

**Effects of deforestation and climate change on
tropical montane forests
- A case study from the Bolivian Andes -**

Denis Lippok

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Cover photo

A fragmented landscape in the Bolivian Andes (photo by D. Lippok)

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Summary

Tropical montane forests (TMFs) are very diverse ecosystems and providers of important ecosystem services. The high biodiversity is among others generated by high habitat heterogeneity, resulting from steep gradients in elevation and topography. Population growth and human land use resulted in the deforestation of vast areas of tropical forests, mostly by the use of fire. The remaining forest fragments are degraded by selective logging, over-hunting, fires and edge effects from the surrounding deforested habitats, favoring disturbance-adapted species and discriminating mature forest species. Forest regeneration in deforested habitats is slow due to low seed input from adjacent forests, unsuitable habitat conditions and strong competition by invading ferns. Climate change is additionally threatening TMFs, which are particularly vulnerable to changes in temperatures and precipitation. The management of TMFs in fragmented landscapes is urgently required to prevent the further loss of biodiversity and ecosystem service supply. A better understanding of the factors driving vegetation patterns in forest fragments and of the filters for natural forest regeneration in deforested habitats is therefore urgently needed.

The present thesis aims at better understanding the impacts of deforestation and climate change on TMFs. I studied the effects of fragmentation on woody vegetation and soil seed banks, and natural forest regeneration in deforested habitats in a fragmented landscape in the Bolivian Andes. The thesis comprises four studies. In the first study, I analyzed the effects of elevation, topography and forest edge on woody plant diversity in forest fragments. Gradients in elevation and topography generated a high heterogeneity in habitat conditions and a high variation in species composition. Edge effects from the surrounding deforested habitats altered habitat conditions at forest edges and caused a shift in species composition towards a higher dominance of disturbance-adapted species. Small-scale gradients such as topography and forest edge had stronger effects than elevation. In the second study, I tested the effects of the proximity of adjacent forests, as a proxy for seed input, and of elevation on forest regeneration in deforested habitats. Forest regeneration increased strongly with increasing elevation, while effects of distance to forests were comparably weak. The increase with elevation might be explained by decreased habitat filtering, due to milder habitat conditions, and altered species source pools at higher elevations. In the third study, I analyzed the importance of external and internal regeneration sources (ecological memory), and the effects of fern competition on early post-fire regeneration. Pre-fire vegetation (i.e. internal memory) was more important than the distance to adjacent forests (i.e. external memory), because early post-fire regeneration relied mostly

on resprouting. Bracken fern slowed down forest regeneration by a reduction in light availability. In the fourth study, I analyzed soil seed banks in three habitats characterized by different degrees of disturbance, i.e. the forest interior, at forest edges and in deforested habitats, along an elevational gradient. Soil seed banks in the deforested habitats were depauperate, especially in large seeds and distant from adjacent forests, while small-seeded species accumulated at the forest edges. Elevation only affected species composition.

Deforestation threatens TMFs not only by habitat loss, but also in a long-term manner by edge effects in forest fragments and by strong filters to natural forest regeneration in deforested habitats. Climate change will most likely exacerbate these effects. Edge effects from the surrounding deforested habitats shifted the species composition in forest fragments towards a higher dominance of disturbance-adapted species, in both vegetation and soil seed banks. Restoration of intact vegetation structures at edges might prevent strong alterations in habitat conditions and reduce the invasion by ruderal species from the surrounding deforested habitats. Forest species had narrow elevational ranges indicating their sensitivity to climate change. Topography, which was associated with microclimatic conditions at a small spatial scale, should be considered in modeling climate change effects. Forest regeneration in deforested habitats relied mostly on the resprouting of pre-existing plants, while colonisations from adjacent forests were rare. Forest species, in particular large-seeded species, have therefore to be introduced manually. An increase in temperatures due to climate change will most likely increase habitat filtering due to a higher fire frequency in deforested habitats, which will result in the further degradation of woody vegetation. Furthermore, fires favored the promotion of bracken fern, which reduced light availability and forest regeneration. The establishment of pioneer species, which outshade bracken fern and generate milder climatic conditions with their canopies, might enhance the recruitment of other forest species. *Myrsine coriacea* is suggested as a suitable species for restoration purposes, due to its ability to survive fire-events, its fast growth in deforested habitats and its fleshy fruits that might attract seed dispersers such as birds and bats.

Zusammenfassung

Tropische Bergwälder sind diverse Ökosysteme und erfüllen wichtige Ökosystemdienstleistungen. Die hohe Artenvielfalt resultiert aus hoher Habitatsheterogenität, verursacht durch steile Höhengradienten und sehr variable topographische Gegebenheiten. Populationswachstum und intensive Landnutzung haben zur Abholzung und Brandrodung großer Flächen tropischer Wälder geführt. Die verbliebenen Waldfragmente werden oft durch Holzgewinnung, Überjagung und Randeffekte degradiert, was die Ausbreitung störungsangepasster Arten fördert und zum Verlust Arten reifer Wälder führt. Die Waldregeneration in den Rodungsflächen ist oft gehemmt, unter anderem durch einen geringen Diasporeneintrag aus benachbarten Wäldern, ungünstige Habitatbedingungen und eine starke Konkurrenz von einwandernden Farnen. Tropische Bergwälder sind sehr empfindlich gegenüber Temperatur- und Niederschlagsänderungen und daher besonders durch den Klimawandel bedroht. Ein Management der fragmentierten Bergwälder ist dringend notwendig um die Artenvielfalt und Ökosystemdienstleistungen dieser Wälder zu erhalten. Ein besseres Verständnis der Faktoren, die Vegetation in Waldfragmenten und die Waldregeneration in den Rodungsflächen hemmen, ist hierfür Voraussetzung.

Die vorliegende Arbeit untersucht die Auswirkungen von Entwaldung und Klimawandel auf tropische Bergwälder. Es wurden Fragmentierungs-Effekte und die natürliche Waldregeneration in Rodungsflächen in den bolivianischen Anden untersucht. Die Arbeit umfasst vier Studien. In der ersten Studie untersuchte ich die Effekte von Meereshöhe, Topographie und Waldrand auf den Artenreichtum von Gehölzen in Waldfragmenten. Veränderungen in Meereshöhe und Topographie bewirkten eine hohe Habitatsheterogenität und eine hohe Variation in der Artzusammensetzung. Randeffekte veränderten die Habitatbedingungen an Waldrändern und förderten die Dominanz störungsangepasster Arten. Topographie und Waldrand als kleinräumige Faktoren hatten größere Effekte als Meereshöhe. In der zweiten Studie testete ich die Effekte der Entfernung zum Waldrand, als Maß für den Diasporeneintrag, und der Meereshöhe auf die Waldregeneration in den Rodungsflächen. Die Waldregeneration nahm stark mit zunehmender Meereshöhe zu, wobei die Effekte der Entfernung zum Waldrand vergleichsweise gering waren. Die Zunahme der Regeneration lässt sich wahrscheinlich durch weniger raue Habitatbedingungen und veränderte Artenbestände in höheren Lagen erklären. In der dritten Studie untersuchte ich die Bedeutung interner und externer Regenerations-Quellen („ökologisches Gedächtnis“) sowie die Effekte von Farn-Konkurrenz auf die frühe Waldregeneration nach Brand. Die bereits in den Flächen vorhandene Vegetation („inneres Gedächtnis“) war für die Regene-

ration wichtiger als der Sameneintrag aus benachbarten Wäldern („externes Gedächtnis“), da die frühe Regeneration zum Großteil auf Wiederaustrieb beruhte. Adlerfarn hemmte die Waldregeneration durch Verminderung der Lichtverfügbarkeit. In der vierten Studie untersuchte ich Bodensamenbanken in drei Habitattypen unterschiedlicher Störungsintensität, im Waldesinneren, am Waldrand und in den gerodeten Flächen, entlang eines Höhengradienten. Die Bodensamenbanken in den Rodungsflächen waren verarmt, besonders an großen Samen und entfernt vom Waldrand, wogegen sich kleinsamige Arten an Waldrändern ansammelten. Die Meereshöhe beeinflusste nur die Artzusammensetzung.

Waldrodung bedroht tropische Bergwälder nicht nur durch Habitatsverlust, sondern auch langfristig durch Randeffekte in Waldfragmenten und gehemmte Waldregeneration in den Rodungsflächen. Der Klimawandel wird diese Effekte höchst wahrscheinlich weiter verschärfen. Randeffekte führten zur Ausbreitung störungsangepasster Arten in der Vegetation und den Bodensamenbanken. Die Wiederherstellung intakter Vegetationsstrukturen an Waldrändern könnte Veränderungen in Habitatsbedingungen vermindern und die Invasion ruderaler Arten aus den umliegenden Rodungsflächen abschwächen. Waldarten hatten enge vertikale Verbreitungen, was deren besondere Anfälligkeit für den Klimawandel anzeigt. Topographische Gegebenheiten, die mit kleinräumigen mikroklimatischen Veränderungen verknüpft waren, sollten in Modellierungen des Klimawandels berücksichtigt werden. Die Waldregeneration beruhte größtenteils auf dem Wiederaustrieb bereits vorhandener Pflanzen da die Invasion aus benachbarten Wäldern sehr selten war. Waldarten, insbesondere großsamige Arten, müssen daher manuell eingeführt werden. Ein Temperaturanstieg durch den Klimawandel wird sehr wahrscheinlich die Habitatsbedingungen durch eine erhöhte Feuerfrequenz weiter verschärfen, was zur weiteren Degradierung der Vegetation führen wird. Feuer förderten weiterhin die Etablierung von Adlerfarn, der die Lichtverfügbarkeit und Waldregeneration verringerte. Die Etablierung von Pionierarten, die Farne ausschatten und mildere klimatische Bedingungen mit ihren Kronen erzeugen, könnte die Regeneration weiterer Waldarten verbessern. *Myrsine coriacea* wird als geeignete Arte für Wiederaufforstung empfohlen, da sie Feuer überlebt, ein schnelles Wachstum in den Rodungsflächen aufweist und mit ihren fleischigen Früchten Ausbreiter wie Vögel und Fledermäuse anlocken kann.

Chapter 1 – General introduction

Threats to tropical forests

Tropical montane forests (TMFs) are very diverse ecosystems, with high species richness and high levels of endemism (Richter et al., 2009; Garavito et al., 2012). They provide important ecosystem services, such as carbon sequestration and regulation of water balance and regional climate (Costanza et al., 1997; Balvanera, 2012). Population growth and human land use resulted in the deforestation of vast areas of tropical forests (Achard et al., 2002; Wright, 2010; FAO, 2011; Aide et al., 2013), in which fire is an often-used agent for the establishment of cultivations and pastures. Associated with the massive loss of forest habitats is the loss of biodiversity and ecosystem service supply (Laurance, 1999; Foley et al., 2007; Parrotta et al., 2012). The restoration of forests is, besides the conservation of remnant forests, a measure to recuperate biodiversity and ecosystem service supply in fragmented landscapes (Brown & Lugo, 1990; Guariguata & Ostertag, 2001; Chazdon, 2008; Chazdon et al., 2009), but strong filters in seed dispersal and habitat conditions in deforested habitats often slow down or even inhibit forest regeneration (Sarmiento, 1997; Holl, 1999; Florentine & Westbrooke, 2004; Hooper et al., 2005). Climate change is an additional threat to TMFs and might exacerbate the effects of deforestation by various synergies (Still et al., 1999; Foster, 2001; Krupnick, 2013). The conservation of remaining forest fragments, the restoration of forests in deforested habitats and the mitigation of climate change effects are urgently required to prevent further loss of biodiversity and ecosystem service supply in fragmented landscapes. While these topics are mostly studied in lowland forests, the tropical montane forests of the Andes are still less studied.

Fragmentation

Many tropical forests are nowadays highly fragmented, with isolated and disconnected forest fragments embedded in a matrix of deforested habitats (Melo et al., 2013a). The remaining forest fragments are degraded by selective logging, overhunting and frequent fires (Peres, 2001; Cochrane & Laurance, 2002; Laurance et al., 2002; Tabarelli et al., 2004). Especially edge effects from the surrounding deforested habitats cause a cascade of alterations in abiotic and biotic conditions (Murcia, 1995; Laurance et al., 2002; Harper et al., 2005). If levels of disturbances are high, species composition is shifted towards a higher dominance of disturbance-adapted species while mature forest species decline in domi-

nance or get extirpated, a process called retrogressive succession (Laurance et al., 2006; Santos et al., 2008; Tabarelli et al., 2008; Santo-Silva et al., 2013). These alterations in species composition affect forest edges and small fragments and lead to the “biotic homogenization” in fragmented landscapes (Lôbo et al., 2011; Tabarelli et al., 2012). The management of fragmented forests is therefore urgently required to prevent the further loss of biodiversity and ecosystem service supply (Gardner et al., 2010; Tabarelli, 2010), considering in particular the importance of forest fragments as the only remaining seed sources for forest recovery in fragmented landscapes (Turner & Corlett, 1996). The knowledge of factors promoting and reducing plant diversity is hereby an important requirement. Montane forests provide a good opportunity to study driving factors for plant diversity, since they are characterized by steep gradient in elevation and topography that are associated with high variation in habitat conditions and high species turnover at different spatial scales (Beck et al., 2008; Gradstein et al., 2008). The underlying mechanisms of the drivers of plant diversity in TMFs are not clearly understood yet (Culmsee & Leuschner, 2013) and especially studies comparing the effects of various drivers are rare.

Filters to forest regeneration

Natural forest regeneration after deforestation is slow or even inhibited by strong filters; e.g. seed sources are missing, habitat conditions are unsuitable and competition by invading grasses and ferns is strong (Holl, 1999; Florentine & Westbrooke, 2004; Hooper et al., 2005). Fires of anthropogenic origin are frequent in deforested habitats, killing most regenerating forest species (Hooper et al., 2004) and reducing the viability of soil seed banks (Garwood, 1989; Miller, 1999; Wijdeven & Kuzee, 2000). Forest regeneration therefore relies on seed input from adjacent forest remnants (Holl, 1999; Chazdon, 2003; Muñiz-Castro et al., 2006), but seed rain is often low and declines with increasing distance from forests (Zimmerman et al., 2000; Cubiña & Aide, 2001). The decrease is especially strong for animal-dispersed seeds because many seed dispersers tend to avoid deforested habitats (Wunderle Jr, 1997; Holl, 1999). Furthermore, habitat conditions are unsuitable for the establishment of forest species, because of hot and dry microclimates and degraded soils (Holl, 1999; Alvarez-Aquino et al., 2004; Hooper, 2008). Grasses and ferns invade the frequently burned sites and compete with regenerating forest species (D’Antonio & Vitousek, 1992; Hartig & Beck, 2003; Schneider, 2004; Hooper et al., 2005; Slocum et al.,

2006). Especially bracken fern (*Pteridium arachnoideum* (Kaulf.) Maxon) is a highly successful invader in many tropical areas (Schneider, 2004; Peters et al., 2010). Caused by the strong filters in seed dispersal and habitat conditions, mature forest species are missing in the regenerating vegetation while disturbance-adapted species are promoted (Finegan, 1996; Howorth & Pendry, 2006; Chazdon et al., 2007; Marín-Spiotta et al., 2007). Due to socioeconomic changes, vast areas of previously used lands are abandoned and now available for forest restoration (Wright & Muller-Landau, 2006; Grau & Aide, 2007). Active restoration in deforested habitats is often suggested to establish forest-like species assemblages (Chazdon, 2003; Lamb et al., 2005) in which a better knowledge of the driving factors for natural forest regeneration will help to improve active restoration (Holl & Aide, 2011). While natural forest regeneration is well studied in tropical lowlands, montane forest regeneration received comparably less attention (Muñiz-Castro et al., 2006). Elevation as a driving factor of forest regeneration was neglected by most studies, but some studies analyzing the effects of elevation on forest regeneration found changes in species composition of regenerating vegetation (Aide et al., 1996; Pascarella et al., 2000; Chinaa, 2002; Marcano-Vega et al., 2002).

Climate change

Mean temperatures are predicted to increase and precipitation patterns to change in the future (Vuille et al., 2003; Bradley et al., 2006; Seiler et al., 2013). Species will have to adapt, or to move polewards or upslope to adjust to the increasing temperatures (Parmesan & Yohe, 2003). Upslope migration might be more effective than latitudinal shifts due to the shorter geographic distances (Colwell et al., 2008). Species of TMFs are adapted to narrow temperature ranges (Feeley & Silman, 2010) and their migratory movements might be restricted by topographic (Forero-Medina et al., 2011) and anthropogenic barriers such as deforested habitats (Travis, 2003; Opdam & Wascher, 2004). TMFs in fragmented landscapes are therefore particularly vulnerable to climate change (Ponce-Reyes et al., 2013) and various TMF species are confronted with extinction in the future (Colwell et al., 2008; Rojas-Soto et al., 2012). Elevational gradients offer a good opportunity to study the effects of changing climatic conditions (Körner, 2007; Jump et al., 2009) and they can therefore be used to predict the effects of increasing temperatures caused by climate change. Predictions of the effects of climate change should be considered in conservation and restoration

measures to ensure the sustainability of management (Brodie et al., 2012; Stein et al., 2013).

Aims and objectives

The present thesis aims at better understanding the effects associated with deforestation and climate change on TMFs. In particular, driving factors for plant diversity in forest fragments and filters to natural forest regeneration in deforested habitats were addressed. The thesis comprises four studies, three of them investigating woody vegetation and one study accessing soil seed banks. Since all studies incorporated an elevational gradient, their results reveal predictions of the effects of climate change.

The first study (**Chapter 2**) focused on drivers for diversity patterns in TMF fragments. I analyzed the effects of elevation, topography and forest edge on habitat conditions and woody plant diversity. Habitat conditions were characterized by microclimate, soil properties and forest structure. Plant diversity was described by species richness, evenness and composition. I hypothesized that gradients in elevation and topography are associated with a high variation in habitat conditions that cause a high variation in species composition. Furthermore, I hypothesized that edge effects generate habitat conditions unsuitable for mature forest species, shifting the species composition towards a higher dominance of disturbance-adapted species at forest edges.

The subsequent two studies focused on natural forest regeneration in deforested habitats. In one study (**Chapter 3**), I investigated habitat conditions and forest regeneration in deforested habitats at two different distances from the adjacent forests and along an elevational gradient. Habitat conditions were characterized by microclimate, soil properties and light availability. Regenerating vegetation was described by basal area, density and species richness of woody plants. I compared habitat conditions in deforested habitats with forest conditions and analyzed the effects of distance to the adjacent forest (as a proxy for seed input) and elevation on forest regeneration. I hypothesized slow forest regeneration and a species composition distinct from forest vegetation, due to strong dispersal and habitat filters in deforested habitats. Furthermore, I hypothesized better regeneration near forests, due to enhanced seed input from adjacent forests, and lower regeneration at higher elevations, due to increased environmental stress.

In the other study (**Chapter 4**), I assessed the first year of post-fire regeneration in deforested habitats at two different distances from adjacent forests. I recorded woody plant density and species richness, and fern frond density and canopy closure 3 and 12 month after burning. I analyzed the effects of regeneration source, i.e., proximity to the adjacent forest (external memory) and pre-fire vegetation (internal memory), and of competition from bracken fern on forest regeneration. I hypothesized stronger effects of internal than external memory, due to resprouting of pre-fire vegetation and low dispersal capacities. Furthermore I hypothesized bracken fern competition inhibiting forest regeneration in deforested habitats.

The fourth study (**Chapter 5**) focused on soil seed banks (SSBs), which are important seed sources for forest regeneration after disturbance. I investigated SSBs in three different habitat types associated with different degrees of disturbance, i.e. in forest interior, at forest edges and in deforested habitats, along an elevational gradient. Seed density, species richness and composition were assessed at morphospecies-level with a sieving method. I analyzed the effects of habitat type (i.e. disturbance) and elevation on different seed size classes, i.e. small, medium and large-sized seeds. I hypothesized that habitat type alters SSBs, with deforested habitats harboring the lowest density and richness. Furthermore, I hypothesized changes in SSBs, in particular in species composition, with differences in elevation, due to changes in the species composition of the vegetation.

The results of this thesis will contribute to a better understanding of the effects of deforestation on TMF biodiversity, in particular in face of climate change. Furthermore, the results have various implications for the management of TMFs in fragmented landscapes.

The study area - A fragmented landscape in the Bolivian Andes

The tropical Andes are one of the biodiversity hotspots, which are characterized by high levels of species richness and endemism (Myers et al., 2000; Brummitt & Lughadha, 2003; Mittermeier et al., 2011). The Yungas, a phyto-geographic region of the Andes (Garavito et al., 2012), harbor about 7000 known and about 10'000 estimated plant species (Kessler & Beck, 2001). They are situated on the eastern side of the Central Andes in Peru and Bolivia extending from 6° to 13° S and cover an area of approximately 50'500 km² (Ibisch & Mérida, 2004). The fieldwork for this thesis was conducted in the Bolivian Yungas in the

surroundings of the village of Chulumani (1750 asl), 120 km east of La Paz, Bolivia. Annual precipitation in the area is about 1459 mm and annual mean temperature is 20.8 °C (Molina-Carpio, 2005). Precipitation peaks in January and February with more than 200 mm per month while from April to August mean monthly precipitation is below 100 mm. Forests in the area are classified as “Yungas montane seasonal evergreen forest” (Mueller et al., 2002; Navarro, 2011). Due to previous and present anthropogenic land use pressure, the forests in the area were subject to deforestation at large spatial scales with only a few forest fragments remaining (Killeen et al., 2005; Fig. 1). Deforested sites are used for plantations, mainly of coca (*Erythroxylum coca* Lam.), as pastures, or remain without any land use. The areas without land use are regularly burned by fires that originate from slash-and-burn practice or that are set intentionally (personal observations). As a result of the frequent burnings, sites are massively invaded by bracken fern (*Pteridium arachnoideum* (Kaulf.) Maxon).

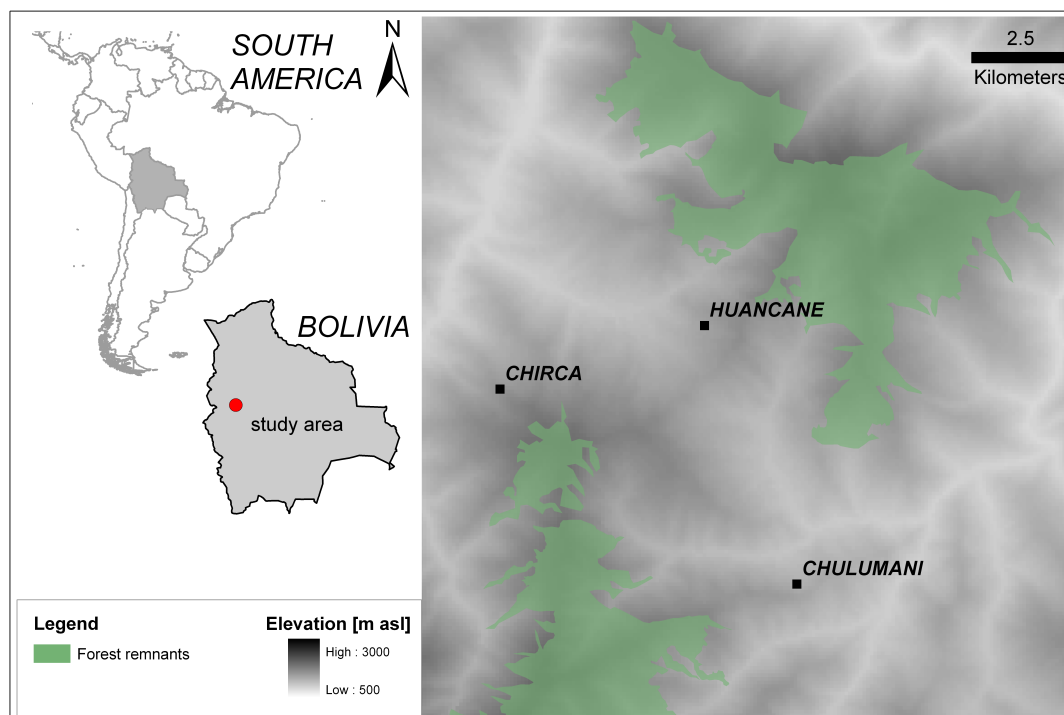


Fig. 1. Location of the study area in Bolivia. Shown are the two largest forest fragments (green area).

Chapter 2 - Topography and edge effects are more important than elevation as drivers of vegetation patterns in a neotropical montane forest

Denis Lippok, Stephan G. Beck, Daniel Renison, Isabell Hensen, Amira E. Apaza & Matthias Schleuning

Journal of Vegetation Science (2013), 10.1111/jvs.12132

Abstract

Aims: The high plant species diversity of tropical mountain forests is coupled with high habitat heterogeneity along gradients in elevation and topography. We quantified the effects of elevation, topography and forest edge on habitat conditions and woody plant diversity of tropical montane forest fragments.

Location: Tropical montane forest fragments, “Yungas”, Bolivia.

Methods: We measured microclimate and sampled soil properties and woody vegetation at forest edges and in the forest interior on ridges and in gorges along an elevational gradient of 600 m. We analyzed effects of elevation, topography and forest edge on habitat conditions (i.e. microclimate, soil properties and forest structure), species richness, evenness and composition with linear mixed effects models and detrended correspondence analysis (DCA).

Results: Changes in habitat conditions were weaker along the elevational gradient than between forest interior and forest edge and between different topographies. Species richness was not affected by any gradient, while species evenness was reduced at forest edges. All three gradients affected species composition, while effects of topography and forest edge were stronger than that of elevation.

Conclusions: In general, effects of the 600 m elevational gradient were weak compared to effects of forest edge and topography. Edge effects shifted species composition towards pioneer species, while topographical heterogeneity is particularly important for generating high diversity in montane forests. These results underscore that edge effects have severe consequences in montane forest remnants and that small-scale variation between topographical microhabitats should be considered in studies that predict monotonous upslope migrations of plant species in tropical montane forests due to global warming.

Keywords: Andes; Bolivia; Edge effects; Elevation; Soils; Microclimate; Forest structure; Species richness; Species composition; Topography; Tropical montane forests

Chapter 3 - Forest recovery of areas deforested by fire increases with elevation in the tropical Andes

Denis Lippok, Stephan G. Beck, Daniel Renison, Silvia C. Gallegos, Francisco V. Saavedra, Isabell Hensen & Matthias Schleuning

Forest Ecology and Management (2013) **15**: 69-76

Abstract

In the tropical Andes, many montane forests have been destroyed, often through human-induced fires. To facilitate the recovery of these forests, it is important to understand the processes that drive secondary succession at deforested sites, yet studies are rare. Two important filters potentially causing a delay in the recovery of tropical forests are decreasing seed rain with distance to forest edge (seed dispersal limitation) and harsher environmental conditions at deforested sites. Moreover, successional pathways along elevation gradients can differ, yet the factors driving elevation differences are poorly understood. In the Bolivian Andes, we compared soil properties, microclimate and light availability at deforested sites with conditions in the adjacent forests and sampled woody secondary vegetation near (at 20 m distance) and away (at 80 m) from the forest edge at eight sites that had been deforested by fires ranging from 1950 to 2500 m asl. We tested the effects of distance to forest edge and elevation on environmental conditions and on basal area, density, species richness and species composition of forest and non-forest species. Environmental conditions differed between forest interiors and deforested areas in most of the measured parameters. Woody secondary vegetation comprised more non-forest (80%) than forest species (20%), indicating that montane forest recovery was strongly hampered. Unexpectedly, basal area and species richness of both forest and non-forest species were higher away than near the forest edge. Density increased with increasing elevation in both forest and non-forest species, while species richness increased with increasing elevation only in forest species. Species composition did not change with distance to forest edge, but changed significantly with elevation. Our findings reject the hypothesis of a strong effect of seed dispersal limitation on forest recovery, but provide evidence that harsh environmental conditions, i.e., hot and dry microclimates and frequent fires, inhibit forest recovery at deforested sites. With increasing elevation, forest recovery increased, probably due to milder environmental conditions at high elevations and a different species source pool. We conclude that abiotic and biotic changes with elevation are crucial for understanding capabilities of forest recovery in mountain ecosystems and highlight that forest recovery may be further reduced in the future if maximum temperatures are going to increase in the tropical Andes. From a management perspective, we propose *Myrsine coriacea*, the most abundant forest species at deforested sites, to be a suitable species for montane forest restoration, due to its ability for long-distance dispersal and resprouting after fire.

Keywords: Bolivia; Elevation; *Myrsine coriacea*; Secondary succession; Tropical montane forests

Chapter 4 – Ecological memory drives early post-fire regeneration in regularly burned sites in the tropical Andes

Denis Lippok, Daniel Renison, Isabell Hensen, Stephan G. Beck & Matthias Schleuning

Manuscript

Abstract

Aims: Extensive areas of Andean tropical forests have been deforested by recurrent fires, which promote the invasion by ferns into burned areas. A better knowledge of the factors driving forest regeneration in these deforested habitats is needed for active restoration. We tested effects of regeneration source availability (i.e., internal and external ecological memory) and fern competition on early post-fire regeneration of woody plants in regularly burned, deforested habitats in the tropical Andes.

Location: Five frequently burned sites in a fragmented landscape in tropical montane forests in the Bolivian Andes

Methods: We recorded woody plant density and species richness in post-fire vegetation 3 and 12 months after prescribed burning. We analyzed the effects of regeneration source availability (i.e., distance to adjacent forest and pre-fire vegetation properties) and fern competition (i.e., density and canopy closure of bracken fern) on density and richness of post-fire vegetation with linear mixed-effects models.

Results: Pre-fire density and richness were the strongest predictors in the regeneration resource models. High pre-fire density and richness were associated with high post-fire density and richness, due to high rates of resprouting. Distance to adjacent forest had no effects. Fern canopy closure was the best predictor in the fern competition models and high fern canopy cover reduced density and richness in post-fire vegetation. Fern frond density had only weak effects. The effects of pre-fire vegetation and fern canopy closure increased over time.

Conclusions: We conclude that the internal ecological memory (i.e. resprouting of existing pre-fire vegetation) was the major regeneration source for early post-fire regeneration and that the negative effect of fern competition on regeneration was mostly mediated by light competition. We confirm previous suggestions that *Myrsine coriacea* is a suitable species for restoration due to its resprouting ability and its potential facilitative effects on other regenerating forest species.

Keywords: Bolivia; elevation; external and internal ecological memory; fire; passive restoration; resprouting; tropical forest; vegetation

Chapter 5 – Effects of disturbance and altitude on soil seed banks of tropical montane forests

Denis Lippok, Florian Walter, Isabell Hensen, Stephan G. Beck and Matthias Schleuning

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Abstract

Vast areas of tropical forests have been deforested by human activities, resulting in landscapes comprising forest fragments in matrices of deforested habitats. Soil seed banks (SSB) are essential sources for the regeneration of tropical forests after disturbance. In a fragmented montane landscape in the Bolivian Andes, we investigated SSB in three different habitat types that were associated with different degrees of disturbance, i.e. in forest interior, at forest edges and in deforested habitats. Sampling of habitats was replicated at six sites ranging in altitude from 1950 to 2450 m asl. We extracted seeds from dried soil samples by sieving, classified seeds into morphospecies and size classes, and characterized SSB in terms of density, species richness and composition. We tested effects of disturbance (i.e. habitat type) and altitude on SSB characteristics. Overall, small seeds (<1 mm) dominated SSB (81% of sampled seeds). Seed density and species richness were lowest in deforested habitats, especially in large seeds and distant from adjacent forests (≥ 20 m), while small-seeded species were most numerous near forest margins. Species turnover between habitats was high. Altitude altered the composition of SSB, but had no effects on seed density and species richness. We conclude that the potential of SSB for natural regeneration of deforested habitats is low and decreases with increasing distance from forest remnants and that forest edges may be eventually invaded by small-seeded species from deforested habitats.

Keywords: Andes; Bolivia; deforestation; edge effects; natural regeneration

Chapter 6 - Synthesis

General discussion

Deforestation had manifold long-term effects besides the direct effects due to habitat loss on TMFs. Forest fragmentation and associated edge effects resulted in the retrogressive succession of vegetation at forest edges (Chapter 2 & 5), while strong filters inhibited forest regeneration in deforested habitats (Chapter 3–5). Climate change will most likely exacerbate these effects, threatening the persistence of TMFs in the future.

Effects of fragmentation

Disturbance-adapted species dominated vegetation at forest edges (Chapter 2), confirming the retrogressive succession in forest remnants reported by previous studies (Melo et al., 2007; Santos et al., 2008; Prieto et al., 2013; Santo-Silva et al., 2013). Habitat conditions at forest edges were characterized by warm and dry microclimates and low canopy heights (Chapter 2) in accordance to other studies (Kapos, 1989; Saunders et al., 1991; Murcia, 1995; Jose et al., 1996; Sizer & Tanner, 1999). These conditions favored disturbance-adapted species, i.e., small-seeded and light-demanding pioneer species (Melo et al., 2007; Santos et al., 2008; Tabarelli et al., 2012; Santo-Silva et al., 2013). Likewise to the shifts in woody vegetation, changes in soil seed banks at forest edges were observed (Chapter 5). The accumulation of small-seeded species reflected altered seed input from the vegetation at forest edges (Melo et al., 2006) and indicated likely an invasion of ruderal species from the surrounding deforested habitats (Lin & Cao, 2009; López-Toledo & Martínez-Ramos, 2011). While edge effects and retrogressive succession did not affect woody plant species richness at plot level (Chapter 2), they reduce the richness in landscapes by favoring a small set of disturbance-adapted species and cause the loss of rare mature forest species (Tabarelli et al., 2012; Arroyo-Rodríguez et al., 2013). Edge effects will most likely be accelerated by climate change, since temperatures, the main driver for alterations in habitat conditions, will increase in the future. Forest fragments, already susceptible for droughts and fires (Laurance & Williamson, 2001), will be even more susceptible to fires from the surrounding deforested habitats due to desiccation during prolonged dry periods (Malhi et al., 2008; Nepstad et al., 2008; Brodie et al., 2012). Fragmentation and the associated alterations in structure and species composition by edge effects diminish the potential of ecosystem service supply by the remaining forests (Foley et al., 2007; Barlow & Peres,

2008). As matrix quality influences environmental conditions in forest fragments (Prevedello & Vieira, 2009; Driscoll et al., 2013), reforestation near forest edges might attenuate edge effects (Didham & Lawton, 1999; Mesquita et al., 1999) and reduce the area of edge-affected forest habitats. The maintenance of an intact forest structure, in particular a closed canopy, will furthermore help to prevent the invasion (Cadenasso & Pickett, 2001) and establishment of small-seeded disturbance-adapted species from surrounding deforested habitats (Lin & Cao, 2009).

Species turnover along the elevational gradient, which corresponded to a difference in air temperature of 3 °C, was high (Chapter 2 & 5), confirming the narrow temperature ranges of TMF species and thus their vulnerability to climate change (Feeley & Silman, 2010). Topographical heterogeneity contributed at a small spatial scale to the high variation in habitat conditions, as previously suggested (Ledo et al., 2012; Metz, 2012), and in particular gorges were characterized by a distinct species composition (Chapter 2). Topographical heterogeneity should therefore be considered in conservation planning to preserve the high diversity in forest fragments (Homeier, 2008) and in predictions of the effects of climate change (Ashcroft, 2010; Suggitt et al., 2011; Gillingham et al., 2012). On the one hand, plant species associated with the high humidity in gorge microhabitats might be particularly vulnerable to climate change (Liancourt et al., 2012) due to restricted movements by topographical barriers such as drier ridges (Forero-Medina et al., 2011). On the other hand, horizontal migration to topographical refugia, such as more humid gorges, might be an alternative for some species to vertical migratory movements (Hopkins et al., 2007; Corlett & Westcott, 2013). The reforestation of corridors connecting forest fragments will enhance migratory movements and thus the possibility for forest species to adjust to the changing temperatures.

Filters to forest regeneration

Forest regeneration in deforested habitats was slow and regenerating vegetation was dominated by disturbance-adapted species with only few mature forest species (Chapter 5), as reported by other studies (Finegan, 1996; Chazdon et al., 2007). Low seed input from adjacent forests, frequent fires, competition from bracken fern and hot and dry microclimates were identified as the major filters in deforested habitats (Chapter 3 - 5). My study on soil seed banks revealed short dispersal distances from remnant forests into deforested habitats

and significant changes in density, richness and composition below 20 m distance (Chapter 5), in line with results from other studies (Aide & Cavelier, 1994; Cubiña & Aide, 2001). Especially large-seeded species, which are characteristic for mature forest species (Foster & Janson, 1985), were missing in the soil seed banks in deforested habitats (Chapter 5). The few forest species occurring in the deforested habitats at distances above 20 m originated most likely from occasionally long distance dispersal events (Lenz et al., 2010), for what *Myrsine coriacea* was a prominent example (Cubiña & Aide, 2001; Muñiz-Castro et al., 2006). An alternative pathway to the recruitment from seeds was the reprofiting of established plants (Chapter 4), which is also a common pathway in the forest recuperation from hurricanes (Yih et al., 1991; Bellingham et al., 1994; Zimmerman et al., 1994) or in periodical burned, fire-prone ecosystems (Kennard et al., 2002; Sampaio et al., 2007; Torres et al., 2013). If plants with the ability to resprout after fire were present in the pre-fire vegetation in deforested habitats, resilience of woody vegetation to fire was high (Chapter 4). However, the contribution of resprouting to the recovery of forest-like species assemblages was low since fire sensitive species got lost and invasions from forest species pools were very rare. Forest species will have to be introduced manually to overcome the dispersal limitation in the regenerating vegetation (Cole et al., 2010).

Additionally, the establishment of forest species in deforested habitats was confronted with strong environmental filters (Chapter 3), which might be even more important for regeneration than seed availability (Holl, 1998; Reid & Holl, 2013). Frequent fires reduce large parts of the soil seed banks (Ewel et al., 1981; Uhl et al., 1981; Miller, 1999) and remove aboveground biomass of regenerating vegetation. Bracken fern grew very fast after fire and established a closed fern canopy that reduced woody plant regeneration (Chapter 4), in line with reports from other tropical regions (Douterlungne et al., 2010; Roos et al., 2010). Its highly flammable litters promote furthermore higher fire severity (Adie et al., 2011). To restore forests in the deforested habitats, the first crucial step is therefore to control the frequent fires and the invasion of bracken fern into deforested habitats (Aide et al., 2000, 2011; Dezzio et al., 2008). Roos et al. (2011) suggest the consecutive frond cutting or the use of herbicides, while Douterlungne & Thomas (2013) successfully applied outshading of bracken fern by a fast-growing pioneer species. *Myrsine coriacea*, a common species in deforested habitats and in the forest fragments (Chapter 2 & 3), might be a suitable species for restoration purposes due to its fast growth and the ability to resprout after fire events (Chapter 4). It might be suitable for outshading bracken fern

and as recruitment focus, attracting seed dispersers such as bird and bats by its fleshy fruits and generating mild microclimatic conditions below its canopy (Guevara et al., 1992; Slocum, 2001; Martínez-Garza & Howe, 2003). If a closed canopy is established by pioneer species, additional direct seeding of shade tolerant, mature forest species is a cost efficient approach to enrich species composition (Guevara et al., 1992; Cole et al., 2011).

The decrease in temperatures with increasing elevation attenuated the strong environmental filtering and increased forest regeneration (Chapter 3). An increase in temperatures caused by climate change will result in hotter and drier microclimatic conditions and enhanced fire frequency (Nepstad et al., 2008; Brodie et al., 2012), thus decreasing forest regeneration. If the time between consecutive fires is short, the resilience of woody vegetation in deforested habitats will decrease due to a reduction in the resprouting source availability (Hoffmann, 1999; Medeiros & Miranda, 2008). In the study area, the advanced degradation was already apparent at lower elevations where woody plant occurrence in deforested habitats was rare and early post-fire regeneration very slow (Chapter 3 & 4). If degradation proceeds, soils erode and grasses establish together with species originating from savanna vegetation that are well adapted to frequent fires (Scott, 1977; Beck, 1993). If forest succession is arrested in such stages, biodiversity and ecosystem service supply will be lost permanently.

Outlook

As shown, deforestation and climate change have manifold negative effects on biodiversity and ecosystem service supply of TMF. Moreover, there are strong synergies among these threats that exacerbate the negative effects. Active measures are urgently required to mitigate the degradation and loss of TMFs in many landscapes. Further studies should consider other early plant life stages such as seedlings and saplings, as these reveals the possibility to predict future changes in vegetation without the need of long-term observations. Other aspects of biodiversity such as functional diversity should also be considered since this approach reveal more detailed insights into the modes of action of disturbance effects (Diaz & Cabido, 2001; Lavorel et al., 2011; Mason & de Bello, 2013; Mouillot et al., 2013). Field surveys comprising different spatial scales combined with remote sensing methods will enable predictions on multiple spatial scales (Blundo et al., 2011; López-Martínez et al., 2013). Results gained by such complex approaches are expected to reveal

more generalized insights. Furthermore, the linkage between biodiversity and ecosystem services (Cardinale et al., 2013) and their monetary value should receive more attention, since this knowledge will assist conservation efforts by justifying the benefits of intact forest ecosystems (Duffy, 2009; Melo et al., 2013b). While there are various studies on the manifold effects of anthropogenic disturbance on biodiversity, the knowledge of measures to mitigate these effects is still rare and should have high priority regarding the fast rates of habitat loss and degradation (Ghazoul, 2013; Lindenmayer et al., 2013). There is still a broad gap between suggestions resulting from scientific studies and their implementation, which should be filled also by conservation scientist themselves (Sayre et al., 2013).

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Appendix A

Curriculum vitae

Contact information

Name: Denis Lippok
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04177 Leipzig
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Birth date and place: 14.06.1980 in Lübben, Germany

Education

2009 – present PhD thesis, Martin-Luther-University Halle-Wittenberg, Institute of Biology / Geobotany and Botanical garden
Topic: “Effects of deforestation and climate change on tropical montane forests -A case study from the Bolivian Andes-“
Supervisors: Prof. Dr. Isabell Hensen and Dr. Matthias Schleuning

2002 – 2009 Studies of Biology, Leipzig University
Major subjects: Tropical ecology, systematic botany and microbiology
Minor subjects: Pharmaceutical biology
Topic diploma thesis: “Vegetation dynamics of anthropogenic montane savannas in the Bolivian Yungas”
Supervisor: Prof. Dr. Isabell Hensen and Dr. Martin Freiberg

2000 – 2002 Studies of Indology, Philosophy and Biology, Leipzig University

1999 Abitur, Thomasschule Leipzig

Work experience

2009 – 2012	Scientific assistant, Martin-Luther-University Halle-Wittenberg, Institute of Biology / Geobotany and Botanical garden
2007 – 2012	Various field trips of several month to Bolivia for scientific work
2009	Part time employment, gardener, Leipzig Botanical Garden
2007	Internship, UFZ Leipzig supervised by Prof. Dr. Carsten Dormann, Topic: „Analysis of the effects of disturbance on pollination networks“

Publications of the dissertation

Denis Lippok, Stephan G. Beck, Daniel Renison, Silvia C. Gallegos, Francisco V. Saavedra, Isabell Hensen & Matthias Schleuning (2013): Forest recovery of areas deforested by fire increases with elevation in the tropical Andes. *Forest Ecology and Management* 15: 69-76.

Denis Lippok, Florian Walter, Isabell Hensen, Stephan G. Beck & Matthias Schleuning (2013): Effects of disturbance and altitude on soil seed banks of tropical montane forests. *Journal of tropical Ecology* 29: 523-529.

Denis Lippok, Stephan G. Beck, Daniel Renison, Isabell Hensen, Amira E. Apaza & Matthias Schleuning (2013): Topography and edge effects are more important than elevation as drivers of vegetation patterns in a neotropical montane forest. *Journal of Vegetation Science*, 10.1111/jvs.12132.

Denis Lippok, Daniel Renison, Isabell Hensen, Stephan G. Beck & Matthias Schleuning (Manuscript): Ecological memory drives early post-fire regeneration in regularly burned sites in the tropical Andes.

Conference contributions

Denis Lippok, Matthias Schleuning & Isabell Hensen (2012): Secondary growth in the Bolivian Andes: Effects of dispersal limitation, altitude & habitat conditions. *Annual meeting of the Society of tropical ecology (GTÖ)*, 22. - 25.2.2012 Erlangen (Germany). Poster.

Denis Lippok & Isabell Hensen (2012): Montane forest remnants in the Bolivian Andes: Effects of altitude, edge & topography (preliminary results). *Annual meeting of the Society of tropical ecology (GTÖ)*, 22. - 25.2.2012 Erlangen (Germany). Poster.

Florian Walter, Denis Lippok & Isabell Hensen (2012): Dispersal limitation of soil seed banks in tropical montane forest secondary growth in the Yungas, Bolivia. *Annual meeting of the Society of tropical ecology (GTÖ)*, 22. - 25.2.2012 Erlangen (Germany). Poster.

Appendix B

Erklärung über den persönlichen Anteil an den Publikationen

1. Study (Chapter 2):

Denis Lippok, Stephan G. Beck, Daniel Renison, Isabell Hensen, Amira E. Apaza & Matthias Schleuning (2013): Topography and edge effects are more important than elevation as drivers of vegetation patterns in a neotropical montane forest. *Journal of Vegetation Science*, 10.1111/jvs.12132.

Data collection: **Denis Lippok** (70%), Amira E. Apaza (20%), Stephan G. Beck (10%)

Analysis: **Denis Lippok** (80%), Matthias Schleuning (20%)

Writing: **Denis Lippok** (70%), Matthias Schleuning (20%), Daniel Renison (10%), corrections by Stephan G. Beck and Isabell Hensen

2. Study (Chapter 3):

Denis Lippok, Stephan G. Beck, Daniel Renison, Silvia C. Gallegos, Francisco V. Saavedra, Isabell Hensen & Matthias Schleuning (2013): Forest recovery of areas deforested by fire increases with elevation in the tropical Andes. *Forest Ecology and Management* 15: 69-76.

Data collection: **Denis Lippok** (80%), Stephan G. Beck (20%)

Analysis: **Denis Lippok** (80%), Matthias Schleuning (20%)

Writing: **Denis Lippok** (80%), Matthias Schleuning (20%), corrections by Daniel Renison, Stephan G. Beck, Isabell Hensen, Silvia C. Gallegos and Francisco V. Saavedra

3. Study (Chapter 4):

Denis Lippok, Daniel Renison, Isabell Hensen, Stephan G. Beck & Matthias Schleuning (Manuscript): Ecological memory drives early post-fire regeneration in regularly burned sites in the tropical Andes.

Data collection: **Denis Lippok** (90%), Stephan G. Beck (10%)

Analysis: **Denis Lippok** (80%), Matthias Schleuning (20%)

Writing: **Denis Lippok** (60%), Matthias Schleuning (20%), Daniel Renison (20%), corrections by Stephan G. Beck and Isabell Hensen

4. Study (Chapter 5):

Denis Lippok, Florian Walter, Isabell Hensen, Stephan G. Beck & Matthias Schleuning (2013): Effects of disturbance and altitude on soil seed banks of tropical montane forests. *Journal of tropical Ecology* 29: 523-529.

Data collection: Florian Walter (100%)

Analysis: **Denis Lippok** (80%), Matthias Schleuning (20%)

Writing: **Denis Lippok** (70%), Matthias Schleuning (20%), Florian Walter (10%), corrections by Stephan G. Beck and Isabell Hensen

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel *“Effects of deforestation and climate change on tropical montane forests - A case study from the Bolivian Andes -“* bisher weder der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), den

Unterschrift: _____ (Denis Lippok)