1   Parallel functional and stoichiometric trait shifts in South-American and African forest

2   communities with elevation

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22   Abstract

23   The Amazon and Congo basin are the two largest continuous blocks of tropical forest with a central

24   role for global biogeochemical cycles and ecology. However, both biomes differ in structure and

25   species richness and composition. Understanding future directions of the response of both biomes

26   to environmental change is paramount. We used one elevational gradient on both continents to

27   investigate functional and stoichiometric trait shifts of tropical forest in South America and Africa.

28   We measured community-weighted functional canopy traits and canopy and topsoil $\delta^{15}N$

29   signatures. We found that the functional forest composition response along both transects was

30   parallel, with a shift towards more nitrogen conservative species at higher elevations. Moreover,

31   canopy and topsoil $\delta^{15}N$ signals decreased with increasing altitude, suggesting a more conservative

32   N cycle at higher elevations. This cross-continental study provides empirical indications that both

33   South-American and African tropical forest show a parallel response with altitude, driven by

34   nitrogen availability along the elevational gradients, which in turn induces a shift in the functional

35   forest composition. More standardized research, and more research on other elevational gradients

36   is needed to confirm our observations.

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38

39

 Introduction

41 A good understanding of the future response of tropical forest ecosystems to global change is

42 required because of their vital role in global biogeochemical cycles and ecology. However, due to

43 the long turnover times in forest ecosystems, it is hard to acquire insight in these future responses.

44 As a result, empirical research has since long turned to studying ecosystems along natural

45 gradients, which can greatly advance our understanding of ecosystem ecology and function in

46 response to environmental shifts. Elevational gradients in particular offer open-air space-for-time

47 experiments. Contrary to latitudinal gradients or elevational gradients in the higher latitude zones,

48 they are not complicated by changes in seasonality, and with careful interpretation can offer great

49 insights in tropical forest functioning (Körner, 2007; Malhi et al., 2010; Sundqvist et al., 2013).

50 Hence, elevational transects have been postulated as a viable and useful setup to assess long-term

51 ecosystem responses to environmental changes, and serve as an empirical tool to assess future

52 trajectories of forest ecosystems under global change (Malhi et al., 2010; Sundqvist et al., 2013).

53 This has invoked research efforts on transects in South America, but no such studies have been

54 carried out in central African forests, leaving the second-largest continuous block of tropical forest

55 understudied. Nevertheless, recent work has shown that African and South-American tropical

56 forest currently show important differences in structure (Banin et al., 2012) and species richness

57 and composition (Slik et al., 2015). These differences call for cross-continental empirical research

58 in both the Amazon and the Congo basin (Corlett and Primack, 2006), and in this context we can

59 raise questions about the universality of tropical forest biogeochemistry and functioning across

60 both continents, and subsequently their response to future global change scenarios. Additionally,

61 due to the central role of nutrient availability that drives both net ecosystem productivity (NEP)

62 and ecosystem carbon use efficiency (CUEe) (Fernandez-Martinez et al., 2014), the effect of

63 climatic gradients on nutrient availability should be better understood.

64

65 Indeed, recent efforts have shown that biosphere-atmosphere carbon exchange in forests is

66 regulated by nutrient availability (Fernandez-Martinez et al., 2014) and therefore, changes in

67 nutrient bio-availability induced by global change need to be accounted for. Canopy chemical traits

68 are proxies that are relatively easy to assess, and from which ecosystem functioning and

69 biogeochemistry can be inferred (Asner et al., 2015; Wright et al., 2004). Nutrient ratios and

70 concentrations in leafs, along with specific leaf area (SLA), are traits that are known to cluster

71 around the leaf economic spectrum, which expresses a trade-off in photosynthetic efficiency and

72 leaf turnover. Indeed, canopy nutrients play key roles in photosynthesis, and are hence vital for

73 carbon exchange processes at the leaf level (Evans, 1989; Reich et al., 2009). Consequently,

74 species with high SLA, N and P are associated with high photosynthesis rates (Poorter et al., 2009;

75 Reich et al., 1997; Wright et al., 2004), but have an 'expensive' nutrient economy (fast leaf

76 turnover). Previous work has shown that these traits vary systematically with landscape

77 biogeochemistry (Asner et al., 2014, 2015) and hence the functional canopy signature of forests

78 across gradients express the ecological response to changes in nutrient availability. Canopy

79 chemistry has received increasingly more attention because of its inherent link to the plant strategy.

80 Nevertheless, and as rightfully noted by Asner and Martin (2016), there are only limited surveys

81 on canopy functional signatures in the tropics, while this information is vital for a landscape-scale

82 understanding of tropical forest assembly. In addition to leaf traits, both leaf and soil $\delta^{15}N$ are

83 known integrators of the local N cycle and analysis of natural abundance of stable N isotope ratios

84 is a powerful and extensively studied proxy for N cycling in ecosystems (Högberg, 1997). Previous

85   efforts have shown that shifts towards lower δ^{15}N values indicate a more closed N cycle with lower

86   N availability, and *vice versa* (Brookshire et al., 2012; Craine et al., 2015; Houlton et al., 2006).

87   This shift in isotopic ratios is caused by increased rates in fractioning processes such as

88   denitrification, where ^{14}N is preferentially consumed, leaving the source pool enriched with ^{15}N

89   (Hobbie and Ouimette, 2009). Hence δ^{15}N values have been used to infer shifts in N openness

90   across natural gradients (Martinelli et al., 1999; Menge et al., 2011; Vitousek et al., 1989), and

91   subsequently, combining both leaf traits and δ^{15}N values is an interesting approach to assess

92   ecosystem responses to environmental gradients.

93

94   In this study we address the existing lack of standardized cross-continental research and assessed

95   shifts in nutrient availability and forest functional composition along two similar transects in

96   Ecuador and Rwanda. We assessed these shifts through indicative (I) community-level functional

97   traits and (II) nitrogen isotope ratios in topsoil and canopy. We hypothesized that (I) both these

98   community-level traits and stable isotope signals would indicate a shift in nitrogen availability

99   with altitude, and that (II) these shifts would be similar on both continents in terms of direction

100   and magnitude, given a standardized research protocol and a similar adiabatic lapse rate.

101   Materials and Methods

102   **Field inventories, sampling and trait analyses**

103   We selected plots at different altitudes on the West flank of the Andes in Ecuador (ranging

104   from 400-3200 masl) and in the Nyungwe national Park Rwanda (1600-3000 masl), in the

105   Southern Great Rift Valley (figure S1 and Table S1 for location and overview maps). Due to

106   reduced accessibility, the gradient in Rwanda was shorter than the South-American transect. We

107   delineated and inventoried plots following an international standardized protocol for tropical forest

108   inventories (RAINFOR, Malhi et al. 2002), with an adapted plot size of 40 by 40 m. In each plot,

109   the diameter of all live stems with a diameter larger than 10 cm was measured at 1.3 m height and

110   the trees were identified to species or genus level. Besides diameters also tree heights were

111   measured, in order to estimate the aboveground carbon storage (AGC) using pan-tropical

112   allometric relationships (Chave et al., 2014). The canopy of every plot was characterized by

113   selecting the most abundant tree species, aiming at a sampling percentage of 80% of the basal area

114   of the plots. For the selected species of all plots, we sampled mature leaves of a minimum of three

115   individuals per species per plot using tree climbers. For most of the individuals we sampled fully

116   sunlit leaves, but this was not always possible for the safety of the climbers, in which case we

117   sampled partly shaded leaves under the top canopy. Previous work on elevational transects has

118   shown that the vertical profile of leaves within a canopy has little effect on the trait values (Fisher

119   et al., 2013). Additionally, composite samples of the topsoil (0-5 cm) were collected at five

120   different places within each plot, and mixed per plot prior to drying. Soil and leaf samples were

121   dried for 48 hours at 60°C. Roots were picked out of the soil samples before grinding and

122   subsequently carbon (C), nitrogen (N) content and δ^{15}N of plant and soil samples were analyzed

123   using an elemental analyzer (Automated Nitrogen Carbon Analyser; ANCA-SL, SerCon, UK),

124   interfaced with an Isotope Ratios Mass Spectrometer (IRMS; 20-20, SerCon, UK). Leaf samples

125   were dry-ashed at 550°C for 5.5 hours; the ash was dissolved in 2M HCl solution and subsequently

126   filtered through a P-free filter. The aliquots where then analyzed for total P by AAS method No.G-

127   103-93 Rev.2 (Multitest MT7/MT8; Ryan and others 2001). SLAs were calculated by dividing the

128   leaf areas of all the sampled leafs per individual by their summed dry mass. Leaf areas were

129   determined by either photographing leafs with on white paper with a reference scale or by drawing

130   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:

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

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):

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

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

152   different leaf traits and elevation using mixed effects models for the different traits, with a random

153   error structure. The plots were spatially clustered around four altitudes on both transects, hence we

154   introduced these elevational clusters as a random effect, and treated altitude and transect as fixed

155   effects. Models were then fitted using maximum likelihood methods in the 'lme4' package in R

156   (Bates et al., 2007). P-values of the fixed effects –elevation, transect and their interaction - were

157   determined based on the denominator degrees of freedom calculated with the Satterhwaite

158   approximation, in the lmerTest package (Kuznetsova et al., 2014). The P-values for the interaction

159   term, along with the Akaike Information Criterion (AIC) for models with and without this

160   interaction term were used to decide whether or not to exclude the interaction term. For reasons of

161   linearity we used the inverse C:N (hence rather N:C) in these analyses. Models for $\delta^{15}N$ were

162   assessed for each transect, using mixed effects models, with elevational cluster as a random effect.

163   To explicitly determine divergence and convergence of plant and soil $\delta^{15}N$ with altitude,

164   compartment (i.e. canopy leaves or topsoil) was introduced as a fixed effect and the interaction

165   term was left in the model. For the statistical analysis, the R-software was used (R Core Team,

166   2014).

167

168   Results

169   The pooled trait datasets from both transects showed a consistent and similar correlation structure

170   (Fig. S2), with both the separate and the pooled data showing significant correlations between all

171   traits, except SLA and N:P. The structural vegetation parameters on both transects showed

172   important differences: for the same altitude range, we found a higher stem density, but less species

173   on the Rwandan transect (Table 1). Tree height and basal area were comparable, and the carbon

174   stocks showed high variability along both transects. Climatic conditions were similar, with a highly

175   consistent temperature gradient (Fig. S3, Table 1), and similar mean annual precipitation in the

176   concurring elevational ranges. The linear mixed effects models with altitude as fixed effect, were

177   able to explain a significant proportion of variation in all traits. This is reflected by both the

178   marginal (m) and conditional (c) R^2_{adj}, respectively proxies for the variation explained by the fixed

179   effects, and the random and fixed effects together (Schielzeth and Nakagawa, 2013) (Table 2). The

180   interaction term was not significant in any case, hence the trait responses to altitude were parallel

181   on both continents. LNC, N:C, LPC and N:P significantly decreased with altitude ($R^2_{adj,m}$ of

182   respectively 0.83, 0.87, 0.68 and 0.60), with the Rwanda transect showing higher overall values.

183   SLA also decreased significantly, but with a slightly higher intercept for the Ecuadorian transect

184   ($R^2_{adj,m} = 0.83$). $\delta^{15}N$ decreased on both continents with altitude, with a similar effect on both

185   continents (Table 3). There was a significant divergence between slope and soil $\delta^{15}N$ along the

186   Ecuadorian transect, while Rwanda showed a significant convergence ($R^2_{adj,m} = 0.93$ and 0.55 for

187   respectively Ecuador and Rwanda).

188

189   Discussion

190   Elevational transects are viable setups to assess long-term ecosystem responses to environmental

191   gradients. We assessed canopy chemistry, functional composition and $\delta^{15}N$ signals along one

192   elevational gradient in South-America and one in Central Africa. The measured traits are indicative

193   proxies for the underlying biogeochemistry of the forest ecosystems. The shifts of these proxies

194   along both transects were parallel in both setups. They indicated a lowering N availability with

195   increasing altitude, with a subsequent parallel shift in functional forest composition on both

196   continents.

197

198 The vegetation structure was varying differently along both transects. The high variability in the

199 stem number, basal area and carbon stocks is potentially caused by the relatively small plot size.

200 Other research efforts, targeting these variables in specific, use plot sizes of 1 hectare, as set

201 forward by the RAINFOR protocol, in tropical forests worldwide (Phillips et al., 2009). As such,

202 the differing carbon stocks probably do not integrate important stochastic events (e.g. tree fall)

203 from the forest along both slopes. However, interestingly enough we found a lower average carbon

204 stocks and higher number of trees in the upper two Rwandan clusters in comparison to the

205 Ecuadorian forests. This contrasts to what has been reported from large scale forest monitoring

206 networks across the lowland forests of Amazon and the Congo basin (Lewis et al., 2013). More

207 research in larger plots, including dynamics and productivity should validate if this is a consistent

208 observation in highland forest on both continents. On the other hand, the lower species number on

209 the African transect fits well within the recent findings of a pantropical study, reporting a lower

210 tree species diversity in the African tropical forest (Slik et al., 2015).

211

212 Different environmental variables are influenced by altitudinal changes, i.e. atmospheric pressure,

213 temperature, cloudiness, moisture, etc. (Körner, 2007). Accordingly, elevation is an indirect proxy

214 for the related changes in these variables. In this view, the air temperature decrease with elevation

215 was highly similar on both transects, which means that we can validly assess similar temperature-

216 driven responses of both forest functional composition and the underlying nutrient dynamics. The

217 high collinearity in the trait datasets corresponds well to known trade-offs described as the "leaf

218 economics spectrum" (LES); basically a leaf-level trade-off between leaf construction cost, i.e.

219 low specific leaf area (SLA), leaf nitrogen content (LNC) and leaf phosphorus content (LPC); and

220 photosynthetic efficiency, i.e. high SLA, LNC and LPC (Wright et al., 2004). LNC, LPC and SLA

221 showed a highly significant decrease with altitude (Fig. 1 and Table 2), indicating a functional

222 shift towards more nutrient conservative species communities at higher altitudes on both transects.

223 Indeed, leaves at lower altitudes with high LNC, LPC and SLA and hence a more efficient

224 photosynthetic apparatus and rapid turnover, are replaced by leaves with low LNC, LPC and SLA

225 values at higher altitudes. We've added previous published work of South America and South-

226 East Asia, with similar temperature gradients by Asner et al, Kitayama and Aiba and Van de Weg

227 et al. to our transects (Asner et al., 2016b; Kitayama and Aiba, 2002; Van de Weg et al., 2009; Fig.

228 S3) to assess the consistency of our observed trends. We added the limited amount of studies where

229 community-weighted means were reported along one 'single mountain range system', hence

230 neglecting a recent and relevant contribution from Asner et al. (Asner and Martin, 2016). Our

231 comparison showed that the decreasing trend in LNC was consistent with the other studies from

232 South-America (Asner et al., 2016b; Van de Weg et al., 2009), but not with South-East Asia where

233 no significant trend was found (Kitayama and Aiba, 2002). However, leaf mass area (LMA; the

234 inverse of SLA) of all studies showed a similar, increasing trend with elevation. LPC shows a

235 strong and significant trend along both transects in this study, while the other studies report no

236 significant trend. This is consistent with the meta-analysis presented by Tanner et al., which shows

237 consistent negative LNC trends on 'same mountain' studies and inconsistent LPC trends (Tanner

238 et al., 1998). A recent effort on a larger scale in Peru has shown that LES trade-off between LNC-

239 LPC or SLA-LPC is indeed decoupled by climatic and geophysical filters, while the leaf SLA-

240 LNC trade-off is more robust (Asner et al., 2016a). Regarding the studies we included for

241 comparison (Fig. S3), only Van de Weg et al. assessed N:P ratio. Although no significant trend

242 was found, they reported that N:P ratio was lowest in the highest sites (Van de Weg et al., 2009).

243 Additionally, decreasing N:P ratios have also been reported on other transects on the Andes (Fisher

244   et al., 2013; Soethe et al., 2008), and recently in Peru using airborne imaging spectroscopy (Asner

245   et al., 2016a).

246

247   In addition to the above community-level functional traits, the decreasing $\delta^{15}N$ values on both

248   continents (Fig. 1) are another strong indication of the decreasing N availability in the upper

249   forests. Along the transects, both topsoil and canopy leaves showed decreasing $\delta^{15}N$ values with

250   increasing altitude (Fig. 1), indicating a more closed N cycle with lower N availability at the higher

251   altitudes of both transects. It has been shown that lowland tropical rainforests exhibit high values

252   of $\delta^{15}N$ mainly caused by the high gaseous nitrogen losses via denitrification, a strongly

253   fractionating process (Houlton et al., 2006). The decreasing trends with altitude are interesting and

254   seem to support the existing paradigm that tropical forests shift from P to N limitation in transition

255   from lowland to montane tropical forest (Townsend et al., 2008). This is also reflected in the

256   stoichiometric shifts, as canopy N:P is decreasing with increasing elevation (Fig. 1). Hence plants

257   incorporate relatively less N compared to P in canopies at higher altitudes. The higher soil $\delta^{15}N$

258   values along the lower part of the Rwanda transect suggests a more open N-cycle compared to the

259   lower part of the Ecuadorian transect. This corroborates with a recent finding of very high N losses

260   at 1900 masl at the Rwanda site (Rütting et al., 2014), and the observation of high retention

261   potential of bio-available N in Chilean Andisols (Huygens et al., 2008). Further research is needed

262   to explain the notable divergence in soil and foliage $\delta^{15}N$ along the Ecuadorian transect, mainly

263   driven by the highest elevational cluster. As previously reported this can be due to different degrees

264   of dependence upon ectomycorrhizal fungi (EcM) (Hobbie et al., 2005), different mycorrhizal

265   association types (Craine et al., 2009) or shifts in the uptake of different forms of nitrogen (Averill

266   and Finzi, 2011; Kahmen et al., 2008). EcM-associated plant species are expected to show more

267 depleted isotopic ratios, due to isotope fractionation during N transfer to the host plant. This effect

268 is obscured in lowland N rich tropical forests and might just not be detectable at lower altitudes,

269 but might become apparent in N poorer environments such as the higher altitude forests (Mayor et

270 al., 2014). Secondly, a study from a temperate elevational transect has shown that plants

271 increasingly switch to organic N sources with decreasing temperature, without fractionation upon

272 N transfer from EcM to plants (Averill and Finzi, 2011). Resulting from that, they found a

273 convergence rather than divergence of δ^{15}N soil – canopy along altitude, because plants draw N

274 increasingly from a source pool close to the bulk isotopic signature. We have no data on EcM

275 colonization or δ^{15}N of sporocarps in the study plots, so we are not able to disentangle both

276 mechanisms. However, by characterizing both community functional traits and canopy and soil

277 δ^{15}N, the data of these transects is consistent with a decreasing availability of soil N as elevation

278 increases. We suggest the reduced N availability to be caused by an indirect temperature effect on

279 the N-cycle, consistent with observations from a direct fertilization experiment (Fisher et al.,

280 2013). Lower temperatures slow down depolymerization and N mineralization processes, hence

281 also N bio-availability, thereby invoking changes in the functional plant communities along the

282 transects (Coûteaux et al., 2002; Marrs et al., 1988). Future global change will most likely distort

283 N availability both directly via increased reactive N deposition (Galloway et al., 2008; Hietz et al.,

284 2011) and indirectly via a temperature effect on N mineralization in forest soils. This raises

285 questions on the future of plant species within the already threatened montane tropical forest

286 biome, where higher N availability and temperature increase might distort the existing ecological

287 niches and in turn also increase N losses. Further research should therefore focus on process-based

288 knowledge of N and P cycle dynamics along such transects to further assess if the availability is

289 actually limiting the ecosystems. These observations also have repercussions for carbon fluxes:

290   since nutrient availability exerts a stronger control on NEP than on gross primary production (GPP)

291   (Fernandez-Martinez et al., 2014), it is likely that the CUE_e will be lower at higher altitudes. It has

292   been hypothesized that this decrease in CUE_e is due to an increased investment of photosynthates

293   to non-biomass components, such as root symbionts for nutrient mining and root exudates, in

294   expense of net primary production (NPP) (Vicca et al., 2012). However, recent empirical evidence

295   has shown for one transect in the Andes, that a decrease in GPP with increasing altitude is not

296   accompanied by a trend in CUE (Malhi et al., 2016). More work on carbon budgets along

297   elevational transects is needed to fully understand the role of N and P availability and its interaction

298   with climate gradients for the tropical forest carbon cycle.

299

300   **Conclusions**

301   Altogether, this study evidences parallel functional shifts with a similar direction and magnitude

302   along two comparable elevation gradients, in tropical forests on two different continents. The data

303   suggests, in two different ways, that this shift is caused by temperature-driven response of nutrient

304   availability. With the first data on an elevational transect in Central Africa, this work adds to the

305   existing set of elevational transects in the tropics. However, more transects are needed, especially

306   in Africa, to validate a universal response of tropical forests to environmental change.

307   Furthermore, work on process-based nutrient dynamics is important to unravel the importance of

308   different global change factors for both forest basins.

309

310   **Supplementary information**

311   **Fig. S1** Overview map

312   **Fig. S2** Structure and correlations of the trait data

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

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

315 **Table S2** Summary of the plot-level characteristics

316 **Table S3** Fixed effects estimates for the different canopy-level response variables for the full
317 model including interaction term

318

319 **Author contributions**

320 *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*
321 *work and analyzed the data. All authors contributed to the ideas presented and edited the*
322 *manuscript.*

323

324 **Competing interests**

325 The authors declare that they have no conflict of interest.

326

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532 **Table 1** General characteristics, vegetation structure, climate (mean annual temperature (MAT) and mean annual precipitation (MAT),

533 WorldClim - Fick, 2017) and soil characteristics of the elevational clusters on both transects. Number of trees and species (in the 40

534 by 40 m plots), basal area (BA), mean tree height (MTH) and above-ground carbon (AGC) are averages per plot ± the standard

535 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

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538 **Table 2** Fixed effects estimates (altitude in km asl) for the different canopy-level response

539 variables; leaf nitrogen content (LNC), inverse C:N ratio, specific leaf area (SLA), leaf phosphorus

540 content (LPC) and N:P ratio, along with the estimated marginal (m) and conditional (c) R^2_{adj} (sensu

541 Nakagawa and Schielzeth (5)). The interaction term for altitude x transect was not significant in

542 any case, and was hence not retained in any model.

543

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 (cm^2 g^{-1})	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		

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548 **Table 3** Fixed effects estimates (altitude in km asl) for $\delta^{15}N$ in both canopy and topsoil

549 (compartment) on both transects, along with the estimated marginal (m) and conditional (c) R^2_{adj}

550 (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		

551
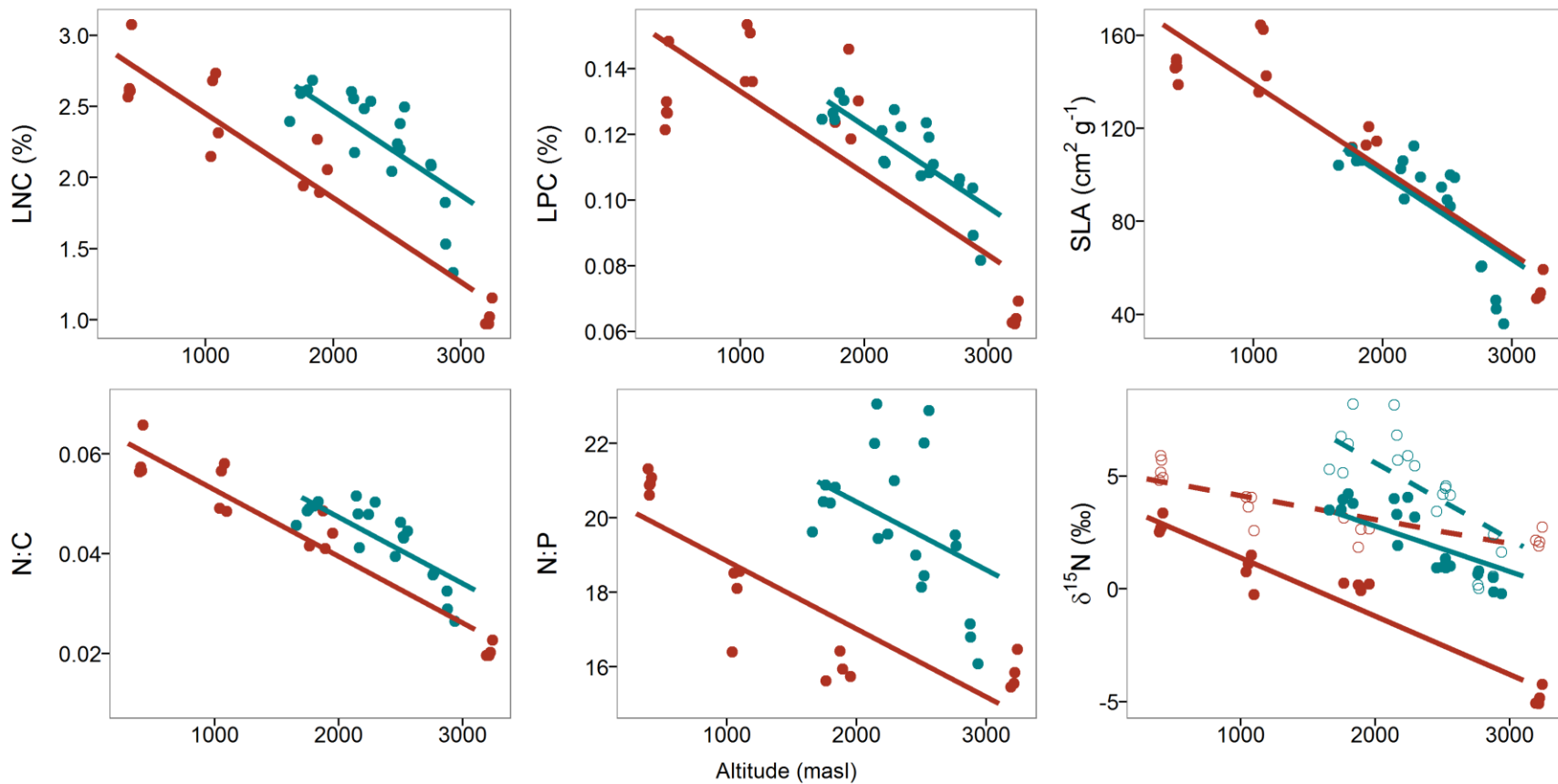
Fig. 1. Trends in community-level functional traits and leaf (full line, closed circles) and topsoil (dashed line, open circles) $\delta^{15}N$ of the elevation transects in Ecuador (red) and Rwanda (blue). Leaf nitrogen content (LNC), leaf phosphorus content (LPC), specific leaf area (SLA), and leaf N:C, P:C and N:P ratio decrease with increasing altitude on both transects. Both transect showed decreasing values of $\delta^{15}N$, 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).