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

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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 m 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.

1. Introduction

Vast areas of tropical forests are deforested by human activities and deforestation still continues at high rates (FAO, 2011). Due to the decreasing area of primary forests, secondary forests become more important as providers of important ecosystem functions and are crucial for the long-term recovery of primary forests (Brown and Lugo, 1990; Guariguata and Ostertag, 2001). In order to restore forest habitats in deforested areas, knowledge of processes that drive secondary succession is needed (Aide et al., 1995). Despite the fact that recovery rates of montane forests are slow in comparison to lowland forests (Ewel, 1980; Aide et al., 1995; Kappelle et al., 1996; Oosterhoorn and Kappelle, 2000), the majority of studies on secondary succession of tropical rain forests were carried out in lowlands, whereas studies in montane areas are still rare (Muñiz-Castro et al., 2006, 2012).

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Recovery of tropical forests after anthropogenic disturbances is often delayed in comparison to recovery after natural disturbances (Aide and Cavelier, 1994; Aide et al., 1995; Kappelle et al., 1996). Missing sources of plant seeds for recovery and altered environmental conditions at deforested sites are important filters potentially causing a delay in the recovery process (Holl et al., 2000; Zimmerman et al., 2000; Myster, 2004). Seed rain is a pivotal condition for forest recovery, due to exhausted seed banks at deforested sites (Wijdeven and Kuzee, 2000), especially after burning (Ewel et al., 1981; Uhl et al., 1981). Adjacent forest remnants are therefore important seed sources for forest recovery (Aide and Cavelier, 1994; Oosterhoorn and Kappelle, 2000; Muñiz-Castro et al., 2006). Seed rain usually decreases with distance to the forest edge, resulting in a decline of seed density and species richness (Aide and Cavelier, 1994; Holl, 1999; Zimmerman et al., 2000; Cubiña and Aide, 2001). Associated with this gradient in seed rain, the secondary vegetation of deforested sites changes with distance to the forest edge and most studies have found higher density and species richness near forest edges (Myster, 2003; Rodrigues et al., 2004; Muñiz-Castro et al., 2006).

Environmental conditions at deforested sites, for instance in soil properties, microclimate and light availability, differ from those in forests and can impede the establishment of forest species (Uhl and Kauffman, 1990; Holl, 1999; Alvarez-Aquino et al., 2004; Hooper, 2008). Environmental conditions also change with elevation because temperature decreases and precipitation increases with increasing elevation (Bendix et al., 2008; Gerold et al., 2008). Forest recovery may thus differ along elevation gradients and secondary succession at higher elevations might be delayed by environmental stress (Del Moral and Ellis, 2004; Ding et al., 2006). The few studies investigating effects of elevation on secondary succession of tropical forests (Aide et al., 1996; Hooftman, 1998; Pascarella et al., 2000; Chinea, 2002) mostly found changes in species composition.

In this study, we aim at improving our understanding of forest recovery along an elevation gradient in the eastern cordillera of the Bolivian Andes. The region is characterized by a vegetation mosaic comprising tropical montane forest remnants located in a matrix of human-induced secondary growth that has been formed by frequent burning. The deforested sites are dominated by ferns that delay the succession of woody vegetation (Hartig and Beck, 2003; Schneider, 2004; Douterlungne et al., 2010). The regenerating vegetation at the deforested sites is composed of forest species that disperse from adjacent forest remnants and non-forest species that only occur in the deforested habitats (Hartig and Beck, 2003; Müller et al., 2007). In order to identify limiting factors of forest recovery, we compared characteristics of secondary vegetation near (at 20 m distance) and away (at 80 m) from the forest edge along an elevation gradient of 550 m from 1950 m to 2500 m asl. We tested the effects of distance to forest edge, of elevation and of the interaction between distance to forest edge and elevation on basal area, density, richness and composition of forest and non-forest species. Additionally, we compared soil properties, microclimate and light availability at the deforested sites with conditions in adjacent forest interiors and along the elevation gradient. We tested the following hypotheses: (I) Distance to the forest edge reduces basal area, density and richness and alters composition of forest species in the secondary vegetation, due to seed dispersal limitation, but has no effect on non-forest species. (II) Effects of elevation influence forest and non-forest species, resulting in a reduced basal area, density and species richness and a different species composition at higher elevations, due to increasing harshness in environmental conditions with increasing elevation.

2. Methods

2.1. Study area

The study was conducted at the eastern cordillera of the Bolivian Andes, about 120 km east of La Paz in the province Sud Yungas, close to Chulumani (1750 m asl, 16° 24′ 29″ S, 67° 31″ W). In Chulumani, the mean annual temperature is 20.8 °C and mean annual precipitation is about 1459 mm (Molina Carpio, 2005). Precipitation is very low during the dry season from May to July, with less than 50 mm precipitation per month. Vast areas of the tropical montane forests around Chulumani have been deforested by frequent human-induced fires (Killeen et al., 2005). Only a small fraction of the deforested areas are used for agriculture, mainly for coca (*Erythroxylon coca*) cultivation, albeit uncontrolled burning has deforested huge areas that are not used for agriculture. These areas are in an early stage of secondary succession and are dominated by two fern species: *Pteridium aquilinum* var. *arachnoideum* (bracken fern) and *Lophosoria quadripinnata*. The invasion of bracken fern is supported by stimulating effects of fires on rhizome expansion and frond growth (Roos et al., 2010). The woody secondary vegetation comprises a mixture of montane forest species and species, which do not naturally occur in montane forests.

We sampled eight sites along an elevation gradient of 550 m ranging from 1950 to 2500 m asl (for site characteristics see Supplementary material Table S1). Each site comprised a deforested area dominated by bracken fern adjacent to the unburned forest edge. Information on disturbance history of sites is sparse and it was not possible to determine exactly time since last fire. Based on information from locals and personal observations, we estimated that sites had been burned not more than 5 years ago. Former agricultural land use was only evident at a single site. Neither inclination nor aspect of sites was correlated with elevation (inclination: Spearman's rho = 0.060, $P = 0.888$; northness: Spearman's rho = 0.571, $P = 0.151$; eastness: Spearman's rho = −0.548, $P = 0.171$).

2.2. Vegetation sampling

We sampled secondary vegetation at the eight sites ranging in elevation from 1950 to 2500 m asl. We set up two vegetation-sampling plots of 100 m^2 (10 m × 10 m) in the deforested areas at two different distances from the forest edge, near (at 20 m distance) and away from the forest edge (at 80 m). The exact location of each sampling plot was determined randomly along two 50 m lines parallel the forest edge. In each plot, all non-climbing woody plants with height $\geqslant$1 m were determined and their basal diameter was measured. Stems were checked for underground connections to provide counts of individuals. Individuals were grouped in the field into morphospecies, and specimens of each morphospecies were identified and stored in the Herbario Nacional de Bolivia in La Paz (LPB). Nomenclature follows the Missouri Botanical Garden (http://www.tropicos.org).

All recorded species were classified to be forest (i.e., also occurring in the forest remnants) or non-forest species (i.e., restricted to secondary vegetation). This classification was based on a previous vegetation study of the forest remnants in the study area at the same elevation range with more than 2000 recorded individuals from more than 250 species (Lippok, unpublished data). Classification was validated by specimens collected in previous studies, stored at the LPB, and by expert knowledge. Furthermore, species were classified according to their dispersal syndrome as anemochorous (dispersed by wind), endozoochorous (mainly dispersed by birds and bats), or baro-synzoochorous (dispersed by gravity and animals) in accordance to Muñiz-Castro et al. (2006) based on specimen information at the LPB and personal observations. For