We would like to thank both reviewers and the editor for the thoughtfull comments. We feel that we have substantially improved the manuscript, and that it is now ready for publication in Biogeosciences.

The authors

<u>Response to RC1</u>

General Comments: I found the paper well written and of general importance to the scientific community given the rarity of elevational transects in tropical forests. My concerns with the current version are generally technical, based on a few somewhat easily modified statistical and linguistic approaches that would greatly improve the manuscript.
We want to thank the reviewer for his appreciation, and his thorough, constructive and qualitative review. We have addressed the comments in bold in this response, and have adapted the MS as noted below. All the edits are indicated in the manuscript (MS) text below with track changes.

(1) Consider that altitude itself is not biologically meaningful, only factors that change with altitude (temperature, pressure, UV). So, in essence you are statistically comparing a proxy for climatic variables that influence plant and soil processes. This is certainly acceptable when climatic variables are not representative, as in the case where climate stations are too remote (or at the wrong elevation) from study plots. However, if you believe your MAT/MAP data reported in Table 1 are real then those metrics would be more sensible to use than altitude. This is because 2000 m elevation means nothing to a plant, and does not represent the same temperatures at different latitudes, aspects, distances from oceans, etc.
We fully agree with the referee on this point, including direct variables instead of the elevation proxy is highly interesting for elevational transects. There are 2 reasons why we did not do this in the manuscript, and by which we would also defend the current version of the manuscript:

1. **Most important: as the referee rightfully states, there are variables other than precipitation or temperature that covary with elevation (such as irradiance, cloud cover, UV...). We merely use elevation in the MS as a proxy because we feel that using all these covarying independent variables would at this point be too suggestive, given the limited size of the dataset (two transects) and the limited orthogonality of the setup. However, we do report MAT and MAP (and the coordinates of the sites in Table S1) to allow future meta-analysis with more transects/plots to disentangle these effects, and as a background for the study.**
2. **The data reported in the tables is WorldClim data (we have also more clearly stated that in the new version of the MS), and indeed the climate stations are both remote and at different locations. One of the notorious challenges in higher elevation is to assess fog deposition, and which probably contributes a lot to the hydrological cycle of high elevation forest. We believe that for before including MAP and MAT in the analyses, advances in this field and in the quantification of this phenomenon are needed, since it is likely that MAP is heavily underestimated at higher elevations.**

(2) Improving the statistical approach is unlikely to change the authors overall conclusions but currently does not represent the best practices in the field. I outline several specific areas for improvement below.
See below for specific answers. We are grateful for these comments and have implemented them in the new MS version, although indeed the overall conclusions did not change, as the referee rightfully states.

(3) The authors use functional characteristics and ecosystem function interchangeably. I believe this to be invalid but acknowledge that there are many whom would disagree with this semantic distinction. I agree that sometimes SLA or LNC is related to leaf function (e.g., photosynthetic rates) but it does not necessarily represent ecosystem function. Similarly, leaf and soil d15N values can integrate ecosystem N cycles but the authors to not demonstrate firm understanding of the caveats and alternatives. Specifics below.
This is a thoughtful comment, which we have already adapted in the new MS. The MS should be objective and correct in the first place, and we would like to avoid any confusion in the text. We have now more explicitly added a section on functional traits in the introduction, which states more clearly that these are 'only' proxies. See also below for more detailed answers.

Specific Comments:
L140 Consider that lme4 is the preferred package as nlme is no longer supported and therefore uses older estimators.
Ok, thank you for this comment. We have now reprocessed the data with the lme4 package.

L141 Including the interaction and then dropping it from final models based on P values is in essence manual stepwise selection, which is generally not recommended when selecting from nested models. Consider using AIC or just leaving the interaction in. Also, there is no description of how these P values were estimated from an nlme model and this is a topic of great debate in the literature as determining the denominator degrees of freedom for random error variance is not a straightforward exercise. For instance, when using mixed effect models and P values the authors need to report something to the effect of: "hypothesis testing was evaluated using likelihood ratio tests with type III ANOVA Satterthwaite approximation of degrees of freedom in the lmerTest package".
This was not well described, the referee is right. In practice we used AIC, BIC and the default ML ratio testing in the anova.nlme function, which is not documented very well in the package. I see now that lme4 has better documentation on this, hence we have shifted to that and better described the methods used in a next MS version. As stated above, we have now re-analysed the data with the lme4 package, and better discribed the methodology (significant fixed effect) using the lmerTest package. We now also included an extra table in supplementary information with the models including the interaction term, along with their respectives AIC scores.

L142 The authors mention they assessed linearity (normality?) but do not discuss what other model fitting metrics they evaluated. Heteroscedascitity? LPC certainly looks non-normally distributed, thus in violation of the pearson correlation statistics that are reported on Fig. S2.
Yes, normality and heteroscedascity of the residuals, qualitatively via qqplots and residual plots. We now more clearly state this in the MS. Please see answer on comment below for the correlation matrix.

Fig. S2 While on the subject, correlation among variables that contain the same variables will always be correlated. Therefore, reporting correlation statistics (with P values!) between LNC, C:N, and N:P is nonsensical.
The referee is right. Actually, the main information we wanted to give the reader was the structure of the trait data sets. And we felt that reporting the correlation statistics in supplementary information, gives the reader the opportunity to gain insight. Mainly when considering the link to ecosystem functionality, the links between traits representing the so called 'trade-offs' are in our opinion valuable to report. In the new version, we have log-transformed the data prior to reporting the correlation statistics. This did still not render normal distributions for some of the parameters, so we now report Spearman's correlation tests, which do not rely on the normality assumption.

L152 "Climatic conditions were similar" is simply not true. Rwanda gets wetter and the Ecuador gets drier with increasing elevation. This is a major problem with elevational transects in the tropics as sites that get wetter at high elevations also receive less solar inputs and will typically contain less foliar N as a result of reduced photosynthetic variability (not to mention either greater hydrological or gaseous outputs of soil N). It is true that both transects get colder but they do so within very different temperature ranges and magnitudes (12.8◦ vs. 4.7◦ changes that barely overlap) owing to the vastly (~300%) different altitudinal ranges among transects (2811 vs. 1084 m). How can these authors claim they are similar? Where did the temperature data come from? What are the latitude and longitudes of the sites? Instead, the author should refer to the similar adiabatic declines (e.g., 219 m per -1◦ in E, 230 m per -1◦ in R), then graphically depict temperatures of the plots; same goes for Fig. S3. This is one of the most important comments I provide on this manuscript.
The latitude and longitudes are listed in Table S1 of the original MS. We agree, and acknowledge in the manuscript, that the transects are different in range for elevation and temperature (see e.g. L 89-90), there was unfortunately no other option in the field (neither in any part of eastern DRC or eastern central Africa for that matter!). Additionally, line 152 completes to '*Climatic conditions were similar, with a highly consistent temperature gradient (Fig S3, Table 1), and similar mean annual precipitation in the concurring altitudinal ranges*.' We do acknowledge that the formulation is a bit misfortunate, but we actually mainly wanted to focus on the very similar adiabatic lapse rate '*highly consistent temperature gradient'* (as we refer to the parallels in fig S3), as noticed by the referee indeed. Additionally, the Ecuadorian transect is 'enveloping' the Rwanda transect, and the amounts of rainfall and temperature conditions within the overlapping altitudinal zone are similar. This boils down to the discussion above; we fully agree that altitude is only a proxy, but we do believe that directly including more climatic predictors instead would be more useful for a larger meta-analyses. But exactly for that reason, empirical research results on 'smaller' datasets (which are very labour and time intensive to acquire, and therefor rare in the tropics) have to get published.

L163 Consider explicitly examining the difference between foliar and soil d15N as ˙ this may better represent aspects of the N cycle (shameless plug: see Mayor et al. 2016, Eco. Lett. 18 for an in depth discussion of the patterns among tropical d15N values).
Please see answer below (on comment of L 234) for an elaborate response on this.

L181 The authors should refer to the similar adiabatic declines (e.g., 219 m per -1◦ in E, 230 m per -1◦ in R.
We now do this explicitly in the results section.

L203 One could also find elevation transects where the parent material changes from low to high along the same mountain as well. Also, you imply that your transects have consistent geology, aspect, slope etc. when they clearly do not based on Table 1 and Fig. S1. So the position you invoke, based on Ed Tanner's defense of low replication, is invalidated by your own data. In addition, there was a recent large scale global elevation gradient study published in Nature (another shameless plug) that suggests within-regional variability is negligible when comparing cross-continents. Given this, your selection of datasets based used in Fig. S3 to those with only single mountain transects may limit your conclusions and does not appear well justified.
Good point. We have reformulated this in a new version. However, the point raised is debatable in our opinion, and we would like to keep the meta-analyses as is in the new version. 1) There are other environmental variables than parent material that are also important when not working with single mountain studies (seasonality, atmospheric deposition, continentality). Additionally, although the parent material is 'varying' in Ecuador along the slope, the soils are all Andisols and are from volcanic origin. In our opinion, the best proof that we should restrict in this study to single mountain studies, is the shift in intercept between both of our own two transects (although the slopes are parallel). 2) Our own transects are 'same mountain' transects, the MS might lose focus with a more extensive meta-analyses using 'non-same mountain' studies (and this has been reported already by Asner et al. 2016 GBC), and 3) much as can be seen in the latter paper, there is simply no data (not from same mountain studies, but also not in a broader approach) on African forests. So would a more elaborate meta-analysis genuinly contribute much more to our story, given the strong focus we have on the African continent currently? (We don't think so)

L206-207 So Van de Weg data is from both SA and SE Asia? Why don't the lines reflect that on Fig. S3? Why don't the lines simply state the location of the transects rather than the authors?
Thanks for this, this is wrong in the MS. SE Asia should be Kitayama! We've added the locations in the legend now.

L222 As mentioned, what may be more informative is the enrichment of plants relative to soil d15N values (˙ Δ15Nplant-soil) is increasing at both sites. This may indicate either greater fractionating pathways during N uptake/translocation or a shift from one N form to another, rather than simply a more closed N cycle. Also, the Rwanda soil line does not appear to fit those data. Were any nonlinear lines compared? Refs to consider here: D. N. L. Menge, W. Troy Baisden, S. J. Richardson, D. A. Peltzer, M. M. Barbour, New Phytol , no- (2011). E. A. Davidson, C. J. R. de Carvalho, A. M. Figueira, F. Y. Ishida, et al., Nature 447, 995-8 (2007). J. Mayor, M. Bahram, T. Henkel, F. Buegger, et al., Ecol Lett 18, 96-107 (2015). C. Averill, A. Finzi, Ecology 92, 883-91 (2011). E. Bai, B. Z. Houlton, Global Biogeochem. Cycles 23, GB2011 (2009).
This was partly discussed in the previous MS version L232-236. See a more elaborate answer below.

L234 You mean to say "different degrees of dependence upon ectomycorrhizal fungi" in particular. (Although there is no discussion about the mycorrhizal type of your tree communities, I would assume they are AM which do not appreciably fractionate). Also, there is no talk about why higher soil 15N suggests and open N cycle when there is a large body of literature that clearly discusses that it may be due to greater gaseous N losses to denitrifiers.
We have responded here to all the concern raised by the referee on the d15N trends. The reviewer's comments on this are very valuable for this MS. We did include a more elaborate discussion on this in an earlier draft, but felt that it might render the discussion to suggestive. Given the parallel comments of the other referee on this, we have now more elaborately discussed the d15N patterns in a following MS version. First of all the soil patterns as such, with a more in-depth discussion on why decreasing d15N values suggest a closing N cycle. Additionally, the Δ15N (canopy-soil) patterns, with the work of especially Mayor et al. 2015 and Averill et al. 2011. We have now also changed the statistics for the d15N values. We considered each transect as such, and then fitted a mixed effect model to the d15N data, including the compartment it was measured in (soil or canopy) as a fixed effect, with interaction term with altitude. This allows us to elegantly discuss the divergence

or convergence of soil-canopy d15N values (so, Δ15N) along both transects, given the significance of the interaction terms in both cases.

L240 “Confirmed”? No, not confirmed, as you say above, only suggestive of declining bioavailable N.
Ok, was indeed overstating! The sentence did not contribute a lot, so we deleted it.

L242 Here is a statement that would be much stronger if you were actually looking at the same temperature ranges across all transects in Fig. S3.
Please see answers above.

L245 What is “this evolutionary conditions for N” mean?
We have rephrased this. We meant that temperature ranges are likely to shift in the future, which will affect N cycling along slopes.

Technical Corrections:
Thanks for these!! We have adapted this in the new version
L53 Extra comma.
L156 “ajd” subscript incorrect.
L160 Spacing between R2 is off.
L227 What does “C:N increase dominates over the C:P increase along the transects” âA˘´lmean? Also, Fig. 1 lists N:C, not C:N, and there is no C:P. . .
L228 Consider replacing “build in” with “incorporate” or “use”.
L239 Delete “both”.
L508 Fix 15N superscript.
L509 Fix R2adj subscript.
L517 It would be useful to those conducting meta-analyses if these raw data were made available.
Raw data was and is available in the supplementary information of the original submission.

<u>Response on Revierwer 2</u>
General comments
The manuscript by Bauters et al. presents an interesting analysis based on a detailed survey of tree species occurrences and their functional traits along two altitudinal transects. The main findings concerning the similar shifts in community weighted means of the key leaf traits for American and African altitudinal transects is stunning and of potential interest to a broad audience. Having that said, there are several issues that need to be improved.
We would like to thank referee 2 for the thoughtful and qualitative review. We have addressed the comments in bold in this response, and have adapted the MS as noted below. All the edits are indicated in the manuscript (MS) text with track changes.

Specific comments
My major point concerns a decoupling between results and theoretical background.
The reasoning behind the study needs to be better developed and introduced.
Understanding the links between nutrient availability and species composition or biomass production is certainly a key for tropical forests. Nevertheless, it is not fully clear how particularly this study contributes to this understanding. For instance, the first two lines in Abstract state: “Elevational gradients are an empirical tool to assess long-term forest responses to environmental change. We studied whether functional composition of tropical forest along elevational gradients in South America and in Africa showed similar shifts.” I do not understand how these sentences are connected. If the shifts are similar, what can this result tell us about forest responses to environmental change?
We have reformulated and rewritten the framework of the study in the new MS version, so that this is clearer. See also comment on point 3 raised by the referee. We use the elevational transects as space for time tools, where the limited spatial range subjects the forest to strong shifts in environmental – mainly climatic – conditions. We believe the main contribution of this MS is the report of highly parallel shifts across continents, of ecosystem properties which have been previously linked to ecosystem functioning. The reported shifts show that forest communities and biogeochemical cycles on both continents respond to the drastic change in some of the environmental variables along the slope (temperature). The observation of shifts in both biogeochemical proxies (d15N) and ecological functioning proxies (leaf traits) shows that the biogeochemical cycles are strongly linked to the ecological shifts.

Similarly, lines 33-34: "This highlights the importance of nutrient availability for tropical forest in a changing world.“ I feel that this sentence is not a sufficient explanation for the main result found here. Why is nutrient limitation important and how this study contributed to this conclusion?

As written above, the shift in forest composition along the slope, with the reported N cycle proxies, shows that forest composition responds to the shifts in nutrient cycling along the transect.

Moreover, as nitrogen concentration changes with both elevation and altitude, how can we know that nutrient concentration (and not temperature) is the key driver of species composition?

We are a bit confused by this comment. The baseline of the story is that temperature shifts with altitude, which in turn affects the N cycling along the slope, and subsequently the species composition. We have now more elaborately described the state-of-the-art and the background on the used proxies in the new MS version, and hope that this is clearer.

I recommend authors to better develop and explain the hypotheses tested.

Second, it is being argued that phosphorus rather than nitrogen is the key nutrient limiting biomass production (and perhaps also species distribution) in tropical forests (Aragao et al. 2009, Quesada et al. 2009). Why this study focuses on nitrogen concentration only? This issue should be discussed.

Aragão, L. et al. 2009. Above-and below-ground net primary productivity across ten Amazonian forests on contrasting soils. – Biogeosciences 6: 2759–2778. Quesada, C. A. et al. 2009. Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties. – Biogeosci. Discuss. 6: 3993–4057.

We have discussed this more in depth in the new MS version. We deliberately caution the use of ‘limitation’ in the MS, since there are different forms of nutrient limitation, and none are easily assessed in the field (see also reference). P is indeed considered the limiting nutrient for the bulk of the tropical forest. However, several reports show that forests shift from P to N limitation along elevational transects, for two reasons; 1) replacing the lowland oxisols, which are strongly weathered and P-depleted, with P-richer and geologically younger soils, and 2) slowing down of the N-cycle with lower temperatures in higher forest. Given the fact that we are indeed working on higher elevation forest, the nitrogen cycle is the main focus of the paper. See also discussion at L 224-228.

1. **P. M. Vitousek, S. Porder, B. Z. Houlton, O. a Chadwick, Terrestrial phosphorus limitation : mechanisms, implications , and nitrogen – phosphorus interactions. *Ecol. Appl.* 20, 5–15 (2010).**

Third, If “Elevational gradients are an empirical tool to assess long-term forest responses to environmental change” (first line of Abstract), how general these results can be? E.g. could we find similar pattern along latitudinal transects?

Elevational transects are an acknowledged tool for long-term forest responses, so called space-for-time experiments, and are in general better setups than latitudinal transects. Part of the reason is that the seasonality shifts with latitude (and the length of the growing season) along with other factors, which render latitudinal setups non-orthogonal. This is elaborately discussed in following introduction paper in a special issue on elevational transects in 2010:

Malhi, Y. *et al.* Introduction: Elevation gradients in the tropics: Laboratories for ecosystem ecology and global change research. *Glob. Chang. Biol.* 16, 3171–3175 (2010).

Lastly, the first paragraph of Discussion is difficult to read. I recommend starting with the main results, how are these results linked with the predictions and what is the possible implication. It is unclear what “the general characteristics” means and what “vegetation structure” means and what “structural characteristics” means

We agree with the referee and have reformulated in the new MS version.

Technical comments:

Thanks for these, we have adapted this in the new MS version.

Line 53: extra “,”

Line 95: Unclear whether tree height or carbon stock was estimated using pantropical relationship. Perhaps delete the comma after “(AGC)“?

Line 509: "2“ in upper case (R2adj)

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

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Keywords : tropical forests, leaf traits, elevational transects, canopy chemistry, ~~altitudinal~~elevational gradient, cross-continental comparison, leaf economics spectrum

Short Title: Parallel trait shifts in South-American and African elevational forest transects

Word count Abstract: 177

Word count Body: 3164

Numbers of references: 47

Abstract

~~Elevational gradients~~The Amazon and Congo basin are ~~an empirical tool to assess long-term forest responses~~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 ~~studied whether functional composition of tropical forest along~~used elevational gradients on both continents to investigate functional and stoichiometric trait shifts of tropical forest in South America and ~~in~~ Africa~~ showed similar shifts.~~. We ~~assessed~~measured community-weighted functional canopy traits and ~~indicative~~canopy and topsoil δ^{15}N ~~shifts along two new altitudinal transects in the tropical forest biome of both South America and Africa~~signatures. We found that the functional forest composition response along both transects was parallel, with a ~~species~~ shift towards more nitrogen conservative species at higher elevations. Moreover, canopy and topsoil δ^{15}N signals decreased with increasing altitude, suggesting a more conservative N cycle at higher elevations. This cross-continental study provides ~~two~~ empirical indications that both South-American and African tropical forest show a parallel response ~~along~~with altitude, driven by nitrogen availability along the ~~altitudinal~~elevational gradients, ~~inducing a parallel~~which in turn induces a shift in the functional forest composition.~~ This highlights the importance of nutrient availability for tropical forest in a changing world.~~ 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 ~~changes is required because of their vital role in the global carbon cycle. Recent efforts have shown that biosphere-atmosphere carbon exchange in forests is regulated by nutrient availability (Fernandez-Martinez et al., 2014). Therefore, changes in nutrient bio-availability induced by global change need to be taken into account. Uncertainties on future responses of forest ecosystems to global change are perhaps most prominent in the tropics, where monitoring is underdeveloped compared to the temperate region. Recent work has shown that African and South-American tropical forest show important differences in structure (Banin et al., 2012) and species richness and composition (Slik et al., 2015a). Additionally, there is a lack of cross-continental empirical research in both the Amazon and the Congo basin, and most model projections are parameterized on either South-American tropical or even temperate forests (Corlett and Primack, 2006). Moreover, earth system model projections typically do not account for nutrient dynamics (Anav et al., 2013) and models that account for nutrient cycling in their land component are still under development (Goll et al., 2012; Reed et al., 2015; Smith et al., 2014). , 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. This leaves us with an important bottleneck to further optimize Earth system models (Ciais et al., 2011). Hence, cross-continental comparisons of tropical forest ecosystem responses to environmental gradients are needed. Additionally, due to the central role of nutrient availability that drives both net ecosystem productivity (NEP) and ecosystem carbon use efficiency (CUE_e) (Fernandez-Martinez et al., 2014), the effect of climatic gradients on nutrient availability should be better understood. Elevation transects offer such gradients.~~

~~Elevation transects have been postulated as a viable and useful setup to assess long-term ecosystem responses to environmental changes, and hence serve as an empirical tool to assess future trajectories of forest ecosystems under global change (Malhi et al., 2010; Sundqvist et al., 2013). In the tropics, this has invoked research efforts on transects in South America, but no such studies have been carried out in central African forests.~~

~~In this study we address this 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. Canopy chemistry has received increasingly more attention, and has been identified as a proxy for landscape-scale biogeochemistry (Asner et al., 2015; Fyllas et al., 2009), 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 a standard set of leaf traits, both leaf and soil δ^{15}N are known integrators of the local N-cycle. 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* (Craine et al., 2009, 2015). Hence combining both leaf traits and δ^{15}N values is an interesting approach to assess ecosystem responses to environmental gradients. 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 in terms of direction and magnitude, given a standardized research protocol and a similar adiabatic lapse rate.~~

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 $\delta^{15}N$ 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 $\delta^{15}N$ 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 ~~altitudinal~~elevational transects has shown that the vertical profile of leaves within a canopy has little effect on the trait values (Fisher et al., 2013). ~~This sampling was carried out at the level of the total inventory.~~ 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):

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

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 ~~altitudinal~~elevational clusters as a random effect, and treated altitude and transect as fixed effects. Models were then fitted using maximum likelihood methods in the ‘~~nlme’ package in R (Pinheiro et al., 2013). An interaction term for transect (Rwanda or Ecuador) and elevation was tested using likelihood ratio test and was retained in the final models when significant at the P<0.05 level. For reasons of linearity we used the inverse C:N (hence rather N:C) in these analyses.~~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 δ^{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 δ^{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 ~~in~~ 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 ~~altitudinal~~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 ~~R^2_{ajd}~~(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 ~~and δ^{15}N~~ responses to altitude were parallel on both continents. LNC, N:C, LPC and N:P significantly decreased with altitude ($R^2_{adj,}$~~$_{marg}$~~$_{m}$ 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 ($R^2_{adj,}$~~$_{marg}$~~$_{m}$ = 0.83). ~~In addition to the functional trait and stoichiometric shifts, canopy and topsoil~~ δ^{15}N decreased on both continents with altitude, with a ~~stronger decrease for canopy than for topsoil~~similar effect on both continents (Table 3). There was a significant divergence between slope and soil δ^{15}N along the Ecuadorian transect, while Rwanda showed a significant convergence ($R^2_{adj,}$~~$_{marg}$~~$_{m}$ = 0.93 and 0.55 for respectively ~~0.92~~Ecuador and ~~0.43 for canopy and soil).~~Rwanda).

Discussion

The ~~general characteristics, averaged for the altitudinal clusters, show that the~~ vegetation structure ~~is different~~was varying differently along both transects. The high variability in ~~these structural characteristics as such,~~the stem number, basal area and carbon stocks is potentially caused by the relatively small plot size. ~~However investigating the variation in structural characteristics is~~

~~beyond the scope of this research.~~ Other research efforts, targeting ~~structural characteristics and carbon stocks~~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 ~~the~~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).~~(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., 2015b). More importantly for this paper, the air temperature decrease with elevation is~~(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. ~~Along the transects, both topsoil and canopy leaves showed decreasing δ^{15}N values with increasing altitude (Fig. 1), inferring a more closed N-cycle with lower N availability at the higher altitudes of both transects.~~ We’ve added previous published work ~~in~~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 (12, 16, 17; Fig.~~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 ~~a~~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), ~~in studies of general altitude patterns from different mountain ranges, elevational trends might be obscured by a range of local environmental characteristics, such as soil type and orientation. Forests~~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~~Fig. S3. Our comparison showed that the decreasing trend in LNC~~ (mass basis)~~ 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 ~~(Van de Weg et al., 2009).~~(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). ~~Of~~Regarding the studies we included ~~studies in~~ 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. ~~In addition to our community-level traits (decreasing LNC, increasing C:N and N:P ratio), the decreasing δ^{15}N values on both continents (fig. 1) are another strong indication of the limited access of the upper forests to bio-available N. This data is only indicative and we cannot conclude that there is actual limitation. However, the trends~~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 ~~the C:~~canopy N ~~increase dominates over the C~~:P ~~increase along the transects, leading to a general decrease of N:P~~is decreasing with increasing elevation (~~fig~~Fig. 1). Hence plants ~~build in~~incorporate relatively less N compared to P in canopies at higher altitudes. The higher soil $\delta^{15}N$ 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 ~~finding~~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 $\delta^{15}N$ along the Ecuadorian transect~~.~~, mainly driven by the highest elevational cluster. As previously reported this can be due to different degrees of ~~mycorrhizal infection~~dependence upon ectomycorrhizal fungi (EcM) (Hobbie et al., 2005), different mycorrhizal association types (Craine et al., 2009) or ~~species-specific preferences for~~shifts in the uptake of different forms of nitrogen ~~(Kahmen et al., 2008).~~

~~By characterizing both community functional traits and canopy and soil $\delta^{15}N$, the data of these both transects is consistent with a decreasing availability of soil N as elevation increases, which is here for the first time confirmed for the African continent.~~(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., 2013). Future global change will most likely distort this evolutional conditions for N availability;~~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 ~~tropical forests.~~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. ~~This advocates the explicit need for implementing nutrient dynamics and availability in ecosystem models.~~ With the first data on an ~~altitudinal~~elevational transect in Central Africa, this work adds to the existing set of elevational transects in the tropics~~, but~~. 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~~)) and soil characteristics of the altitudinal clusters on both transects.~~), 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~~.1~~	18.3 ± 1.0	96 ± 19	23.7	3720	Lahars	Andisol
	2	1068 ± 25	84 ± 38	39 ± 15	33 ± 9~~.4~~	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 ~~masl~~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, ~~canopy and topsoil δ15N,~~ 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		

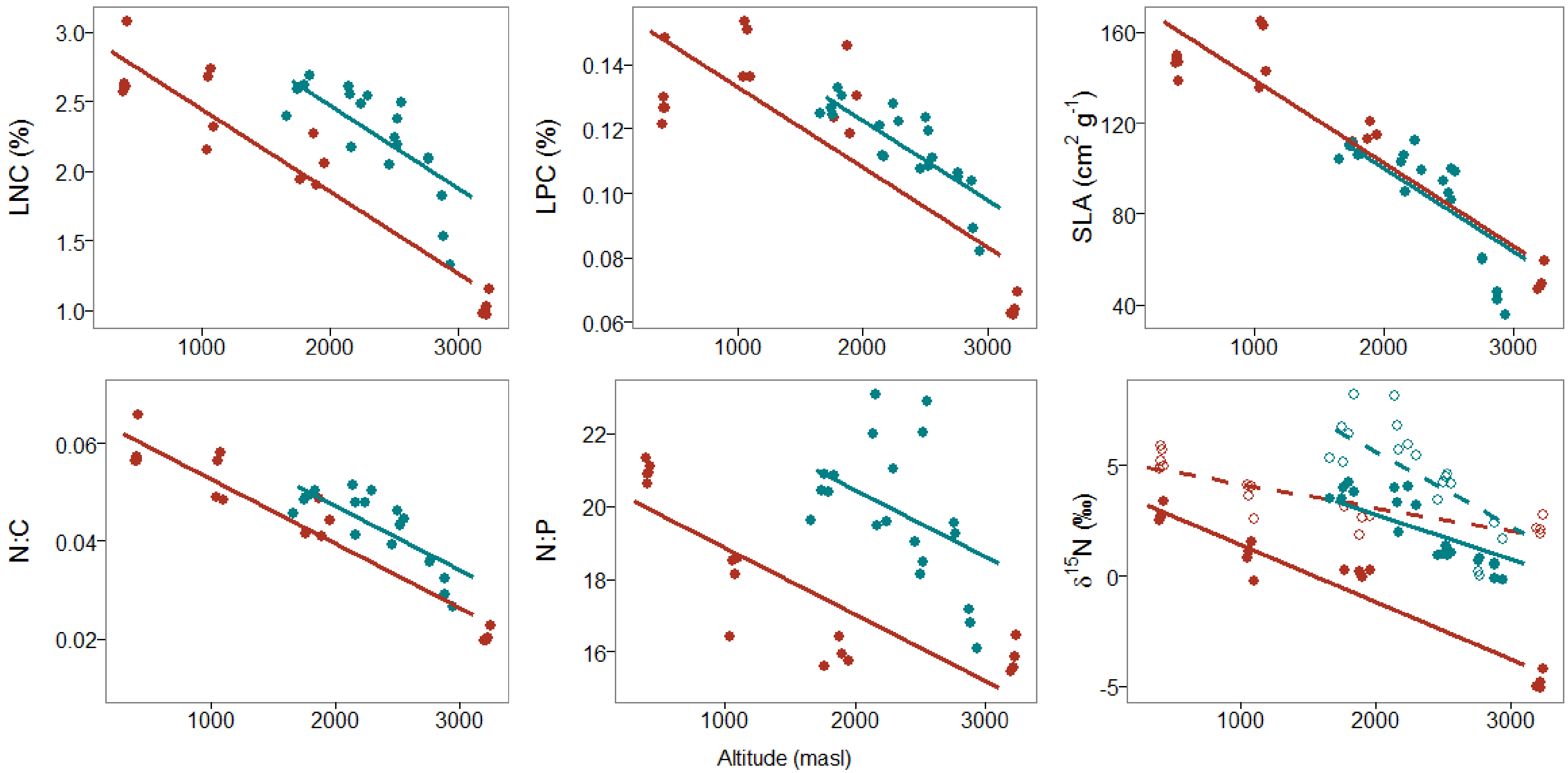

Fig. 1. Trends in community-level functional traits and leaf (full line, closed circles) and topsoil (dashed line, open circles) δ^{15}N of the elevation transects in Ecuador (red) and Rwanda (blue). Leaf nitrogen content (LNC), leaf phosphorus content (LPC), specific leaf area (SLA), and leaf N:C, P:C 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).