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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

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Lippok, D. (corresponding author, denis.lippok@yahoo.de), **Hensen, I.** (isabell.hensen@botanik.uni-halle.de), **Apaza, A.E.** (amiraelvia@yahoo.es) & **Schleuning, M.** (matthias.schleuning@senckenberg.de): Institute of Biology/Geobotany and Botanical Garden, Martin-Luther-University Halle-Wittenberg, Am Kirchtor 1, D-06108, Halle, Germany
Beck, S.G. (lpbstephan@gmail.com) & **Apaza, A.E.** : National Herbarium of Bolivia, UMSA, Campus Universitario, CotaCota, La Paz, Bolivia
Renison, D. (darenison@yahoo.com.ar): Centro de Ecología y Recursos Naturales Renovables, Instituto de Investigaciones Biológicas y Tecnológicas (CONICET – Universidad Nacional de Córdoba), Av. Vélez Sarsfield 1611, X5016GCA, Córdoba, Argentina
Hensen, I. : German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, D-04103, Leipzig, Germany
Schleuning, M. (matthias.schleuning@senckenberg.de): Biodiversity and Climate Research Centre (BiK-F) and Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, 60325, Frankfurt (Main), Germany

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 analysed 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.

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Introduction

Tropical montane forests are highly diverse ecosystems (Henderson et al. 1991; Kier et al. 2005). The tropical Andes are one of the global hotspots of diversity with ca. 45 000 plant species, whereof 20 000 species are endemic to this area (Myers et al. 2000). The high diversity of these forests is associated with high habitat heterogeneity along gradients in elevation and topography (Beck et al. 2008).

Elevational gradients in tropical mountains are characterized by a decrease in temperature (Bendix et al. 2008; Gerold et al. 2008), and soil nutrient availability usually decreases with increasing elevation (Tanner et al. 1998; Soethe et al. 2008; but see Unger et al. 2010). Vegetation of montane forests is altered by such changes in abiotic conditions. Consequently, above-ground productivity, tree height and plant species richness usually decrease with increasing elevation (Gentry 1988; Kitayama & Aiba 2002; Moser et al. 2008; Homeier et al. 2010). Species composition also changes with elevation (Gentry 1995; Lieberman et al. 1996), and the rapid species turnover with elevation is one of the main drivers of the high diversity in tropical montane forests (Homeier et al. 2010).

Tropical montane forests are not only shaped by elevational gradients but also by a mosaic of different microhabitats within elevational belts. Variation in topography is a crucial factor influencing abiotic conditions and vegetation characteristics at a small spatial scale (Webb et al. 1999; Homeier 2008; Weaver 2010). Towards lower slopes, availability of soil water (Daws et al. 2002; Markesteijn et al. 2010) and soil nutrients (Wilcke et al. 2011; Wolf et al. 2011) increases, while wind exposure and associated damage are reduced (Lawton 1982; Herwitz & Young 1994; Webb et al. 1999). As a consequence of these different abiotic conditions, productivity and canopy height are higher at lower slopes (i.e. in gorges) than in upslope conditions (i.e. on ridges; Webb et al. 1999; Oesker et al. 2008). Conditions for plant establishment are also contingent on topographic variation among microhabitats and causes differences in plant species composition (Homeier 2008; Punchi-Manage et al. 2013), contributing to the high diversity in montane forests (Kubota et al. 2004; Homeier 2008).

Nowadays, tropical montane forests are being deforested and the forest remnants are further fragmented by human activities (FAO 2011). Small forest fragments are exposed to edge effects with altered abiotic conditions (Saunders et al. 1991; Williams-Linera et al. 1998). As a consequence of high wind speeds at forest edges, canopy height is reduced and canopy openness increases (Saunders et al. 1991; Oosterhoorn & Kappelle 2000), leading to elevated irradiation (Kapos 1989; Williams-Linera et al. 1998). Consequently, forest edges pose altered environmental conditions for plant establishment, which may favour pioneer species and may lead to a loss of forest interior species (Santos et al. 2008).

In this study, we simultaneously tested effects of elevation, topography and forest edge on habitat conditions and plant diversity of tropical montane forests. We aimed at contributing to a better understanding of the major drivers that generate the high plant diversity in tropical mountains. This knowledge is essential for conservation and restoration of tropical montane forest remnants that are important refugia for biodiversity and providers of ecosystem functions (Brown & Lugo 1990; Guariguata & Ostertag 2001). We measured microclimate and sampled soil properties and woody vegetation of tropical montane forest fragments in the eastern cordillera of the Bolivian Andes. Along an elevational gradient of 600 m, we sampled human-induced forest edges and less disturbed forest interiors on ridges and in gorges. We compared the direction and strength of the effects of these three gradients (i.e. elevation, topography and forest edge) on:

1. habitat conditions (i.e. microclimate, soil properties and forest structure), and
2. woody plant diversity (i.e. species richness, species evenness and species composition).

The results of this study help to quantify and disentangle the effects of three major determinants of habitat conditions and forest vegetation in tropical mountains, and may also contribute to a more comprehensive understanding of vegetation responses to global warming in the tropical Andes.

Methods

Study site

The study was conducted in the eastern cordillera of the Bolivian Andes in the province of Sud Yungas, close to the village of Chulumani (1750 m a.s.l., 16°24′29″ S, 67°31′16″ W), about 120 km east of La Paz. The mean annual precipitation is about 1459 mm (Molina-Carpio 2005) and mean annual temperature is 20.8 °C. Precipitation decreases from May to July, resulting in a dry season with less than 50 mm precipitation per month. We expected an increase of precipitation with increasing elevation, according to earlier studies in the region (Molina-Carpio 2005; Gerold et al. 2008).

The tropical montane forests in the Area (‘Yungas’) are highly diverse ecosystems, with an estimated species richness of ca. 10 000 plant species (Kessler & Beck 2001). Vast areas of these forests have been deforested by frequent burnings (Killeen et al. 2005), resulting in fragmented landscapes comprising few forest remnants in a matrix of deforested habitats. In the study area, only two major forest fragments have remained; both are characterized by highly dissected forest margins and thus high proportions of forest edges relative to the remaining forest area (Appendix S1). At deforested areas adjacent to forest fragments, the vegetation is characterized by an early stage of secondary succession, dominated by bracken fern and wind-dispersed shrubs and only a few regenerating forest species (Lippok et al. 2013).

Sampling design

The forest fragments were sampled at six sites (Appendix S1a), which were equally distributed along an elevational gradient of 600 m, ranging from 1900 to 2500 m a.s.l. (Appendix S1b). At each sampling site, we set up two sampling plots at forest edges (20 m from forest margin) and two plots in the forest interior (>100 m from forest margin), each plot measuring 400 m^2 (20 × 20 m). Sampling plots in the forest interior were set up in two contrasting topographic microhabitats, i.e. on ridges (and upper slopes) and in gorges (and lower slopes). Slopes were steepest in gorges (median = 40°, range = 40–45°) and flatter on ridges (median = 17°, range = 11–19°). A topographical classification for forest edges was not meaningful because of the absence of forest edges in gorges. Instead, we sampled a wide range of slope inclinations at forest edges (median = 20°, range = 6–35°) to eliminate the possibility of confounding effects of edge with slope. We had to exclude one edge and one ridge plot because fire and logging destroyed the vegetation during data collection. In total, we sampled 22 plots, comprising 11 plots at forest edges, five plots on ridges and six plots in gorges. We observed former charcoal production and selective logging in forest remnants and recorded former fire impacts at a few forest edges. During plot selection, we dismissed places with obvious former and recent human disturbance in order to exclude confounding effects of direct human disturbance with the three studied gradients, especially with elevation and topography.

Microclimate

In each sampling plot, we recorded microclimatic conditions, i.e. temperature and relative humidity, with iButtons® data loggers (Maxim/Dallas Semiconductor Corp., Dallas, TX, US) installed 20 cm above the ground. Because the number of data loggers was too low (n = 12 data loggers) to measure differences between all sampling plots at all sites simultaneously, we measured all sampling plots within each site for at least 1 mo and after that equipped another randomly chosen site. We calculated mean and maximum temperature and minimum humidity for the respective sampling periods.

Soil properties

We analysed chemical soil properties in each sampling plot. Mineral soil samples covered an area of 100 m^2, where we took 12 subsamples to a depth of 20 cm. The combined subsamples were air dried and sieved (2 mm). Using the fine fraction (<2 mm), soil pH was measured potentiometrically in a 1:2.5 soil–H_2O suspension. Content of exchangeable cations (Ca^{2+}, Mg^{2+} and K^+) was determined with atomic absorption spectrometry (AAS vario 6; Analytik Jena, Jena, DE) using 0.2 N $BaCl_2$ as extracting solution. We used the sum of these three cations for further analysis. C:N ratio was determined on milled samples after heat combustion (Vario ELIII elemental analyzer; Elementar, Hanau, DE).

Woody vegetation

We sampled all non-climbing woody plants (without tree ferns) with diameter ≥2.5 cm at 1.3 m above the ground (DBH). We estimated the height of each stem and measured its DBH. Individuals were grouped in the field into morpho-species, and specimens of each morpho-species were identified and stored in the Herbario Nacional de Bolivia in La Paz (LPB). In total, we sampled 2178 individuals from 259 taxa (Appendix S2), each taxon representing a distinct species. In total, 164 taxa (representing 83% of sampled individuals) were indentified to species level, 72 taxa (13% of sampled individuals) were identified to genus level. A small number of 11 taxa were only identified to family level and 12 taxa remained undefined (together 5% of sampled individuals).

We calculated tree basal area (of stems with DBH ≥ 10 cm) and canopy height (95th quantile of stem lengths with DBH ≥ 10 cm) of each sampling plot. We analysed canopy openness based on nine hemispherical photographs (Nikon Coolpix 4500, equipped with Nikon FC-E8 lens, Nikon, Tokyo, Japan), taken at the nine intercepts of a 10-m grid inside the plot limits at 1.30 m above the ground; digital images were analysed with WinScanopy2005® (Regent Instruments Inc., Quebec, CA).

We computed observed and rarefied species richness (Hurlbert 1971) and species evenness (Pielou 1975) for all woody plants (DBH ≥ 2.5 cm) and for trees only (DBH ≥ 10 cm). For analysis of species composition, we compiled a community matrix based on species abundances of all woody plants for each sampling plot. We square root-transformed the matrix to reduce the influence of the most abundant species on species turnover. A Mantel test performed on Bray–Curtis distances of species abundances and geographic distances between sampling plots revealed no significant spatial autocorrelation in species composition ($n = 22$, $r = 0.11$, $P = 0.089$, 999 permutations).

Statistical analysis

All statistical analysis were carried out with R 2.15.2 (R Core Team 2012; R Foundation for Statistical Computing, Vienna, AT) and the associated packages 'labdsv', 'nlme'and 'vegan'. Because of non-normal distribution of data, pH and content of exchangeable cations were $\log_{10}$-transformed, and basal area was square root-transformed prior to analysis.

In a first step, we tested the effects of the three gradients (i.e. elevation, forest edge and topography) on habitat conditions. We applied linear mixed effects models with elevation and habitat type (i.e. forest edge, ridge and gorge) as fixed factors and site as random factor to test for effects on microclimate, soil properties and forest structure, while accounting for random variation among study sites. We applied two orthogonal contrasts on habitat type to compare edges and forest interior and to compare ridges and gorges within the forest interior. The significance of the individual effect sizes were obtained from *t*-tests of the model estimates for elevation and for the two orthogonal contrasts of habitat types.

In a second step, we tested the effects of the three gradients on the diversity of woody plants and trees, respectively. Effects of the three gradients on measures of species richness (observed and rarefied) and species evenness were also tested with linear mixed effects models. Model design and hypothesis testing were analogous to the analysis of habitat conditions. To visualize and quantify gradients in species composition, we applied detrended correspondence analysis (DCA), based on the community matrix of species abundances. The axis length of DCA axes was used to quantify species turnover, where an axis length ≥3.5 SD indicates that species turnover along the axis is complete (Jongman et al. 1995). We *post-hoc* correlated the three gradients (i.e. elevation, forest edge and topography) and the habitat conditions (i.e. microclimate, soil properties and forest structure) with gradients in species composition derived from DCA; the significance of environmental predictors on species composition was tested with Monte-Carlo Permutations ($n = 999$). Permutations were stratified at the site level for effects of forest edge and topography to account for the hierarchical sampling design. Indicator species of habitat types (i.e. forest edge, ridge and gorge) were evaluated by indicator species analysis (Dufrene & Legendre 1997), with the community matrix including species with more than five individuals. Significance of indicator values was tested with Monte-Carlo Permutations ($n = 9999$).

Results

Habitat conditions

Mean temperatures decreased by 0.5 °C per 100 m of elevation, while maximum temperature and minimum humidity did not change with elevation (Fig. 1a–c). Mean and maximum temperatures at forest edges were higher and minimum humidity lower than in the forest interior (Fig. 1a–c). Ridges and gorges differed only in minimum humidity, which was higher in gorges (Fig. 1a–c).

The pH, content of exchangeable cations and C:N ratio did not change along the elevational gradient (Fig. 1d–f). The pH and content of exchangeable cations was not altered by edge effects, but both were higher in gorges than on ridges (Fig. 1d, e). The C:N ratio was higher at edges than in the interior and higher on ridges than in gorges (Fig. 1f).

Tree basal area increased with elevation (Fig. 1g), whereas canopy height and openness were not influenced by elevation (Fig. 1h, i). Forest edge and topography did not influence tree basal area (Fig. 1g). Canopy height was lower at edges compared to the interior, whereas topography had no effects (Fig. 1h). Canopy openness was not affected by edge effects and topography (Fig. 1i).

Plant diversity

The three gradients had no significant effects on observed species richness of woody plants (Fig. 2a, b). Rarefied richness and evenness of woody plants tended to be lower at forest edges compared to the forest interior, but this effect was only significant for species evenness (Fig. 2c). Elevation and topography did not affect rarefied richness and evenness of woody plants (Fig. 2c). Effects of the three gradients on tree diversity were qualitatively identical to those on all woody plant species (Appendix S3).

The first gradient in species composition (DCA axis 1) was correlated with forest edge ($P = 0.002$) and topography ($P = 0.034$; Fig. 3, Appendix S4). Sampling plots at edges and in gorges were widely separated, while sampling plots on ridges were placed in between. The axis length of 5.5 SD indicated full species turnover along this gradient. Microclimate, soil properties and canopy openness were associated with species turnover along this gradient, with forest edges being associated with warmer temperatures, high canopy openness and high C:N ratio, and gorges with humid conditions, high pH and high content of exchangeable cations (Fig. 3, Appendix S4). The second gradient in species composition (DCA axis 2) was associated with elevation ($P = 0.001$); axis length (2.9 SD) was twofold lower compared to the first gradient (Fig. 3, Appendix S4). The elevational gradient in species composition was mostly

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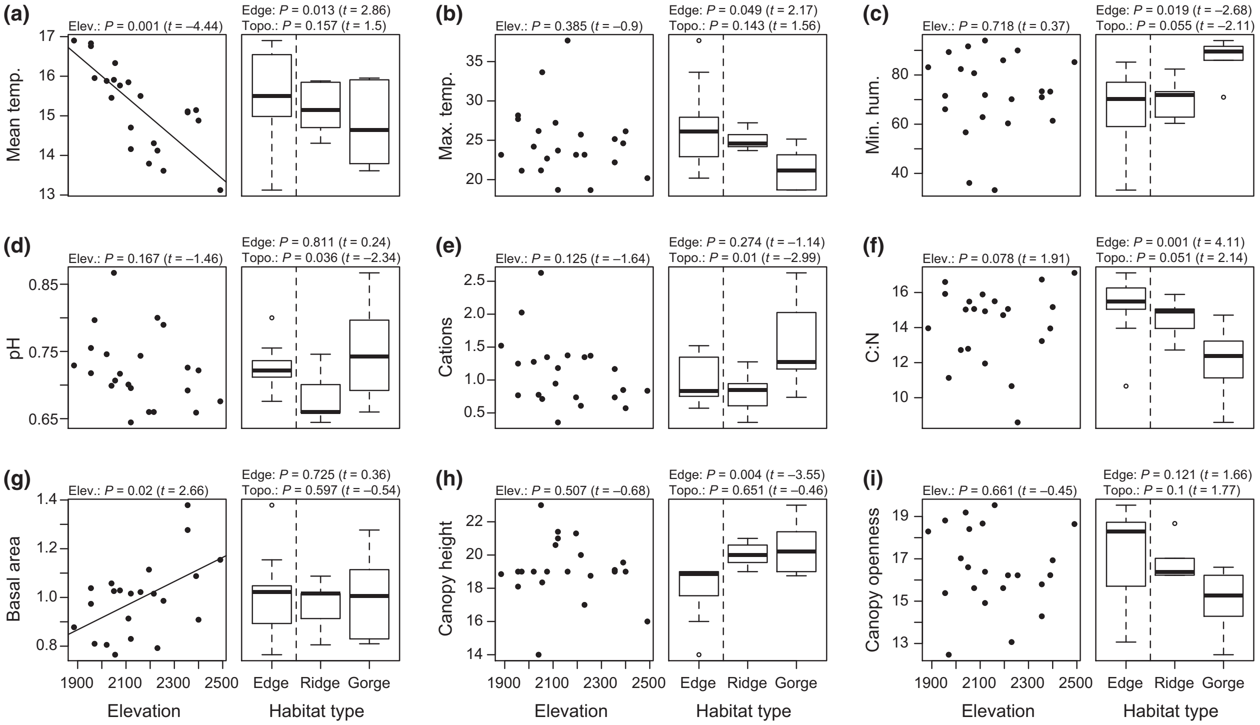

Fig. 1. Habitat conditions (i.e. microclimate, soil properties and forest structure) in tropical montane forest remnants in the Bolivian Eastern cordillera along an elevational gradient of 600 m at forest edges and in the forest interior, on ridges and gorges. **(a)** Mean temperature (°C), **(b)** maximum temperature (°C), **(c)** minimum humidity (%), **(d)** pH ($\log_{10}$-transformed), **(e)** content of exchangeable cations ($\mu mol \cdot g^{-1}$; $\log_{10}$-transformed), **(f)** C:N ratio, **(g)** tree basal area (m^2 400 m^{-2}, square root-transformed), **(h)** canopy height (m) and **(i)** canopy openness (c.o.;%). *P*- and *t*-values were derived from linear mixed effects models, accounting for random variation among sites, and are based on *t*-tests of the model estimates for elevation and for the two orthogonal contrasts of habitat type, i.e., edge vs interior, and ridge vs gorge. The dashed line in the box plots visualizes the comparison between forest edges (left side) with the forest interior (right side). Horizontal lines across boxes are medians, boxes indicate 25th and 75th percentiles, whiskers indicate the data range, and circles are outliers.

associated with decreasing mean temperature and increasing tree basal area with increasing elevation (Fig. 3, Appendix S4).

Indicator species analysis revealed only two indicator species for forest edges and three and six species for ridges and gorges, respectively ($P < 0.05$ in all cases). Indicator species at forest edges were the two pioneer species *Myrsine coriacea* (indicator value = 0.57) and *Cecropia elongata* (0.45). In the forest interior, *Piper hispidum* (0.64), *Palicourea flavifolia* (0.48) and *Faramea candelabrum* (0.40) were typical for ridges. *Psychotria viridis* (0.55), *Eugenia* cf. *feijoi* (0.50), *Miconia barbeyana* (0.50), *Miconia* cf. *centrodesma* (0.50), *Myriocarpa stipitata* (0.47) and *Guarea* sp. (0.42) were restricted to gorges.

Discussion

Gradients in habitat conditions

Habitat conditions were altered by each of the three gradients, and changes in habitat conditions tended to be strongest at the small spatial scale, due to effects of forest edge and topography. Although temperatures decreased with increasing elevation, changes along the here-investigated elevational gradient were low, and among the studied nutrients no nutrient shortage at high elevations could be found. Edge effects altered habitat conditions at forest edges towards warmer and drier microclimates and lower canopy heights. In the forest interior, habitat conditions in gorges were characterized by higher content of exchangeable cations and more humid air conditions than on ridges.

We observed a decrease in temperature with increasing elevation by 0.5 °C 100 m^{-1} (i.e. 3 °C along the 600-m elevational gradient), which is in accordance with other studies in tropical mountains (Bendix et al. 2008; Gerold et al. 2008). Mean temperature was higher at forest edges than in the forest interior. Temperature differences between edges and forest interior were of similar magnitude to a change in elevation of 100 m. Our findings underscore that dry and warm microclimates of the surrounding open habitat matrix alter microclimates at forest edges, at least to a distance of 20 m inside the forest (Kapos 1989). Topography had no effects on temperature, but had

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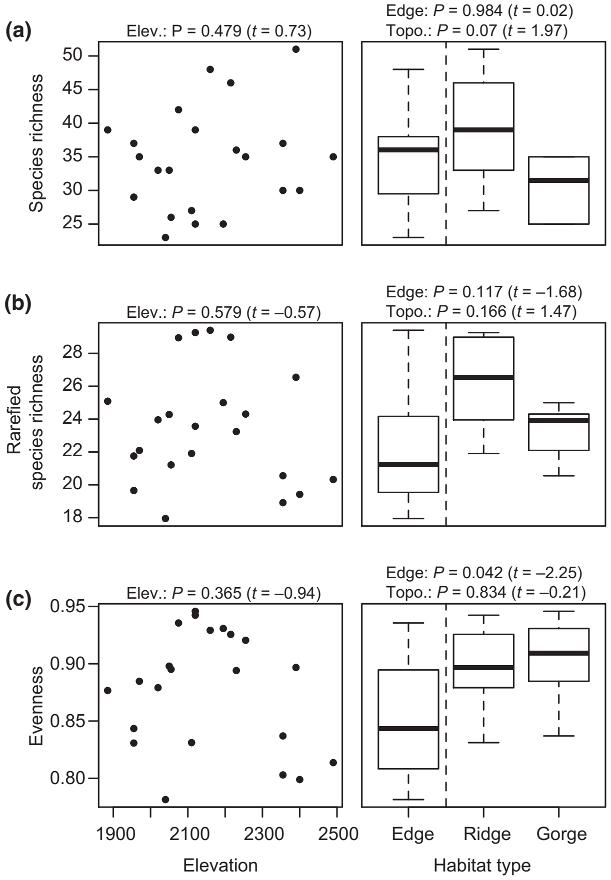

Fig. 2. Woody plant diversity in tropical montane forest remnants in the Bolivian Eastern cordillera along an elevational gradient of 600 m at forest edges and in the forest interior, on ridges and gorges. **(a)** Observed species richness (species 400 m^{-2}), **(b)** rarefied species richness (species per 46 individuals) and **(c)** species evenness. *P*- and *t*-values were derived from linear mixed effects models, accounting for random variation among sites, and are based on *t*-tests of the model estimates for elevation and for the two orthogonal contrasts of habitat type, i.e. edge vs interior, and ridge vs gorge. The dashed line in the box plots visualizes the comparison between forest edges (left side) and forest interior (right side). Horizontal lines across boxes are medians, boxes indicate 25th and 75th percentiles, whiskers indicate the data range, and circles are outliers.

effects on minimum humidity, although they were only marginally significant. Differences in minimum humidity between ridges and gorges were of similar magnitude compared to differences between edges and forest interior. Soil water movement down-slope (Daws et al. 2002; Markesteijn et al. 2010) and higher wind protection in gorges (Lawton 1982) might cause lower fluctuations of humidity in gorge microhabitats.

The content of the studied soil nutrients did not decrease with increasing elevation. C:N ratios at forest edges were higher than in the forest interior; C:N ratios in gorges were lower than on ridges. High C:N ratios might be indicative of low decomposability of soil organic matter (Taylor et al. 1989; Unger et al. 2010) that may be caused, among other factors, by the dry conditions in these habitats (Zhang & Zak 1995; Takyu et al. 2003). The effects of forest edge and topography on C:N ratios were of similar magnitude. The higher content of exchangeable cations in gorges likely results from elutriation of soil nutrients down slopes (Tanner 1977; Chen et al. 1997).

Changes in forest structure were evident along the elevational gradient and between forest edges and forest interior. The observed increase in basal area with elevation might indicate changes in human disturbance regimes with elevation (Midgley & Niklas 2004; Leithead et al. 2012). For example, Lovett et al. (2006) explained the increase of basal area with elevation in Tanzanian montane forests as higher logging intensities at lower elevations. However, we did not find indications for higher logging intensities at low elevations and maximum DBH in the study plots was unrelated to elevation in our study area ($n = 22$, Person's rho = 0.23, $P = 0.296$). Lower canopy height at forest edges than in the forest interior might be associated with high wind speeds and increased damage to canopy trees at edges (Saunders et al. 1991; Oosterhoorn & Kappelle 2000). Gorges and ridges in the forest interior did not differ in forest structure, and thus might experience similar levels of anthropogenic and natural disturbances.

Gradients in plant diversity

Species turnover was high along the three gradients, while species richness responded only weakly. Changes in species composition with elevation and topography contribute to the high diversity of tropical montane forests. In contrast to expectations, effects of topography on species turnover were stronger than that of elevation. Changes in species composition at edges caused an impoverishment of forest vegetation, indicated by lower species evenness and higher importance of pioneer species at forest edges.

Species turnover along elevational gradients may be attributed to changes in temperature (Ghalambor et al. 2006), whereas differences in species composition between ridges and gorges might be caused by differences in soil fertility and humidity (Homeier 2008). Since species turnover was higher between the topographical microhabitats than along the elevational gradient, it seems that soil properties and humidity affected species composition more than mean temperature at the here-investigated spatial scale. Topographical heterogeneity increases vegetation heterogeneity and thus plant species diversity of tropical montane forests (Homeier 2008), and should therefore be considered in conservation measures for tropical montane forests.

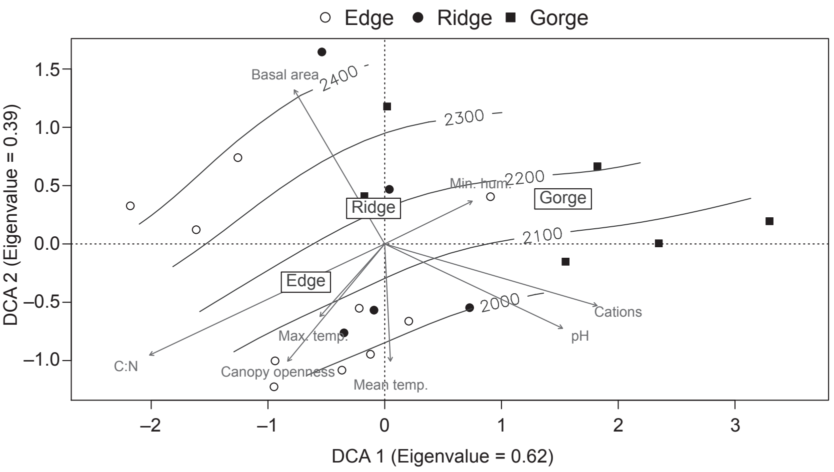

Fig. 3. Species composition of tropical montane forest remnants in the Bolivian Eastern cordillera along an elevational gradient of 600 m at forest edges and in the forest interior, on ridges and gorges. Detrended correspondence analysis (DCA) based on square root-transformed abundances of 259 species. Surface lines indicate elevation and centroids habitat types (i.e. edge, ridge and gorge). Arrows indicate significant effects of habitat conditions on species composition ($P < 0.05$ in Monte–Carlo permutations). Shown are effects of mean temperature, maximum temperature, minimum humidity, pH, content of exchangeable cations, C:N ratio, tree basal area and canopy openness; detailed statistical information is provided in Appendix S4.

Species composition was shifted by edge effects towards higher dominance of pioneer species at edges, e.g. *Myrsine coriacea* (Primulaceae) and *Cecropia elongata* (Urticaceae). Hot and dry microclimates (Kapos 1989; Didham & Lawton 1999), high irradiation caused by higher canopy openness (Saunders et al. 1991) and frequent fires (Laurance 2004) at edges promote the establishment of such pioneer species. While these changes in habitat conditions did not result in a loss of species richness, species evenness was reduced at forest edges, driven by the dominance of pioneer species. These findings highlight that studies that investigate effects of environmental gradients on plant diversity should not only focus on responses of taxonomic species richness but should also investigate changes in evenness and composition (Baraloto et al. 2012). Because the edge effects observed in this study were driven by increasing temperature and decreasing humidity, global warming might further increase the deleterious impacts of edge effects on forest structure and plant diversity, especially by an increased susceptibility to fire (Laurance & Williamson 2001).

Implications for plant responses to climate change

Studies of elevational gradients are essential for gaining insights into effects of climate change on vegetation in tropical mountains (Körner 2007). In response to climate change, a shift in species distribution has been observed in many taxa, including plants (Chen et al. 2011). For the tropical Andes, a previous study detected upslope migration of many plant species, likely due to global warming, of about 2.5–3.5 $\text{m}\cdot\text{yr}^{-1}$ (Feeley et al. 2011). However, observed migration rates were lower than expected based on the increase in temperature (Feeley et al. 2011). Almost all species distribution models and derived projections of species movements do not consider the high topographical heterogeneity and the associated small-scale climatic gradients (Ashcroft 2010; Suggitt et al. 2011) of tropical mountain forests. According to our findings, and at a vertical scale of 600 m in elevation, topographic gradients may be even more important as drivers of plant species turnover than climatic gradients associated with elevation. The importance of topographical variation has two important implications for plant responses to climate change. First, horizontal migration between different microhabitats characterized by specific climatic conditions might be as important as upslope migrations for many plant species, at least under the current rates of climatic warming. Such horizontal migrations could explain why a meta-analysis of species responses to climate change only found weak upslope migrations compared to expected elevational shifts (Chen et al. 2011). If this is the case, topographic heterogeneity could compensate to some extent for changes in climatic conditions, and topographic microhabitats could form microrefugia in tropical mountain ecosystems (Hopkins et al. 2007; Suggitt et al. 2011). This underscores the importance of topographic heterogeneity for conservation efforts in the tropical Andes. Second, the strong dependency of plant species on specific microhabitats, as indicated by the high number of plant species restricted either to ridge or gorge habitats, illustrates that upslope migrations of plant species could be constrained by the availability of specific microhabitats at higher elevations. Hence, plant species would not only need to move upslope but they would need to move in a directed fashion to appropriate microhabitats at higher elevations (Forero-Medina et al. 2011). This is likely to hamper upslope movements of many plant species in tropical mountain forests.

Conclusions

Gradients in elevation and topography and associated species turnover are the main drivers of the high diversity of tropical montane forests. Noteworthy, effects of the 600-m elevational gradient were weak compared to the small-scale effects of forest edge and topography on soil properties, species evenness and species turnover. These findings have two important implications for the conservation of tropical mountain forests. First, the dominance of disturbance-adapted species at forest edges likely leads to an impoverishment of forest vegetation in the long term. Second, in response to current climate change, horizontal migration of plant species between different microhabitats should be considered in simplified models of upslope migrations in tropical mountains.

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References

Ashcroft, M.B. 2010. Identifying refugia from climate change. *Journal of Biogeography* 37: 1407–1413.

Baraloto, C., Hérault, B., Paine, C.E.T., Massot, H., Blanc, L., Bonal, D., Molino, J.-F., Nicolini, E.A. & Sabatier, D. 2012. Contrasting taxonomic and functional responses of a tropical tree community to selective logging. *Journal of Applied Ecology* 49: 861–870.

Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. 2008. *Gradients in a tropical mountain ecosystem of Ecuador*. Springer, Berlin, DE.

Bendix, J., Rollenbeck, R., Richter, M., Fabian, P. & Emck, P. 2008. Climate. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (eds.) *Gradients in a tropical mountain ecosystem of Ecuador*, pp. 63–74. Ecological Studies. Springer, Berlin, DE.

Brown, S. & Lugo, A.E. 1990. Tropical secondary forests. *Journal of Tropical Ecology* 6: 1–32.

Chen, Z.-S., Hsieh, C.-F., Jiang, F.-Y., Hsieh, T.-H. & Sun, I.-F. 1997. Relations of soil properties to topography and vegetation in a subtropical rain forest in southern Taiwan. *Plant Ecology* 132: 229–241.

Chen, I.-C., Hill, J.K., Ohlemuller, R., Roy, D.B. & Thomas, C.D. 2011. Rapid range shifts of species associated with high levels of climate warming. *Science* 333: 1024–1026.

Daws, M.I., Mullins, C.E., Burslem, D.F.R.P., Paton, S.R. & Dalling, J.W. 2002. Topographic position affects the water regime in a semideciduous tropical forest in Panama. *Plant and Soil* 238: 79–89.

Didham, R.K. & Lawton, J.H. 1999. Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* 31: 17–30.

Dufrene, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.

FAO (Food and Agriculture Organization) 2011. *State of the World's forests 2011*. FAO, Rome, IT.

Feeley, K.J., Silman, M.R., Bush, M.B., Farfan, W., Cabrera, K.G., Malhi, Y., Meir, P., Revilla, N.S., Quisiyupanqui, M.N.R. & Saatchi, S. 2011. Upslope migration of Andean trees. *Journal of Biogeography* 38: 783–791.

Forero-Medina, G., Joppa, L. & Pimm, S.L. 2011. Constraints to species' elevational range shifts as climate changes. *Conservation Biology* 25: 163–171.

Gentry, A.H. 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75: 1–34.

Gentry, A.H. 1995. Patterns of diversity and floristic composition in neotropical montane forests. In: Churchill, S.P., Balslev, H., Forero, E. & Luteyn, J.L. (eds.) *Biodiversity and conservation of Neotropical montane forests*, pp. 103–126. The New York Botanical Garden, New York, NY, US.

Gerold, G., Schawe, M. & Bach, K. 2008. Hydrometeorologic, pedologic and vegetation patterns along an elevational transect in the montane forest of the Bolivian Yungas. *Die Erde* 139: 141–168.

Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J. & Wang, G. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology* 46: 5–17.

Guariguata, M.R. & Ostertag, R. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* 148: 185–206.

Henderson, A., Churchill, S.P. & Luteyn, J.L. 1991. Neotropical plant diversity. *Nature* 351: 21–22.

Herwitz, S.R. & Young, S.S. 1994. Mortality, recruitment, and growth rates of montane tropical rain forest canopy trees on Mount Bellenden-Ker, Northeast Queensland, Australia. *Biotropica* 26: 350–361.

Doi: 10.1111/jvs.12132

Homeier, J. 2008. The influence of topography on forest structure and regeneration in an Ecuadorian mountain forest. In: Gradstein, S.R., Homeier, J. & Gansert, D. (eds.) *The tropical mountain forest – Patterns and processes in a biodiversity hotspot*, pp. 97–107. Biodiversity and Ecology Series. Universitätsverlag Göttingen, Göttingen, DE.

Homeier, J., Breckle, S.-W., Günter, S., Rollenbeck, R.T. & Leuschner, C. 2010. Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species-rich Ecuadorian montane rain forest. *Biotropica* 42: 140–148.

Hopkins, J.J., Allison, H.M., Walmsley, C.A., Gaywood, M. & Thurgate, G. 2007. *Conserving biodiversity in a changing climate: guidance on building capacity to adapt*. Department for the Environment, Food and Rural Affairs, London, UK.

Hurlbert, S.H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52: 577–586.

Jongman, R.H., Ter Braak, C.J. & Van Tongeren, O.F. 1995. *Data analysis in community and landscape ecology*. Cambridge University Press, Cambridge, UK.

Kapos, V. 1989. Effects of isolation on the water status of forest patches in the Brazilian Amazon. *Journal of Tropical Ecology* 5: 173–185.

Kessler, M. & Beck, S.G. 2001. Bosques nublados del Neotropico. In: Kappelle, M. & Brown, A.D. (eds.) *Bosques Nublados del Neotropico*, pp. 581–622. Instituto Nacional de Biodiversidad INBio, Santo Domingo de Heredia, CR.

Kier, G., Mutke, J., Dinerstein, E., Ricketts, T.H., Küper, W., Kreft, H. & Barthlott, W. 2005. Global patterns of plant diversity and floristic knowledge. *Journal of Biogeography* 32: 1107–1116.

Killeen, T., Siles, T., Soria, L. & Correa, L. 2005. Estratificación de vegetación y cambio de uso de suelo en los Yungas y Alto Beni de La Paz. *Ecología en Bolivia* 40: 32–69.

Kitayama, K. & Aiba, S.-I. 2002. Ecosystem structure and productivity of tropical rain forests along altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu, Borneo. *Journal of Ecology* 90: 37–51.

Körner, C. 2007. The use of "altitude" in ecological research. *Trends in Ecology & Evolution* 22: 569–574.

Kubota, Y., Murata, H. & Kikuzawa, K. 2004. Effects of topographic heterogeneity on tree species richness and stand dynamics in a subtropical forest in Okinawa Island, Southern Japan. *Journal of Ecology* 92: 230–240.

Laurance, W.F. 2004. Forest–climate interactions in fragmented tropical landscapes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 359: 345–352.

Laurance, W.F. & Williamson, G.B. 2001. Positive feedbacks among forest fragmentation, drought, and climate change in the Amazon. *Conservation Biology* 15: 1529–1535.

Lawton, R.O. 1982. Wind stress and elfin stature in a montane rain forest tree: an adaptive explanation. *American Journal of Botany* 69: 1224.

Leithead, M., Anand, M., Duarte, L. & D. Pillar, V. 2012. Causal effects of latitude, disturbance and dispersal limitation on richness in a recovering temperate, subtropical and tropical forest. *Journal of Vegetation Science* 23: 339–351.

Lieberman, D., Lieberman, M., Peralta, R. & Hartshorn, G.S. 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *Journal of Ecology* 84: 137–152.

Lippok, D., Beck, S.G., Renison, D., Gallegos, S.C., Saavedra, F.V., Hensen, I. & Schleuning, M. 2013. Forest recovery of areas deforested by fire increases with elevation in the tropical Andes. *Forest Ecology and Management* 295: 69–76.

Lovett, J.C., Marshall, A.R. & Carr, J. 2006. Changes in tropical forest vegetation along an altitudinal gradient in the Udzungwa Mountains National Park, Tanzania. *African Journal of Ecology* 44: 478–490.

Markesteijn, L., Iraipi, J., Bongers, F. & Poorter, L. 2010. Seasonal variation in soil and plant water potentials in a Bolivian tropical moist and dry forest. *Journal of Tropical Ecology* 26: 497–508.

Midgley, J.J. & Niklas, K.J. 2004. Does disturbance prevent total basal area and biomass in indigenous forests from being at equilibrium with the local environment? *Journal of Tropical Ecology* 20: 595–597.

Molina-Carpio, J. 2005. Régimen de precipitación en la cuenca de Huarinilla-Cotapata, La Paz-Bolivia. *Ecología en Bolivia* 40: 43–55.

Moser, G., Röderstein, M., Soethe, N., Hertel, D. & Leuschner, C. 2008. Altitudinal changes in stand structure and biomass allocation of tropical mountain forests in relation to microclimate and soil chemistry. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (eds.) *Gradients in a tropical mountain ecosystem of Ecuador*, pp. 229–242. Ecological Studies. Springer, Berlin, DE.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A. & Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Oesker, M., Dalitz, H., Günter, S., Homeier, J. & Matezki, S. 2008. Spatial heterogeneity patterns — a comparison between gorges and ridges in the upper part of an evergreen lower montane forest. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F. & Mosandl, R. (eds.) *Gradients in a tropical mountain ecosystem of Ecuador*, pp. 267–274. Ecological Studies. Springer, Berlin, DE.

Oosterhoorn, M. & Kappelle, M. 2000. Vegetation structure and composition along an interior–edge–exterior gradient in a Costa Rican montane cloud forest. *Forest Ecology and Management*. 26: 291–307.

Pielou, E.C. 1975. *Ecological diversity*. Wiley, New York, NY, US.

Punchi-Manage, R., Getzin, S., Wiegand, T., Kanagaraj, R., Savitri Gunatilleke, C.V., Nimal Gunatilleke, I.A.U., Wiegand, K. & Huth, A. 2013. Effects of topography on structuring local species assemblages in a Sri Lankan mixed dipterocarp forest. *Journal of Ecology* 101: 149–160.

Santos, B.A., Peres, C.A., Oliveira, M.A., Grillo, A., Alves-Costa, C.P. & Tabarelli, M. 2008. Drastic erosion in functional attributes of tree assemblages in Atlantic forest fragments of northeastern Brazil. *Biological Conservation* 141: 249–260.

Saunders, D.A., Hobbs, R.J. & Margules, C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5: 18–32.

Soethe, N., Lehmann, J. & Engels, C. 2008. Nutrient availability at different altitudes in a tropical montane forest in Ecuador. *Journal of Tropical Ecology* 24: 397–406.

Suggitt, A.J., Gillingham, P.K., Hill, J.K., Huntley, B., Kunin, W.E., Roy, D.B. & Thomas, C.D. 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. *Oikos* 120: 1–8.

Takyu, M., Aiba, S.-I. & Kitayama, K. 2003. Changes in biomass, productivity and decomposition along topographical gradients under different geological conditions in tropical lower montane forests on Mount Kinabalu, Borneo. *Oecologia* 134: 397–404.

Tanner, E.V.J. 1977. Four montane rain forests of Jamaica: a quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. *Journal of Ecology* 65: 883–918.

Tanner, E.V.J., Vitousek, P.M. & Cuevas, E. 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology* 79: 10–22.

Taylor, B.R., Parkinson, D. & Parsons, W.F. 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70: 97–104.

Unger, M., Leuschner, C. & Homeier, J. 2010. Variability of indices of macronutrient availability in soils at different spatial scales along an elevation transect in tropical moist forests (NE Ecuador). *Plant and Soil* 336: 443–458.

Weaver, P. 2010. Forest structure and composition in the lower montane rain forest of the Luquillo Mountains, Puerto Rico. *Interciencia* 35: 640–646.

Webb, E.L., Stanfield, B.J. & Jensen, M.L. 1999. Effects of topography on rainforest tree community structure and diversity in American Samoa, and implications for frugivore and nectarivore populations. *Journal of Biogeography* 26: 887–897.

Wilcke, W., Boy, J., Goller, R., Fleischbein, K., Valarezo, C. & Zech, W. 2011. Effect of topography on soil fertility and water flow in an Ecuadorian lower montane forest. In: Bruijnzeel, L.A., Scatena, F.N. & Hamilton, L.S. (eds.) *Tropical montane cloud forests: science for conservation and management*, pp. 402–409. Cambridge University Press, Cambridge, UK.

Williams-Linera, G., Domínguez-Gastelú, V. & García-Zurita, M.E. 1998. Microenvironment and floristics of different edges in a fragmented tropical rainforest. *Conservation Biology* 12: 1091–1102.

Wolf, K., Veldkamp, E., Homeier, J. & Martinson, G.O. 2011. Nitrogen availability links forest productivity, soil nitrous oxide and nitric oxide fluxes of a tropical montane forest in southern Ecuador. *Global Biogeochemical Cycles* 25: GB4009

Zhang, Q. & Zak, J.C. 1995. Effects of gap size on litter decomposition and microbial activity in a subtropical forest. *Ecology* 76: 2196.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Map of the study area. (a) Sampling plots (red triangles) were spatially blocked in six sampling sites distributed over two major forest remnants (green), embedded in a matrix of deforested habitats (grey). (b) Sampling plot distribution of the three habitat types, i.e. forest edge, ridge and gorge, along the elevational gradient.

Appendix S2. Tree diversity (all woody plants with DBH ≥ 10 cm) in tropical montane forest remnants in the Bolivian Eastern cordillera along an elevational gradient of 600 m at forest edges and in the forest interior, on ridges and gorges. (a) Observed species richness (species 400 m^{-2}), (b) rarefied species richness (species per 14 individuals) and (c) species evenness. P- and t-values were derived from linear mixed effects models, accounting for random variation among sites, and are based on t-tests of the model estimates for elevation and for the two orthogonal contrasts of habitat type, i.e. edge vs interior, and ridge vs gorge. The dashed line in the box plots visualizes the comparison between forest edges (left side) and forest interior (right side). Horizontal lines across boxes are medians, boxes indicate 25th and 75th percentiles, whiskers indicate the data range, and circles are outliers.

Appendix S3. Species list of 259 taxa recorded in tropical montane forest remnants in the Bolivian Eastern cordillera along an elevational gradient of 600 m at forest edges and in the forest interior, on ridges and gorges. Abundance (and number of sampling plots) of species in the three habitat types (i.e. edge, ridge and gorge) are shown. Asterisks indicate endemic species.

Appendix S4. Correlations of (a) the three gradients (i.e. elevation, forest edge and topography) and (b) habitat conditions (i.e. soil properties, microclimate and forest structure) with patterns in species composition derived from detrended correspondence analysis (DCA). Score 1 and score 2 indicate the ordination centroids (for factors) or arrow endpoints (for continuous predictors). Squared correlation coefficients (R^2) and their associated P-values (based on 999 permutations) indicate the proportion of variance in species composition that is explained by the respective predictor variable.