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### Spatial patterns of above-ground structure, biomass and composition in a network of six Andean elevation transects

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## Spatial patterns of above-ground structure, biomass and composition in a network of six Andean elevation transects

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**Background:** The Amazon to Andes transition zone provides large expanses of relatively pristine forest wilderness across environmental gradients. Such elevational gradients are an excellent natural laboratory for establishing long-term interactions between forest ecosystems and environmental parameters, which is valuable for understanding ecosystem responses to environmental change.

**Aims:** This study presents data on elevational trends of forest structure (biomass, basal area, height, stem density), species richness, and composition from six elevational transects in the Andes.

**Methods:** We analysed the spatial patterns of forest structure, above-ground biomass and composition from 76 permanent plots, ranging from lowland Amazonian rain forest to high-elevation cloud forests in Ecuador, Peru, and Bolivia.

**Results:** Forest above-ground woody biomass stocks ranged from 247 Mg ha<sup>-1</sup> (Peru, 210 m) to 86 Mg ha<sup>-1</sup> (Peru, 3450 m), with significantly decreasing trends of tree height and biomass and an increasing trend of stem density with increasing elevation. We observed an increase in forest richness at three taxonomic levels at mid-elevation, followed by a decrease in richness within the cloud immersion zone.

**Conclusions:** The transects show an increase in stem density, a decline in tree height and above-ground coarse wood biomass and a hump-shaped trend in species richness with increasing elevation. These results suggest that environmental change could lead to significant shifts in the properties of these ecosystems over time.

**Keywords:** Andes; ecophysiology; elevation gradient; biomass; forest composition; precipitation; temperature; tropical montane forests

### Introduction

Elevation gradients in tropical forests are a powerful tool to improve our understanding of the relationship between environmental parameters and ecosystem structure (Malhi et al. 2010). Andean elevational gradients have harboured studies on temperature and biodiversity (Jørgensen et al. 2011; Larsen et al. 2011; Jankowski et al. 2012), species distributional ecology (Feeley et al. 2011a; Rapp et al. 2012), ecosystem function (Graefe et al. 2008; Zimmerman et al. 2009a, 2009b; Girardin et al. 2010; Salinas et al. 2011) and response to global change drivers (Feeley et al. 2011b) of forest ecosystems. In particular, tropical montane forests (TMF) and the adjoining Amazonian lowlands are amongst the most poorly studied terrestrial ecosystems on earth (Curchill 1993; Kapelle and Brown 2001) and developed along strong environmental gradients over short distances (Pounds et al. 1999; Still et al. 1999; Myers et al. 2000; Bubb et al. 2004; Killeen et al. 2007). As they provide short distances to migrate, these ecotones may become potential

refuges for adjoining lowland ecosystems, depending on species-specific upward migration rates (Colwell et al. 2008; Feeley et al. 2011a).

Whereas large quantities of data on carbon cycling in lowland tropical forests have become available in the past few years (Malhi et al. 2004; Luyssaert et al. 2007; Aragão et al. 2009; Malhi et al. 2009, 2014) there remains little information on patterns of carbon cycling in montane forests (Pitman et al. 2011) (see also Table 2). Difficulty of access and focus on lowland rather than montane regions have resulted in a lack of qualitative and quantitative baseline data needed to make accurate scientific predictions on the fate of the Andes to Amazon corridor. A clear mechanistic understanding of how Andean TMF ecosystems are correlated with climatic parameters is an essential step towards understanding their carbon cycle, the CO<sub>2</sub> feedback processes likely to further affect climatic change, and formulating adequate policy responses to mitigate increasing climatic pressures. The effects of predicted changes in

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Table 1. Metadata on elevation, plot numbers, sampling intensity and availability of weather data in each elevation transect.

Country	Department/Region	Minimum elevation (m a.s.l.)	Maximum elevation (m a.s.l.)	Number of plots	Trees per hectare ( <i>n</i> )	Weather data available (y/n)
Bolivia	Beni	800	480	3	521	Yes
Bolivia	Santa Cruz	60	1200	7	796	Yes
Bolivia	Madidi	175	3116	33	700	No
Ecuador	Cordillera del Cóndor	130	1200	8	631	No
Peru	Junin	1075	2100	6	522	Yes
Peru	Cusco	194	3025	14	753	Yes

temperature, rainfall and cloud cover seasonality on these TMF are potentially very significant, but remain poorly understood (Bruijnzeel and Proctor 1995; Houghton et al. 2000).

However, few data exist on the structure and functioning of TMF, particularly in South America: the difficulty of access and disproportionate funding flows to lowland rather than montane tropical regions have resulted in a lack of baseline qualitative and quantitative data to make accurate scientific predictions. One of the reasons for our greater knowledge of lowland Amazonian ecosystems is the success of networks of permanent plots, such as RAINFOR (The Amazon Forest Inventory Network; Malhi et al. 2002; Peacock et al. 2007), to act as research foci and allow large-scale studies of spatial and temporal changes in forest dynamics (e.g. Higgins et al. 2011; Quesada et al. 2012; Butt et al. 2014). However, no such networks have previously existed in TMF in South America. This study therefore presents data from a new network of permanent plots in Andean forests and adjoining lowlands, to provide a platform for monitoring the impacts of climate change. Specifically, we have compiled data from 76 permanent 1 ha inventory plots, ranging from high-elevation cloud forests to lowland Amazonia from Ecuador, Peru, and Bolivia (Table 1). These data allow us to identify the main trends in forest structure, plant richness at different taxonomic levels and above-ground biomass along Andean elevation gradients (Table 2).

The present study aimed to:

- (i) Provide baseline information from the first elevational transect network in the tropics.
- (ii) Understand how forest structure, richness, composition and biomass changes with elevation.
- (iii) Discuss the potential for these Andean sites to become a network to monitor forest dynamics, biodiversity and ecosystem function.

## Materials and methods

### Study sites

The present study reports data compiled from six, independently run, TMF elevation transects located in Bolivia, Peru and Ecuador (Figure 1). Table 1 provides information on sampling intensity, elevation, location, and protocols for

each of the six elevational transects. At all sites, forest inventory data were collected using the RAINFOR protocol (Metcalf et al. 2009). In each plot, every tree was identified, labelled and tracked through time. Typically, plots provide information on all trees  $\geq 10$  cm diameter at a reference height of 1.3 m. For each plot, there is at least one census, information on the taxonomy of the trees, the diameter at breast height (DBH) and tree height. All data were standardised according to RAINFOR protocols.

Data on precipitation, temperature, and soil properties were available for 19 plots in Peru and 10 plots along one of the Bolivian transects. Weather data were collected from local weather stations located within 3 km of each site. In Peru, solar radiation, air temperature, relative humidity and precipitation time series were collected from automatic weather stations (AWS, Campbell Scientific) located at 3000, 1500, and 200 m elevation (Halladay et al. in review). Data were measured with at least 30 min resolution for the period July 2005 to December 2010. These data were quality controlled to remove outliers and gap-filled using data from a nearby Peruvian Servicio Nacional de Meteorología e Hidrología (SENAMHI) stations at Acjanaco (13.20°S, 71.62°W, 3000 m a.s.l.), Chontachaca (13.02°S, 71.47°W, elevation 880 m), and Puerto Maldonado (12.58°S, 69.20°W, 200 m a.s.l.), according to the methodology described in Halladay et al. (in review).

### Forest structure, carbon stocks and composition

For each plot, we used measurements of canopy height, basal area and stem density to estimate above-ground biomass. DBH and tree height measurements were converted into estimates of coarse wood biomass, using allometric equations for moist forest stands that relate tree diameter and height to biomass (Chave et al. 2005):

$$AGB = 0.0776 * (\rho \cdot DBH^2 \cdot H)^{0.94} \quad (1)$$

where *AGB* is above-ground biomass in kg,  $\rho$  is wood density (family or genus means, or species-specific values) obtained from a global tropical forest wood density database (Chave et al. 2009; Zanne et al. 2009), *DBH* is diameter at breast height in cm, and *H* is height in m. Where tree height was not available for particular trees, it was estimated by fitting an exponential model to existing height

Table 2. Trends in forest structure along elevation transects in the ecological literature. Arrows indicate the trend reported in each study; N/A, data not available; MAT, mean annual temperature; ANPP, annual net primary production.

Transect	Elevation (m)	MAT (°C)	Rainfall (mm year <sup>-1</sup> )	Soil type	Canopy height	Leaf Area Index	Stem density (trees/ha)	Basal area	Diameter at breast height	Soil organic matter	Species richness	Reference
Ecuadorian Andes, SE of Loja	1890–3060	14.9–8.6	1950 (1890 m); 5000 (2380 m); 4500 (3060 m)	Humic cambisols								Röderstein et al. (2005); Leuschner et al. (2007)
Mauna Loa, Hawaii, USA	290–1660	22–13	4000 (290 m); 5900 (700 m); 2500 (1660 m)	Volcanic ash substrate and 3400-yr-old 3400-yr-old pahoehoe lava flow.	↓	N/A	↓	↓	N/A	↑	↑	Raich et al. (1997).
Hawaian Islands: Hawaii Molokai, Kauai.	915–1200	16	2500	Organic soil on aa lava and ejecta; Histic Placaquept; Terric Troposaprist	N/A	↓	↑	↑	↔	↑	N/A	Herbert and Fownes (1999); Townsend et al. (1995)
Mount Kinabalu, Borneo	700–3100	24–21	2509–3285	Sedimentary and ultrabasic soils	↓	↓	↑	↑	↔	N/A	↓	Aiba and Kitayama (1999, 2002); Takyu (2002)
Luquillo Mountains, Puerto Rico	200–1075	23–19	2300–4500	Clays and loams; ultisols and inceptisols	↓	↓	↑	↑	↓	↑	↓	Weaver (1986, 1990)
Volcan Brava (forest structure) & Monteverde (ANPP), Costa Rica	32–2600	24–10.5	2900 (32 m); 8000 (700 m); 3300 (2600 m)	Basaltic and andesitic lavas of Pilo-Pleistocene age	↓	N/A	N/A	↑	↔	N/A	↓	Lieberman (1996)

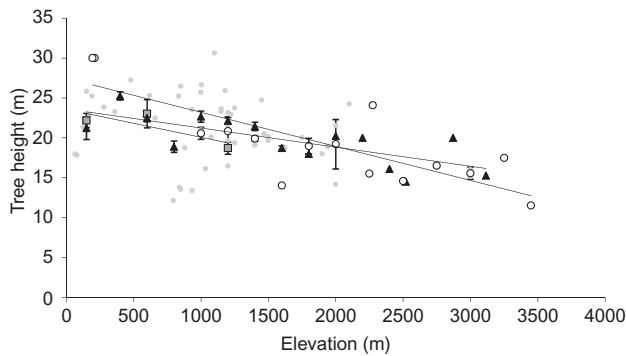


Figure 1. Tree height along elevation for all Andean 1 ha permanent plots included in this study. Grey circles represent average height values for each plot (m), all other points represent average values in Ecuador (grey squares), Bolivia (black triangles), and Peru (open circles). Aggregated average values were obtained in every 200 m elevational steps. Only plots with height data are included.

and DBH data from other transects for trees at that elevation. Tree ferns and palms were identified and their biomass was estimated, assuming they had a cylindrical shape and by using their height where available. Where fern height data were unavailable, we estimated the average height of tree ferns in that plot to gap-fill the data. Above-ground biomass was estimated by summing all tree above-ground biomass in the area of each plot. To convert biomass values into carbon, we assumed that stem biomass was 50% C (Chave et al. 2005). Canopy height was estimated as the mean height of all trees with DBH  $\geq 40$  cm. Basal area was calculated as the summed cross-sectional area at breast height for all trees  $\geq 10$  cm DBH. Stem density was the number of stems ( $\geq 10$  cm DBH) per ha.

We present data on forest composition at family, genus and species level and compared the frequency of tree families, genera and species along the elevational gradients. Identifications were made based on herbarium specimens collected from the plots and deposited at relevant institutions (in Peru: CUZ, USM, MOL, in Bolivia LPB, USZ, in Ecuador: QCNE; most of the sites also have duplicates in MO (USA)). Identifications were carried out by local botanists with the support of specialists from MO. This project began in 2007–08 (prior to the launch of the Angiosperm Phylogeny Group III system), hence we used MOBOT (<http://www.tropicos.org/>) and the RAINFOR data base as taxonomic conventions. We standardised the species names across plots and transects, and the identifications were compared across plots for the Peruvian sites. However, identifications (species and morphospecies) were not compared across transects. We estimated the elevation of the lowest, highest, and most frequent occurrence of each genus in the six transects. For the entire dataset, 49% of stems were identified to species, 68% to genus, 54% to family level. Understanding Andean vascular plant richness patterns is complicated by the fact that perhaps more than 50% of tropical Andean biodiversity

remains undescribed (Larsen et al. 2011). Hence, genus-level analysis helps minimise possible errors due to individuals that could not be reliably identified to species (Feeley et al. 2011b).

#### Analytical techniques

Linear regression analyses were conducted to identify significant elevational trends in forest characteristics and allocation to above-ground biomass. All statistical analyses were performed with the R version 2.9.0 statistical package (R Development Core Team, 2011). All uncertainty estimates are given as the standard errors of the mean.

## Results

### Climate

Mean annual temperatures (MAT) decreased linearly with elevation along all gradients, ranging from 25.45 °C (250 m) to 8.93 °C (3450 m). These results are similar to the temperature lapse rates of ca. 5.5 °C km<sup>-1</sup> reported from Peru by previous studies (Treborgh 1996; Bush et al. 2004; Girardin et al. 2010; Rapp et al. 2012). However, precipitation, soil water content (SWC) and light incidence were not related to elevation. In the Andes, annual precipitation obtained from local weather stations varied between approximately 900 mm year<sup>-1</sup> (Bolivia, 1200 m) and 5000 mm year<sup>-1</sup> at ca. 1500 m (Peru). Precipitation patterns may be explained by microsite effects along the elevational gradient, due to topographic effects rather than elevation (Killeen et al. 2007; Moser et al. 2008). As we did not obtain information on the elevation of the cloud cover base for each transect, we assumed that cloud cover influenced vegetation formations at 1500–2000 m throughout the Andes.

### Forest structure and biomass

We found a significant decline in tree height with increasing elevation in Peru (slope =  $-0.0043$ ,  $r^2 = 0.63$ ,  $P < 0.01$ ), Bolivia (slope =  $-0.0035$ ,  $r^2 = 0.65$ ,  $P < 0.01$ ) and Ecuador (slope =  $-0.0024$ ,  $r^2 = 0.54$ ,  $P < 0.01$ ), with no significant difference in slopes among countries (Figure 1). We found no trend in basal area along elevational gradients, with values of basal area ranging between 13 and 49 m<sup>2</sup> ha<sup>-1</sup> (Figure 2). Stem density increased significantly with elevation (decreasing MAT) in Ecuador (slope = 0.36,  $r^2 = 0.99$ ,  $P < 0.01$ ), Bolivia (slope = 0.59,  $r^2 = 0.91$ ,  $P < 0.01$ ), but was constant in the Peruvian Andes (Figure 3).

There was a decline in above-ground coarse woody biomass along elevational gradients in Peru (slope =  $-0.034$ ,  $r^2 = 0.57$ ,  $P < 0.01$ ), Bolivia (slope =  $-0.032$ ,  $r^2 = 0.42$ ,  $P < 0.05$ ) and Ecuador (slope =  $-0.050$ ,  $r^2 = 0.41$ ,  $P < 0.05$ ) (Figure 4). As there was no trend in basal area with elevation, we conclude that the biomass decline was largely driven by reduced tree height with increasing elevation.



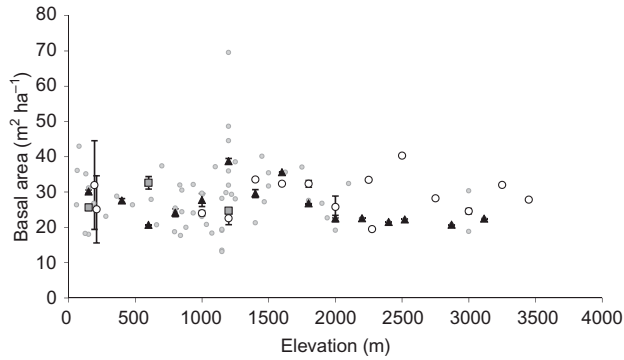


Figure 2. Basal area along elevation in all 1 ha plots of the Andean network (grey circles,  $\text{m}^2 \text{ha}^{-1}$ ) and averaged in groups of 200 m elevational steps for Ecuador (grey squares), Bolivia (black triangles), and Peru (open circles). Error bars are SE of the mean.

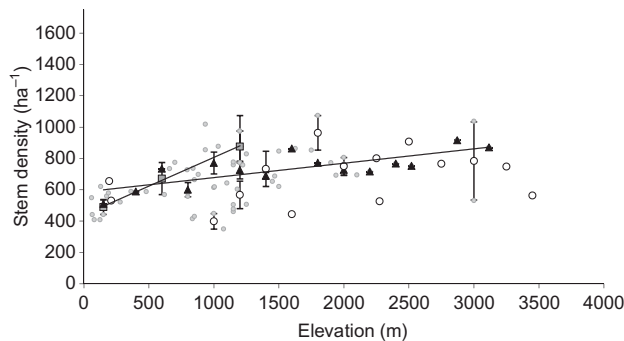


Figure 3. Stem density along elevation gradients in all 1 ha plots of the Andean network (grey circles) and averaged in groups of 200 m elevational steps for Ecuador (grey squares), Bolivia (black triangles), and Peru (open circles). Error bars are SE of the mean.

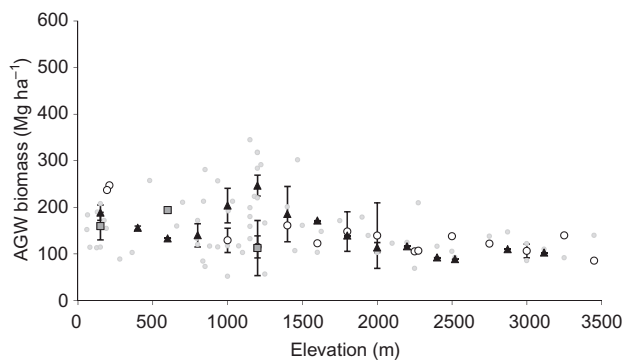


Figure 4. Above-ground dry coarse wood (ACW) biomass from Andes plots (grey circles,  $\text{Mg ha}^{-1}$ ) and averages for Ecuador (open squares), Bolivia (filled triangles), and Peru (open circles), grouped in 200 m elevational steps. Error bars are SE of the mean.

#### Family, genera and species richness

There were mid-elevational peaks (1000–1500 m) in numbers of families, genera and species and a steady decline in species richness above 1500 m in all transects (Figure 5). Combining genus-level data from all elevational gradients showed that most genera had a narrow elevational range and that many were most abundant at the top or bottom of their

elevational range (Figure 6). In Peru and Bolivia, 49% and 34 % of genera peaked in stem abundance between 1200 m and 1800 m, at the base or below the cloud base (Figure 6). This trend emphasised the importance of the cloud formation as a driver of species composition turnover along Andean elevation gradients.

## Discussion

### Tree height, basal area and stem density

Height decreased, stem number increased and basal area decreased along the Andean altitudinal transect. We searched the literature to review existing information on forest structure of TMFs (Grubb and Whitmore 1966; Bruijnzeel and Veneklaas 1998; Schuur and Matson 2001; Röderstein et al. 2005; Girardin et al. 2010); our observations of decreasing tree height and increased stem density in particular are consistent with observations from Borneo, Puerto Rico, Costa Rica and Ecuador (Table 2). In each of the six transects, species composition varied considerably among plots, significantly impacting the spatial variability of above-ground carbon stocks as above-ground biomass of mature trees is linked species species attain large sizes. Most published studies report structural and functional differences in Tropical Montane Cloud Forests (TMCF) compared with lowland rainforests, with most notably an increase in stem density, basal area and soil organic matter depth and a decline in tree height, leaf area index, species richness (Table 2), above-ground carbon stocks (Table 3) and net primary productivity (Tanner 1980; Raich et al. 1997; Schuur and Matson 2001; Kitayama and Aiba 2002) with increasing elevation. The Raich et al. (1997) study in Mauna Loa, Hawaii, provides conflicting findings which may be explained by a variation in soil parent material among sites (volcanic ash and pahoehoe lava) as well as overall low species richness. All of the studies associate these trends with cooler temperatures, fog, reduced light incidence and higher relative humidity. These factors are thought to interact to result in cool, saturated soils and therefore slower mineralisation of dead organic matter and slow nutrient cycling (Salinas et al. 2011).

We found relatively consistent patterns of key forest structure characteristics with elevation (hence temperature) gradients. However, our analysis also highlights a high spatial variability comparable with that reported from Amazonian lowlands (Anderson et al. 2009). This is best illustrated by plots located around 1200 m, with tree height (10–21 m), stem density (460–975 stems), basal area (13–70  $\text{m}^2 \text{ha}^{-1}$ ) and stem biomass (56–345  $\text{Mg ha}^{-1}$ ) displaying high spatial variability across the transects.

It is important to stress that our analysis treats elevation as a way of presenting data along a gradient, not as a direct controlling factor (Körner 1998). Nonetheless, the close correlations observed between elevation and MAT in all elevational transects suggests that any significant relationship observed between forest ecosystem characteristics and elevation implies a significant relationship with MAT.

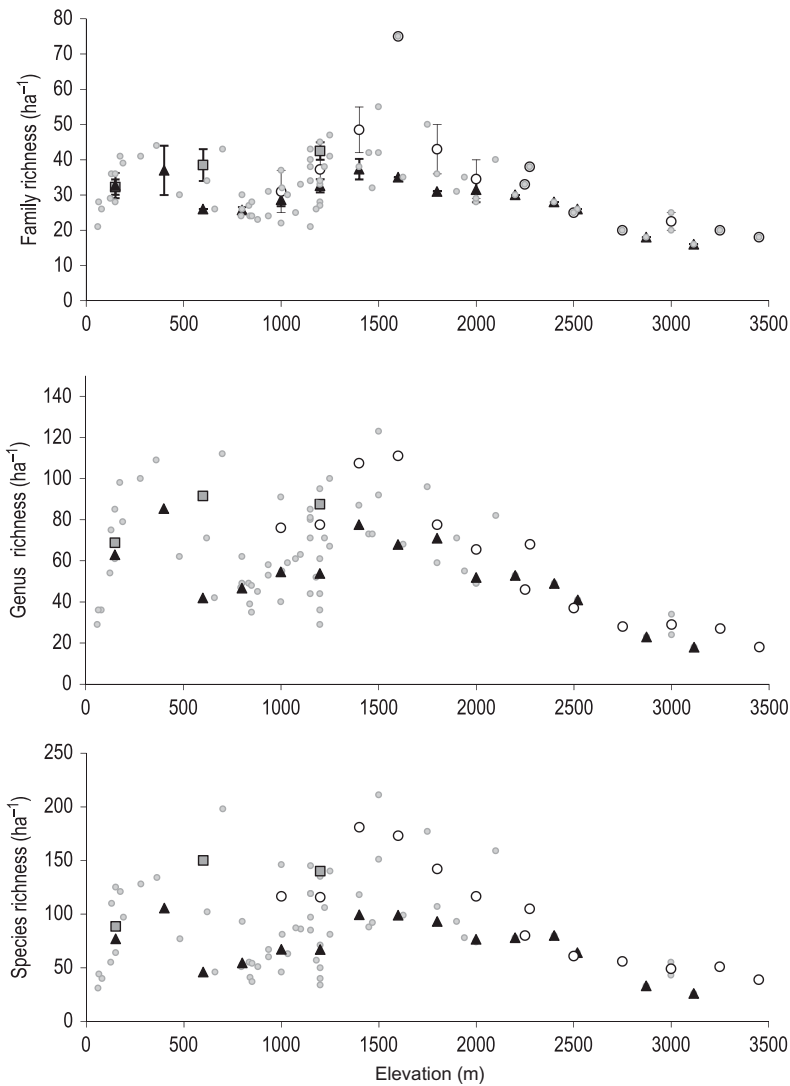


Figure 5. Number (ha<sup>-1</sup>) of families, genera, species and individuals (grey circles) vs. elevation in all plots of the Andean network, in Peru (open circles), Bolivia (black triangles) and Ecuador (grey squares).

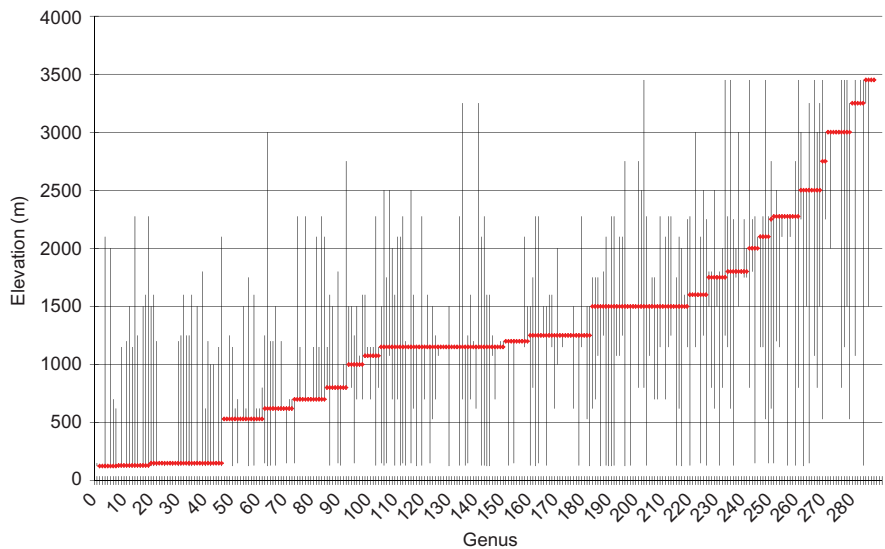


Figure 6. Analysis of forest composition at the genus level. Horizontal lines indicate the estimated approximate elevations of the cloud base at the sites. Vertical bars indicate the estimated limits of genus range, red diamonds indicate elevation of highest abundance. The genera are ranked by increasing elevation of highest abundance.



Table 3. Above-ground coarse woody (ACW) biomass, mean annual temperature (MAT) and rainfall trends in tropical montane forests.

Site	Elevation (m)	MAT (°C)	Rainfall (mm year <sup>-1</sup> )	ACW biomass (Mg ha <sup>-1</sup> )	Source
Ecuadorian Andes	1050	18.9	—	207	Leuschner et al. (2007)
	1540	16.7	—	118	Graefe et al. (2008)
	1890	14.9	1950	133	
	2380	12.3	5000	746	
	3060	8.6	4500	738	
Hawaii	915	16	1200	109–202	Herbert and Fownes (1999), Crews (1995)
New Guinea (Mt Kerigom)	2400–2500	13	3985	155	Edwards and Grubb (1977)
Puerto Rico	500	—	—	74–99	Ovington (1970)
Venezuela	2640–3000	—	—	197	Delaney et al. (1997)
	2310–2450	—	—	177	
	210–270	—	—	198	
Peruvian Andes	194	26.4	2730	237.04	Girardin et al. (2010)
	210	26.4	2730	246.99	
	1000	20.7	3087	158.90	
	1500	18.8	5302	205.65	
	1855	18.03	2472	111.15	
	2020	17.4	1827	77.24	
	2720	13.5	2318	131.87	
	3020	11.8	1776	94.06	
	3025	11.8	1560	129.88	

#### Above-ground coarse woody biomass

As allometric equations for TMFs have not been developed, we used a lowland forest allometry equation for moist tropical forests, including height (Equation (1)). Our observations on forest structure lead us to attribute the consistently recorded decline in stem biomass solely to the change in tree height with increasing elevation, highlighting the importance of including tree height when estimating stem carbon stocks in tropical montane forests. Girardin et al. (2010) estimated that assuming lowland forest allometry while omitting tree height in biomass estimates would result in a systematic overestimation of  $52\% \pm 10\%$  biomass at higher elevations.

Our analysis of the Andean plots network indicates that a decrease in above-ground biomass is a characteristic feature of TMFs across the study sites (Figure 4). Although there is a long record of forest above-ground biomass measurement studies in the ecological literature, only a handful of studies focus on TMFs. Studies of above-ground biomass in tropical elevational transects in Ecuador (Moser et al. 2008), Hawaii (Kitayama et al. 1997), Borneo (Takyu et al. 2003), Puerto Rico (Ovington, 1970), Venezuela (Delaney et al. 1997), and New Guinea (Edwards and Grubb 1977) suggest that above-ground biomass declines with increasing elevation (Table 3). This decline in biomass appears to result from a decrease in net primary productivity (NPP), without increasing residence time (Malhi et al. 2011; Galbraith et al. 2013). A number of causal factors have been proposed to explain the decline in NPP, including temperature limitation of nutrient supply (Vitousek and Sanford 1986; Tanner et al. 1998; Benner et al. 2010); temperature limitation of physiology (Grubb

1977; Kitayama and Aiba 2002); limitation of nutrient uptake (Bruijnzeel et al. 1993; Bruijnzeel 2004); anaerobic conditions in waterlogged soils (Hetsch and Hoheisel 1976; Schuur and Matson 2001); increased leaf sclerophylly and lignin/phenolic content slowing the rate of mineralisation (Bruijnzeel and Veneklaas 1998; Hafkenscheid 2000); high ultraviolet light exposure (Flenley 1992); low light levels (Grubb 1977); and strong winds (Sugden 1986). More recently, Girardin et al. (2010) found that NPP did not show a steady decline with elevation and provided evidence of a sharp transition in productivity in the cloud immersion zone. This implies that the main controls of NPP do not vary linearly with elevation (e.g. temperature) and are likely to be associated with the cloud cover (e.g. light, humidity). Based on data from the Kosñipata transect (Peru), Rapp et al. (2012) demonstrated that growth showed no consistent trend with altitude within species, although higher-elevation species had lower growth rates than lower-elevation species, suggesting that species composition is a key determinant of forest NPP.

Published studies on below-ground carbon allocation of TMFs have demonstrated that the consistently reported decrease in above-ground biomass did not necessarily translate into a loss in total ecosystem biomass. Instead, above-ground biomass from trees declines as a result of a shift from above- to below-ground carbon stocks with increasing elevation. Whereas most plots from the reported Andean network do not provide information on below-ground carbon allocation, two of the transects contributed data on fine root biomass along TMF altitudinal gradients in Ecuador (Röderstein et al. 2005; Moser et al. 2008), and Peru (Girardin et al. 2013). These studies observed

an increase in fine root biomass with increasing elevation, consistent with an altitudinal change in how trees allocate carbon. For example, in Ecuador, the authors found that fine root biomass increased from 270 to 1080 g m<sup>-2</sup> between 1050 and 3060 m a.s.l. (Moser et al. 2011), and in Peru Girardin et al. (2013) observed that fine root biomass increased from 679 to 1448 g m<sup>-2</sup> between 1000 and 3000 m a.s.l. These findings from Andean transects corroborate those of Kitayama and Aiba (2002), who found a marked increase in fine root biomass with elevation from 520 to 1440 g m<sup>-2</sup> in two altitudinal transects from 700 to 3100 m on Mount Kinabalu, Borneo. Further, all published studies on TMF reported a significant increase in soil organic matter with elevation, resulting in soils with thick organic horizons (acidic, tannin rich, humic layer) (Salinas et al. 2011; Table 2).

In Ecuador (Röderstein et al. 2005; Leuschner et al. 2007; Graefe et al. 2008) and Peru (Girardin et al. 2010), the apparent decrease in ecosystem C stocks was therefore in fact a shift in C stocks from above to below ground. Here, we hypothesise that this shift in C stocks with elevation may be a consistent feature of the carbon cycle throughout the Andes. Whereas this study provides some clues as to the abiotic parameters and ecophysiological processes driving this shift, a clearer mechanistic understanding of the factors driving this shift in carbon allocation is needed to fully understand the effects of a rapidly changing climate on the distribution of carbon in TMFs. Malhi et al. (2011) highlight the high uncertainty associated with the response of tropical forest carbon stocks to future climate change and the importance of understanding the full carbon cycle to determine the response of these ecosystems to future climate changes. We agree, and stress the importance of extending the measurements of existing Andean plots to collect information on below-ground carbon stocks and above and below-ground carbon fluxes (i.e. NPP, autotrophic and heterotrophic respiration) (Röderstein et al. 2005; Zimmermann et al. 2009a, 2009b; Girardin et al. 2010).

#### *Family, genera and species richness*

As elevation is strongly correlated with temperature, the similar bell-shaped curves of family, genus and species richness against elevation (Figure 5) results in a similar relationship when these variables are plotted against temperature, with a peak in richness at a temperature range of 21.9–20.2 °C. The strong decline in numbers of individuals at the families, genera and species level between 1500 m and 3500 m coincides with the formation of a cloud immersion zone at that altitudinal range in Andean transects (Gentry 1995), emphasising the key role of cloud formation for the composition of TMFs (Huaraca Huasco et al. 2014). Similarly, there is a high genus richness observed at mid-elevations, between 1500 and 1000 m (Figure 6), below the base of the cloud immersion zone.

Inevitably, our forest composition analysis presents some caveats. The Andean network's dataset remains

limited to above ground biomass data (Table 1). Notwithstanding these caveats, our analysis across all sites points to a number of genera displaying a narrow altitudinal range, with highest number of individuals at the top or bottom of their altitudinal range. Although some of these will be able to migrate rapidly to adapt, many require particular conservation science attention if they are to be protected from the impending threats from climate change (Feeley et al. 2011a). On the other hand, a number of genera appear less closely related to environmental parameters and occur across wide elevations, and consequently are likely to show more resistance to climate change (Hedberg 1969). A key priority for research is to determine the migration rate of these genera (Feeley et al. 2011b). In a recent review of vascular plant richness and endemism across the Andes, Jörgensen et al. (2011) argued that the high spatial variability of Andean topography and the interweaving of edaphic and microclimatic gradients explain the great species richness recorded in the Andes. However, since we do not fully understand the mechanisms that create and maintain the richness patterns, based on our correlative analyses alone, it is almost impossible to foresee what will happen to the biodiversity in the area when change is induced in one or more parameters.

#### **Conclusions and research recommendations**

Andean tropical forests are an ideal laboratory for understanding the mechanistic interactions between forest ecosystems and environmental parameters. Here, we present data from the first network of elevational transects established in the tropics. The Andean network dataset points to evidence of a change in forest structure, and a decrease in above-ground biomass and woody plants richness along elevation gradients. Notably, we found an increase in stem density, but a decline in tree height and above-ground coarse wood biomass with increasing elevation. We found a hump-shaped trend in woody plant richness along all elevation gradients, with a peak in family, genera and species richness in lower montane forests, followed by decreasing richness within the cloud immersion zone. A preliminary analysis of woody plant richness at three taxonomical levels highlights the need for accurate baseline data on species richness distribution along elevation gradients to provide information on the Andean woody plant species most vulnerable to rapid climatic changes.

Finally, the present network of replicated elevational transects in the Andes provides a unique opportunity for understanding the long-term mechanistic interactions between forest ecosystems and environmental parameters, and the global change response of forest ecosystems. A comprehensive study of all components of the carbon cycle of these plots would considerably increase our understanding of the biotic and abiotic parameters driving shifts in carbon stock and flux. This would require information on above- and below-ground NPP and respiration, allowing us to estimate the spatial variability of gross primary productivity and carbon use efficiency across the Andes. Such

detailed monitoring has been carried out in the Kosñipata elevation transect (Girardin et al. 2014; Huaraca Huasco et al. 2014; Malhi et al. 2014). This existing network of Andean plots provides an ideal opportunity for using the RAINFOR-GEM methodologies (Marthews et al. 2012) to develop a mechanistic understanding of the complete carbon cycle and ecosystem functions across the Andes.

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