Parallel functional and stoichiometric trait shifts in South-American and African forest communities with elevation

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Abstract

The Amazon and Congo basin are the two largest continuous blocks of tropical forest with a central role for global biogeochemical cycles and ecology. However, both biomes differ in structure and species richness and composition. Understanding future directions of the response of both biomes to environmental change is paramount. We used elevational gradients on both continents to investigate functional and stoichiometric trait shifts of tropical forest in South America and Africa. We measured community-weighted functional canopy traits and canopy and topsoil $\delta^{15}N$ signatures. We found that the functional forest composition response along both transects was parallel, with a shift towards more nitrogen conservative species at higher elevations. Moreover, canopy and topsoil $\delta^{15}N$ signals decreased with increasing altitude, suggesting a more conservative N cycle at higher elevations. This cross-continental study provides empirical indications that both South-American and African tropical forest show a parallel response with altitude, driven by nitrogen availability along the elevational gradients, which in turn induces a shift in the functional forest composition. More standardized research, and more research on other elevational gradients is needed to confirm our observations.

Introduction

A good understanding of the future response of tropical forest ecosystems to global change is required because of their vital role in global biogeochemical cycles and ecology. However, due to the long turnover times in forest ecosystems, it is hard to acquire insight in these future responses. As a result, empirical research has since long turned to studying ecosystems along natural gradients, which can greatly advance our understanding of ecosystem ecology and function in response to environmental shifts. Elevational gradients in particular offer open-air space-for-time experiments. Contrary to latitudinal gradients or elevational gradients in the higher latitude zones, they are not complicated by changes in seasonality or growing season length, and with careful interpretation can offer great insights in tropical forest functioning (Körner, 2007; Malhi et al., 2010; Sundqvist et al., 2013). Hence, elevational transects have been postulated as a viable and useful setup to assess long-term ecosystem responses to environmental changes, and serve as an empirical tool to assess future trajectories of forest ecosystems under global change (Malhi et al., 2010; Sundqvist et al., 2013). This has invoked research efforts on transects in South America, but no such studies have been carried out in central African forests, leaving the second-largest continuous block of tropical forest understudied. Nevertheless, recent work has shown that African and South-American tropical forest currently show important differences in structure (Banin et al., 2012) and species richness and composition (Slik et al., 2015). These differences call for cross-continental empirical research in both the Amazon and the Congo basin (Corlett and Primack, 2006), and in this context we can raise questions about the universality of tropical forest biogeochemistry and functioning across both continents, and subsequently their response to future global change scenarios. Additionally, due to the central role of nutrient availability that drives both net ecosystem productivity (NEP) and ecosystem carbon use efficiency (CUEe) (Fernandez-

Martinez et al., 2014), the effect of climatic gradients on nutrient availability should be better understood.

Indeed, recent efforts have shown that biosphere-atmosphere carbon exchange in forests is regulated by nutrient availability (Fernandez-Martinez et al., 2014) and therefor, changes in nutrient bio-availability induced by global change need to be accounted for. Canopy chemical traits are proxies that are relatively easy to assess, and from which ecosystem functioning and biogeochemistry can be inferred (Asner et al., 2015a; Wright et al., 2004). Nutrient ratios and concentrations in leafs, along with specific leaf area (SLA), are traits that are known to cluster around the leaf economic spectrum, which expresses a trade-off in photosynthetic efficiency and leaf turnover. Indeed, canopy nitrogen (N) and phosphorus (P) play key roles in photosynthesis, and are hence vital for carbon exchange processes at the leaf level. Consequently, species with high SLA, N and P are associated with high photosynthesis rates (Poorter et al., 2009; Reich et al., 1997; Wright et al., 2004), but have an ‘expensive’ nutrient economy (fast leaf turnover). Previous work has shown that these traits vary systematically with landscape biogeochemistry (Asner et al., 2014, 2015b) and hence the functional canopy signature of forests across gradients express the ecological response to changes in nutrient availability. Canopy chemistry has received increasingly more attention because of its inherent link to the plant strategy. Nevertheless, and as rightfully noted by Asner and Martin (2016), there are only limited surveys on canopy functional signatures in the tropics, while this information is vital for a landscape-scale understanding of tropical forest assembly. In addition to leaf traits, both leaf and soil δ^{15}N are known integrators of the local N-cycle and analysis of natural abundance of stable N isotope ratios is a powerful and extensively studied proxy for N cycling in ecosystems (Högberg, 1997). Previous efforts have shown that shifts towards lower δ^{15}N values indicate a more closed N-cycle with lower N availability, and *vice versa* (Brookshire et al., 2012; Craine et al., 2015; Houlton et al., 2006). This shift in isotopic ratios is caused by increased rates in fractioning processes such as denitrification, where ^{14}N is preferentially consumed, leaving the source pool enriched with ^{15}N (Hobbie and Ouimette, 2009). Hence δ^{15}N values have been used to infer shifts in N openness across natural gradients (Martinelli et al., 1999; Menge et al., 2011; Vitousek et al., 1989). Hence combining both leaf traits and δ^{15}N values is an interesting approach to assess ecosystem responses to environmental gradients.

In this study we address the existing lack of standardized cross-continental research and assessed shifts in nutrient availability and forest functional composition along two similar transects in Ecuador and Rwanda. We assessed these shifts through indicative (I) community-level functional traits and (II) nitrogen isotope ratios in topsoil and canopy. We hypothesized that (I) both these community-level traits and stable isotope signals would indicate a shift in nitrogen availability with altitude, and that (II) these shifts would be similar on both continents in terms of direction and magnitude, given a standardized research protocol and a similar adiabatic lapse rate.

Materials and Methods

Field inventories, sampling and trait analyses

We selected plots at different altitudes on the West flank of the Andes in Ecuador (ranging from 400-3200 masl) and in the Nyungwe national Park Rwanda (1600-3000 masl), in the Southern Great Rift Valley (figure S1 and Table S1 for location and overview maps). Due to reduced accessibility, the gradient in Rwanda was shorter than the South-American transect. We delineated and inventoried plots following an international standardized protocol for tropical forest inventories (RAINFOR, Malhi et al. 2002), with an adapted plot size of 40 by 40 m. In each plot, the diameter of all live stems with a diameter larger than 10 cm was measured at 1.3 m height and the trees were identified to species or genus level. Besides diameters also tree heights were measured, in order to estimate the aboveground carbon storage (AGC) using pan-tropical allometric relationships (Chave et al., 2014). The canopy of every plot was characterized by selecting the most abundant tree species, aiming at a sampling percentage of 80% of the basal area of the plots. For the selected species of all plots, we sampled mature leaves of a minimum of three individuals per species per plot using tree climbers. For most of the individuals we sampled fully sunlit leaves, but this was not always possible for the safety of the climbers, in which case we sampled partly shaded leaves under the top canopy. Previous work on elevational transects has shown that the vertical profile of leaves within a canopy has little effect on the trait values (Fisher et al., 2013). Additionally, composite samples of the topsoil (0-5 cm) were collected at five different places within each plot, and mixed per plot prior to drying. Soil and leaf samples were dried for 48 hours at 60°C. Roots were picked out of the soil samples before grinding and subsequently carbon (C), nitrogen (N) content and $\delta^{15}N$ of plant and soil samples were analyzed using an elemental analyzer (Automated Nitrogen Carbon Analyser; ANCA-SL, SerCon, UK), interfaced with an Isotope Ratios Mass Spectrometer (IRMS; 20-20, SerCon, UK). Leaf samples were dry-ashed at 550°C for 5.5 hours; the ash was dissolved in 2M HCl solution and subsequently filtered through a P-free filter. The aliquots where then analyzed for total P by AAS method No.G-103-93 Rev.2 (Multitest MT7/MT8; Ryan and others 2001). SLAs were calculated by dividing the leaf areas of all the sampled leafs per individual by their summed dry mass. Leaf areas were determined by either photographing leafs with on white paper with a reference scale or by drawing leaf contours and scanning the drawings. Both the scans and the pictures were processed using the ImageJ software (Schneider et al., 2012). For one abundant species of the higher altitudes on the

Rwandan transect (*Podocarpus latifolius* (Thunb.) R.Br. ex Mirb.) we could not obtain good area estimates, so we adopted SLA figures from literature (Midgley et al., 1995).

Statistical analysis

Average leaf trait values as specific leaf area (SLA), leaf nitrogen content on mass basis (LNC), leaf phosphorus content on mass basis (LPC), δ^{15}N, C:N and N:P ratio were calculated for every selected species, based on the sample values for the different individuals of the species. Subsequently, to calculate community-level traits and leaf δ^{15}N per plot, we calculated a basal area weighted-average canopy value and standard deviation using the species composition and the species averages, following Asner et al. (2016b). Hence:

$$\bar{x}_w = \frac{\sum_{i=1}^{N} w_i . x_i}{\sum_{i=1}^{N} x_i}$$

with x_w the weighted value for trait x, x_i the mean trait value for species i and w_i the basal-area based weight of that species in the specific plot. Subsequently for the weighted standard deviations (σ_w):

$$\sigma_w = \sqrt{\frac{\frac{\sum_{i=1}^{N} w_i . (x_i - \bar{x}_w)^2}{(N-1)\sum_{i=1}^{N} w_i}}{N}}$$

with N the number of nonzero weights.

The structure of the trait datasets was assessed qualitatively using Pearson correlation statistics after log-transforming the trait data for normality. Finally, we studied the relations between the different leaf traits and elevation using mixed effects models for the different traits, with a random error structure. The plots were spatially clustered around four altitudes on both transects, hence we introduced these elevational clusters as a random effect, and treated altitude and transect as fixed effects. Models were then fitted using maximum likelihood methods in the ‘lme4’ package in R (Bates et al., 2007). P-values of the fixed effects –elevation, transect and their interaction - were determined based on the denominator degrees of freedom calculated with the Satterhwaite approximation, in the lmerTest package (Kuznetsova et al., 2014). The P-values for the interaction term, along with the Akaike Information Criterion (AIC) for models with and without this interaction term were used to decide whether or not to exclude the interaction term. For reasons of linearity we used the inverse C:N (hence rather N:C) in these analyses. Models for $\delta^{15}N$ were assessed for each transect, using mixed effects models, with elevational cluster as a random effect. To explicitly determine divergence and convergence of plant and soil $\delta^{15}N$ with altitude, compartment (i.e. canopy leaves or topsoil) was introduced as a fixed effect and the interaction term was left in the model. For the statistical analysis, the R-software was used (R Core Team, 2014).

Results

The pooled trait datasets from both transects showed a consistent and similar correlation structure (Fig. S2), with both the separate and the pooled data showing significant correlations between all traits, except SLA and N:P. The structural vegetation parameters on both transects showed important differences: for the same altitude range, we found a higher stem density, but less species on the Rwandan transect (Table 1). Tree height and basal area were comparable, and the carbon stocks showed high variability along both transects. Climatic conditions were similar, with a highly consistent temperature gradient (Fig. S3, Table 1), and similar mean annual precipitation in the concurring elevational ranges. The linear mixed models with altitude as fixed effect, were able to explain a significant proportion of variation in all traits. This is reflected by both the marginal (m) and conditional (c) R^2_{adj}, respectively proxies for the variation explained by the fixed effects, and the random and fixed effects together (Schielzeth and Nakagawa, 2013) (Table 2). The interaction term was not significant in any case, hence the trait responses to altitude were parallel on both continents. LNC, N:C, LPC and N:P significantly decreased with altitude ($R^2_{adj,m}$ of respectively 0.83, 0.87, 0.68 and 0.60), with the Rwanda transect showing higher overall values. SLA also decreased significantly, but with a slightly higher intercept for the Ecuadorian transect ($R^2_{adj,m}$ = 0.83). $\delta^{15}N$ decreased on both continents with altitude, with a similar effect on both continents (Table 3). There was a significant divergence between slope and soil $\delta^{15}N$ along the Ecuadorian transect, while Rwanda showed a significant convergence ($R^2_{adj,m}$ = 0.93 and 0.55 for respectively Ecuador and Rwanda).

Discussion

The vegetation structure was varying differently along both transects. The high variability in the stem number, basal area and carbon stocks is potentially caused by the relatively small plot size. Other research efforts, targeting these variables in specific, use plot sizes of 1 hectare, as set forward by the RAINFOR protocol, in tropical forests worldwide (Phillips et al., 2009). As such, the differing carbon stocks probably do not integrate important stochastic events (e.g. tree fall) from the forest along both slopes. However, interestingly enough we found a lower average carbon stocks and higher number of trees in the upper two Rwandan clusters in comparison to the Ecuadorian forests. This contrasts to what has been reported from large scale forest monitoring networks across the lowland forests of Amazon and the Congo basin (Lewis et al., 2013). More research in larger plots, including dynamics and productivity should validate if this is a consistent observation in highland forest on both continents. On the other hand, the lower species number on the African transect fits well within the recent findings of a pantropical study, reporting a lower tree species diversity in the African tropical forest (Slik et al., 2015).

Different environmental variables are influenced by altitudinal changes, i.e. atmospheric pressure, temperature, cloudiness, moisture, etc. (Körner, 2007). Using all these variables in a meta-analysis would be highly interesting, but nonsensical for this study's new data alone, hence we chose to indirectly use elevation as a proxy for the related changes. In this view, the air temperature decrease with elevation was highly similar on both transects, which means that we can validly assess similar temperature-driven responses of both forest functional composition and the underlying nutrient dynamics. The high collinearity in the trait datasets corresponds well to known trade-offs described as the "leaf economics spectrum" (LES); basically a leaf-level trade-off between leaf construction cost, i.e. low specific leaf area (SLA), leaf nitrogen content (LNC) and leaf phosphorus content (LPC); and photosynthetic efficiency, i.e. high SLA, LNC and LPC (Wright et al., 2004). LNC, LPC and SLA showed a highly significant decrease with altitude (Fig. 1 and Table 2), indicating a functional shift towards more nutrient conservative species communities at higher altitudes on both transects. Indeed, leaves at lower altitudes with high LNC, LPC and SLA and hence a more efficient photosynthetic apparatus and rapid turnover, are replaced by leaves with low LNC, LPC and SLA values at higher altitudes. We've added previous published work of South America and South-East Asia, with similar temperature gradients by Asner et al, Kitayama and Aiba and Van de Weg et al. to our transects (Asner et al., 2016b; Kitayama and Aiba, 2002; Van de Weg et al., 2009; Fig. S3) to assess the consistency of our observed trends. We deliberately only added the limited amount of studies where community-weighted means were reported along one ‘single mountain range system’, hence neglecting a recent and relevant contribution from Asner et al. (Asner and Martin, 2016). As argued by Tanner et al. (Tanner et al., 1998), forests with low, intermediate and high nutrient concentrations can be found globally at any altitude, hence neglecting the effect of local environmental characteristics (atmospheric deposition, seasonality etc.) might lead to wrong conclusions. This is also shown by the different intercepts, or the vertical *shift* in trends in Fig. S3. Our comparison showed that the decreasing trend in LNC was consistent with the other studies from South-America (Asner et al., 2016b; Van de Weg et al., 2009), but not with South-East Asia where no significant trend was found (Kitayama and Aiba, 2002). However, leaf mass area (LMA; the inverse of SLA) of all studies showed a similar, increasing trend with elevation. LPC shows a strong and significant trend along both transects in this study, while the other studies report no significant trend. This is consistent with the meta-analysis presented by Tanner et al., which shows consistent negative LNC trends on ‘same mountain’ studies and inconsistent LPC trends (Tanner et al., 1998). A recent effort on a larger scale in Peru has shown that LES trade-off between LNC-LPC or SLA-LPC is indeed decoupled by climatic and geophysical filters, while the leaf SLA-LNC trade-off is more robust (Asner et al., 2016a). Regarding the studies we included for comparison (Fig. S3), only Van de Weg et al. assessed N:P ratio, and although no significant trend was found, they reported that N:P ratio was lowest in the highest sites (Van de Weg et al., 2009). Additionally, decreasing N:P ratios have also been reported on other transects on the Andes (Fisher et al., 2013; Soethe et al., 2008), and recently in Peru using airborne imaging spectroscopy (Asner et al., 2016a).

In addition to the above community-level functional traits, the decreasing δ^{15}N values on both continents (Fig. 1) are another strong indication of the decreasing N availability in the upper forests. Along the transects, both topsoil and canopy leaves showed decreasing δ^{15}N values with increasing altitude (Fig. 1), indicating a more closed N-cycle with lower N availability at the higher altitudes of both transects. It has been shown that lowland tropical rainforests exhibit high values of δ^{15}N mainly caused by the high gaseous nitrogen losses via denitrification, a strongly fractionating process (Houlton et al., 2006). The decreasing trends with altitude are interesting and seem to support the existing paradigm that tropical forests shift from P to N limitation in transition from lowland to montane tropical forest (Townsend et al., 2008). This is also reflected in the stoichiometric shifts, as canopy N:P is decreasing with increasing elevation (Fig. 1). Hence plants incorporate relatively less N compared to P in canopies at higher altitudes. The higher soil δ^{15}N values along the lower part of the Rwanda transect suggests a more open N-cycle compared to the lower part of the Ecuadorian transect. This corroborates with a recent finding of very high N losses at 1900 masl at the Rwanda site (Rütting et al., 2014), and the observation of high retention potential of bio-available N in Chilean Andisols (Huygens et al., 2008). Further research is needed to explain the notable divergence in soil and foliage δ^{15}N along the Ecuadorian transect, mainly driven by the highest elevational cluster. As previously reported this can be due to different degrees of dependence upon ectomycorrhizal fungi (EcM) (Hobbie et al., 2005), different mycorrhizal association types (Craine et al., 2009) or shifts in the uptake of different forms of nitrogen (Averill and Finzi, 2011; Kahmen et al., 2008). EcM-associated plant species are expected to show more depleted isotopic ratios, due to isotope fractionation during N transfer to the host plant. This effect is obscured in lowland N-rich tropical forests and might just not be detectable at lower altitudes, but might become apparent in N-poorer environments such as the higher altitude forests (Mayor et al., 2014). Secondly, a study from a temperate elevational transect has shown that plants increasingly switch to organic N sources with decreasing temperature, without fractionation upon N transfer from EcM to plants (Averill and Finzi, 2011). Resulting from that, they found a convergence rather than divergence of δ^{15}N soil – canopy along altitude, because plants draw N increasingly from a source pool close to the bulk isotopic signature. We have no data on EcM colonization or δ^{15}N of sporocarps in the study plots, so we are not able to disentangle both mechanisms. However, by characterizing both community functional traits and canopy and soil δ^{15}N, the data of these transects is consistent with a decreasing availability of soil N as elevation increases. We suggest the reduced N availability to be caused by an indirect temperature effect on the N-cycle, consistent with observations from a direct fertilization experiment (Fisher et al., 2013). Lower temperatures slow down depolymerization and N mineralization processes, hence also N bio-availability, thereby invoking changes in the functional plant communities along the transects (Coûteaux et al., 2002; Marrs et al., 1988). Future global change will most likely distort N availability both directly via increased reactive N deposition (Galloway et al., 2008; Hietz et al., 2011) and indirectly via a temperature effect on N mineralization in forest soils. This raises questions on the future of plant species within the already threatened montane tropical forest biome, where higher N availability and temperature increase might distort the existing ecological niches and in turn also increase N-losses. Further research should therefore focus on process-based knowledge of N and P cycle dynamics along such transects to further assess if the availability is actually limiting the ecosystems. These observations also have repercussions for carbon fluxes: since nutrient availability exerts a stronger control on NEP than on gross primary production (GPP) (Fernández-Martínez et al., 2014), it is likely that the CUE_e will be lower at higher altitudes. It has been hypothesized that this decrease in CUE_e is due to an increased investment of photosynthates to non-biomass components, such as root symbionts for nutrient mining and root exudates, in expense of net primary production (NPP) (Vicca et al., 2012). However, recent empirical evidence has shown for one transect in the Andes, that a decrease in GPP with increasing altitude is not accompanied by a trend in CUE (Malhi et al., 2016). More work on carbon budgets along elevational transects is needed to fully understand the role of N and P availability and its interaction with climate gradients for the tropical forest carbon cycle.

Conclusions

Altogether, this study evidences parallel functional shifts with a similar direction and magnitude along two comparable elevation gradients, in tropical forests on two different continents. The data suggests, in two different ways, that this shift is caused by temperature-driven response of nutrient availability. With the first data on an elevational transect in Central Africa, this work adds to the existing set of elevational transects in the tropics. However, more transects are needed, especially in Africa, to validate a universal response of tropical forests to environmental change. Furthermore, work on process-based nutrient dynamics is important to unravel the importance of different global change factors for both forest basins.

Supplementary information

Fig. S1 Overview map

Fig. S2 Structure and correlations of the trait data

Fig. S3 Trends in community-level functional traits of previously reported studies

Table S1 Coordinates, elevation and cluster membership of the different plots on both transects

Table S2 Summary of the plot-level characteristics

Author contributions

M.B., H.V. and P.B. developed the project; M.B, M.D., S.B., C.T. and D.V. carried out the field work and analyzed the data. All authors contributed to the ideas presented and edited the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

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Table 1 General characteristics, vegetation structure, climate (mean annual temperature (MAT) and mean annual precipitation (MAT), WorldClim - Fick, 2017) and soil characteristics of the elevational clusters on both transects. Number of trees and species (in the 40 by 40 m plots), basal area (BA), mean tree height (MTH) and above-ground carbon (AGC) are averages per plot ± the standard deviation on the plot-level results, based on the inventories.

	Cluster	Altitude (masl)	Number of trees per plot	Number of species per plot	BA (m^2 ha^{-1})	MTH (m)	AGC (Ton C ha^{-1})	MAT (°C)	MAP (mm)	Soil parent material	Soil classification
Ecuador	1	406 ± 10	86 ± 13	30 ± 2	25 ± 3	18.3 ± 1.0	96 ± 19	23.7	3720	Lahars	Andisol
	2	1068 ± 25	84 ± 38	39 ± 15	33 ± 9	16.9 ± 0.7	140 ± 25	20.0	3227	Lahars	Andisol
	3	1871 ± 79	69 ± 11	31 ± 2	33 ± 11	13.5 ± 1.3	112 ± 57	17.5	1619	Redbed volcaniclastics	Andisol
	4	3217 ± 21	90 ± 25	18 ± 2	49 ± 11	13.0 ± 1.4	161 ± 34	10.9	1241	Granitic/acid	Andisol
Rwanda	1	1760 ± 66	70 ± 18	21 ± 4	34 ± 4	13.9 ± 0.7	121 ± 11	17.6	1518	Shale and Quartzite	Inceptisol/Ultisol
	2	2200 ± 64	71 ± 18	18 :± 3	45 ± 9	14.3 ± 0.3	179 ± 27	15.9	1628	Shale and Quartzite	Inceptisol/Ultisol
	3	2512 ± 37	122 ± 60	11 ± 1	31 ± 9	12.0 ± 1.0	99 ± 36	14.7	1716	Shale and Quartzite	Inceptisol/Ultisol
	4	2844 ± 77	109 ± 56	8 ± 2	34 ± 4	11.5 ± 0.5	89 ± 10	12.9	1835	Shale and Quartzite	Inceptisol/Entisol

Table 2 Fixed effects estimates (altitude in km asl) for the different canopy-level response variables; leaf nitrogen content (LNC), inverse C:N ratio, specific leaf area (SLA), leaf phosphorus content (LPC) and N:P ratio, along with the estimated marginal (m) and conditional (c) R^2_{adj} (sensu Nakagawa and Schielzeth (5)). The interaction term for altitude x transect was not significant in any case, and was hence not retained in any model.

Response	Effect	Estimate	SE	P-value	$R^2_{adj,m}$	$R^2_{adj,c}$
LNC (%)	Ecuador intercept	3.04	0.131	<0.001	0.80	0.85
	Rwanda intercept	3.65	0.115	0.003		
	Altitude	-0.59	0.000	<0.001		
SLA	Ecuador intercept	175.28	14.107	<0.001	0.77	0.95
	Rwanda intercept	172.55	12.504	0.835		
	Altitude	-36.24	0.007	0.002		
N:C	Ecuador intercept	0.07	0.003	<0.001	0.83	0.91
	Rwanda intercept	0.07	0.003	0.033		
	Altitude	-0.01	0.000	<0.001		
LPC (%)	Ecuador intercept	0.16	0.012	<0.001	0.60	0.88
	Rwanda intercept	0.17	0.011	0.247		
	Altitude	-0.02	0.000	0.009		
N:P	Ecuador intercept	20.66	1.055	<0.001	0.54	0.74
	Rwanda intercept	24.06	0.926	0.014		
	Altitude	-1.82	0.001	0.018		

Table 3 Fixed effects estimates (altitude in km asl) for $\delta^{15}N$ in both canopy and topsoil (compartment) on both transects, along with the estimated marginal (m) and conditional (c) R^2_{adj} (sensu Nakagawa and Schielzeth (5)).

Response	Effect	Estimate	SE	P-value	$R^2_{adj,m}$	$R^2_{adj,c}$
$\delta^{15}N$ Ecuador(‰)	Canopy intercept	3.96	0.406	<0.001	0.93	0.94
	Soil intercept	5.19	0.440	0.009		
	Altitude	-2.59	0.000	<0.001		
	Altitude x compartment	1.53	0.000	<0.001		
$\delta^{15}N$ Rwanda (‰)	Canopy intercept	6.83	3.193	0.21103	0.55	0.82
	Soil intercept	12.37	1.749	0.004		
	Altitude	-2.02	0.001	0.310		
	Altitude x compartment	-1.37	0.001	0.074		

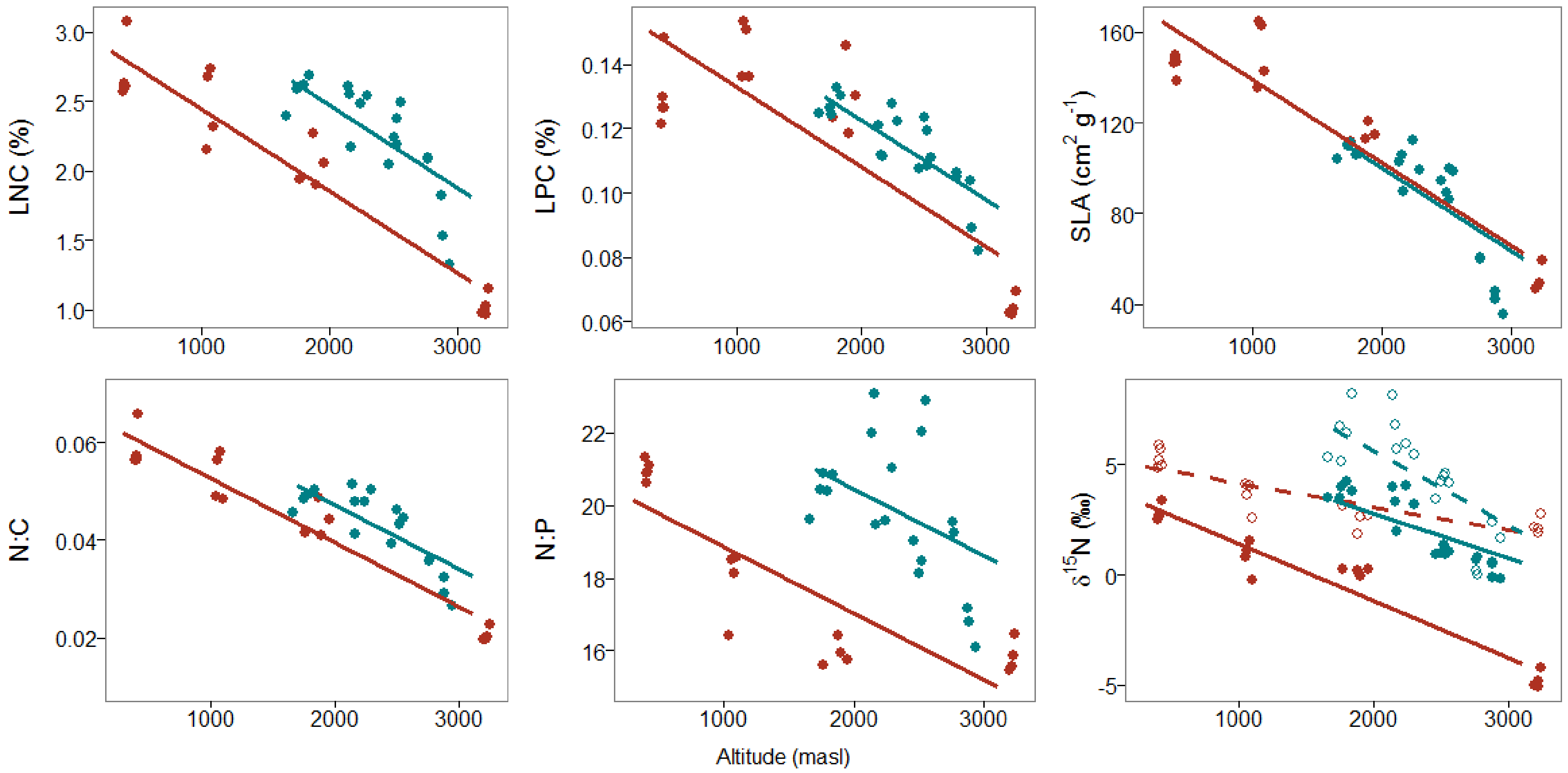

Fig. 1. Trends in community-level functional traits and leaf (full line, closed circles) and topsoil (dashed line, open circles) δ^{15}N of the elevation transects in Ecuador (red) and Rwanda (blue). Leaf nitrogen content (LNC), leaf phosphorus content (LPC), specific leaf area (SLA), and leaf N:C, P:C and N:P ratio decrease with increasing altitude on both transects. Both transect showed decreasing values of δ^{15}N, providing additional evidence for a more closed N-cycle with increasing altitude. Lines represent the fixed altitude effects in the respective statistical models for both Ecuador (red, 400-3200 masl) and Rwanda (blue, 1600-3000 masl).