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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 each plot, we calculated basal area (m^2 100 m^{-2}), density (individuals 100 m^{-2}) and observed species richness (species 100 m^{-2}) for both forest and non-forest species. We compiled quantitative matrices of species composition for each sampling plot, based on counts of individuals.

2.3. Environmental conditions

We compared environmental conditions at the deforested sites at two distances from the forest edge, i.e. near (at 20 m distance) and away from the edge (at 80 m), with forest interior conditions (>100 m inside from edge). Soil properties were sampled at eight sites, microclimate at six sites and light availability at five sites, covering the entire elevation gradient (Supplementary material Table S1). Soil samples were taken in a plot of 100 m^2, where we took 12 sub-samples to a depth of 20 cm. The combined sub-samples were air dried and sieved (2 mm). Using the fine fraction, soil pH was measured potentiometrically in a 1:2.5 soil–H_2O suspension. Contents of exchangeable cations (Ca^{2+}, Mg^{2+} and K^+) were determined by atomic-absorption spectrometry (AAS vario 6, Analytik Jena, Jena, Germany) using 0.2 N $BaCl_2$ as extracting solution. C:N ratio was determined on milled samples after heat combustion (Vario ELIII elemental analyzer, Elementar, Hanau, Germany). We used iButtons® data loggers (Maxim/Dallas Semiconductor Corp., Dallas, Texas), installed 20 cm above ground, to record temperature and relative humidity. Because the number of data loggers was too low to measure microclimate differences between forest interiors and deforested areas at all sites simultaneously, we measured microclimate conditions within each site for 1 month and after that equipped another site. To determine the effect of elevation on microclimate, we simultaneously measured the microclimate of six deforested sites (at 40 m distance from the forest edge with surrounding vegetation cleared) for 2 months. To characterize light availability, we took four hemispherical photos 1 m above ground, i.e. at the corners of a 1-m^2 quadrat. We calculated quadrat means for canopy openness and leaf area index (Bonhomme and Chartier, 1972), using WinScanopy2005® (Regent Instruments Inc., Quebec, Canada).

2.4. Data analysis

All statistical analysis were carried out with R (R Development Core Team, 2010) and dedicated packages 'multcomp' (Hothorn et al., 2008), 'MuMIn' (Bartoń, 2011), 'nlme' (Pinheiro et al., 2010) and 'vegan' (Oksanen et al., 2011). Effect of habitat type (forest interior, deforested sites at 20 m and 80 m) on environmental conditions was tested with a linear mixed effect model with site as random factor. We applied Tukey's all pair comparison with Bonferroni correction to test for differences between the three habitat types. Effects of species origin (forest versus non-forest species), distance to forest edge (near versus away) and elevation on basal area, density and species richness were tested with linear mixed effect models, with species origin, distance to forest edge, elevation and their interaction terms as fixed factors and site and plot identity as nested random factors. We fitted all possible combinations of fixed effects and identified the best model according to the Akaike information criterion, corrected for small sample size, AICc (Zuur et al., 2009). In case of non-normality or heteroscedasticity, dependent variables were $\log_{10}$- or square-root-transformed.

We also analyzed patterns in species community turnover, separately for forest and non-forest species. We quantified species dissimilarity between plots with the Morisita-Horn-Dissimilarity, which is independent of sample size and species richness (Wolda, 1981; Chao et al., 2006). Analyses were based on quantitative community matrices, excluding two plots from the analysis of the forest species community because of very low densities of forest species (<2 individuals). We partitioned differences in community turnover associated with the distance to forest edge, elevation and their interaction term with a multivariate analyze of variance (MANOVA) (McArdle and Anderson, 2001). Significant effects of predictor variables on community turnover were tested with a Monte Carlo permutation ($n = 999$). Permutations for main and interaction effects of distance were stratified at the site level to account for the nested sampling design, whereas permutations for changes with elevation were unconstrained.

3. Results

3.1. Secondary vegetation

In total, we sampled 2046 individuals from 57 species at the deforested sites (for species list see Supplementary material Table S2). Forest species included 22 taxa, representing 19% of all sampled individuals. Species numbers were evenly distributed across 21 different plant families. The majority of forest species were endozoochorous (73% of forest species). The most abundant forest species was *Myrsine coriacea* (Primulaceae) accounting for 66% of all forest individuals. Non-forest species included 35 taxa, accounting for 81% of all sampled individuals. The most diverse families of non-forest species were Asteraceae (17 species) and Melastomataceae (6 spp.) and the most abundant dispersal modes were anemochory (57% of non-forest species) and endozoochory (29%). The most abundant non-forest species was *Collaea speciosa* (Fabaceae) accounting for 45% of all non-forest individuals.

3.2. Environmental conditions

The deforested sites differed from the forest interiors in soil properties, microclimate and light availability (Table 1), whereas environmental conditions did not change with distance from the forest edge. Soil pH, content of exchangeable Mg^{2+} and K^+ and C:N ratio were significantly higher at deforested sites than in the forest interiors (Table 1A). Content of exchangeable Ca^{2+} was elevated at deforested sites, but did not differ significantly from forest interiors. Microclimatic conditions at deforested sites were characterized by higher temperatures and lower humidity than in the forest interiors (Table 1B). The leaf area index was significantly lower at deforested sites than at forest interiors, whereas canopy

Table 1

Environmental conditions in forest interiors and at deforested sites at 20 m and 80 m distance from the forest edge along an elevation gradient ranging from 1950 m to 2500 m asl in the Bolivian Andes. Mean ± standard deviation of (A) soil properties (8 sites), (B) microclimate (6 sites) and (C) light availability (5 sites) are shown.

	Forest	Deforested area	
	Interior	20 m	80 m
(A) Soil properties			
pH	3.8 ± 0.4*a*	4.3 ± 0.3*b*	4.5 ± 0.2*b*
Mg^{2+} (μmol c/g)	3.3 ± 3.6*a*	7.5 ± 7.3*b*	11.8 ± 7.8*b*
Ca^{2+} (μmol c/g)	1.6 ± 3.1*a*	7.2 ± 12.4*a*	14.2 ± 24.2*a*
K^+ (μmol c/g)	2.2 ± 0.8*a*	5.3 ± 1.6*b*	5.5 ± 1.8*b*
C:N	15.1 ± 1.9*a*	17.1 ± 1.3*b*	16.8 ± 0.9*b*
(B) Microclimate			
Mean temperature (°C)	14.9 ± 1.0*a*	16.1 ± 1.0*b*	16.7 ± 1.2*b*
Maximal temperature (°C)	25.7 ± 4.4*a*	34.1 ± 3.5*b*	34.5 ± 6.6*b*
Mean humidity (%)	98.1 ± 1.7*a*	92.6 ± 2.8*b*	92.1 ± 3.7*b*
Minimal humidity (%)	63.8 ± 20.5*a*	36.1 ± 9.6*b*	35.3 ± 13.6*b*
(C) Light availability			
Leaf area index	2.6 ± 0.2*a*	1.5 ± 0.5*b*	1.4 ± 0.7*b*
Canopy openness (%)	18.7 ± 1.7*a*	31.3 ± 14.0*a*	38.5 ± 24.4*a*

Different letters in rows indicate significant ($P < 0.05$) differences (Tukey's all-pair comparison with Bonferroni-Correction).

Table 2
Effects of species origin (forest versus non-forest species), distance to forest edge, elevation and their interaction terms on basal area, density and observed species richness of secondary vegetation at eight deforested sites along an elevation gradient ranging from 1950 to 2500 m asl in the Bolivian Andes. Given are model estimates from minimal adequate models according to AICc derived from comparisons of all possible combinations of main and interaction effects of species origin, distance to forest edge and elevation on the respective response variables. Terms not included in the minimal adequate models are not shown.

	Df	Basal area[a]		Density[b]		Species richness[a]	
		t	*P*	*t*	*P*	*t*	*P*
Species origin (non-forest)	1	4.172	0.001	6.425	<0.001	3.352	0.005
Distance to forest edge	1	2.545	0.038	1.915	0.097	2.880	0.024
Elevation	1	2.135	0.077	3.782	0.009	2.465	0.049
Species origin × elevation	1	Not applicable		Not applicable		−2.807	0.014

[a] Square-root-transformed.
[b] $\log_{10}$-transformed.

openness, albeit strongly elevated at most deforested sites, did not differ significantly (Table 1C). Changes in environmental conditions at deforested sites along the elevation gradient were less pronounced (Appendix A). Content of exchangeable Ca^{2+} and Mg^{2+} and mean temperature decreased with increasing elevation, while there were no changes in light availability.

3.3. Basal area, density and species richness

Basal area of woody plants (forest and non-forest species) ranged from 0.004 to 0.084 m^2 100 m^{-2}. The basal area of forest species (mean ± SD = 0.008 ± 0.008 m^2 100 m^{-2}) was threefold lower compared to that of non-forest species (0.023 ± 0.02 m^2 100 m^{-2}). Basal area of forest and non-forest species was higher at 80 m distance than at 20 m distance from the forest edge (Table. 2, Fig. 1A) and increased slightly with elevation (Table. 2). Density ranged from 3 to 521 individuals 100 m^{-2}. The density of forest species (24.2 ± 30.6 individuals 100 m^{-2}) was fourfold lower than the density of non-forest species (103.7 ± 112.3 individuals 100 m^{-2}). The density of both groups tended to be higher at 80 m distance than at 20 m distance from the forest edge and strongly increased with increasing elevation (Table. 2, Fig. 1B). Observed species richness ranged from 2 to 22 species 100 m^{-2}. Richness of forest species (3.5 ± 2.6 species 100 m^{-2}) was half as much as of non-forest species (6.8 ± 3.7 species 100 m^{-2}). Observed species richness of both groups was higher at 80 m than at 20 m distance (Table. 2, Fig. 1C) and increased with increasing elevation (Fig. 1D). The increase in species richness with elevation, however, was only evident in forest species.

3.4. Species turnover

Species turnover along the elevation gradient was strong and accounted for 42% and 33% of species turnover in forest and non-forest species, respectively (Table. 3). In forest species communities, *Clethra scabra* and *Inga* cf. *fendleriana* were frequent at lower elevations, whereas *M. coriacea*, *Bejaria aestuans* and *Viburnum seemanii* were frequent at higher elevations. Among the non-forest species, species such as *Chromolaena laevigata* and *Tibouchina stenocarpa* were replaced at higher elevations by *C. speciosa* and *Baccharis platypoda.* In contrast to the strong effect of elevation, communities of forest and non-forest species were not influenced by the distance to the forest edge (Table. 3). However, dissimilarities between species communities at 20 m and 80 m distance from the forest edge decreased with elevation for forest species but not for non-forest species (see interaction terms in Table. 3).

4. Discussion

4.1. Secondary vegetation

Forest species belonged to typical montane forest families (e.g. Clethraceaea, Cunoniaceae, Ericaceae and Myrtaceae) with most species dispersed by endozoochory, as typical for tropical forest species (Howe and Smallwood, 1982). The most common forest species at the deforested sites was the light-demanding pioneer species *M. coriacea*, a small-seeded species that is dispersed by birds into open areas (Cubiña and Aide, 2001; Muñiz-Castro et al., 2006) and which is a dominant tree of montane forests (Bach et al., 2003). In contrast, species of Asteraceae and Melastomataceae, which are typical non-forest species (Hartig and Beck, 2003; Peters et al., 2010), invaded deforested sites mostly by anemochouros dispersal (Hartig and Beck, 2003). The most abundant non-forest species, the baro-synzoochorous *C. speciosa*, might benefit from burnings that stimulate germination in many hard-seeded Fabaceae (Keeley and Fotheringham, 2000). Most of the non-forest species have their origins in neotropical savannas and cerrados (Beck, 1993; Miranda et al., 2010) and are adapted to dry microclimates and frequent fires, while a small proportion has an Andean distribution.

Montane forest recovery at the deforested sites was hampered, indicated by the low proportion of forest species (<20% of the individuals) in the secondary vegetation. Low seed rain might be one limiting factor for forest recovery at deforested sites (Holl et al., 2000; Zimmerman et al., 2000; Myster, 2004). Recovery of forest species may be limited by hot and dry microclimates (Engelbrecht and Kursar, 2003; Poorter and Markesteijn, 2008; Markesteijn and Poorter, 2009). Another important filter might be frequent burning that kills the seedlings and the majority of the established vegetation (Uhl and Kauffman, 1990; Aide and Cavelier, 1994; Hooper et al., 2005). We observed that most species occurring at the deforested sites were actually able to resprout after fire, e.g. the two most abundant species at the deforested sites *M. coriacea* and *C. speciosa* among many other species, e.g. *Raulinoreitzia crenulata* and *C. scabra* (personal observation; Beck, 1993; Hartig and Beck, 2003; Kennedy and Horn, 2008). Thus, frequent fires can shift the regeneration pathways from seeds towards resprouting (Hoffmann, 1998; Hooper et al., 2004), altering species composition by favoring species with resprouting ability. Fire effects are enhanced in bracken fern-dominated stands because of the flammable litter of this species, causing increased fire temperatures and damage (Adie et al., 2011).

4.2. Environmental conditions

The transformation of montane forests into deforested lands by frequent burning leads to significant changes in environmental conditions, particularly in soil properties, microclimate and light availability. The elevated pH and content of exchangeable cations likely results from the mineralization of biomass by frequent burnings (Nye and Greenland, 1964; Certini, 2005; Notario del Pino et al., 2008), while the elevated C:N ratio indicates a loss of N at deforested sites (Hamer et al., 2012). Consistent with expectations, microclimatic conditions were harsher at deforested sites with higher temperatures and lower humidity, also reported by other

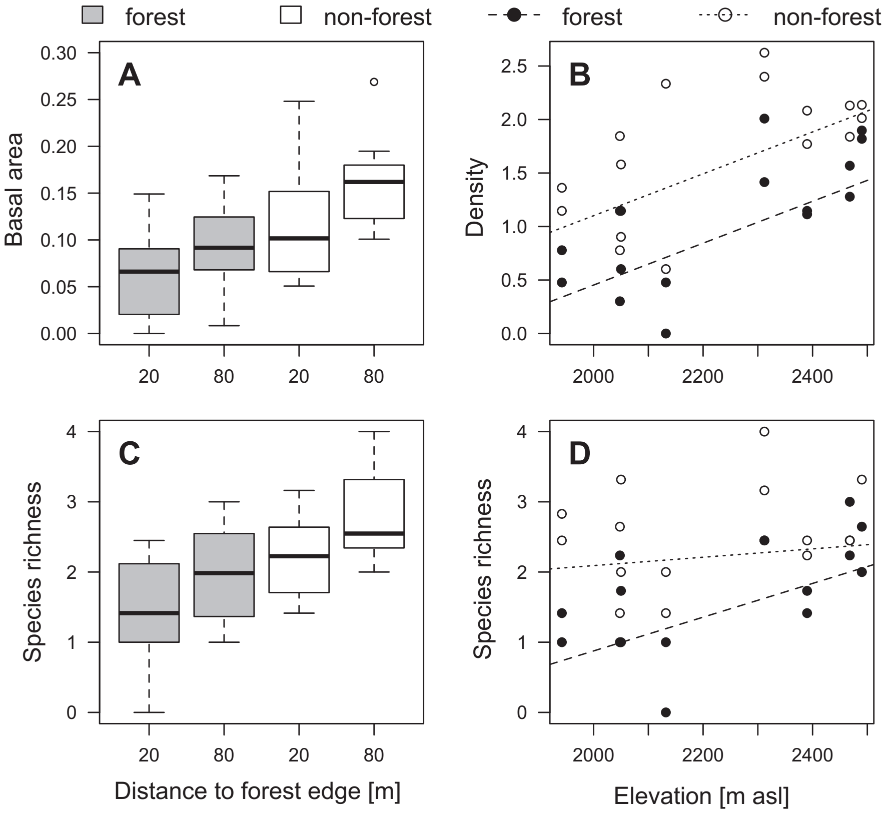

Fig. 1. (A) Basal area (m^2 100 m^{-2}, square-root-transformed), (B) density (individuals 100 m^{-2}, log_{10}-transformed) and (C and D) observed species richness (number of species 100 m^{-2}, square-root-transformed) of forest and non-forest species in secondary vegetation at eight deforested sites along an elevation gradient ranging from 1950 to 2500 m asl in the Bolivian Andes. In box plots, grey color indicates forest species and white color non-forest species. In scatter plots, solid circles and long-dashed lines refer to forest species; empty circles and short-dashed lines to non-forest species. In box plots, horizontal lines across boxes are medians, boxes indicate 25th and 75th percentiles, whiskers indicate the data range, and circles are outliers.

Table 3
Non-parametric multivariate analysis of variance (MANOVA) of the effects of distance to forest edge, elevation and their interaction term on species composition of (A) forest and (B) non-forest species in secondary vegetation at deforested sites along an elevation gradient ranging from 1950 to 2500 m asl in the Bolivian Andes. Dissimilarities were measured with the Morisita-Horn index. R^2-values indicate the proportion of variance explained by the factor and *P-values* indicate the significance of each factor derived from a permutation model.

	Df	*F*	R^2	*P*
(A) Forest species				
Distance	1	1.19	0.05	0.246
Elevation	1	9.824	0.415	0.001
Distance × elevation	1	2.656	0.112	0.023
Residuals	10		0.422	
(B) Non-forest species				
Distance	1	0.297	0.016	0.853
Elevation	1	6.153	0.328	0.001
Distance × elevation	1	0.322	0.017	0.635
Residuals	12		0.639	

studies (Uhl and Kauffman, 1990; Holl, 1999; Alvarez-Aquino et al., 2004; Hooper, 2008). Because canopy cover at 1 m above the ground was rather low at deforested sites, competition with ferns for light does not appear to be a limiting factor at deforested sites. These findings illustrate that environmental conditions are strongly altered by fire and deforestation in the tropical Andes and that these changes are likely to pose important environmental filters on the regenerating forest vegetation. One particular important filter could be the harsh microclimatic conditions at deforested sites because maximum temperatures were increased by about 10°C and minimum humidity was half as high at deforested sites compared to the forest interior. Because temperatures decreased with increasing elevation in our study and in other studies (Bendix et al., 2008; Gerold et al., 2008), the strength of this environmental filter may be relaxed towards higher elevations.

4.3. Effects of seed dispersal limitation

In contrast to previous studies (Myster, 2003; Rodrigues et al., 2004; Muñiz-Castro et al., 2006) and to our initial hypothesis, distance to the forest edge did not reduce the basal area, density and richness of forest species in the secondary vegetation. In contrast, we recorded higher basal area and species richness away from the forest edge, for both forest as non-forest species. Previous seed rain studies found thresholds for seed dispersal at about 10 m from forest edges (Aide and Cavelier, 1994; Zimmerman et al., 2000; Cubiña and Aide, 2001). Because effects of seed-dispersal distances in the transition zone between forest edge and degraded vegetation were not the focus of our study, we are unable to test whether dispersal limitation occurs in direct vicinity to the forest edge in our system. Given the post-fire age of the sites and the dispersal capability of bird-dispersed plant species (Lenz et al. 2010; Breitbach et al. 2012), it is likely that many forest species are able to colonize microsites at distances of 20 m or 80 m from the forest edge. This hypothesis is supported by our finding that most forest species were endozoochorous and that we found no distinct species composition for the two different distances to the forest edge. Thus, animal-mediated seed dispersal moved seeds medium to large distances from the forest edges, suggesting that limitations in seed rain were less important than environmental filters. This is nicely illustrated by the high recruitment success of the bird-dispersed small-seeded forest species *M.coriacea* at deforested sites (Cubiña and Aide, 2001; Muñiz-Castro et al., 2006). More detailed studies of montane forest recovery should compare dispersal distances between small- and large-seeded plant species because large-seeded plant species are more likely to suffer from human disturbance than small-seeded species (Markl et al., 2012). The higher values for basal area and species richness at 80 m distance might be caused by post-dispersal factors, such as enhanced seed and seedling predation near the forest edge. However, we did not investigate post-dispersal filters in this study and refrain from explaining this spatial pattern with the presented data.

4.4. Effects of elevation

In contrast to our hypothesis, density of forest and non-forest species increased with increasing elevation. One explanation for this surprising effect could be a relaxed environmental filter at high elevations because the decrease of temperature with increasing elevation might compensate for hot and dry microclimates at deforested sites. In addition, higher precipitation and less short wave radiation, due to increased cloudiness, result in lower evaporation at higher elevations (Gerold et al., 2008) and might attenuate the severe effects of the dry season on water supply. Consequently, frequency and intensity of fires might be lowered at higher elevations due to more humid climatic conditions and the higher remoteness from human populations (Hooftman, 1998; Pascarella et al., 2000; Marler and del Moral, 2011). Hooper et al. (2004) reported that the effect of the distance to the forest edge on species composition decreased with increasing time since fire. We found an increased similarity of forest species composition between 20 and 80 m plots with increasing elevation, which might also reflect a lower fire frequency at high elevations.

Consistent with other studies (Aide et al., 1996; Pascarella et al., 2000; Chinea, 2002), species composition of forest and non-forest species changed along the elevation gradient. The composition of the forest species colonizing the deforested sites changed with elevation, likely because of changes in the forest species pool with elevation (Gentry, 1995; Lieberman et al., 1996; Vázquez et al., 1998). In concert with milder environmental conditions at deforested sites at high elevations, the altered species pool could explain the increasing species richness of forest species with increasing elevation. Species from higher altitudes are potentially better adapted to fluctuations in microclimatic conditions because high elevation forests have a more open forest structure (Bach et al., 2003; Homeier et al., 2010) and thus may have a higher capability to recruit in open deforested areas. It is likely that the source pool of non-forest species also changed with elevation gradually from origins at lower elevations, i.e. neotropical savannas and cerrados, towards origins at higher elevations, which explains the high species turnover.

The increase in the density of forest species was mostly caused by a strong increase of *M. coriacea* at higher elevations. It might be a suitable species for facilitating montane forest recovery due to its ability to be dispersed for long distances into deforested sites (Muñiz-Castro et al., 2006) and to resprout after fire (Kennedy and Horn, 2008). Its fleshy fruits might attract frugivorous birds and bats and enhance seed rain in the deforested sites (Wunderle, 1997). If fires are suppressed, it can establish a close canopy and shade out the bracken fern (Oosterhoorn and Kappelle, 2000) and serve as a recruitment focus for other forest species (Holl et al., 2000).

5. Conclusions

Montane forest recovery at deforested sites was low and is likely to be limited by harsh environmental conditions, particularly by hot and dry microclimate and high fire frequencies. Forest recovery was not enhanced near forest edges and most forest species establishing at deforested sites were animal-dispersed, suggesting that seed dispersal limitation was less important than environmental filters. Interestingly, we found that community composition strongly changed with elevation and that this effect was associated with an increase in forest recovery with elevation, corroborated by higher density and species richness of forest species at high elevations. We propose that the effect of elevation on forest recovery is mediated by changes in the species source pool and in particular by milder environmental conditions at deforested sites at high elevations. Our findings highlight that environmental changes with elevation are crucial for understanding capabilities of forest recovery in mountain ecosystems and implies that forest recovery may be further reduced if maximum temperatures are going to increase in the tropical Andes in the near future.

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Appendix A

See Table A1.

Table A1
Correlations between elevations and (A) soil properties (8 sites), (B) microclimate (6 sites) and (C) light availability (5 sites) at deforested sites along an elevation gradient ranging from 1950 to 2500 m asl in the Bolivian Andes.

	Spearman's rho	*P*
(A) Soil properties		
pH	−0.385	0.141
Mg^{2+} (μmol c/g)	−0.485	0.057
Ca^{2+} (μmol c/g)	−0.551	0.027
K^{+} (μmol c/g)	−0.112	0.679
C:N	−0.331	0.210
(B) Microclimate		
Mean temperature (°C)	−1.000	0.003
Maximal temperature (°C)	−0.257	0.658
Mean humidity (%)	0.371	0.497
Minimal humidity (%)	0.200	0.714
(C) Light availability		
Leaf area index	0.394	0.260
Canopy openness (%)	−0.049	0.893

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.01.011.

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