from Control (little disturbance) to Intensive (a lot of disturbance) (Peters, 2005; PISLP, 2000) .

Amphibian abundance and species richness have been monitored in three sampling points per treatment (Maldenado, 2005). Only one block per site was sampled. This means there were a total of 2 sites x 1 block x 4 treatments x 3 sampling points = 24 sampling points. At each of these sampling points amphibian abundance and species richness have been monitored by Mayra Maldonado in 2005 and 2006 (Maldenado 2006). Traps were used as shown in figure 1. It consisted of four buckets dug into the ground so the open part is level with the ground surface. In between the buckets transparent plastic screens were placed to "force" the animals towards the buckets. The buckets were spaced 10 meters apart. Animals were collected and measured on a daily basis. When the traps were not used they were covered with a lid.

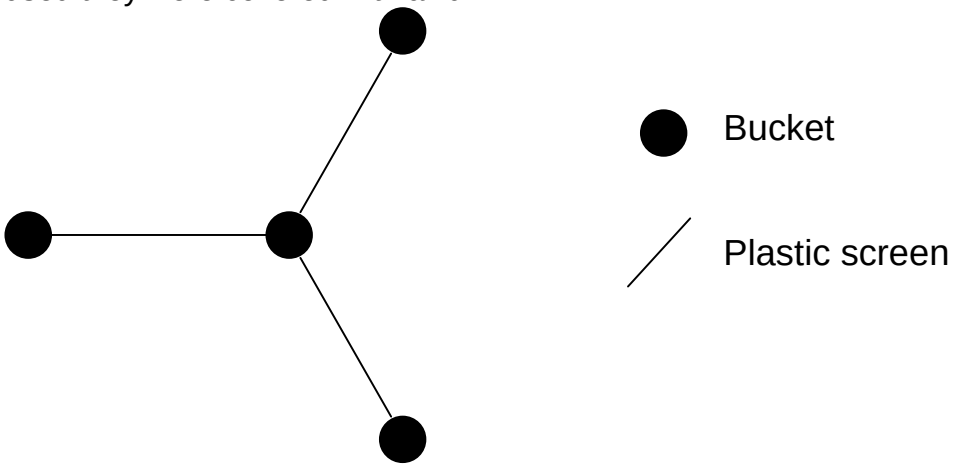

Figure 1. Trap setup for the logging effect study by Mayra Maldonado. Four dug-in buckets are linked by plastic screens which are approximately 40 cm. high. This way frogs following the screens will end up in one of the buckets.

2.2.2 Study on the effect of small scale heterogeneity on amphibians

Amphibian and reptile species richness, composition and abundance have been monitored by Wilma Lasthuis in November and December of 2006. The aim of the study was to look at the home range of amphibians, and how they respond to small scale environmental heterogeneity. The study was conducted outside the treatment blocks of IBIF. Buckets were placed in ground in a similar fashion as with Mayra Maldonado's traps. This was done a in a grid shape of 6 by 7 buckets (figure 2) at four different sites in La Chonta in October 2006. Two of the sites were next to a water stream and two were not near water. The sites are within 3 kilometers from each other. The buckets were spaced 5 meters apart.

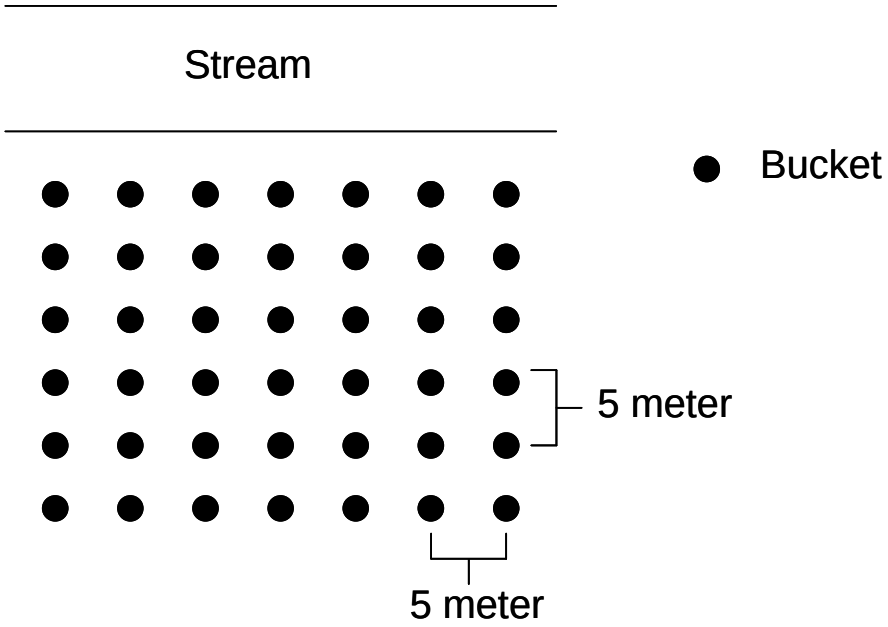

Figure 2. Trap setup by Wilma Lasthuis. Buckets were dug into the ground in a grid-like fashion with 5 meters between each. Two sites were next to a stream (as in this figure) and two sites did not have a stream nearby.

2.3 Data collection

To test the hypotheses, data collection was done at each sampling point in the experiments of Mayra Maldonado and Wilma Lasthuis. For Mayra Maldonado each trap site (4 buckets) was considered a sample point. The sample points in the heterogeneity study were single buckets. The measured variables were abiotic factors and vegetation variables. Predation and food availability were not studied, because this is logistically very time consuming, and temporal variation in predators and food ability makes it more difficult to draw firm conclusions.

Measurements were done in November and December in 2006 and for the logging effect study extra measurements were made in January and February 2007. All measurements were carried out in the wet season.

Several abiotic and biotic factors were measured that have a direct or indirect effect on amphibians. Firstly it is described why certain groups of variables were measured and secondly an explanation is given how each of these variables was measured.

- Litter (litter depth, litter moisture, number of stacked leaves, litter mass). The litter is the part of the forest layer where most amphibians occur. Differences in the amount of litter and its composition can greatly affect the moisture levels in the litter. Since it is important for the amphibians to have a humid environment a number of litter factors were measured.
- Light (canopy openness, gap number, distance to nearest gap). Light does not affect amphibians directly, but when more light reaches the forest floor it

changes local temperatures greatly. It is therefore important to know how much light reaches the forest floor.

- Temperature (mean temperature). Since amphibians are exothermic their activity is directly dependent on temperature. Temperature is also important because it has a strong effect on the litter moisture content, and relative humidity and vapor pressure deficit of the air.
- Water relations (relative humidity of the air, litter moisture, soil water content). Relative humidity is very important for amphibians as desiccation is a big risk for most of them.
- Wood (fine and coarse woody debris). Wood debris holds water and provides protection.
- Vegetation cover (tree density, basal area, understory vegetation density, understory height). Basal area tells something about the tree volume, and is therefore important for tree frogs as well as an overall measure for the openness of the forest.
- Vegetation composition (understory species composition, tree species richness). This gives an idea how the plant composition changes with different treatments. Patches with an abundance of *Aiphanes aculeata*, for instance, have a very different understory composition and litterlayer than a part of forest with other tree species. Species can also have a direct effect. Litter from chonta's for instance has lots of prickly spines in it, providing excellent protection against larger predators.
- Water availability (distance to water, slope). These factors each have different effects. The availability of standing water Is very important for the breeding habits of some amphibians. And slope has an effect on light climate and water runoff.

All these variables were measured for both studies. But because of differences in experimental design, different methods were used for each of the studies.

2.3.1 Methods to study amphibian responses to logging

Litter

- Litter depth (cm) is measured by putting a ruler into the ground until it reaches the soil layer. This is done at three 15 meter transects pointing away from the centre bucket and in the middle between the screens (Fig. 3). On these transects a measurement is taken every three meters starting 3 meter from the centre bucket. The average of these 15 measurements is taken as the average litter depth of one trap site.
- Number of stacked leaves (#) is measured by putting a knife into the ground and counting the number of pierced leaves. This is done at the same points where litter depth is measured.
- A measure for litter mass (g/m^2) is taken by weighing the collected leaves of a 1 by 1 meter patch. This is done six times per trap. Two times on each of

the transects; between the 3 and 6 meter points and between the 9 and 12 meter point (fig. 3).

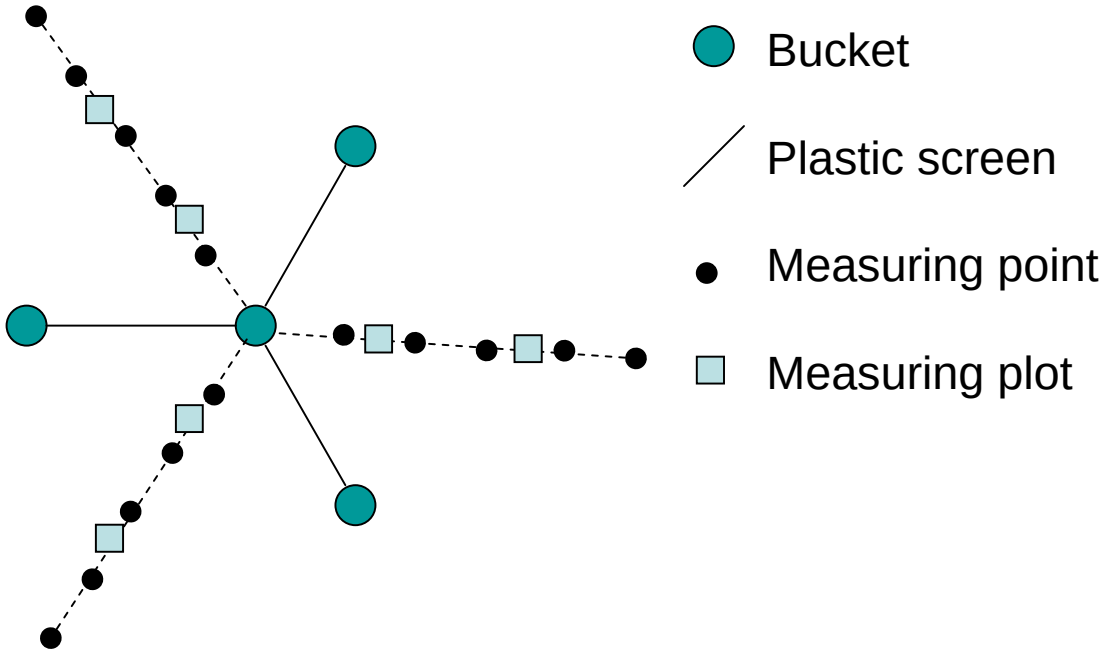

Fig. 3 Measuring points and plots on transects for a trap site of Mayra Maldonado

Light

- Canopy openness

Canopy openness (%) is measured using a spherical densiometer. At each of the three outer buckets an estimation of openness is made in four directions. The average of these 12 measurements is the average for the trap.

- Understory density

Understory density (#) is measured by counting the number of leaves that touch a 2 meter long pole standing straight up in the understory. This is done at the same points where litter depth is measured.

- Understory height

Understory height (cm) is measured in six 2 by 2 meter plots at the same place as the litter mass plots. The average height per species (only species used in vegetation composition measurements) is measured with a measuring tape. Vegetation composition gives the relative abundance for one plant family in a measuring plot. By multiplying the height with the relative abundance for each species the understory height could be computed by adding them all up for one plot. The average of these six plots is then taken as the average height for the trap site.

- Gap number

The number of gaps (#/ha), in a 30 meter radius from the central bucket, is counted.

- Distance to nearest gap

The distance (m) from the central bucket to the nearest gap is measured.

- Tree density

The number of trees in a 15 meter radius from the middle bucket is counted.

- Basal area

Of these trees the DBH is measured (in cm) and from that the basal area (m^2/ha) is calculated per tree. To get the basal area for the site all basal areas of the individual trees were added up.

Basal area (tree) = $(DBH / 2)^2 * \pi * 10000 / Asite$, where $Asite = \pi (15m)^2$

Basal area (site) = Basal area (tree1+tree2+tree3+tree4….)

Temperature

- Using data loggers (Hobo, H08-032-08, Onset) temperature was measured every half hour for a 24 hour period. Average temperature is calculated for the day (6:00 to 18:00) and the night (18:00 to 6:00). Measurements were done from 24/01/2007 to 28/01/2007. Only La Chonta was measured. Due to time constraints Inpa could not be measured.

Humidity

- Relative humidity of the air

The same data loggers that measure temperature, measure air relative humidity (%) at the same time. A daily average is used for further analysis. Fluctuations found were so small (0,1% to 4,3% RH) that separating day and night was unnecessary.

- Litter water content

Litter water content (%) is calculated by comparing the fresh and dry weight of samples the litter samples.

Litter moisture = (fresh litter weight – dry litter weight) / fresh litter weight

For every trap two samples were taken by mixing the leaves used for litter mass. from this mix two samples were put in envelopes, then the fresh mass is measured, hereafter the samples were oven-dried for 8 days at 60 degrees C and reweighed for their dry mass.

- Soil water content

To get the soil water content (%) a similar method is used as with litter moisture. Samples were taken from mixed soil which is taken from the six litter mass plots. These were then put in envelopes, weighted and put in the oven. After 8 days in the oven they were weighted again for the dry weight. Then soil water content was calculated using the following formula: Soil water content = (fresh soil weight – dry soil weight) / fresh soil weight. For soil water content only one sample per trap is used.

- Woody Debris

Between two of the outer buckets a transect is laid out. This is done for all the outer buckets (three in total). Next the number of times the transect crosses woody debris is counted. This is done for two size classes; branches between 1 and 5 cm. in diameter and branches and tree trunks larger then 5 cm. Only dead wood was included.

Vegetation composition

- Understory species composition

In the 2 by 2 meter plots used for vegetation height the ground cover is estimated per species. Each of the plots was split up in twenty-five 40 by 40 cm squares. For each of the squares the dominant species is evaluated. Four types of species were commonly present; *Costaceae* (shade tolerant herbaceous species), *Heliconiaceae spp (*light demanding herbaceous species), and two species of fern (herbaceous species). All the other plant species (when big enough or with sufficient individuals to occupy the 40 by 40 cm square) were put in the category “small plants”. This category included tree small plants, lianas, grasses, bushes and herbaceous species.

- Tree species richness

For all the trees counted in tree density, the name was noted down. Then the number of species was counted for each trap site (#/707m^2).

Water availability

- Near water

The number of streams and standing open water larger than 2 by 2 meters was recorded when it was within a 30 meter radius from the middle bucket (#/707m^2).

- Slope

The inclination (degrees) was measured using an inclinometer. To do this a tree was marked at eye level when standing next to it. Then a measurement was made from 20 meters uphill. To do this the measurer uses his left eye to look at the mark and uses his right eye to read the corresponding inclination on the inclinometer.

2.3.2 Methods for the study on the effect of environmental heterogeneity on amphibians

For Wilma Lasthuis traps similar measurement methods were used. There were some differences.

- Instead of using transects, all measurements were done in the middle between each of the buckets.
- Instead of specific measuring plots, each quadrant (area between 4 buckets). was used. By taking the average of the four surrounding quadrants a value was obtained for each bucket, so data could be more easily linked to the amphibian data.

- For woody debris an estimation was made for each quadrant. Fine debris was between 1 and 5 cm in diameter. Coarse has a diameter larger than 5 centimetres. The plot was then estimated to have 'few' (up to 7 fine branches or 2 coarse branches), 'medium' (more than 2 coarse debris and up to 7 fine debris or 4 coarse debris) or 'much' (more than 7 fine debris or 4 coarse debris) woody debris.
- For basal area all the trees in the whole plot (between the buckets, 30 by 35 meters) were measured.

There were only 30 (5 x 6 quadrants) environmental measuring points per site. Amphibians were caught in each of the buckets. Since there were 42 buckets per site (6 x 7) it was difficult to match the data. Therefore the data from the quadrants was extrapolated to the buckets. This meant that for each bucket the average of the surrounding quadrants was taken as the value for that bucket. It should be noted that this is not a perfect extrapolation. For 18 buckets there were 4 quadrants surrounding it, for 20 buckets on the edge of the plot there were only 3 quadrants "surrounding" it. And for the 4 buckets on the corners of the plot the average was derived from only 2 quadrants. The result of this was that border quadrants were estimated less well.

2.4 Data-analysis

The same analyses were used for both experiments. For both experiments it consisted of two parts; one describing the environment and the other part describing the effect this has on the amphibian populations. In the heterogeneity experiment data on the reptile population were gathered as well. These will be analyzed separately, in the same way as the amphibians were analyzed.

ANOVA's were carried out to test how silvicultural treatments (for the logging-effect experiment). or sites (for the heterogeneity experiment) differ in their environmental characteristics. To use the treatments as a disturbance gradient it was coded on an ordinal scale from 1-4: control is 1, normal is 2, improved is 3 and intensive is 4. Then Principal Component Analyses were carried out to see which of the environmental variables describes the variation between traps best. A PCA shows how all of the measured variables were related to each other. Two axes were calculated from all the variables. These represent differences between areas best, because they were strongly related to most of the other variables.

Then, to analyze the effect of environment on amphibian populations, correlations, multiple regressions and ANCOVA's were carried out. The amphibians were caught by Mayra Maldonado in the wet season (November 2006 to February 2007). To calculate abundance and species richness all caught animals were used. For the heterogeneity experiment these were for the reptiles: *Stenocercus caducus, Ameiva ameiva, Prionodactylus eigenmani, Mabuya cf.frenata, Kentropics, Tupinamis, Bachia dorbignyi, Amphisbaena fuliginosa.* For the amphibians these were: *Bufo paracnemis, Bufo margaritifer, Epipedobates*

pictus, Chiasmocleis albopunctata, Leptodactylus mystaceus, Leptodactylidae Adenomera, Leptodactylus leptodactyloides, Leptodactylidae Lithodytes lineatus, Hamptophryne boliviana, Physolameus albonotatus. In the logging-effect study amphibian abundance and species richness for La Chonta were comprised of: *Bufo margaritifer, Epipedobates pictus, Chiasmocleis albopunctata, Leptodactylus mystaceus, Leptodactylidae Adenomera, Microhylidae, Hamptophryne boliviana, Leptodactylus leptodactyloides, Leptodactylidae proceratophrys, Leptodactylidae Enanos, Eleutherodactylus sp, Proceratophrys.* In Inpa the following amphibian species were caught for the logging-effect experiment: *Bufo paracnemis, Leptodactylus elenae, Leptodactylus fuscus, Leptodactylus mystacinus, Leptodactylus syphax, Physalaemus cf. albonotatus, Proceratophrys sp., Phyllomedusa boliviana, Chiasmocleis albopunctata, Dermatonotus muelleri, Elachistocleis ovalis.*

Pearsons correlations were done, between environmental variables and abundance and species richness. Then multiple regressions were carried out to evaluate which variables predict abundance and richness best model. A forward regression was used, to use the simplest model possible, because there were only a low number of replicates. To analyze the effects of the treatments taking these relations (from the correlations) into account, ANCOVA's were done. Doing the ANCOVA's also made it clearer which environmental variables showed relations with amphibian abundance and species richness, when the treatments are compensated for..

All statistical tests were done with SPSS (version 12.0).

3 Results

3.1 Logging effect study in La Chonta

Table 1; ANOVA of environmental variables between 4 treatments; (T(control), N(normal), M(improved), and I(intensive), n=3 replicates per treatment. F is the variance between groups divided by the variance within groups. The higher the value of F, the bigger the relative difference is between the sites. The number of stars beneath p shows how strong the significance is (ns stands for not significant, * is p<0,05, ** is p<0,01 and *** is p<0,001). Values in the same row, followed by a different letters are significantly different from each other (S-N-K post-hoc test, p<0.05).

Treatment	Unit	F	p	T	N	M	I
Pteris sp.	(%)	2,64	ns	0,57a	0,18a	0,17a	0,35a
Adiantum sp.	(%)	0,71	ns	0,02a	0,14a	0,04a	0,07a
Costaceae	(%)	1,28	ns	0,02a	0,02a	0,08a	0,08a
Heliconiaceae	(%)	1,56	ns	0,02a	0,05a	0,13a	0,03a
Small plants	(%)	2,62	ns	0,04a	0,18a	0,20a	0,22a
Ground cover	(%)	0,54	ns	0,66a	0,57a	0,62a	0,75a
Herb height	(cm)	3,24	ns	43,3a	47,9a	70,8a	85,3a
Litter mass	(g/m^2)	9,83	**	700a	373b	211b	431b
Litter layers	(-)	1,74	ns	3,91a	2,67a	3,09a	3,04a
Litter depth	(cm)	2,25	ns	4,2a	2,72a	3,56a	3,37a
Understory density	(#/2m)	1,80	ns	1,8a	1,42a	1,76a	2,62a
Tree density	(#/ha)	1,12	ns	273,51a	183,91a	183,91a	254,65a
Tree richness	(#/707m^2)	0,55	ns	11,33a	9,33a	8,67a	9,33a
Basal area	(m^2/ha)	0,65	ns	19,87a	11,92a	13,51a	23,87a
Canopy openness	(%)	12,45	**	10,4a	4,8b	8,1a	4,0b
Inclination	(%)	7,09	**	20,00a	5,33b	4,00b	13,00ab
Water sources	(y/n)	1,00	ns	0a	0,33a	0a	0a
Gap number	(#/ha)	2,46	ns	5,9a	15,3a	3,5a	10,6a
Gap distance	(m)	5,48	*	16,00ab	26,33a	3,67b	8,33b
Tday	(℃)	2,62	ns	23,54a	24,35a	23,78a	24,15a
Tnight	(℃)	2,22	ns	22,56a	23,03a	22,59a	23,17a
RH	(%)	0,22	ns	94,79a	99,03a	95,57a	97,17a
Litter water content	(%)	5,73	*	50,8a	57,8b	58,2b	56,4b
Soil water content	(%)	1,14	ns	19,7a	27,2a	22,4a	22,4a
Fine woody debris	(#/17m)	0,60	ns	12,72a	10,11a	8,67a	12,67a
Coarse woody debris	(#/17m)	0,58	ns	4,65a	4,89a	3,67a	5,22a
Axis 1	-	7,10	**	1,36b	-0,80a	-0,39a	-0,17a
Axis 2	-	1,04	ns	0,49a	0,07a	-0,84a	0,27

Differences in environmental variables between treatments

ANOVA's were to done to look into environmental differences between treatments. In general there were few significant differences between treatments (Table 1). Differences between treatments can only be found in the litter mass (p=0,005), canopy openness (p=0,002), inclination (p=0,012), gap distance

(p=0,024), and litter water content (p=0,022). The control treatment had a significantly higher litter mass and inclination, and lower litter water content compared to the other treatments. The treatment normal had the largest gap distance and the control and improved treatment had the largest canopy openness.

Table 2a Pearson correlation between environmental variables, pooling all data from the twelve sites (n=12). All correlations in bold script are significant (p<0.05). Tday (day temperature), Tnight (night temperature), RH (relative humidity)

	Pteris sp.	*Adiantum* sp.	Costaceae	Heliconiaceae	Small plants	Ground cover	Herb height	Litter mass	Litter number	Litter depth	Understory density	Tree density	Tree richness	Basal area
Treatment	-0,33	0,07	0,52	0,17	**0,62**	0,21	**0,72**	-0,55	-0,34	-0,24	0,45	-0,08	-0,31	0,14
Pteris sp.		-0,41	0,15	-0,05	**-0,84**	**0,66**	-0,41	**0,67**	**0,67**	**0,75**	0,02	0,30	0,09	0,38
Adiantum sp.			-0,21	-0,22	0,36	0,11	0,26	-0,18	-0,33	-0,37	0,08	-0,20	-0,29	-0,17
Costaceae				0,13	-0,09	0,41	0,14	-0,33	0,06	0,41	0,07	-0,07	-0,42	0,38
Heliconiaceae					-0,03	0,25	-0,14	-0,22	0,21	0,03	-0,20	0,10	-0,04	0,03
Small plants						-0,38	0,55	**-0,70**	**-0,81**	**-0,79**	0,16	-0,30	-0,23	-0,37
Ground cover							-0,09	0,19	0,35	0,48	0,12	0,13	-0,35	0,33
Herb height								-0,32	-0,16	-0,13	**0,62**	-0,03	0,04	0,11
Litter mass									**0,70**	0,50	0,19	**0,72**	**0,62**	0,53
Litter number										**0,80**	0,16	0,51	0,30	0,45
Litter depth											0,03	0,39	0,15	0,56
Understory density												0,15	0,17	0,35
Tree density													**0,72**	**0,79**
Tree richness														0,55
Basal area														
Canopy openess														
Inclination														
Water sources														
Gap number														
Gap distance														
Tday														
Tnight														
RH														
Litter water content														
Soil water content														
Fine woody debris														
Coarse woody debris														

Table 2b Pearson correlation between environmental variables, pooling all data from the twelve sites (n=12). All correlations in bold script are significant (p<0.05). Tday (day temperature), Tnight (night temperature), RH (relative humidity)

	Canopy openess	Inclination	Water sources	Gap number	Gap distance	Tday	Tnight	RH	Litter water content	Soil water content	Fine woody debris	Coarse woody debris
Treatment	**-0.63**	-0.33	-0.13	0.44	-0.49	0.23	0.31	0.15	0.53	0.08	-0.04	0.04
Fern 1	0.39	0.48	0.20	0.10	-0.09	-0.20	0.02	0.08	**-0.64**	0.00	-0.10	-0.21
Fern 2	-0.33	-0.02	-0.10	-0.22	0.28	0.61	0.26	0.38	0.03	-0.20	0.38	**0.59**
Costaceae	-0.06	-0.37	-0.13	0.44	-0.33	0.06	0.09	-0.02	0.22	0.06	-0.45	-0.47
Heliconiaceae	0.05	**-0.58**	0.25	0.51	-0.10	-0.39	-0.54	0.09	0.22	0.27	-0.35	-0.11
Seedlings	-0.54	-0.30	-0.19	0.14	-0.17	0.32	0.24	-0.10	0.53	0.09	0.36	0.35
Bare soil	-0.01	-0.11	-0.17	-0.45	0.21	-0.19	-0.12	-0.44	0.39	-0.06	-0.02	-0.09
Ground cover	0.01	0.11	0.17	0.45	-0.21	0.19	0.12	0.44	-0.39	0.06	0.02	0.09
Herb height	-0.41	0.03	-0.34	0.14	-0.56	0.12	0.23	0.17	0.47	-0.39	0.02	0.10
Litter mass	0.28	**0.64**	-0.02	-0.51	0.38	-0.27	-0.12	0.02	**-0.67**	-0.33	0.08	0.09
Litter number	0.44	0.36	-0.18	-0.07	-0.01	-0.56	-0.53	0.34	-0.50	-0.40	-0.24	-0.16
Litter depth	0.46	0.25	-0.10	0.12	-0.27	-0.31	-0.21	0.21	-0.49	-0.28	-0.36	-0.44
Understory density	-0.18	0.49	-0.48	-0.21	-0.24	0.02	0.17	-0.16	0.10	**-0.67**	0.04	-0.02
Tree density	-0.08	0.16	-0.05	-0.29	0.26	-0.36	-0.21	0.08	-0.38	-0.18	-0.01	0.12
Tree richness	0.03	0.20	0.17	-0.52	0.23	-0.29	-0.01	-0.31	-0.03	-0.18	-0.23	-0.15
Basal area	-0.18	0.02	0.04	-0.25	0.11	0.02	0.18	-0.02	-0.11	-0.19	-0.42	-0.31
Canopy openess		0.40	-0.27	0.17	-0.14	**-0.78**	**-0.75**	-0.53	-0.45	-0.40	0.03	-0.20
Inclination			-0.42	-0.30	-0.07	-0.25	-0.01	-0.22	**-0.64**	**-0.62**	0.51	0.23
Water sources				0.08	0.16	0.38	0.47	.	0.25	**0.80**	-0.40	-0.21
Gap number					**-0.71**	-0.26	-0.24	0.02	0.11	0.28	0.02	-0.02
Gap distance						0.18	-0.01	0.05	-0.15	0.12	0.05	0.26
Tday							**0.86**	0.24	0.29	0.31	-0.05	0.02
Tnight								-0.05	0.35	0.34	-0.15	-0.17
RH									-0.25	0.28	0.15	0.41
Litter water content										0.25	-0.52	-0.31
Soil water content											-0.18	-0.07
Fine woody debris												**0.84**
Coarse woody debris												

Associations amongst environmental variables

A correlation was done to see how the environmental variables are correlated amongst each other (Table 2). The variable treatment represents the intensity of logging disturbance in the forest (1 = control, 2 = normal, 3 = improved, 4 = intensive). An increase in treatment intensity causes the canopy to be less open, a higher herb height and more small plants. There was a positive relation between herb height and understory density. Litter mass was positively correlated

with litter number and negatively with litter water content. Litter number was also positively correlated with litter depth, so all litter variables are closely related. Tree density, tree species richness and basal area were also closely related. The relation between canopy openness and temperature seems strange. One would expect more extreme temperatures in a more open forest (higher during the day, lower during the night). However, it appears that temperature was always lower in a more open forest. The last important result was that in areas were water was found nearby, the soil water content was higher.

Table 3 Principal Component Analysis for environmental variables to show how variables relate to each other. Two axes were extracted to represent these relations in a two dimensional field. The numbers are the scores of the variables on each of the two axes (2 components extracted); RH (relative humidity). The bold correlations are significant (p<0,05).

	Axes	
	1	2
Pteris sp.	**0,79**	-0,22
Adiantum sp.	-0,43	0,50
Costaceae	0,01	**-0,61**
Heliconiaceae	0,00	**-0,58**
Small plants	**-0,85**	0,27
Ground cover	0,33	-0,28
Herb height	-0,33	0,20
Litter mass	**0,85**	0,34
Litter number	**0,89**	-0,09
Litter depth	**0,81**	-0,34
Understory density	0,13	0,38
Tree density	**0,61**	0,15
Tree species richness	0,43	0,19
Basal area	0,53	-0,14
Canopy openess	0,56	-0,05
Inclination	0,54	**0,64**
Water count	-0,16	-0,50
Gap count	-0,15	-0,57
Gap distance	0,05	0,31
Tday	-0,51	0,06
Tnight	-0,37	0,01
RH	-0,01	0,04
Litter water content	**-0,68**	-0,34
Soil water content	-0,40	-0,55
Fine woody debris	-0,11	**0,73**
Coarse woody debris	-0,19	**0,66**

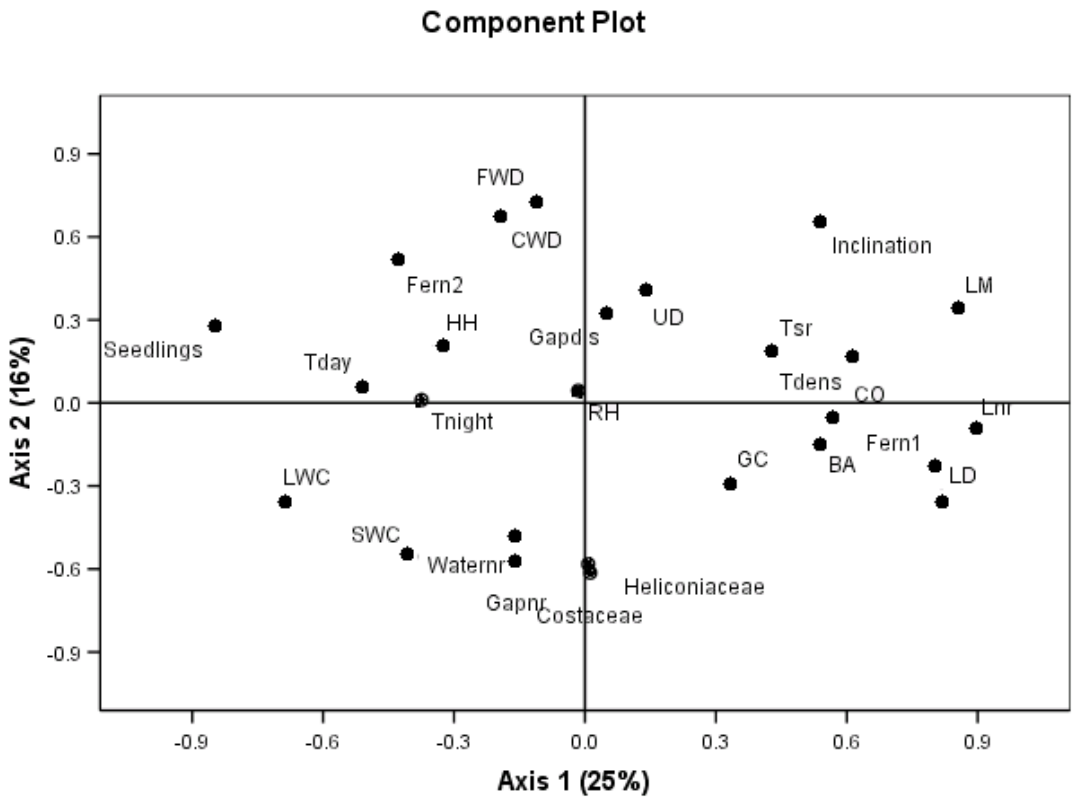

Fig. 4 Graph of axes scores from Table 3. PCA on 26 environmental factors in the logging-effect study in La Chonta. The percentages indicate how much variation is explained by each axis. Together they explain 42,3% of the variation; GC (ground cover), HH (herb height), LM (litter mass), LN (litter layers), LD (litter depth), UD (understory density), TD (tree density), TSR (tree species richness), BA (basal area), CO (canopy openness), RH (relative humidity), LWC (litter water content), SWC (soil water content), FWD (fine woody debris), CWD (coarse woody debris)

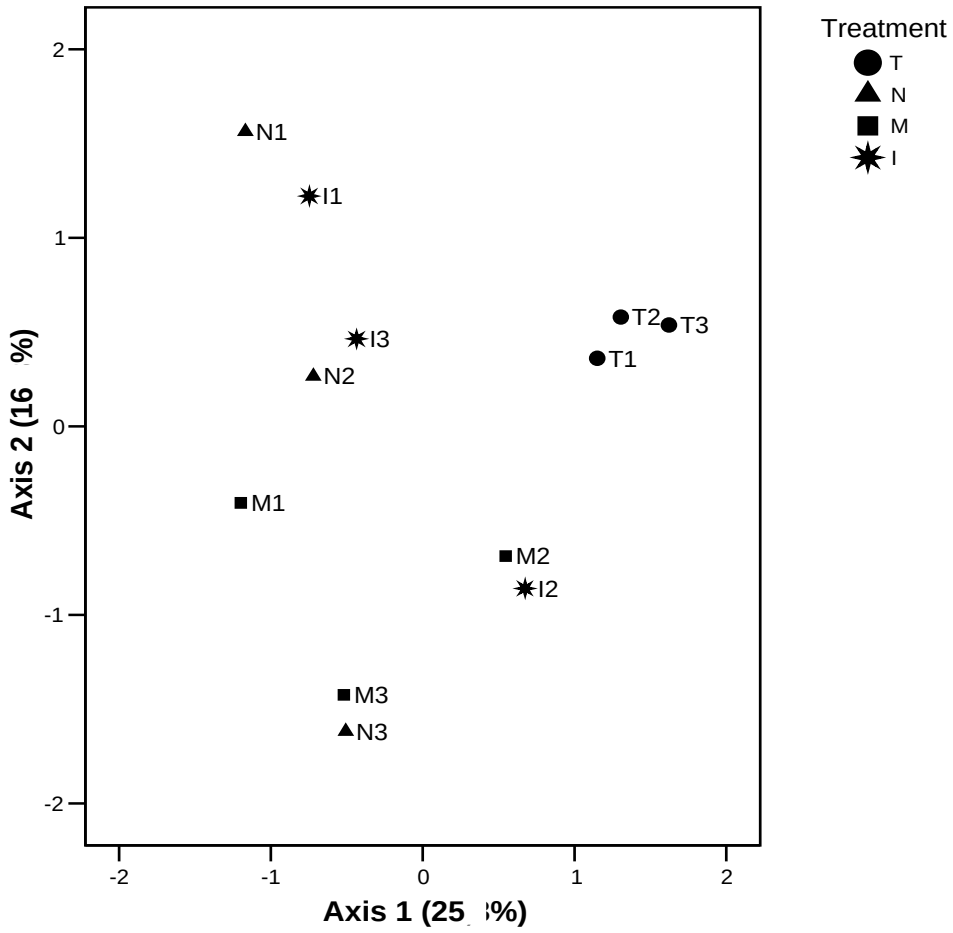

Fig. 5; Scatter plot of both regression factors resulting from the PCA. The letter are the treatments: T (control), N (normal), M (improved), I (intensive). The numbers behind the letters represent the different replicates.

A PCA was run to summarize the 26 environmental variables into two axes. To get a clearer picture of the relations among the environmental variables (Fig. 4, Table 3). Together they explain 41% of the variance in the data. The first axis explains 25%, of the variation and is associated with a high cover of *Pteris* sp., few small plants and high litter mass, litter number and litter depth (Fig. 4). This new explanatory variable was significantly different between treatments (p=0,012, Table 1). with the control treatment having significantly higher axis scores (i.e., a higher fern cover, few small plants and high litter mass, number and depth). than the other treatments (S-N-K post-hoc, Table 1, Fig. 5). The second axis explained 16% of the variation, with Costaceae and Heliconiaceae cover being negatively correlated with this axis, and coarse and fine woody debris being positively correlated. The treatments did not differ significantly in their scores for the second axis (Table 1). The great spread in the axis scores of the plots shows that the plots differ largely in their biotic and abiotic conditions and all treatments were mixed, with the exception of the control treatment, which has a higher first axis scores (Fig. 5).

Effects of environmental variables on amphibians

It is clear that some environmental variables differed between treatments. Therefore it is interesting to see what effect environmental variables have on amphibian abundance and species richness. To get a better understanding of this, correlations, ANCOVA's and multiple regressions were done.

Table 4 Correlation between abundance and richness of amphibians and environmental variables, pooling the traps of all twelve sites (n=12). All correlations in bold are significant ($p<0.05$). For the abundance and species richness all animals were pooled together. *Aab (amphibian abundance), Asr (amphibian species richness), Bm (*Bufo margaritifer*), Ep (*Epipedobates pictus*), Ca (*Chiasmocleis albopunctata*), Lm (*Leptodactylus* mystaceus), La (*Leptodactylidae adenomera*), Mh (*Microhylidae Hamptophryne boliviana*), Le (*Leptodactylus leptodactyloides*), Lp (*Leptodactylidae Proceratophrys*), Le (*Leptodactylidae enanos*), Tday (day temperature), Tnight (night temperatura), RH (relative air humidity). Only species with five individuals or more were used for correlation analysis.

	Aab	Asr	Bm	Ep	Ca	Lm	La	Mh	Lle	Lp	
Number of captures	236	236	24	23	71	21	24	7	49	5	
Treatment	-0,10	-0,26	-0,17	-0,04	0,07	-0,27	-0,17	-0,16	-0,15	-0,23	
Pteris sp.	-0,07	0,09	-0,23	0,12	-0,26	-0,16	0,10	0,02	0,13	-0,37	
Adiantum sp.	-0,09	-0,05	0,24	0,04	-0,13	0,00	-0,07	-0,18	-0,14	**0,89**	-
Costaceae	0,07	0,10	-0,32	0,07	0,27	0,15	0,02	-0,07	-0,10	-0,30	
Heliconiaceae	0,17	-0,04	0,10	0,34	-0,08	-0,18	0,30	0,27	0,28	-0,32	
Small plants	-0,08	-0,24	0,12	-0,09	0,06	0,00	-0,22	-0,13	-0,18	0,20	-
Ground cover	0,11	0,04	-0,16	0,28	-0,36	-0,25	0,10	-0,08	0,07	-0,08	
Herb height	-0,45	-0,53	-0,43	-0,45	-0,18	-0,28	-0,37	-0,44	-0,40	0,01	-
Litter mass	-0,28	-0,09	-0,12	-0,25	-0,26	-0,52	-0,15	-0,19	-0,10	0,00	-
Litter number	-0,28	-0,06	-0,40	-0,30	-0,11	-0,34	-0,18	-0,24	-0,20	-0,24	-
Litter depth	-0,31	-0,02	-0,55	-0,18	-0,27	-0,14	-0,04	-0,27	-0,16	-0,23	
Understory density	**-0,61**	**-0,77**	-0,45	**-0,71**	-0,15	-0,52	-0,53	**-0,61**	**-0,58**	-0,13	**-**
Tree density	-0,33	-0,15	-0,15	-0,20	-0,32	**-0,81**	-0,16	-0,25	-0,13	-0,03	-
Tree richness	-0,21	-0,28	-0,03	-0,25	-0,34	-0,56	0,08	-0,02	0,08	-0,10	-
Basal area	-0,25	-0,20	-0,20	-0,17	-0,25	**-0,68**	0,04	-0,21	-0,07	-0,08	-
Canopy openess	-0,29	-0,18	-0,52	-0,26	-0,17	0,40	-0,22	-0,23	-0,25	-0,22	
Inclination	**-0,61**	-0,43	-0,47	-0,59	-0,31	-0,18	**-0,58**	-0,56	-0,51	-0,02	**-**
Water presence	**0,70**	0,44	**0,67**	**0,86**	-0,14	0,06	**0,94**	**0,87**	**0,97**	-0,11	
Gap number	-0,01	-0,04	-0,33	0,36	-0,20	0,24	0,04	0,06	0,10	-0,47	
Gap distance	0,40	0,41	**0,66**	0,21	0,38	-0,10	0,20	0,29	0,21	0,49	-
Tday	0,29	0,20	0,52	0,44	-0,04	0,08	0,45	0,23	0,32	0,57	-
Tnight	0,25	0,09	0,36	0,29	-0,11	-0,02	0,44	0,27	0,38	0,19	-
RH	0,34	0,57	0,43	0,31	0,27	-0,23	0,07	0,13	0,20	0,38	
Litter water content	0,41	-0,03	0,25	0,18	0,34	0,19	0,36	0,39	0,31	-0,16	
Soil water content	**0,82**	**0,70**	**0,71**	**0,93**	0,20	0,22	**0,75**	**0,86**	**0,86**	-0,18	
Fine woody debris	-0,39	-0,13	-0,09	-0,21	-0,19	-0,07	**-0,60**	-0,42	-0,42	0,34	-
Coarse woody debris	-0,16	0,02	0,15	0,02	-0,10	-0,22	-0,39	-0,20	-0,20	0,47	-

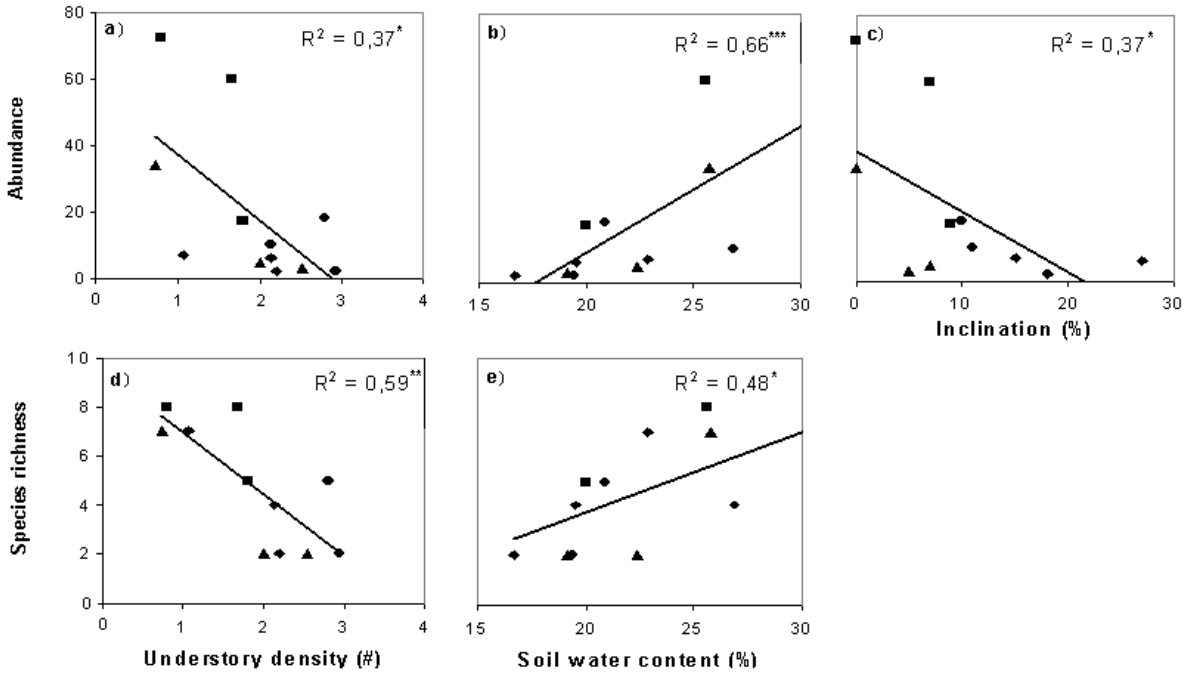

Figure 6; Correlations between amphibian abundance (a,b and c). or species richness (d and e). and environmental variables. The four treatments are shown as different symbols. Control (diamond), Normal (square), Improved (triangle), Intensive (circle), regression lines, coefficients of determination and significance levels are shown.

Correlations were done to see how amphibians relate to single environmental variables (Table 4, Fig. 6). Amphibian abundance and richness show a positive relation with soil water content and presence of water sources, and a negative relation with inclination and understory density. No other significant correlations with environmental variables were found. Soil water content showed the strongest correlation with abundance (Fig. 6). Understory density had the strongest effect on amphibian species richness (Fig. 6). All species respond in a similar manner to the environmental variables as the general abundance does. *Epipedobates pictus* responds strongest to the environmental variables. *Leptodactylidae proceratophrys* is the only one that responds to ferns. Basal area and tree density only has an effect on *Leptodactylus mystaceus* . For *Bufo margaritifer* the proximity of gaps is important and the amount of fine woody debris is important for *Leptodactylidae Adenomera*.

Table 5; ANCOVA table, showing the effect of treatment and environmental covariates on amphibian abundance. The interaction between treatment and covariate is shown if significant otherwise results are presented of an ANCOVA without the interaction term. F and p values, and coefficients of determination (r^2). are shown. TSR (Tree species richness), RH (relative humidity). (ns stands for not significant, * is p<0,05, ** is p<0,01 and *** is p<0,001). Significant F values are shown in bold.

	Treatment		Covariate		Interaction		
Covariable	F	p	F	p	F	p	r^2
Pteris sp.	**7,05**	*	4,14	ns			0,75
Adiantum sp.	**14,63**	*	**9,22**	*			0,83
Costaceae	2,21	ns	**29,36**	**	**19,49**	**	0,98
Heliconiaceae	4,04	ns	0,76	ns			0,65
Small plants	**6,09**	*	3,01	ns			0,73
Ground cover	3,76	ns	0,29	ns			0,62
Herb height	3,21	ns	0,10	ns			0,61
Litter mass	3,35	ns	0,27	ns			0,21
Litter number	3,75	ns	0,92	ns			0,65
Litter depth	3,91	ns	4,76	ns			0,77
Understory density	2,96	ns	0,04	ns			0,61
Tree density	3,48	ns	0,17	ns			0,62
TSR	3,22	ns	0,00	ns			0,61
Basal area	3,50	ns	0,53	ns			0,63
Canopy openess	3,46	ns	3,87	ns			0,75
Inclination	2,07	ns	3,14	ns			0,73
Water sources	**7,31**	*	4,39	ns			0,76
Gap number	2,93	ns	0,39	ns			0,63
Gap distance	2,79	ns	1,07	ns			0,66
Tday	2,12	ns	0,03	ns			0,59
Tnight	0,16	ns	0,28	ns			0,24
RH	2,74	ns	0,16	ns			0,62
Litter water content	2,60	ns	**10,52**	*			0,84
Soil water content	**63,59**	***	**26,43**	**	**20,36**	**	0,98
Fine woody debris	**12,22**	*	0,00	ns	**6,56**	*	0,95
Coarse woody debris	**17,35**	**	0,23	ns	**10,36**	*	0,96

Correlations only give a superficial look at the relations. It is possible that the treatments have such a big impact on amphibians that the effects of other variables are no longer visible. Therefore a series of ANCOVAs was carried out to evaluate whether treatments and environmental variables had independent, direct effects on amphibian abundance (Table 4). and richness (Table 5). Amphibian abundance differed significantly among treatments, if *Pteris* sp., *Adiantum* sp., small plants, water number, soil water content, and woody debris were included as covariates. The normal treatment differed from the control treatment in all these cases. The improved and intensive treatment were always similar and had an abundance that was between the abundances of the control and normal treatment. Treatments differed especially in abundance when corrected for differences in soil water content. Similarly, *Adiantum* sp., Costaceae, litter water content and soil water content have a significant effect on amphibian abundance, when differences among treatments have been taken into

account.

Table 6 ANCOVA's for species richness. Interaction between treatment and covariate is shown if significant; otherwise results are presented of an ANCOVA without the interaction term. TSR (Tree species richness), RH (relative humidity). (ns stands for not significant, * is p<0,05, ** is p<0,01 and *** is p<0,001). Significant F values are shown in bold.

	Treatment		Covariate		Interaction		
Covariable	F	p	F	p	F	p	r2
Pteris sp.	1,93	ns	1,22	ns	-	-	0,46
Adiantum sp.	1,95	ns	1,22	ns			0,46
Costaceae	**15,50**	*	0,01	ns	**15,02**	*	0,96
Heliconiaceae	1,33	ns	0,03	ns	-	-	0,37
Seedling	1,70	ns	1,19	ns	-	-	0,45
Ground cover	1,44	ns	0,23	ns	-	-	0,38
Litter mass	1,50	ns	0,40	ns	-	-	0,40
Litter number	1,46	ns	0,28	ns	-	-	0,39
Litter depth	2,22	ns	1,73	ns	-	-	0,49
Understory density	2,28	ns	**14,55**	**	-	-	0,79
Tree density	1,24	ns	0,00	ns	-	-	0,36
TSR	1,61	ns	1,17	ns	-	-	0,45
Basal area	1,18	ns	0,02	ns	-	-	0,36
Canopy openess	1,21	ns	0,01	ns	-	-	0,36
Inclination	2,68	ns	4,77	ns	-	-	0,62
Water count	0,73	ns	0,27	ns	-	-	0,39
Gap count	2,55	ns	2,36	ns	-	-	0,53
Gap distance	0,77	ns	0,11	ns	-	-	0,37
Tdag	0,89	ns	0,13	ns	-	-	0,37
Tnacht	0,94	ns	0,09	ns	-	-	0,37
RH	0,17	ns	1,86	ns	-	-	0,42
Litter water content	1,65	ns	0,63	ns	-	-	0,42
Soil water content	1,00	ns	0,68	ns	-	-	0,83
Herb height	1,74	ns	**9,70**	*	-	-	0,90
Fine woody debris	1,30	ns	0,08	ns	-	-	0,37
Coarse woody debris	1,35	ns	0,05	ns	-	-	0,37

There is a strong relation between amphibian abundance and species richness (Pearson correlation, df=11, r=0,81, p=0,001). However, when looking at the ANCOVA's for species richness, the results are different from those for abundance. When accounting for Costaceae there was a difference between treatments in species richness, with the highest species richness in the normal treatment and the lowest in the control treatment. Understory density and herb height had a significant effect on species richness, when differences between treatments have been taken into account. Costaceae was the only factor for which the effect varies with different treatments (Table 6).

What environmental variables are the best predictors?

A forward regression was carried out for amphibian abundance on all 26 environmental variables to see which of the environmental variables are needed to be able to predict amphibian abundance and species richness. Soil water content was the only variable included in this parsimonious model for abundance. It shows that increase of soil water content leads to a rise in amphibian abundance. This relation explains 66,7% of the variations between traps (forward regression; F=20,1 ; p=0,001; Amphibian abundance (# of animals caught in trap). = 375,9 * Soil Water Content -66,5 (Fig. 6))

For amphibian species richness a forward regression was carried out as well. Understory density was selected as the only variable that significantly affected amphibian richness. This relation explains 59% of the variation between traps (forward regression ; F=14,4 ; p=0,004; Amphibian species richness (# of species caught in trap). = -2,5 * Understory Density + 9,5 (Fig. 6).). It shows that a more open understory had a more species rich amphibian population.

3.2 Logging effects in Inpa

Table 7 ANOVA how environmental variables differ among 4 treatments; (T(control), N(normal), M(improved). and I(intensive), n=3 replicates per treatment. F is the variance among groups divided by the variance within groups. The number of stars beneath p shows how strong the significance is (ns stands for not significant, * is p<0,05, ** is p<0,01 and *** is p<0,001). Values in the same row, followed by a different letters are significantly different from each other (S-N-K post-hoc test, p<0.05)

Treatment	Unit	F	p	T	N	M	I
Bromeliaceae	(%)	1.91	ns	0,08a	0,17a	0,15a	0,00a
Small plants	(%)	3.20	ns	0,25a	0,39a	0,42a	0,54a
Ground cover	(%)	1.73	ns	0,33a	0,56a	0,56a	0,54a
Herb height	(cm)	2.12	ns	51,3a	59,8a	57,9a	115,3a
Litter mass	(g)	1.47	ns	243a	289a	319a	255a
Litter layers	(#)	4.98	*	1,00a	2,00(ab)	1,67(ab)	2,33(b)
Litter depth	(cm)	2.76	ns	1,33a	2,00a	2,00a	2,33a
Understory density	(#)	3.44	ns	1,33a	1,50a	1,33a	2,67a
Tree density	(#/ha)	0.76	ns	349a	431a	330a	344a
Tree species richness	(#/707m²)	0.87	ns	9,3a	10,0a	7,6a	9,7a
Basal area	(m²/ha)	2.58	ns	20,0a	22,0a	15,3a	11,3a
Canopy openness	(%)	0.10	ns	0,06a	0,07a	0,06a	0,06a
Inclination	(%)	1.56	ns	9,0a	3,50a	8,33a	2,33a
Water sources	(y/n)	0.85	ns	0,33a	0,00a	0,00a	0,00a
Gap number	(#/ha)	3.95	ns	14,0a	35,0a	33,0a	61,3a
Gap distance	(m)	1.27	ns	16,33a	14,0a	17,3a	6,67a
Litter water content	(%)	2.03	ns	0,39a	0,28a	0,25a	0,32a
Soil water content	(%)	0.79	ns	0,17a	0,12a	0,13a	0,22a
Fine woody debris	(#/17m)	3.02	ns	10,11a	13,11a	11,17a	20,78a
Coarse woody debris	(#/17m)	1.50	ns	5,22a	3,78a	4,83a	7,89a
Axis 1	-	5,72	*	-1,01a	-0,12ab	-0,03ab	1,15b
Axis 2	-	3,76	ns	0,49a	-0,91a	0,64a	0,84a

Differences in environmental variables among treatments

ANOVA's were done to see how the treatments differ from each other (Table 7). Only the number of litter layers differs significantly among treatments (p=0,037), with more litter layers in the intensive than in the control treatment.

Table 8a Pearson correlation among environmental variables, pooling all data from the twelve sites (n=12). All correlations in bold script are significant (p<0.05).

	Treatment	Bromeliaceae	Small plants	Ground cover	Herb height	Litter mass	Leaf stack	Litter depth	Understory density	Tree density	Tree species richness
Treatment		-0,31	**0,70**	0,46	**0,60**	**0,81**	**0,68**	**0,67**	**0,67**	0,10	0,21
Bromeliaceae			-0,23	0,42	-0,16	-0,14	-0,08	-0,21	-0,21	0,07	-0,39
Small plants				**0,78**	**0,72**	0,61	**0,61**	**0,79**	**0,79**	0,31	0,27
Ground cover					0,57	0,49	0,51	0,59	0,59	0,33	0,01
Herb height						0,37	0,26	**0,79**	0,79	0,14	0,15
Litter mass							**0,78**	**0,63**	0,02	-0,11	-0,20
Leaf stack								**0,64**	**0,63**	-0,06	0,11
Litter depth									**0,64**	0,25	-0,20
Understory density										0,26	0,16
Tree density											0,30
Tree species richness											
Basal area											
Canopy openess											
Inclination											
Water count											
Gap count											
Gap distance											
Litter water content											
Soil water content											
Fine woody debris											
Coarse woody debris											

Table 8b Pearson correlation among environmental variables, pooling all data from the twelve sites (n=12). All correlations in bold script are significant (p<0.05).

	Basal area	Canopy openess	Inclination	Water count	Gap count	Gap distance	Litter water content	Soil water content	Fine woody debris	Coarse woody debris
Treatment	-0,44	0,13	**-0,61**	-0,40	**0.77**	-0.52	-0.25	0.24	**0.64**	0.44
Bromeliaceae	0,44	0,11	0,21	-0,30	0.06	-0.12	**-0.68**	-0.52	-0.42	-0.35
Seedlings	-0,19	0,36	-0,22	-0,33	**0.68**	-0.32	-0.36	0.19	**0.72**	0.52
Ground cover	0,09	0,40	-0,08	-0,50	**0.68**	-0.37	**-0.77**	-0.16	0.40	0.26
Herb height	-0,27	0,57	-0,35	-0,24	**0.77**	-0.50	-0.21	0.02	**0.76**	**0.82**
Litter mass	-0,14	0,08	0,20	-0,56	0.09	-0.14	-0.36	-0.10	0.07	0.01
Leaf stack	-0,39	-0,26	**-0,69**	-0,37	0.53	-0.53	-0.45	0.49	0.27	0.16
Litter depth	-0,20	-0,33	-0,23	-0,56	0.40	-0.52	-0.40	0.55	0.28	0.06
Understory density	-0,15	0,18	-0,31	-0,31	**0.67**	**-0.67**	-0.25	0.48	0.59	0.59
Tree density	**0,74**	0,21	0,18	0,05	-0.08	0.17	-0.05	0.00	0.02	0.06
Tree species richness	0,27	0,23	-0,37	0,53	0.05	0.25	0.19	-0.02	0.05	0.23
Basal area		0,03	0,29	0,35	-0.42	0.38	-0.13	-0.18	-0.54	-0.35
Crown openess			0,22	-0,22	0.50	-0.12	0.05	**-0.65**	**0.63**	**0.67**
Inclination				-0,20	-0.32	0.19	0.26	-0.27	-0.03	-0.14
Water count					-0.51	**0.71**	0.27	0.10	-0.43	-0.31
Gap count						**-0.66**	-0.45	-0.14	**0.74**	0.56
Gap distance							0.19	-0.22	-0.40	-0.51
Litter water content								0.15	0.09	0.26
Soil water content									-0.01	-0.07
Fine woody debris										**0.76**
Coarse woody debris										

The large number of significant correlations among treatment and environmental variables shows that the treatments (presented as a measure of disturbance) do have an effect (Table 8), whereas this could not be shown with the ANOVA (Table 1). It is also interesting to see that the number of gaps correlates positively with the structural variables of the understory, namely ground cover, herb height and understory density.

Table 9: Principal Component Analysis for environmental variables to show how variables relate to each other. Two axes were extracted to represent these relations in a two dimensional field. The numbers are the scores of the variables on each of the two axes.

	Axes	
	1	2
Bromeliaceae	-0.08	-0.88
Small plants	0.86	0.05
Ground cover	0.75	-0.51
Herb height	0.82	0.28
Litter mass	0.29	-0.56
Leaf number	0.71	-0.07
Litter depth	0.65	-0.24
Understory density	0.86	0.16
Tree density	0.08	-0.08
Tree species richness	0.03	0.51
Basal area	-0.40	-0.31
Canopy openess	0.37	0.12
Inclination	-0.33	-0.27
Water count	-0.59	0.47
Gap count	0.87	-0.01
Gap distance	-0.71	0.10
Litter water content	-0.38	0.73
Soil water content	0.16	0.29
Fine woody debris	0.76	0.37
Coarse woody debris	0.66	0.48

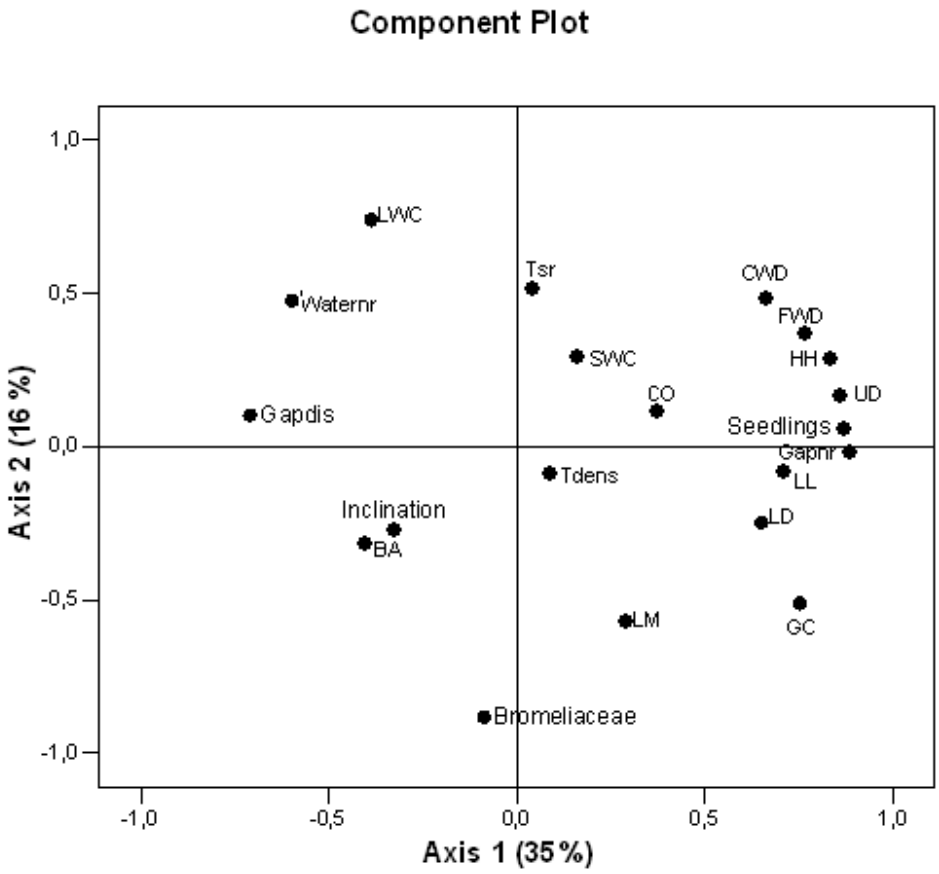

Fig. 8 Graph of axes scores from Table 3. PCA on 20 environmental factors in the logging-effect study in Inpa. The percentages show how much variations each axis explains. Together they explain 51,3% of the variation; GC (ground cover), HH (herb height), LM (litter mass), LN (litter layers), LD (litter depth), UD (understory density), TD (tree density), TSR (tree species richness), BA (basal area), CO (canopy openness), LWC (litter water content), SWC (soil water content), FWD (fine woody debris), CWD (coarse woody debris)

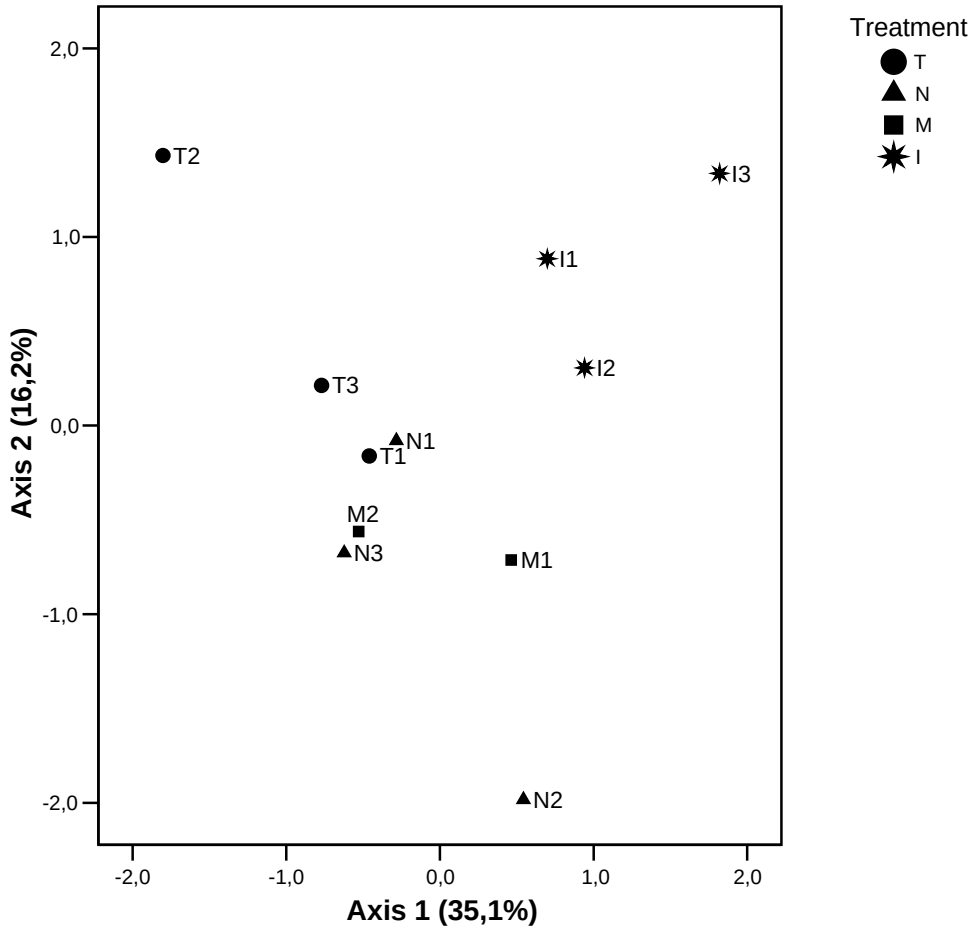

Fig. 9 ; Scatter plot of both regression factors resulting from the PCA. T (control), N (normal), M (improved), I (intensive)

A PCA was run to summarize the 20 environmental variables into two axes to get a better insight into the relations among them (Fig.8). The first axis explained 35,1% of the variation and was positively correlated with the variation in small plants, herb height, understory density, and gap count and negatively correlated with gap distance. This new explanatory variable differed significantly among treatments ($ANOVA_{df=2,8,}$ F=5,72, p=0,027; table 7). with the intensive treatment having significantly higher axis scores (i.e., more small plants, a higher herb height, a denser understory, and more and closer gaps). than the control. The second axis explains 16,2% of the variation, with Bromeliaceae being the negative extreme and litter water content being the positive extreme. The treatments did not differ significantly in their scores for the second axis.

Table 10 Correlation between abundance and richness of all amphibians (pooled together and abundance of individual species). and environmental variables in Inpa, pooling the traps of all sites (n=11). All correlations in bold are significant (p<0.05); Le (*Leptodactylus elenae*), Lm (*Leptodactylus mystacinus*), Ls (*Leptodactylus syphax*), Pa (*Physalaemus cf. albonotatus*), Pr (*Proceratophrys* sp.), Ca (*Chiasmocleis albopunctata*), Dm (*Dermatonotus muelleri*), Eo (*Elachistocleis ovalis*)

	Abundance 188	Species richness 188	Le 46	Lm 7	Ls 12	Pa 43	Pr 15	Ca 29	Dm 21	Eo 8
Treatment	-0.39	-0.13	-0.25	-0.22	-0.13	-0.34	-0.58	-0.38	-0.37	-0.12
Bromeliaceae	-0.34	-0.50	-0.36	0.39	0.07	-0.31	-0.26	-0.32	-0.35	-0.29
Small plants	-0.36	-0.25	-0.35	-0.04	-0.51	-0.24	-0.42	-0.33	-0.35	-0.32
Ground cover	-0.55	-0.56	-0.55	0.20	-0.43	-0.42	-0.56	-0.50	-0.54	-0.48
Herb height	-0.22	0.17	-0.21	0.00	-0.35	-0.18	-0.30	-0.23	-0.19	-0.29
Litter mass	**-0.63**	**-0.69**	**-0.66**	0.10	-0.13	-0.57	-0.56	-0.57	-0.59	**-0.63**
Leaf stack	-0.35	-0.16	-0.32	-0.02	0.21	-0.22	-0.54	-0.37	-0.33	-0.11
Litter depth	-0.49	-0.14	-0.52	0.15	0.21	-0.24	-0.58	-0.56	-0.55	-0.05
Understory density	-0.21	0.23	-0.26	0.30	-0.10	0.02	-0.28	-0.30	-0.25	-0.21
Tree density	0.07	-0.11	0.15	-0.18	-0.34	0.14	0.15	0.04	-0.03	0.12
Tree species richness	0.47	0.01	0.55	-0.25	-0.53	0.33	0.47	0.55	0.48	0.01
Basal area	0.37	-0.10	0.36	0.10	-0.16	0.39	0.50	0.34	0.28	0.19
Canopy openness	-0.29	-0.27	-0.16	-0.12	**-0.78**	-0.41	-0.20	-0.21	-0.24	-0.59
Inclination	-0.19	-0.15	-0.27	0.30	-0.24	-0.11	0.06	-0.21	-0.25	-0.24
Water sources	**0.98**	0.43	**0.93**	-0.26	-0.03	**0.84**	**0.92**	**1.00**	**0.99**	**0.68**
Gap count	-0.53	-0.22	-0.47	0.17	-0.36	-0.47	-0.63	-0.50	-0.49	-0.46
Gap distance	**0.61**	-0.11	**0.62**	-0.54	-0.23	0.42	0.61	0.70	**0.63**	0.54
Litter water content	0.32	0.53	0.38	-0.27	0.02	0.22	0.41	0.27	0.31	0.12
Soil water content	0.25	0.56	0.15	0.12	0.57	0.51	0.12	0.10	0.19	0.43
Fine woody debris	-0.43	-0.02	-0.34	-0.16	-0.50	-0.40	-0.49	-0.41	-0.39	-0.38
Coarse woody debris	-0.30	0.21	-0.25	-0.03	-0.39	-0.34	-0.25	-0.31	-0.26	-0.55

Effects of environmental variables on amphibians

To see how the amphibians are related to the environmental variables, correlations were carried out. Litter mass correlates negatively and the presence of wáter and the distance to gap correlate positively with amphibian abundance (Table 5). Of these three the presence of water correlates strongest. All individual species respond in a similar fashion as the total abundance does. Canopy openness has a negative effect on the abundance of *Leptodactylus syphax*, while this does not go for the general abundance. For *Leptodactylus elenae* the distance to the nearest gap was important. The presence of water sources has a relation with almost all amphibian species. It correlates positively with *Leptodactylus elenae*, *Physalaemus cf. albonotatus*, Proceratophrys sp., *Chiasmocleis albopunctata*, *Dermatonotus muelleri*, *Elachistocleis ovalis.*

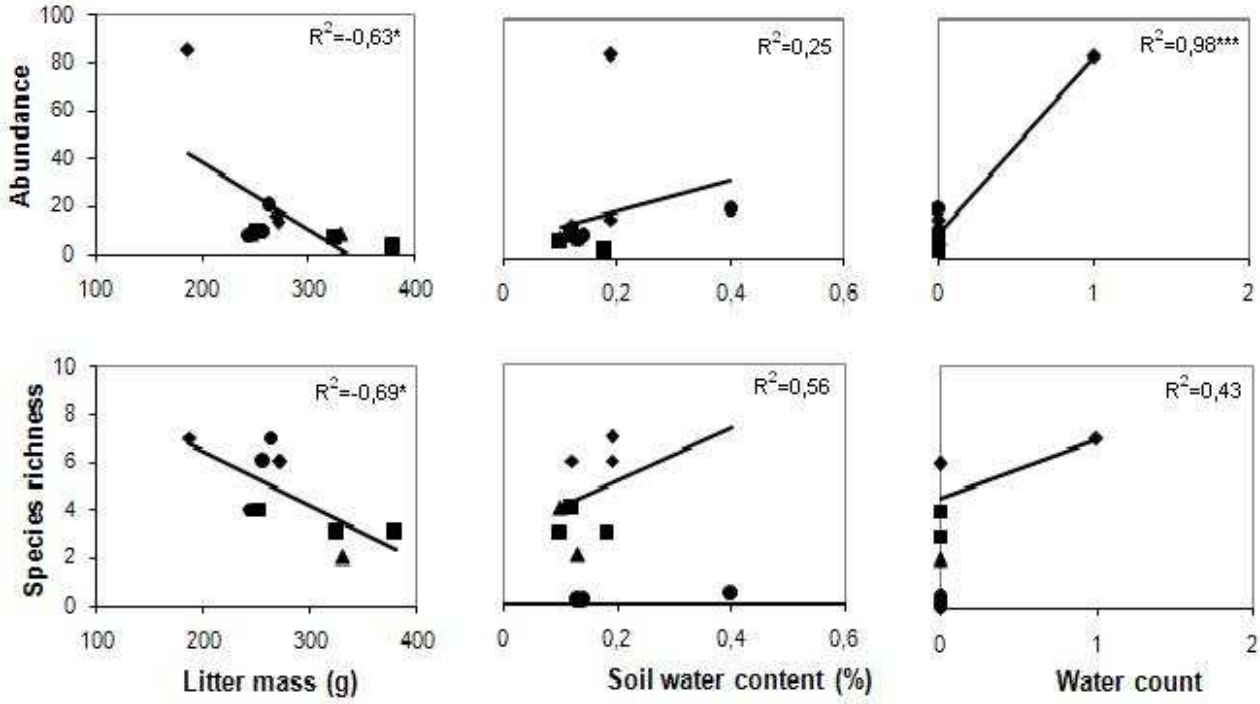

Figure 10; Correlations between amphibian abundance or species richness and environmental variables. The four treatments are shown as different symbols. Control (diamond), Normal (square), Improved (triangle), Intensive (circle), regression lines, coefficients of determination and significance levels are shown.

Table 11; ANCOVA table, showing the effect of treatment and environmental covariates on amphibian abundance. The interaction between treatment and covariate is shown if significant; otherwise results are presented of an ANCOVA without the interaction term..

	Treatment		Covariable		Interaction		
Covariable	F	Sig.	F	Sig.	F	Sig.	r^2
Bromeliaceae	**29.15**	**	1.09	ns	**25.96**	**	0.96
Small plants	0.73	ns	0.00	ns	-	-	0.36
Ground cover	0.35	ns	0.42	ns	-	-	0.40
Herb height	**21.83**	*	**42.53**	**	**18.73**	*	0.89
Litter mass	**87.05**	**	0.91	ns	**78.86**	**	0.99
Leaf number	0.75	ns	0.03	ns	-	-	0.36
Litter depth	0.47	ns	0.27	ns	-	-	0.39
Understory density	1.08	ns	0.21	ns	-	-	0.38
Tree density	1.19	ns	0.18	ns	-	-	0.38
Tree species richness	1.54	ns	2.75	ns	-	-	0.56
Basal area	1.07	ns	0.84	ns	-	-	0.44
Canopy openess	1.28	ns	0.89	ns	-	-	0.44
Inclination	2.77	ns	3.51	ns	-	-	0.60
Watercount	1.80	ns	**164.99**	***	.	.	0.98
Gapcount	0.84	ns	1.63	ns	-	-	0.50
Gapdistance	**23.86**	*	0.17	ns	**56.26**	**	1.00
Litter water content	0.83	ns	0.07	ns	-	-	0.37
Soil water content	1.16	ns	0.48	ns	-	-	0.41
Fine woody debris	1.19	ns	1.54	ns	-	-	0.15
Coarse woody debris	**44.37**	**	**10.66**	*	**35.95**	**	0.96

A series of ANCOVA's was carried out to evaluate whether treatments and environmental variables had independent, direct effects on amphibian abundance and richness (Table 11). When Bromaliaceae, herb height, litter mass, gap distance or coarse woody debris are compensated for, there is a significant difference in abundance among treatments. In each of these cases the control treatment was different from the other treatments. There is a strong interaction with logging disturbance resulting in different relations in different treatments. Herb height, water count and coarse woody debris have a relation with amphibian abundance when differences among treatments are compensated for.

Table 12; ANCOVA table, showing the effect of treatment and environmental covariates on amphibian species richness. The interaction between treatment and covariate is shown if significant; otherwise results are presented of an ANCOVA without the interaction term..F and p values, and coefficients of determination (r^2). are shown.

	Treatment		Covariable		Interaction		
Covariable	F	Sig.	F	Sig.	F	Sig.	r^2
Bromeliaceae	3.74	ns	0.11	ns	-	-	0.74
Small plants	**6.08**	*	0.87	ns	-	-	0.77
Ground cover	3.97	ns	0.91	ns	-	-	0.77
Herb height	**5.32**	*	0.00	ns	-	-	0.56
Litter mass	**46.79**	**	**56.21**	**	**48.57**	**	1.00
Leaf number	**5.67**	*	0.26	ns	-	-	0.75
Litter depth	**6.17**	*	0.62	ns	-	-	0.76
Understory density	**5.14**	*	0.00	ns	-	-	0.74
Tree density	**5.58**	*	0.10	ns	-	-	0.74
Tree species richness	**6.86**	*	1.04	ns	-	-	0.77
Basal area	**5.50**	*	0.02	ns	-	-	0.74
Canopy openess	**8.53**	*	3.04	ns	-	-	0.82
Inclination	**51.18**	**	**56.24**	**	**25.88**	**	0.99
Watercount	4.68	ns	0.55	ns	-	-	0.76
Gapcount	**8.51**	*	2.80	ns	-	-	0.82
Gapdistance	**5.66**	*	0.16	ns	-	-	0.74
Litter water content	3.46	ns	0.00	ns	-	-	0.74
Soil water content	**5.17**	*	2.25	ns	-	-	0.81
Fine woody debris	**7.63**	*	1.66	ns	-	-	0.65
Coarse woody debris	**5.80**	*	0.50	ns	-	-	0.59

For species richness there are very different relations (Table 12). Amphibian species richness differed significantly or nearly significantly among treatments, irrespective of the covariables. With litter mass and inclination there is a relation with abundance when the differences among the treatments have been accounted for. For both it depends on the treatment what kind of relation this is.

What environmental variables are the best predictors?

Again a forward regression was carried out for amphibian abundance on all 20 environmental variables. Water count and soil water content were both included in the model. The model explains 97,9% of the variation (forward regression; F=187,3 ; p<0,000; Amphibian abundance (# of animals caught in trap). = 73,9 * Water count + 40,4 * Soil Water Content + 3,4 (Fig. 10)). It shows that with increase of water in the area (albeit standing water or moisture in the soil). more amphibians are present.

For amphibian species richness litter mass and soil water content were selected for the model (forward regression ; F=10,0 ; p=0,007 Amphibian species

richness (# of species caught in trap). = -0,021 * Litter mass + 10,1 * soil water content + 8,9 (Fig. 10)). It explains 71% of the variation in amphibian species richness.

3.3 Effects of small-scale heterogeneity on amphibians

Table 13. ANOVA of differences in environmental variables among 4 sites (n=42 per site). R1 and R2 are sites near a stream. N1 and N2 are sites that are not close to a stream. F is the variance between groups divided by the variance within groups. The higher the value of F, the bigger the relative difference is between the sites. The number of stars beneath p shows how strong the significance is (ns stands for not significant, * is p<0,05, ** is p<0,01 and *** is p<0,001). Tree SR is tree species richness.

Variable		F	p	R1	R2	N1	N2
Litter depth	(cm)	16,65	***	4,47c	5,05b	4,47c	5,92a
Woody debris	(-)	8,72	***	1,65b	1,64b	2,12a	1,93a
Pteris sp.	(%)	92,86	***	0,15c	0,04d	0,62b	0,72a
Adiantum sp.	(%)	30,52	***	0,29a	0,36a	0,00b	0,00b
Costaceae	(%)	4,58	***	0,10ab	0,04b	0,13a	0,17a
Heliconiaceae	(%)	25,51	***	0,26a	0,04b	0,05b	0,00b
Small plants	(%)	17,32	***	0,18b	0,50a	0,16b	0,11b
Understory density	(#/2m)	36,50	***	1,99c	2,87a	1,25d	2,54b
Distance to stream	(m)	395,94	***	17,50b	17,50b	50,00a	50,00a
PCA Axis 1	(-)	202,5	***	-0,74b	0,87a	0,90a	-1,03c
PCA Axis 2	(-)	21,3	***	-0,77c	-0,26b	0,52a	0,51a

Environmental differences between sites

To see how variables differ between sites ANOVA were carried out. The ANOVA's show that the four sites differ significantly from each other in all variables (Table 13). Woody debris, *Adiantum* sp., Costaceae and distance to stream all show the same pattern, namely that the two stream sites (R1 and R2). are similar, but differ from the two other sites (N1 and N2), which are in turn similar to each other. When comparing the stream sites with the sites without a stream the following differences occur. There is less woody debris on the stream sites. For the understory vegetation *Adiantum* sp. and small plants are more common on sites near the stream, while *Pteris* sp. and Costaceae are more common on sites without a stream. There is a higher basal area on the stream sites.

Table 14 Pearson correlation between environmental variables, pooling all data from the four sites (n=148). All correlations in bold script are significant (p<0.05)

Correlations	Litter depth	WD	*Pteris* sp.	*Adiantum* sp.	Costaceae	Heliconiaceae	Small plants	UD	Stream	Stream distance
Site	**0,29**	-0,05	-0,07	0,09	-0,09	**-0,44**	**0,33**	**0,45**	0,00	0,00
Litter depth	1,00	-0,03	**0,15**	-0,06	**-0,02**	**-0,29**	0,10	**0,16**	**-0,18**	0,06
Woody debris		1,00	**0,25**	**-0,32**	-0,12	-0,10	0,04	-0,07	**-0,35**	**0,44**
Pteris sp.			1,00	**-0,55**	-0,01	**-0,36**	**-0,49**	-0,15	**-0,78**	**0,70**
Adiantum sp.				1,00	**-0,22**	0,06	-0,14	**0,23**	**0,59**	**-0,62**
Costaceae					1,00	0,04	**-0,33**	**-0,17**	**-0,23**	**0,28**
Heliconiaceae						1,00	**-0,23**	**-0,24**	**0,35**	**-0,26**
Seedling							1,00	**0,16**	**0,32**	**-0,29**
Understory density								1,00	**0,28**	**-0,26**

Stream		1,00	**-0,94**

The great number of correlations between environmental variables and the presence of a stream and stream distance stand out. When stream is positively correlated, distance to stream does so negatively and vice versa. The presence or close proximity of a stream results in a denser understory, more *Adiantum* sp. and Heliconiaceae and more and larger trees. If there is no stream present, there is more litter and woody debris. In addition, more *Pteris* sp. and Costaceae can be found. It is clear that understory species respond to different levels of the environmental factors (Table 14)

Table 15; Principal Component Analysis for
environmental variables to show how variables relate to each other. Two axes were extracted to represent these relations in a two diminsional field. The numbers are the scores of the variables on each of the two axes.

Component Matrix(a)

	Axes	
	1	2
Woody debris	0.53	0.16
Pteris sp.	0.81	0.17
Adiantum sp.	-0.72	-0.13
Costaceae	0.30	-0.41
Heliconiaceae	-0.22	-0.73
Small plants	-0.36	0.55
Basalarea	-0.46	0.23
TSR	-0.21	-0.0
Stream distance	0.90	0.04
Litter depth	0.05	0.60
Understory density	-0.29	0.45

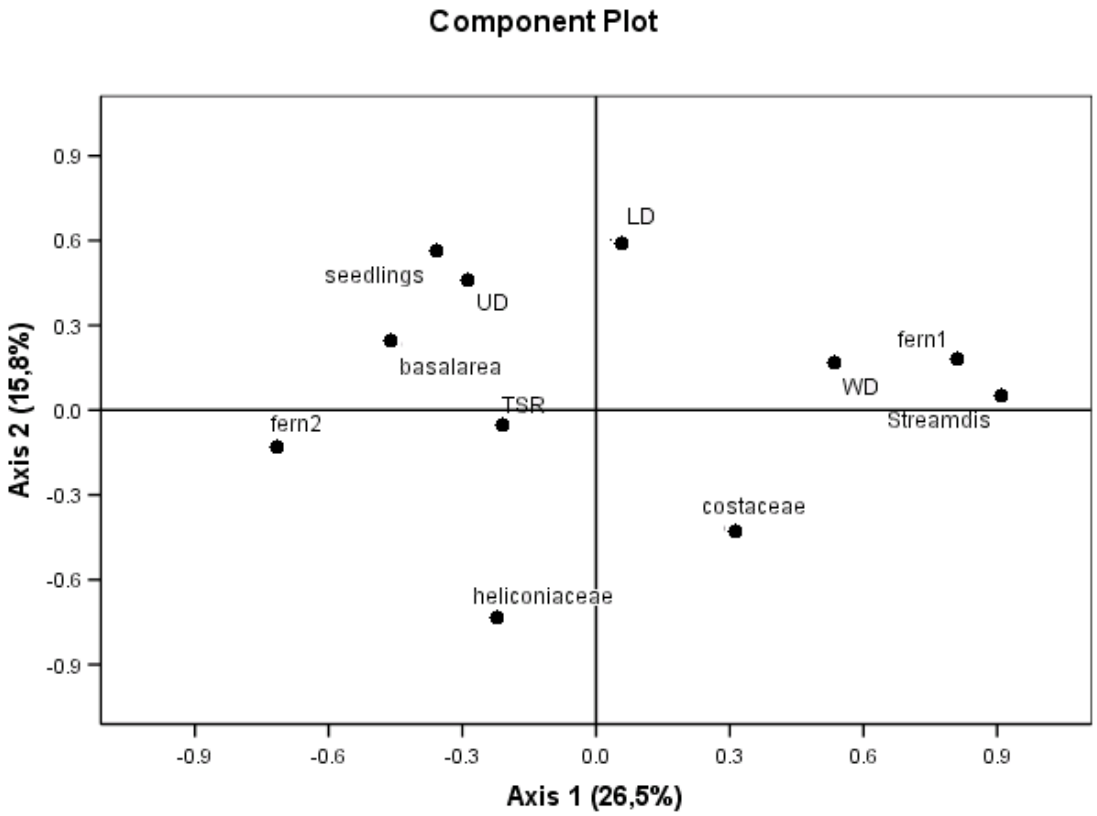

Fig. 11 Graph of axes scores from Table 3. PCA on 11 environmental factors in the heterogeneity study. The percentages show how much variations each axis explains. Together they explain 42,3% of the variation; LD (litter depth), UD (understory density), TSR (tree species richness), WD (woody debris)

j

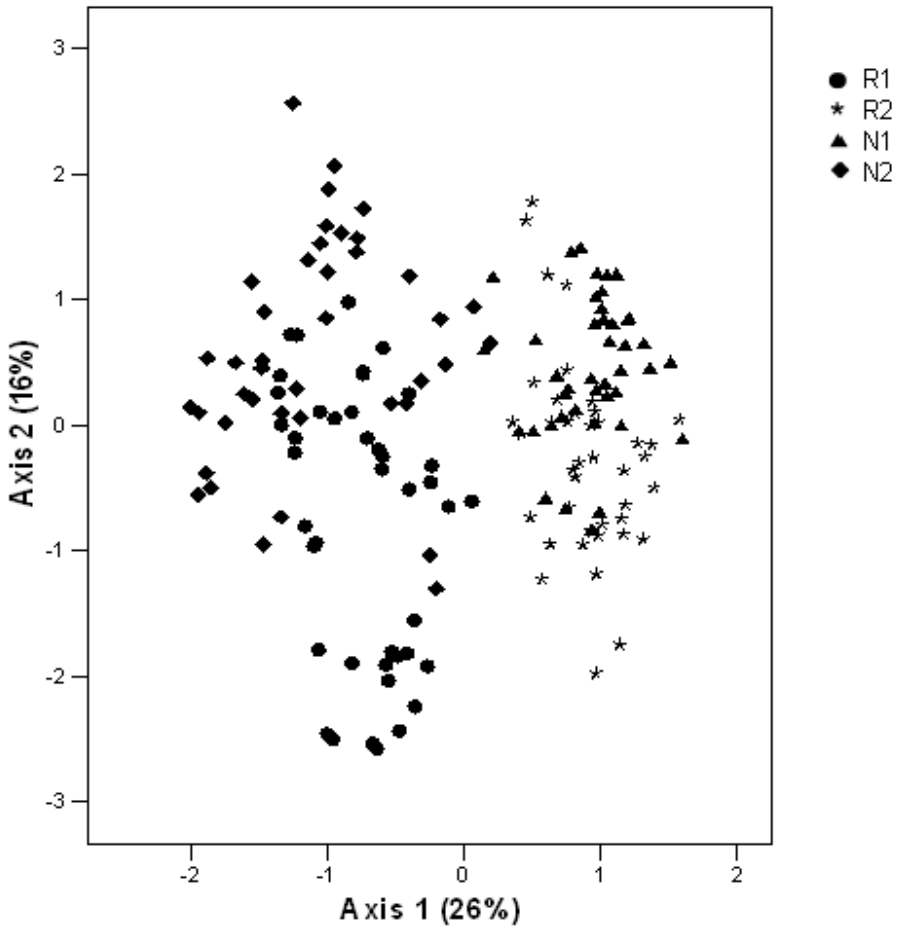

Fig. 12; Using the axes created from Table 3, scores can be calculated for each sample point. Sample points that are similar are shown close to each other. Together the axes explain 42,3% of the variation.

From the correlations it was clear that many environmental variables are related. To give a better overview of these relations a PCA was done. Two summary variables (represented by axis 1 and 2). were created to represent all the variables. Both axes together explain 42% of the variation in environmental variables. The first axis explains 26% of the variation and is positively associated with the distance to the stream and *Pteris* sp., while it was negatively associated with *Adiantum* sp. (Table 15, Fig. 11). The second axis explains 15% of the variation and is negatively associated with Heliconiaceae, and positively associated with small plants, litter depth and understory density. On the first axis the stream sites separate clearly from the other two sites (Table 15, Fig. 12). This means that distance to stream and the abundance of *Pteris* sp. differ greatly between these sites. Also clear is the difference between sites R1 and N1, and sites R2 and N2 according to the second axis (Table 13).

Table 16 Correlation between abundance, species richness and 10 single species of amphibians and environmental variables as well as abundance, species richness and 3 single species of reptiles, pooling the traps of all four sites (n=168). All correlations in bold are significant (p<0.05). Aab (amphibian abundance), Asr (amphibian species richness), Rab (reptile abundance), Rsr (reptile species richness). Ten species of amphibians: Bp (*Bufo paracnemis*), Bm (*Bufo margaritifer*), Ep (*Epipedobates pictus*), Ca (*Chiasmocleis albopunctata*), Lm (*Leptodactylus mystaceus*), La (*Adenomera sp.*), Le (*Leptodactylus leptodactyloides*), Li (*Leptodactylidae Lithodytes lineatus*). and three reptile species: Sc (*Stenocercus caducus*), Aa (*Ameiva ameiva*), Pe (*Prionodactylus Eigenmani*). Only species with five individuals or more were used for correlation analysis.

Correlation Number of captures	Aab 296	Asr 296	Bp 7	Bm 64	Ep 36	Ca 46	Lm 31	La 87	Lle 6	Lli 9	Rab 79	Rsr 79	Sc 50	Aa 6	Pe 14
Litter depth	-0,09	-0,12	-0,05	-0,05	-0,13	-0,05	0,09	-0,02	-0,11	-0,06	**0,16**	**0,19**	0,14	0,01	**0,17**
Woody debris	**-0,23**	**-0,23**	0,06	-0,19	-0,05	-0,03	-0,03	**-0,20**	-0,02	-0,05	0,01	0,03	0,03	-0,06	0,05
Pteris sp.	**-0,40**	**-0,42**	0,14	**-0,29**	**-0,17**	**-0,32**	0,06	**-0,17**	-0,05	**-0,16**	**0,19**	**0,17**	**0,25**	-0,10	0,09
Adiantum sp.	**0,21**	**0,20**	-0,08	**0,34**	-0,06	0,11	-0,07	0,10	0,03	-0,02	-0,03	-0,06	-0,10	**0,16**	-0,05
Costaceae	-0,02	-0,03	0,06	-0,13	0,05	-0,05	0,12	0,04	0,07	-0,04	**-0,18**	**-0,18**	**-0,16**	-0,09	0,01
Heliconiaceae	0,14	0,12	-0,01	0,11	**0,29**	-0,05	-0,05	0,07	0,02	0,11	-0,10	-0,08	-0,06	-0,07	0,00
Seedling	**0,23**	**0,28**	-0,12	0,06	0,04	**0,34**	-0,03	0,08	0,00	**0,17**	-0,03	0,02	-0,07	0,06	-0,06
Understory density	0,08	0,12	-0,05	0,03	-0,04	0,14	0,09	0,01	0,05	-0,08	0,09	0,09	0,03	**0,18**	-0,03
Stream	**0,48**	**0,50**	-0,09	**0,40**	0,19	**0,39**	-0,11	**0,17**	0,13	**0,17**	**-0,12**	-0,09	-0,14	0,04	-0,11
Distance to stream	**-0,40**	**-0,44**	0,07	**-0,35**	-0,10	**-0,33**	0,11	**-0,16**	-0,11	-0,14	**0,12**	0,10	0,15	-0,06	0,11

Amphibian and animal response to environmental variables

Now that the relations between the environmental variables are clear it is interesting to see how amphibians and reptiles respond to these variables. To look into this, correlations were done. The first thing that stands out is that abundance and richness have very similar correlations with the environmental variables (Table 5). This is because there is a strong correlation between abundance and richness both for amphibians (r = 0,89 ; p<0,000). and reptiles (r=0,91 ; p<0,000). This is due to the fact that each data point used here represents only one bucket. In each bucket, on average, only 1,8 amphibians and 0,5 reptiles were caught. This doesn't leave a lot of room for big differences in species richness (only one or sometimes two species per bucket). So in fact these correlations really show the same thing, namely abundance. Therefore species richness will not be discussed further (Table 5)

The second result that stands out is that when amphibians correlate positively with environmental factors, reptiles do so negatively (Table 5).

Amphibian abundance increases with increasing abundance of *Adiantum* sp. and small plants, as well as the presence of a stream. It decreases with increases of woody debris, *Pteris* sp. and distance to stream. Of these the presence of a stream is strongest. Thus it seems that the availability of water has the largest impact on amphibian abundances (Table 5).

Reptiles do not only respond opposite to amphibians, they also find different factors important. Reptile abundance is positively correlated with litter depth, *Pteris* sp. and distance to stream, while the abundance of Costaceae and

the presence of a stream show a negative correlation. Understory composition is most important for reptiles, as *Pteris* sp. and Costaceae show the strongest correlations (Table 5).

Both for reptiles and amphibians the species respond similar to the different variables as their abundance does, albeit with a different strength (Table 5).

Table 17 ANCOVA for amphibian abundance. F is the variance between groups divided by the variance within groups. The higher the value of F, the bigger the relative difference is between the sites. The number of stars beneath p shows how strong the significance is (ns stands for not significant, * is p<0,05, ** is p<0,01 and *** is p<0,001)

Fabun	Site		Covariate		Interaction		r^2
Covariable	F	p	F	p	F	p	
Litter depth	1,50	ns	0,17	ns	0,40	ns	0,27
Woody debris	0,44	ns	1,06	ns	1,26	ns	0,23
Pteris sp.	**3,16**	*****	1,81	ns	2,52	ns	0,29
Adiantum sp.	**15,89**	*******	3,09	ns	0,80	ns	0,28
Costaceae	**16,06**	*******	2,54	ns	0,06	ns	0,28
Heliconiaceae	**16,96**	*******	0,04	ns	0,55	ns	0,27
Seedling	**9,38**	*******	0,21	ns	0,10	ns	0,26
Understory density	**10,03**	*******	**5,51**	*****	**3,56**	*****	0,33
Stream	0,00	ns	**-**	**-**	-	-	0,26
Distance to stream	1,55	Ns	**4,68**	*****	0,03	ns	0,28

Rabun	Site		Covariate		Interaction		r^2
Covariable	F	P	F	p	F	p	
Litter depth	1,71	Ns	2,60	ns	2,37	ns	0,09
Woody debris	0,92	Ns	0,00	ns	1,78	ns	0,08
Pteris sp.	0,21	Ns	2,46	ns	0,32	ns	0,07
Adiantum sp.	**2,68**	*****	0,63	ns	0,23	ns	0,05
Costaceae	**4,00**	******	**6,69**	******	0,66	ns	0,11
Heliconiaceae	1,90	Ns	0,39	ns	0,13	ns	0,05
Seedling	1,54	Ns	0,01	ns	0,27	ns	0,49
Understory density	2,18	Ns	0,39	ns	1,39	ns	0,07
Stream	**4,67**	*****	*	*	*	*	0,04
Distance to stream	0,61	Ns	0,08	ns	0,45	ns	0,05

Table 18 ANCOVA for reptile abundance. F is the variance between groups divided by the variance within groups. The higher the value of F, the bigger the relative difference is between the sites. The number of stars beneath p shows how strong the significance is (ns stands for not significant, * is p<0,05, ** is p<0,01 and *** is p<0,001)

From the ANOVA's it is clear that the sites differ from each other in amphibian abundance (Table 13). From the correlations it is clear that there are strong relations between variables (Table 14). So which of these variables are

causing the-differences between sites for amphibian and reptile abundance? To answer this question ANCOVA's were carried out.

When basal area, understory plant species or understory density are compensated for there is still a difference in amphibian abundance between sites. Understory density and distance to stream have an effect on amphibian abundance even when site differences are compensated for. However, for understory density the site does have an influence on how strong this relation is (Table 17)

For reptiles some understory plant species (*Adiantum* sp. and costaceae), tree species richness and the presence of a stream do not have an effect on differences between sites. Only Costaceae has a relation with amphibian abundance when compensating for site differences (Table 18)

What environmental variables are the best predictors?

A forward regression was done to see which variable predicts amphibian abundance and reptile abundance best. To predict amphibian abundance the presence of water and tree were important (forward regression; F=25,9; p=0,000; Amphibian abundance (# of animals caught in bucket). = 1,65 * Stream + 0,74 * Basal area – 0,74 * Tree species richness + 1,52). This formula predicted 32% of the variation in amphibian abundance.

For reptile abundance *Pteris* sp. and Costaceae were the best predictors (forward regression; F=6,07; p=0,003; Reptile abundance (# of animals caught in bucket). = 0,43 * *Pteris* sp. – 0,88 * Costaceae + 0,40). Only 7% of the variation in reptile abundance was explained by this.

4 Discussion

In this chapter the research questions will be answered by combining the results from the logging effect study and the heterogeneity study. From that the conclusions are drawn and it is seen how these fit into existing literature. The heterogeneity study can only be used for some of the questions since logging was not involved. How do amphibian abundance and species richness change with selective logging? To answer this question several sub questions have to become clear. What are the effects of logging on the environmental conditions? How do amphibians respond to these conditions? Finally, to give an estimation of the impact, it needs to be clear how important these factors are.

How does selective logging change environmental conditions?

From the ANOVA's we can learn how environmental conditions differ among the treatments. The correlations show the effect of logging disturbance on the environmental conditions. And the PCA's show how the overall site conditions are affected by logging. With selective logging I expected an increase in gaps, temperature, and more understory growth caused by the increase in light. Basal area, humidity and soil moisture should have decreased.

Both La Chonta and Inpa show few significant differences between treatments (Tables 1 and 7). This means that both forests are very heterogeneous. The low number of replicates is also cause for the lack of differences among treatments. Many variables do show a clear trend but are not significant, so it is possible that relations with logging exist. Therefore, correlations were done by coding the treatments as a disturbance gradient on an ordinal scale (Table 2 and 8). In La Chonta positive relations with intensity of logging disturbance were found for the amount of small plants and the height of the herbaceous layer. This is contrary to what Felton (2006) found two years after logging. There logging gaps had less understory growth/regeneration then natural gaps. However, the current study measured four years after logging, so that considerable regrowth had occurred in the gaps. Fetcher (1985) found that it took only 2 years for the understory to regenerate. Fredericksen (2002) found a positive relation between disturbance intensity and canopy openness one year after logging. However, we found a negative relation between disturbance intensity and canopy openness. This contrast is caused by tree regeneration during the four years after logging. Apparently, the forest is in the building phase after four years in which there are many small trees competing for light. During this building phase canopy openness is lower than in a mature stand. In Inpa there were positive relations between disturbance intensity and the amount of small plants, the height of the herbaceous layer, the amount of litter (number of layers and depth), the density of the understory and the amount of fine woody debris. These are in line with findings of Urbina-Cardona (2006), who found similar relations in a tropical rainforest in Mexico. A negative relation was found between the number of gaps and disturbance intensity and between inclination and disturbance intensity. Again, this

is because sufficient time has passed for gap closure to take place. It is unlikely that inclination is changed by the treatment, so differences between treatments existed before selective logging was implemented (Vroomans, 2004). Inclination is often associated with amphibian abundance (Scott, 1977; Urbina-Cardona, 2006), but always because it has an effect on the moisture level of the soil. All of these soil moisture variables were measured so inclination will not be included in the rest of the discussion. For both forests the number of gaps increased with disturbance intensity. In Inpa the canopy openness increased as well with disturbance intensity, but in La Chonta the canopy openness declined when more logging was done. The contradictory results can be explained by the recuperation speeds of the forest. In La Chonta growth rates are a lot higher with a longer growing season and with only 30% of the trees shedding leaves in the dry season, while in Inpa all trees shed their leaves during the dry season. Because of this La Chonta recovers more quickly after disturbance. Overall seedlings grow faster in La Chonta then in Inpa (Kennard, 2002; Toledo, 2006). Since the treatments were applied 4 years ago in La Chonta and 5 years ago in Inpa, the forest overstoryhas had time to recuperate (Quispe, 2007). Apparently that was enough time in La Chonta for the plants to grow higher than the understory layer, while in Inpa it was not. The relation between amount of litter and disturbance intensity differs greatly between the forests. In Inpa more logging resulted in more litter, while the opposite seems true for La Chonta. Litter turnover is greatly affected by litter moisture content and canopy openness has a negative relation with this. Thus, the different litter relations with disturbance can be explained by the relation with canopy openness.

Basal area and tree density varied surprisingly little among treatments. Since it is a logging experiment these are the two variables that were expected to be influenced most in the current study because it affects them directly. Previous research in La Chonta and Inpa suggest that these factors do indeed differ between treatments (ref IBIF). Because only small areas were measured per sample point (up to a 15 meter radius), outcomes were heavily influenced by chance as a single big tree in the sample area can change the results.

A lot of these environmental variables are interrelated; small plants and herbaceous height for instance are strongly related in Inpa and both correlate with the treatments. To see how the overall forest is changed a principal component analysis was done (Table 3 and 9; Fig. 4, 5, 8 and 9). In La Chonta the control treatment stood apart from the other treatments. In Inpa the intensive treatment stands apart from the rest. So in La Chonta only a low intensity (normal treatment) is required to change the forest, while in Inpa it takes a high intensity (intensive) to do so. The reason for this is probably the difference in light levels between the forests. Trees in Inpa shed their leaves in the dry season and trees in La Chonta do not causing Inpa to be a lot more open. To go from an open (undisturbed) to a more open forest a bigger disturbance is required. In La Chonta the forest is “opened up” a lot sooner because it had a closed canopy before.

How do amphibians respond to different environmental conditions?

Now that is clear how the environmental variables are affected by logging it is interesting to see how amphibians respond to the environmental variables and hence, to logging. To address this question the heterogeneity study is used as well. This study should provide interesting insights because it describes the environmental heterogeneity on a small scale. Take note that the heterogeneity study was only carried out in La Chonta.

The hypothesis was that amphibian abundance and richness would increase with humidity, temperature and amount of litter. In both La Chonta and Inpa water sources had a strong effect on abundance (Table 4, 10 and 16; Fig 6 and 10), although it did not affect species richness. This is probably because all species depend on water for reproduction. Only tree frogs can reproduce without water and these were hardly captured in this study. The importance of water for abundance also comes back in the heterogeneity study where the dummy variable Stream has the strongest correlation with abundance. It should be noted that all measurements were done in the wet season, which is also the breeding season for many species (Gascon, 1991; Magnusson, 1990; Donnelly, 1994). So it is likely that the breeding migration is an important factor in explaining the importance of water for the amphibians in this study. Temperature and amount of litter were not important for amphibians in La Chonta.

In Inpa the only factors that affect amphibians are litter mass and gap distance. Litter mass had a negative effect on abundance and species richness, and gap distance had a positive effect on abundance. In contrast, Sluys (2007) found out that the humidity of the litter was very important and that it was correlated to the amount of litter. In Inpa, I did not find such a correlation. The positive effect of gap distance indicates that these animals avoid gaps. This could be because of increased predation by reptiles or the lower humidity in and around gaps (Vitt, 1997). In the logging effect study in La Chonta, only understory density decreases abundance and species richness.

In the logging effect study only a 3 out of 26 (La Chonta) and 3 out of 20 (Inpa) variables show a relation with amphibian abundance and species richness, whereas in the heterogeneity study as many as 7 of the 12 variables showed a relation with abundance. *Pteris* sp., woody debris, and distance to stream show a negative relation with abundance. *Adiantum* sp., the number of small plants, basal area and the presence of a stream show a positive relation with abundance. Hypotheses were only made for water, temperature and amount of litter. Water had indeed a positive relation with abundance. However, measurements were done in the wet season during the breeding period, so there is an influence of the breeding migration on relations. The influence is positive on relations with presence of a stream and negative on the relations with distance to stream.

Interestingly, in La Chonta none of the variables that are affected by selective logging show a relation with amphibian abundance or species richness. In contrast, in Inpa logging had a negative effect on litter, and that variable had in turn a negative effect on amphibian abundance and species richness. Logging

increased the number of gaps, and the distance to the nearest gap had in turn a negative influence on the species *Leptodactylus elenae* and *Dematonotus muelleri*.

ANCOVA's were carried out to see if without the effect of the treatments there are independent relations between environmental variables and amphibian abundance and species richness, The ANCOVA's confirm that in La Chonta soil water content and understory density are very important for amphibian abundance and species richness. In Inpa, water sources and litter mass were most important for amphibian abundance and species richness. None of these factors were influenced by logging (Table 5, 6, 11, 12, 17 and 18).

It was expected that abundance and species richness would respond similarly and respond primarily to humidity and temperature. Water was the common environmental variable that is important in both forests for amphibian abundance. It seems that water was more important in Inpa then in La Chonta, because it is able to predict more of the variation. This is probably because Inpa is a dry forest and La Chonta a wet forest and water is thus scarcer in Inpa. The importance of understory density and litter mass for species richness was not expected. For understory density similar relations were found in other studies as well as opposite relations (Pearman, 1997; Cardona, 2006). Relations for litter mass are also found in literature, these are opposite op those found here (Cardona, 2006; Sluys, 2007)

In La Chonta there is next to the relation between water and abundance also a strong influence caused by logging disturbance, with the highest abundance in the normal treatment. In Inpa this is not the case, here water is the only determinant of abundance. There is however another logging effect in Inpa, namely on species richness. In La Chonta no such effects were found.

A lot of the environmental factors found in other studies revolve around water and litter with both having a positive effect on abundance and richness. The biggest factors are the presence of ponds and streams (Dupuis, 1995; Fredericksen, 2004; Marsh, 2001; Ross, 2000; Scott, 1976; Soares, 2007; Scribner, 2001). This is where most animals breed and live year round. Other water variables such as soil moisture (Vonesh, 2001; Kolozsvary, 1999; Seebacher, 1999) and litter moisture (Allmon, 1991) were also important. Negative correlations were found with temperature (Abrunhosa, 2006; Dupuis, 1995; Urbina-Cardona, 2006), which seems strange because amphibians are exothermic. Temperature is always strongly intertwined with relative humidity, which drops with increasing temperatures. Apparently avoidance of desiccation is a lot more important then the need to get warm to get active. Other biotic factors might also be important because of their modifying effect on temperature. Positive correlations between amphibian abundance and understory density are, for example, commonly found (Dupuis, 1995; Marsh, 1997; Pearman, 1997; Urbina-Cardona, 2006; Vonesh, 2001). Pearman (1997) suggested that a dense understory is important because there is more shade, and thus a cooler environment, under it which reduces dessication of the skin for amphibians. The second variable that is often found to be important is litter (Allmon, 1991; Urbina-Cardona, 2006; Sluys,

2007; Vonesh, 2001). This is linked to the availability of food, because more litter houses more insects and spiders (Coleman, 2006; Meehan, 2006; Moretti, 2006). And prey abundance is, in turn, strongly correlated with amphibian abundance (Poulin, 2000).

What environmental factor can be used to predict amphibian abundance and species richness?

The present forest law dictates that the forests should be managed in a sustainable way, with little negative impacts on biodiversity. To accomplish this many rules were formed. The important one for amphibians is the prohibition of logging near streams.

Multiple regressions were done to see what environmental factors can be used to predict abundance and species richness. In La Chonta soil water content was a good predictor for abundance and soil water content together with water sources predicted abundance in Inpa. Species richness can be predicted using only understory density in La Chonta and litter mass with soil water content in Inpa. The amphibians need high soil water content or presence of water to keep their skin moist in order to breath. The fact that amphibians have a preference for litter-poor sites seems strange at first. More litter is usually associated with more food (insects) and higher humidity (Sluys, 2007). It may also be that more humid litter decomposes faster, resulting in less litter. However, less litter also dries up faster resulting in slower decomposition. Neither of these two relations drives litter relations alone. The fact that no relation was found between litter mass and litter water content supports that.

Environmental predictors explain in Inpa a lot more of the variation (98% for abundance and 71% for species richness) than in La Chonta (respectively 67% and 59%). This suggests that the primary need (water) is more important in Inpa than it is in La Chonta as few other variables cause variation in abundance. This is caused by the difference in water between the forests, as La Chonta is a wet forest and Inpa a dry forest.

Reptiles respond to very different environmental variables. Two kinds of understory plant species predict a small fraction of the variation in reptile abundance (Table 16). As no direct relations between reptiles and these plant species are known it is unclear why these plants make good predictors.

Heterogeneity study

The variables that amphibians responded to in the heterogeneity study were similar to those from the logging effect study. This means that those variables already work on a very small scale. So a 5 by 5 meter patch which has more moisture in the soil will already have a different abundance and species richness then the next. It also shows that the forest is very heterogeneous, with the microhabitat changing every couple of meters. This suggests that amphibians show a distinct preference for certain spots and will actively seek them out. It also shows that territorial amphibians do not necessarily use all of their territory but only

use favorable spots. In the heterogeneity study a lot less variation was explained by the predictors. Water is still the most important variable for abundance.

Conclusions

When all this information is put together we can try and answer the main question, namely “How do amphibian abundance and species richness change with selective logging?”

In La Chonta a low disturbance intensity is enough to cause differences in the environment. This change only has an effect on the amphibian abundance. In Inpa a high disturbance intensity is needed to cause differences in the environment. Here, only the amphibian species richness is affected by such a change.

Water is the most important environmental variable for amphibian abundance in both forests, in accordance with the literature. For species richness understory density (in La Chonta), and litter mass (in Inpa) were found to be most important. Both have a negative relation with species richness. None of these variables were affected by the logging, so logging does not have a dramatic effect on amphibian abundance and species richness in either forest. If anything, amphibians in La Chonta benefit from logging, as abundance was highest in the normal treatments. Higher levels of disturbance, as found in the intensive treatment, cause a drop in abundance. Apart from the efttect of these relations there is an effect of selective logging on abundance in La Chonta and species richness in Inpa. It is not clear how this mechanism and more research is required to shed light on this.

Studies from Fredericksen (2002, 2004) in the same area also suggest that there is a higher abundance in logged areas than in unlogged areas. Most studies say that it is very difficult to use general descriptors like amphibian abundance and species richness to assess the effects on amphibian populations (Cushman, 2006; Gascon; 1991; Grover, 2002; Marsh, 2001; Marsh, 1997; Pearman, 1997). In this study, the individual species responded in a similar as total amphibian abundance, suggesting that, in fact, it is possible to use amphibian abundance and richness as indicators.

By far the most important environmental variable for amphibians is water. And as logging near water is prohibited by the present forest law, amphibian populations should not be affected.

5 Limitations and recommendations for further research

The biggest limitation of this study was the limited number of replicates in the logging effect study. Due to this a lot of the small scale heterogeneity could not be filtered out and this caused relations to be insignificant and not representing the treatments well. Therefore, the most important recommendation is that this amphibian study is repeated (or at least for some of the interesting variables) with more replicates. It would be wise to limit the influence of streams as they have big impact on amphibian populations, while no actual logging occurs near them. As only some of the treatments have streams it is best to use only non-stream sites.

There was a lot of pseudo replication in the heterogeneity study. However, the small scale heterogeneity was still highly visible in the data so the effect was minimal. Most of the affecting variables in the heterogeneity study were similar to those from the logging effect study.

The time that the animals were caught was the breeding season. This influenced the study, but it is difficult to do something about this, since amphibians aren't very active during the dry season.

Not enough animals were caught in this single year to do all the analyses at the species level. Instead, all data had to be pooled. Many studies suggest that species-level data are needed to get a good idea of what is happening, so sufficient animals should be caught to be able to do the analyses species-wise.

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