



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

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22 Abstract

23 Elevational gradients are an empirical tool to assess long-term forest responses to environmental
24 change. We studied whether functional composition of tropical forest along elevational gradients
25 in South America and in Africa showed similar shifts. We assessed community-weighted
26 functional canopy traits and indicative $\delta^{15}\text{N}$ shifts along two new altitudinal transects in the tropical
27 forest biome of both South-America and Africa. We found that the functional forest composition
28 response along both transects was parallel, with a species shift towards more nitrogen conservative
29 species at higher elevations. Moreover, canopy and topsoil $\delta^{15}\text{N}$ signals decreased with increasing
30 altitude, suggesting a more conservative N cycle at higher elevations. This cross-continental study
31 provides two empirical indications that both South-American and African tropical forest show a
32 parallel response along altitude, driven by nitrogen availability along the altitudinal gradients,
33 inducing a parallel shift in the functional forest composition. This highlights the importance of
34 nutrient availability for tropical forest in a changing world. More standardized research, and more
35 research on other elevational gradients is needed to confirm our observations.

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39 Introduction

40 A good understanding of the future response of tropical forest ecosystems to global changes is
41 required because of their vital role in the global carbon cycle. Recent efforts have shown that
42 biosphere-atmosphere carbon exchange in forests is regulated by nutrient availability (Fernandez-
43 Martinez et al., 2014). Therefore, changes in nutrient bio-availability induced by global change
44 need to be taken into account. Uncertainties on future responses of forest ecosystems to global
45 change are perhaps most prominent in the tropics, where monitoring is underdeveloped compared
46 to the temperate region. Recent work has shown that African and South-American tropical forest
47 show important differences in structure (Banin et al., 2012) and species richness and composition
48 (Slik et al., 2015a). Additionally, there is a lack of cross-continental empirical research in both the
49 Amazon and the Congo basin, and most model projections are parameterized on either South-
50 American tropical or even temperate forests (Corlett and Primack, 2006). Moreover, earth system
51 model projections typically do not account for nutrient dynamics (Anav et al., 2013) and models
52 that account for nutrient cycling in their land component are still under development (Goll et al.,
53 2012; Reed et al., 2015; Smith et al., 2014). , In this context we can raise questions about the
54 universality of tropical forest biogeochemistry and functioning across both continents, and
55 subsequently their response to future global change scenarios. This leaves us with an important
56 bottleneck to further optimize Earth system models (Ciais et al., 2011). Hence, cross-continental
57 comparisons of tropical forest ecosystem responses to environmental gradients are needed.
58 Additionally, due to the central role of nutrient availability that drives both net ecosystem
59 productivity (NEP) and ecosystem carbon use efficiency (CUE_e) (Fernandez-Martinez et al.,
60 2014), the effect of climatic gradients on nutrient availability should be better understood.
61 Elevation transects offer such gradients.



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

68

69 In this study we address this lack of standardized cross-continental research and assessed shifts in
70 nutrient availability and forest functional composition along two similar transects in Ecuador and
71 Rwanda. We assessed these shifts through indicative (I) community-level functional traits and (II)
72 nitrogen isotope ratios in topsoil and canopy. Canopy chemistry has received increasingly more
73 attention, and has been identified as a proxy for landscape-scale biogeochemistry (Asner et al.,
74 2015; Fyllas et al., 2009), because of its inherent link to the plant strategy. Nevertheless, and as
75 rightfully noted by Asner and Martin (2016), there are only limited surveys on canopy functional
76 signatures in the tropics, while this information is vital for a landscape-scale understanding of
77 tropical forest assembly. In addition to a standard set of leaf traits, both leaf and soil $\delta^{15}\text{N}$ are
78 known integrators of the local N-cycle. Previous efforts have shown that shifts towards lower $\delta^{15}\text{N}$
79 values indicate a more closed N-cycle with lower N availability, and *vice versa* (Craine et al.,
80 2009, 2015). Hence combining both leaf traits and $\delta^{15}\text{N}$ values is an interesting approach to assess
81 ecosystem responses to environmental gradients. We hypothesized that (I) both these community-
82 level traits and stable isotope signals would indicate a shift in nitrogen availability with altitude,
83 and that (II) these shifts would be similar in terms of direction and magnitude, given a standardized
84 research protocol and a similar adiabatic lapse rate.



85 Materials and Methods

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

87 We selected plots at different altitudes on the West flank of the Andes in Ecuador (ranging
88 from 400-3200 masl) and in the Nyungwe national Park Rwanda (1600-3000 masl), in the
89 Southern Great Rift Valley (figure S1 and Table S1 for location and overview maps). Due to
90 reduced accessibility, the gradient in Rwanda was shorter than the South-American transect. We
91 delineated and inventoried plots following an international standardized protocol for tropical forest
92 inventories (RAINFOR, Malhi et al. 2002), with an adapted plot size of 40 by 40 m. In each plot,
93 the diameter of all live stems with a diameter larger than 10 cm was measured at 1.3 m height and
94 the trees were identified to species or genus level. Besides diameters also tree heights were
95 measured, in order to estimate the aboveground carbon storage (AGC), using pan-tropical
96 allometric relationships (Chave et al., 2014). The canopy of every plot was characterized by
97 selecting the most abundant tree species, aiming at a sampling percentage of 80% of the basal area
98 of the plots. For the selected species of all plots, we sampled mature leaves of a minimum of three
99 individuals per species per plot using tree climbers. For most of the individuals we sampled fully
100 sunlit leaves, but this was not always possible for the safety of the climbers, in which case we
101 sampled partly shaded leaves under the top canopy. Previous work on altitudinal transects has
102 shown that the vertical profile of leaves within a canopy has little effect on the trait values (Fisher
103 et al., 2013). This sampling was carried out at the level of the total inventory. Additionally,
104 composite samples of the topsoil (0-5 cm) were collected at five different places within each plot,
105 and mixed per plot prior to drying. Soil and leaf samples were dried for 48 hours at 60°C. Roots
106 were picked out of the soil samples before grinding and subsequently carbon (C), nitrogen (N)
107 content and $\delta^{15}\text{N}$ of plant and soil samples were analyzed using an elemental analyzer (Automated



108 Nitrogen Carbon Analyser; ANCA-SL, SerCon, UK), interfaced with an Isotope Ratios Mass
109 Spectrometer (IRMS; 20-20, SerCon, UK). Leaf samples were dry-ashed at 550°C for 5.5 hours;
110 the ash was dissolved in 2M HCl solution and subsequently filtered through a P-free filter. The
111 aliquots were then analyzed for total P by AAS method No.G-103-93 Rev.2 (Multitest
112 MT7/MT8; Ryan and others 2001). SLAs were calculated by dividing the leaf areas of all the
113 sampled leaves per individual by their summed dry mass. Leaf areas were determined by either
114 photographing leaves with on white paper with a reference scale or by drawing leaf contours and
115 scanning the drawings. Both the scans and the pictures were processed using the ImageJ software
116 (Schneider et al., 2012). For one abundant species of the higher altitudes on the Rwandan transect
117 (*Podocarpus latifolius* (Thunb.) R.Br. ex Mirb.) we could not obtain good area estimates, so we
118 adopted SLA figures from literature (Midgley et al., 1995).

119

120 **Statistical analysis**

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

$$127 \quad \bar{x}_w = \frac{\sum_{i=1}^N w_i \cdot x_i}{\sum_{i=1}^N x_i}$$

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



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

134 with N the number of nonzero weights.

135 The structure of the trait datasets was assessed qualitatively using Pearson correlation statistics.

136 Finally, we studied the relations between the different leaf traits and elevation using mixed effects

137 models for the different traits, with a random error structure. The plots were spatially clustered

138 around four altitudes on both transects, hence we introduced these altitudinal clusters as a random

139 effect, and treated altitude and transect as fixed effects. Models were then fitted using maximum

140 likelihood methods in the ‘nlme’ package in R (Pinheiro et al., 2013). An interaction term for

141 transect (Rwanda or Ecuador) and elevation was tested using likelihood ratio test and was retained

142 in the final models when significant at the P<0.05 level. For reasons of linearity we used the inverse

143 C:N (hence rather N:C) in these analyses. For the statistical analysis, the R-software was used (R

144 Core Team, 2014).

145

146 Results

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

148 (Fig S2), with in both separate and the pooled data significant correlations between all traits, except

149 SLA and N:P. The structural vegetation parameters on both transects showed important

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

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

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



153 consistent temperature gradient (Fig S3, Table 1), and similar mean annual precipitation in the
154 concurring altitudinal ranges. The linear mixed models with altitude as fixed effect, were able to
155 explain a significant proportion of variation in all traits. This is reflected by both the marginal and
156 conditional R^2_{adj} , respectively proxies for the variation explained by the fixed effects, and the
157 random and fixed effects together (Schielzeth and Nakagawa, 2013) (Table 2). The interaction
158 term was not significant in any case, hence the trait and $\delta^{15}\text{N}$ responses to altitude were parallel on
159 both continents. LNC, N:C, LPC and N:P significantly decreased with altitude ($R^2_{\text{adj,marg}}$ of
160 respectively 0.83,0.87,0.68 and 0.60), with the Rwanda transect showing higher overall values.
161 SLA also decreased significantly, but with a slightly higher intercept for the Ecuadorian transect
162 ($R^2_{\text{adj,marg}} = 0.83$). In addition to the functional trait and stoichiometric shifts, canopy and topsoil
163 $\delta^{15}\text{N}$ decreased on both continents, with a stronger decrease for canopy than for topsoil ($R^2_{\text{adj,marg}}$
164 respectively 0.92 and 0.43 for canopy and soil).

165

166 Discussion

167 The general characteristics, averaged for the altitudinal clusters, show that the vegetation structure
168 is different along both transects. The high variability in these structural characteristics as such, is
169 potentially caused by the relatively small plot size. However investigating the variation in
170 structural characteristics is beyond the scope of this research. Other research efforts, targeting
171 structural characteristics and carbon stocks in specific, use plot sizes of 1 hectare, as set forward
172 by the RAINFOR protocol, in tropical forests worldwide (Phillips et al., 2009). As such, the
173 differing carbon stocks probably do not integrate important stochastic events (e.g. tree fall) from
174 the forest along both slopes. However, interestingly enough the lower average carbon stocks and
175 higher number of trees in the upper two Rwandan clusters in comparison to the Ecuadorian forests.



176 This contrasts to what has been reported from large scale forest monitoring networks across the
177 lowland forests of Amazon and the Congo basin (Lewis et al., 2013). More research in larger plots,
178 including dynamics and productivity should validate if this is a consistent observation in highland
179 forest on both continents. On the other hand, the lower species number on the African transect fits
180 well within the recent findings of a pantropical study, reporting a lower tree species diversity in
181 the African tropical forest (Slik et al., 2015b). More importantly for this paper, the air temperature
182 decrease with elevation is highly similar on both transects, which means that we can validly assess
183 similar temperature-driven responses of both forest functional composition and the underlying
184 nutrient dynamics. The high collinearity in the trait datasets corresponds well to known trade-offs
185 described as the “leaf economics spectrum” (LES); basically a leaf-level trade-off between leaf
186 construction cost, i.e. low specific leaf area (SLA), leaf nitrogen content (LNC) and leaf
187 phosphorus content (LPC); and photosynthetic efficiency, i.e. high SLA, LNC and LPC (Wright
188 et al., 2004). LNC, LPC and SLA showed a highly significant decrease with altitude (Fig. 1 and
189 Table 2), indicating a functional shift towards more nutrient conservative species communities at
190 higher altitudes on both transects. Indeed, leaves at lower altitudes with high LNC, LPC and SLA
191 and hence a more efficient photosynthetic apparatus and rapid turnover, are replaced by leaves
192 with low LNC, LPC and SLA values at higher altitudes. Along the transects, both topsoil and
193 canopy leaves showed decreasing $\delta^{15}\text{N}$ values with increasing altitude (Fig. 1), inferring a more
194 closed N-cycle with lower N availability at the higher altitudes of both transects. We’ve added
195 previous published work in South America, with similar temperature gradients by Asner et al,
196 Kitayama and Aiba and Van de Weg et al. to our transects (12, 16, 17; Fig. S3) to assess the
197 consistency of our observed trends. We deliberately only added the limited amount of studies
198 where community-weighted means were reported along a ‘single mountain range system’, hence



199 neglecting a recent and relevant contribution from Asner et al. (Asner and Martin, 2016). As argued
200 by Tanner et al. (Tanner et al., 1998), in studies of general altitude patterns from different mountain
201 ranges, elevational trends might be obscured by a range of local environmental characteristics,
202 such as soil type and orientation. Forests with low, intermediate and high nutrient concentrations
203 can be found globally at any altitude, hence neglecting the effect of local characteristics might lead
204 to wrong conclusions. This is also shown by the different intercepts, or the vertical *shift* in trends
205 in fig S3. Our comparison showed that the decreasing trend in LNC (mass basis) was consistent
206 with the other studies from South-America (Asner et al., 2016b; Van de Weg et al., 2009), but not
207 with South-East Asia where no significant trend was found (Van de Weg et al., 2009). However,
208 leaf mass area (LMA; the inverse of SLA) of all studies showed a similar, increasing trend with
209 elevation. LPC shows a strong and significant trend along both transects in this study, while the
210 other studies report no significant trend. This is consistent with the meta-analysis presented by
211 Tanner et al., which shows consistent negative LNC trends on ‘same mountain’ studies and
212 inconsistent LPC trends (Tanner et al., 1998). A recent effort on a larger scale in Peru has shown
213 that LES trade-off between LNC-LPC or SLA-LPC is indeed decoupled by climatic and
214 geophysical filters, while the leaf SLA-LNC trade-off is more robust (Asner et al., 2016a). Of the
215 included studies in Fig. S3, only Van de Weg et al. assessed N:P ratio, and although no significant
216 trend was found, they reported that N:P ratio was lowest in the highest sites (Van de Weg et al.,
217 2009). Additionally, decreasing N:P ratios have also been reported on other transects on the Andes
218 (Fisher et al., 2013; Soethe et al., 2008), and recently in Peru using airborne imaging spectroscopy
219 (Asner et al., 2016a).

220



221 In addition to our community-level traits (decreasing LNC, increasing C:N and N:P ratio), the
222 decreasing $\delta^{15}\text{N}$ values on both continents (fig. 1) are another strong indication of the limited
223 access of the upper forests to bio-available N. This data is only indicative and we cannot conclude
224 that there is actual limitation. However, the trends are interesting and seem to support the existing
225 paradigm that tropical forests shift from P to N limitation in transition from lowland to montane
226 tropical forest (Townsend et al., 2008). This is also reflected in the stoichiometric shifts, as the
227 C:N increase dominates over the C:P increase along the transects, leading to a general decrease of
228 N:P with increasing elevation (fig. 1). Hence plants build in relatively less N compared to P in
229 canopies at higher altitudes. The higher soil $\delta^{15}\text{N}$ values along the lower part of the Rwanda
230 transect suggests a more open N-cycle compared to the lower part of the Ecuadorian transect. This
231 corroborates with a recent finding of very high N losses at 1900 masl at the Rwanda site (Rütting
232 et al., 2014), and the finding of high retention of bio-available N in Chilean Andisols (Huysgens et
233 al., 2008). Further research is needed to explain the notable divergence in soil and foliage $\delta^{15}\text{N}$
234 along the Ecuadorian transect. As previously reported this can be due to different degrees of
235 mycorrhizal infection (Hobbie et al., 2005), different mycorrhizal association types (Craine et al.,
236 2009) or species-specific preferences for different forms of nitrogen (Kahmen et al., 2008).

237

238 By characterizing both community functional traits and canopy and soil $\delta^{15}\text{N}$, the data of these
239 both transects is consistent with a decreasing availability of soil N as elevation increases, which is
240 here for the first time confirmed for the African continent. We suggest the reduced N availability
241 to be caused by an indirect temperature effect on the N-cycle, consistent with observations from a
242 direct fertilization experiment (Fisher et al., 2013). Lower temperatures slow down
243 depolymerization and N mineralization processes, hence also N bio-availability, thereby invoking



244 changes in the functional plant communities along the transects (Coûteaux et al., 2002; Marrs et
245 al., 2013). Future global change will most likely distort this evolutionary conditions for N
246 availability; both directly via increased reactive N deposition (Galloway et al., 2008; Hietz et al.,
247 2011) and indirectly via a temperature effect on N mineralization in tropical forests. This raises
248 questions on the future of plant species within the already threatened montane tropical forest
249 biome, where higher N availability and temperature increase might distort the existing ecological
250 niches and in turn also increase N-losses. Further research should therefore focus on process-based
251 knowledge of N and P cycle dynamics along such transects to further assess if the availability is
252 actually limiting the ecosystems. These observations also have repercussions for carbon fluxes:
253 since nutrient availability exerts a stronger control on NEP than on gross primary production (GPP)
254 (Fernández-Martínez et al., 2014), it is likely that the CUE_e will be lower at higher altitudes. It has
255 been hypothesized that this decrease in CUE_e is due to an increased investment of photosynthates
256 to non-biomass components, such as root symbionts for nutrient mining and root exudates, in
257 expense of net primary production (NPP) (Vicca et al., 2012). However, recent empirical evidence
258 has shown for one transect in the Andes, that a decrease in GPP with increasing altitude is not
259 accompanied by a trend in CUE (Malhi et al., 2016). More work on carbon budgets along
260 elevational transects is needed to fully understand the role of N and P availability and its interaction
261 with climate gradients for the tropical forest carbon cycle.

262

263 **Conclusions**

264 Altogether, this study evidences parallel functional shifts with a similar direction and magnitude
265 along two comparable elevation gradients, in tropical forests on two different continents. The data
266 suggests, in two different ways, that this shift is caused by temperature-driven response of nutrient



267 availability. This advocates the explicit need for implementing nutrient dynamics and availability
268 in ecosystem models. With the first data on an altitudinal transect in Central Africa, this work adds
269 to the existing set of elevational transects in the tropics, but more transects are needed, especially
270 in Africa, to validate a universal response of tropical forests. Furthermore, work on process-based
271 nutrient dynamics is important to unravel the importance of different global change factors for
272 both forest basins.

273

274 **Supplementary information**

275 **Fig. S1** Overview map

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

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

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

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

280

281 **Author contributions**

282 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
283 work and analyzed the data. All authors contributed to the ideas presented and edited the
284 manuscript.

285

286 **Competing interests**

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

288



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296 **References:**

- 297 Anav, A., Friedlingstein, P., Kidston, M., Bopp, L., Ciais, P., Cox, P., Jones, C., Jung, M.,
298 Myneni, R. and Zhu, Z.: Evaluating the land and ocean components of the global carbon cycle in
299 the CMIP5 earth system models, *J. Clim.*, 26(18), 6801–6843, doi:10.1175/JCLI-D-12-00417.1,
300 2013.
- 301 Asner, G. P. and Martin, R. E.: Convergent elevation trends in canopy chemical traits of tropical
302 forests, *Glob. Chang. Biol.*, 22(6), 2216–2227, doi:10.1111/gcb.13164, 2016.
- 303 Asner, G. P., Anderson, C. B., Martin, R. E., Tupayachi, R., Knapp, D. E. and Sinca, F.:
304 Landscape biogeochemistry reflected in shifting distributions of chemical traits in the Amazon
305 forest canopy, *Nat. Geosci.*, 8(May), 567–573, doi:10.1038/ngeo2443, 2015.
- 306 Asner, G. P., Knapp, D. E., Anderson, C. B., Martin, R. E. and Vaughn, N.: Large-scale climatic
307 and geophysical controls on the leaf economics spectrum, *PNAS*, 4043–4051,
308 doi:10.1073/pnas.1604863113, 2016a.
- 309 Asner, G. P., Martin, R. E., Anderson, C. B., Kryston, K., Vaughn, N., Knapp, D. E., Bentley, L.
310 P., Shenkin, A., Salinas, N., Sinca, F., Tupayachi, R., Sandra, D., Huaypar, K. Q., Pillco, M. M.,
311 Delis, F., Alvarez, C., Malhi, Y., Quispe Huaypar, K., Montoya Pillco, M., Ccori Álvarez, F. D.,
312 Díaz, S., Enquist, B., Malhi, Y., Sandra, D., Huaypar, K. Q., Pillco, M. M., Delis, F., Alvarez, C.
313 and Malhi, Y.: Scale dependence of canopy trait distributions along a tropical forest elevation
314 gradient, *New Phytol.*, 2016b.
- 315 Banin, L., Feldpausch, T. R., Phillips, O. L., Baker, T. R., Lloyd, J., Affum-Baffoe, K., Arets, E.
316 J. M. M., Berry, N. J., Bradford, M., Brienen, R. J. W., Davies, S., Drescher, M., Higuchi, N.,
317 Hilbert, D. W., Hladik, A., Iida, Y., Salim, K. A., Kassim, a. R., King, D. a., Lopez-Gonzalez,



- 318 G., Metcalfe, D., Nilus, R., Peh, K. S.-H., Reitsma, J. M., Sonké, B., Taedoumg, H., Tan, S.,
319 White, L., Wöll, H. and Lewis, S. L.: What controls tropical forest architecture? Testing
320 environmental, structural and floristic drivers, *Glob. Ecol. Biogeogr.*, 21(12), 1179–1190,
321 doi:10.1111/j.1466-8238.2012.00778.x, 2012.
- 322 Chave, J., Réjou-Méchain, M., Burquez, A., Chidumayo, E., Colgan, M. S., Delitti, W. B. C.,
323 Duque, A., Eid, T., Fearnside, P. M., Goodman, R. C., Henry, M., Martinez-Yrizar, A.,
324 Mugasha, W. A., Muller-Landau, H. C., Mencuccini, M., Nelson, B. W., Ngomanda, A.,
325 Nogueira, E. M., Ortiz-Malavassi, E., Péliissier, R., Ploton, P., Ryan, C. M., Saldarriaga, J. G.
326 and Vieilledent, G.: Improved allometric models to estimate the aboveground biomass of tropical
327 trees, *Glob. Chang. Biol.*, 20(10), 3177–3190, doi:10.1111/gcb.12629, 2014.
- 328 Ciais, P., Bombelli, a, Williams, M., Piao, S. L., Chave, J., Ryan, C. M., Henry, M., Brender, P.
329 and Valentini, R.: The carbon balance of Africa: synthesis of recent research studies., *Philos.*
330 *Trans. A. Math. Phys. Eng. Sci.*, 369(1943), 2038–2057, doi:10.1098/rsta.2010.0328, 2011.
- 331 Corlett, R. T. and Primack, R. B.: Tropical rainforests and the need for cross-continental
332 comparisons, *Trends Ecol. Evol.*, 21(2), 104–110, doi:10.1016/j.tree.2005.12.002, 2006.
- 333 Coûteaux, M. M., Sarmiento, L., Bottner, P., Acevedo, D. and Thiéry, J. M.: Decomposition of
334 standard plant material along an altitudinal transect (65 - 3968 m) in the tropical Andes, *Soil*
335 *Biol. Biochem.*, 34, 69–78, 2002.
- 336 Craine, J. M., Elmore, A. J., Aidar, M. P. M., Bustamante, M., Dawson, T. E., Hobbie, E. A.,
337 Kahmen, A., Mack, M. C., Mclauchlan, K. K., Michelsen, A., Nardoto, G. B. and Pardo, L. H.:
338 Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal
339 fungi, foliar nutrient concentrations, and nitrogen availability, *New Phytol.*, 183, 980–992, 2009.



- 340 Craine, J. M., Brookshire, E. N. J., Cramer, M. D., Hasselquist, N. J., Koba, K., Marin-spiotta, E.
341 and Wang, L.: Ecological interpretations of nitrogen isotope ratios of terrestrial plants and soils,
342 *Plant Soil*, 396, 1–26, doi:10.1007/s11104-015-2542-1, 2015.
- 343 Fernandez-Martinez, M., Vicca, S., Janssens, I. A., Sardans, J., Luysaert, S., Campioli, M., Iii,
344 F. S. C., Ciais, P., Malhi, Y., Obersteiner, M., Papale, D., Piao, S. L. and Reichstein, M.:
345 Nutrient availability as the key regulator of global forest carbon balance, *Nat. Clim. Chang.*,
346 4(June), 471–476, doi:10.1038/NCLIMATE2177, 2014.
- 347 Fernández-Martínez, M., Vicca, S., Janssens, I. a., Sardans, J., Luysaert, S., Campioli, M.,
348 Chapin III, F. S., Ciais, P., Malhi, Y., Obersteiner, M., Papale, D., Piao, S. L., Reichstein, M.,
349 Rodà, F., Peñuelas, J., Fernandez-Martinez, M., Vicca, S., Janssens, I. a., Sardans, J., Luysaert,
350 S., Campioli, M., Iii, F. S. C., Ciais, P., Malhi, Y., Obersteiner, M., Papale, D., Piao, S. L. and
351 Reichstein, M.: Nutrient availability as the key regulator of global forest carbon balance, *Nat.*
352 *Clim. Chang.*, 4(June), 471–476, doi:10.1038/NCLIMATE2177, 2014.
- 353 Fisher, J. B., Malhi, Y., Torres, I. C., Metcalfe, D. B., van de Weg, M. J., Meir, P., Silva-Espejo,
354 J. E., Huasco, W. H. and Daniel, T.: Nutrient limitation in rainforests and cloud forests along a
355 3,000-m elevation gradient in the Peruvian Andes, *Oecologia*, 172(3), 889–902,
356 doi:10.1007/s00442-012-2522-6, 2013.
- 357 Fyllas, N. M., Patiño, S., Baker, T. R., Nardoto, G. B., Martinelli, L. A., Quesada, C. A., Paiva,
358 R., Okologie, A., Fyllas, N. M., Patiño, S., Baker, T. R., Nardoto, G. B., Martinelli, L. A.,
359 Quesada, C. A., Paiva, R., Schwarz, M., Horna, V., Mercado, L. M., Santos, A., Arroyo, L.,
360 Jimenez, E. M., Luizao, F. J., Neill, D. a., Silva, N., Prieto, A., Rudas, A., Silviera, M., Vieira, I.
361 C. G., Lopez-Gonzalez, G., Malhi, Y., Phillips, O. L. and Lloyd, J.: Basin-wide variations in
362 foliar properties of Amazonian forest: phylogeny, soils and climate, *Biogeosciences*, 6, 2677–



- 363 2708, doi:10.5194/bgd-6-3707-2009, 2009.
- 364 Galloway, J. N., Townsend, A. R., Erisman, J. W., Bekunda, M., Cai, Z., Freney, J. R.,
365 Martinelli, L. A., Seitzinger, S. P. and Sutton, M. A.: Transformation of the Nitrogen Cycle :
366 Recent Trends, Questions, and Potential Solutions, *Science* (80-.), 320(May), 889–893, 2008.
- 367 Goll, D. S., Brovkin, V., Parida, B. R., Reick, C. H., Kattge, J., Reich, P. B., van Bodegom, P.
368 M. and Niinemets, Ü.: Nutrient limitation reduces land carbon uptake in simulations with a
369 model of combined carbon, nitrogen and phosphorus cycling, *Biogeosciences Discuss.*, 9(3),
370 3173–3232, doi:10.5194/bgd-9-3173-2012, 2012.
- 371 Hietz, P., Turner, B. L., Wanek, W., Richter, a., Nock, C. a. and Wright, S. J.: Long-Term
372 Change in the Nitrogen Cycle of Tropical Forests, *Science* (80-.), 334(2011), 664–666,
373 doi:10.1126/science.1211979, 2011.
- 374 Hobbie, E. a., Jumpponen, A., Trappe, J., Jumpponen, Æ. A. and Trappe, Æ. J.: Foliar and fungal
375 ¹⁵N:¹⁴N ratios reflect development of mycorrhizae and nitrogen supply during primary
376 succession: Testing analytical models, *Oecologia*, 146(2), 258–268, 2005.
- 377 Huygens, D., Boeckx, P., Templer, P., Paulino, L., Van Cleemput, O., Oyarzún, C., Müller, C.
378 and Godoy, R.: Mechanisms for retention of bioavailable nitrogen in volcanic rainforest soils,
379 *Nat. Geosci.*, 1(8), 543–548, doi:10.1038/ngeo252, 2008.
- 380 Kahmen, A., Wanek, W. and Buchmann, N.: Foliar d¹⁵N values characterize soil N cycling and
381 reflect nitrate or ammonium preference of plants along a temperate grassland gradient,
382 *Oecologia*, 156(4), 861–870, doi:10.1007/s00442-008-1028-8, 2008.
- 383 Kitayama, K. and Aiba, S.: Ecosystem structure and productivity of tropical rain forests along
384 altitudinal gradients with contrasting soil phosphorus pools on Mount Kinabalu , Borneo, J.



385 Ecol., 90, 37–51, 2002.

386 Lewis, S. L., Sonké, B., Sunderland, T., Begne, S. K., Lopez-gonzalez, G., Heijden, G. M. F.

387 Van Der, Phillips, O. L., Affum-baffoe, K., Baker, T. R., Banin, L., Bastin, J., Beekman, H.,

388 Boeckx, P., Bogaert, J., Cannière, C. De, Clark, C. J., Collins, M., Djangbletey, G., Djuikouo, M.

389 N. K., Doucet, J., Ewango, C. E. N., Fauset, S., Feldpausch, T. R., Ernest, G., Gillet, J.,

390 Hamilton, A. C., Harris, D. J., Hart, T. B., Haulleville, T. De, Hladik, A., Hufkens, K., Huygens,

391 D., Jeanmart, P., Jeffery, K. J., Leal, M. E., Lloyd, J., Lovett, J. C., Makana, J., Malhi, Y.,

392 Andrew, R., Ojo, L., Peh, K. S., Pickavance, G., Poulsen, J. R., Reitsma, J. M., Sheil, D., Simo,

393 M., Steppe, K., Taedoumg, H. E., Talbot, J., James, R. D., Taylor, D., Thomas, S. C., Toirambe,

394 B., Verbeeck, H., Vleminckx, J., Lee, J., White, T., Willcock, S., Woell, H., Zemagho, L., B, P.

395 T. R. S., Sonke, B., Poulsen, R. and Thomas, C.: Above-ground biomass and structure of 260

396 African tropical forests Above-ground biomass and structure of 260 African tropical forests,

397 Philos. Trans. R. Soc. Lond. B. Biol. Sci., 368, 2013.

398 Malhi, Y., Phillips, O. L., Lloyd, J., Baker, T., Wright, J., Almeida, S., Arroyo, L., Frederiksen,

399 T., Grace, J., Higuchi, N., Killeen, T., Laurance, W. F., Leão, C., Lewis, S., Meir, P.,

400 Monteagudo, a., Neill, D., Núñez Vargas, P., Panfil, S. N., Patiño, S., Pitman, N., Quesada, C.

401 a., Rudas-Ll., a., Salomão, R., Saleska, S., Silva, N., Silveira, M., Sombroek, W. G., Valencia,

402 R., Vásquez Martínez, R., Vieira, I. C. G. and Vinceti, B.: An international network to monitor

403 the structure, composition and dynamics of Amazonian forests (RAINFOR), J. Veg. Sci., 13(3),

404 439, doi:10.1658/1100-9233(2002)013[0439:AINTMT]2.0.CO;2, 2002.

405 Malhi, Y., Silman, M., Salinas, N., Bush, M., Meir, P. and Saatchi, S.: Introduction: Elevation

406 gradients in the tropics: Laboratories for ecosystem ecology and global change research, Glob.

407 Chang. Biol., 16(12), 3171–3175, doi:10.1111/j.1365-2486.2010.02323.x, 2010.



408 Malhi, Y., Girardin, C. A. J., Goldsmith, G. R., Doughty, C. E., Salinas, N., Metcalfe, D. B.,
409 Huaraca Huasco, W., Silva-Espejo, J. E., del Aguilla-Pasquell, J., Farf??n Am??zquita, F.,
410 Arag??o, L. E. O. C., Guerrieri, R., Ishida, F. Y., Bahar, N. H. A., Farfan-Rios, W., Phillips, O.
411 L., Meir, P. and Silman, M.: The variation of productivity and its allocation along a tropical
412 elevation gradient: A whole carbon budget perspective, *New Phytol.*, doi:10.1111/nph.14189,
413 2016.

414 Marrs, R. H., Proctor, J., Heaney, A., Mountford, M. D., Marrs, R. H. and Experimental, M. W.:
415 Changes in Soil Nitrogen-Mineralization and Nitrification Along an Altitudinal Transect in
416 Tropical Rain Forest in Costa Rica, *J. Ecol.*, 76(2), 466–482, 2013.

417 Midgley, J. J., Van Wyk, G. R. and Everard, D. A.: Leaf attributes of South African forest
418 species, *Afr. J. Ecol.*, 33(2), 160–168 [online] Available from: [http://dx.doi.org/10.1111/j.1365-](http://dx.doi.org/10.1111/j.1365-2028.1995.tb00791.x)
419 [2028.1995.tb00791.x](http://dx.doi.org/10.1111/j.1365-2028.1995.tb00791.x) DO - 10.1111/j.1365-2028.1995.tb00791.x, 1995.

420 Phillips, O., Baker, T., Feldpausch, T. and Brien, R.: RAINFOR field manual for plot
421 establishment and remeasurement., 2009.

422 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. and Team, T. R. C.: nlme: Linear and Nonlinear
423 Mixed Effects Models, October, R package [online] Available from:
424 [http://scholar.google.com/scholar?start=10&q=mixed+effects+model&hl=en&as_sdt=2000#8,](http://scholar.google.com/scholar?start=10&q=mixed+effects+model&hl=en&as_sdt=2000#8)
425 2013.

426 R Core Team: R: A Language and Environment for Statistical Computing, R Found. Stat.
427 Comput. Vienna Austria, 0, {ISBN} 3-900051-07-0, 2014.

428 Reed, S. C., Yang, X. and Thornton, P. E.: Incorporating phosphorus cycling into global
429 modeling efforts: A worthwhile, tractable endeavor, *New Phytol.*, 208(2), 324–329,



- 430 doi:10.1111/nph.13521, 2015.
- 431 Rütting, T., Cizungu, L. N., Roobroeck, D., Bauters, M., Huygens, D. and Boeckx, P.: Leaky
432 nitrogen cycle in pristine African montane Rainforest soil, *Global Biogeochem. Cycles*, 29(3),
433 962–973, doi:10.1002/2013GB004593. Received, 2014.
- 434 Ryan, J., Estefan, G. and Rashid, A.: *Soil and Plant Analysis Laboratory Manual*. Second
435 Edition, ICARDA, Aleppo, Syria, Syria., 2001.
- 436 Schielzeth, H. and Nakagawa, S.: Nested by design: Model fitting and interpretation in a mixed
437 model era, *Methods Ecol. Evol.*, 4(1), 14–24, doi:10.1111/j.2041-210x.2012.00251.x, 2013.
- 438 Schneider, C. a, Rasband, W. S. and Eliceiri, K. W.: NIH Image to ImageJ: 25 years of image
439 analysis, *Nat. Methods*, 9(7), 671–675, doi:10.1038/nmeth.2089, 2012.
- 440 Slik, J. W. F., Arroyo-rodríguez, V., Aiba, S., Alvarez-loayza, P., Alves, L. F., Ashton, P.,
441 Balvanera, P., Bastian, M. L., Bellingham, P. J., Berg, E. Van Den, Bernacci, L., Bispo, C.,
442 Blanc, L., Böhning-gaese, K., Boeckx, P., Bongers, F., Boyle, B., Bradford, M., Brearley, F. Q.,
443 Hockemba, M. B., Bunyavejchewin, S., Calderado, D., Matos, L., Castillo-santiago, M.,
444 Catharino, E. L. M., Chai, S., Chen, Y., Colwell, R. K., Robin, C. L., Clark, C., Clark, D. B.,
445 Clark, D. a, Culmsee, H., Damas, K., Dattaraja, H. S., Dauby, G., Davidar, P., Dewalt, S. J.,
446 Doucet, J., Duque, A., Durigan, G., Eichhorn, K. a O., Eisenlohr, P. V., Eler, E., Ewango, C.,
447 Farwig, N., Feeley, K. J., Ferreira, L., Field, R., Oliveira, A. T. De, Fletcher, C., Forshed, O.,
448 Franco, G., Fredriksson, G., Gillespie, T., Gillet, J., Amarnath, G., Griffith, D. M., Grogan, J.,
449 Gunatilleke, N., Harris, D., Harrison, R., Hector, A., Homeier, J., Imai, N., Itoh, A., Jansen, P. a,
450 Joly, C. a, Jong, B. H. J. De, Kartawinata, K., Kearsley, E., Kelly, D. L., Kenfack, D., Kessler,
451 M., Kitayama, K., Kooyman, R., Larney, E., Laumonier, Y., Laurance, S., Laurance, W. F.,
452 Lawes, M. J., Leao, I., Letcher, S. G., Lindsell, J., Lu, X., Mansor, A., Marjokorpi, A., Martin, E.



453 H., Meilby, H., Melo, F. P. L., Metcalfe, D. J., Medjibe, V. P., Paul, J., Millet, J., Mohandass, D.,
454 Montero, J. C., Morisson, M. De, Mugerwa, B., Nagamasu, H., et al.: An estimate of the number
455 of tropical tree species, *Proc. Natl. Acad. Sci.*, 112(24), 7472–7477,
456 doi:10.1073/pnas.1512611112, 2015a.

457 Slik, J. W. F., Arroyo-rodríguez, V., Aiba, S., Alvarez-loayza, P., Alves, L. F., Ashton, P.,
458 Balvanera, P., Bastian, M. L., Bellingham, P. J., Berg, E. Van Den, Bernacci, L., Bispo, C.,
459 Blanc, L., Böhning-gaese, K., Boeckx, P., Bongers, F., Boyle, B., Bradford, M., Brearley, F. Q.,
460 Hockemba, M. B., Bunyavejchewin, S., Calderado, D., Matos, L., Castillo-santiago, M.,
461 Catharino, E. L. M., Chai, S., Chen, Y., Colwell, R. K., Robin, C. L., Clark, C., Clark, D. a D.
462 B., Clark, D. a D. B., Culmsee, H., Damas, K., Dattaraja, H. S., Dauby, G., Davidar, P., Dewalt,
463 S. J., Doucet, J., Duque, A., Durigan, G., Eichhorn, K. a O., Eisenlohr, P. V., Eler, E., Ewango,
464 C., Farwig, N., Feeley, K. J., Ferreira, L., Field, R., Oliveira, A. T. De, Fletcher, C., Forshed, O.,
465 Franco, G., Fredriksson, G., Gillespie, T., Gillet, J., Amarnath, G., Griffith, D. M., Grogan, J.,
466 Gunatilleke, N., Harris, D., Harrison, R., Hector, A., Homeier, J., Imai, N., Itoh, A., Jansen, P. a,
467 Joly, C. a, Jong, B. H. J. De, Kartawinata, K., Kearsley, E., Kelly, D. L., Kenfack, D., Kessler,
468 M., Kitayama, K., Kooyman, R., Larney, E., Laumonier, Y., Laurance, S., Laurance, W. F.,
469 Lawes, M. J., Leao, I., Letcher, S. G., Lindsell, J., Lu, X., Mansor, A., Marjokorpi, A., Martin, E.
470 H., Meilby, H., Melo, F. P. L., Metcalfe, D. J., Medjibe, V. P., Paul, J., Millet, J., Mohandass, D.,
471 Montero, J. C., Morisson, M. De, Mugerwa, B., Nagamasu, H., et al.: An estimate of the number
472 of tropical tree species, *Proc. Natl. Acad. Sci.*, 112(33), E4628–E4629,
473 doi:10.1073/pnas.1512611112, 2015b.

474 Smith, B., Wärlind, D., Arneeth, A., Hickler, T., Leadley, P., Siltberg, J. and Zaehle, S.:
475 Implications of incorporating N cycling and N limitations on primary production in an



- 476 individual-based dynamic vegetation model, *Biogeosciences*, 11(7), 2027–2054, doi:10.5194/bg-
477 11-2027-2014, 2014.
- 478 Soethe, N., Lehmann, J. and Engels, C.: Nutrient availability at different altitudes in a tropical
479 montane forest in Ecuador, *J. Trop. Ecol.*, 24(4), 397–406, doi:10.1017/S026646740800504X,
480 2008.
- 481 Sundqvist, M. K., Sanders, N. J. and Wardle, D. a.: Community and Ecosystem Responses to
482 Elevational Gradients: Processes, Mechanisms, and Insights for Global Change, *Annu. Rev.*
483 *Ecol. Evol. Syst.*, 44(1), 261–280, doi:10.1146/annurev-ecolsys-110512-135750, 2013.
- 484 Tanner, A. E. V. J., Vitousek, P. M. and Cuevas, E.: Experimental Investigation of Nutrient
485 Limitation of Forest Growth on Wet Tropical Mountains, *Ecology*, 79(1), 10–22, 1998.
- 486 Townsend, A. R., Asner, G. P. and Cleveland, C. C.: The biogeochemical heterogeneity of
487 tropical forests, *Trends Ecol. Evol.*, 23(8), 424–431, doi:10.1016/j.tree.2008.04.009, 2008.
- 488 Vicca, S., Luysaert, S., Peñuelas, J., Campioli, M., Chapin, F. S., Ciais, P., Heinemeyer, a.,
489 Högberg, P., Kutsch, W. L., Law, B. E., Malhi, Y., Papale, D., Piao, S. L., Reichstein, M.,
490 Schulze, E. D. and Janssens, I. A.: Fertile forests produce biomass more efficiently, *Ecol. Lett.*,
491 15(6), 520–526, doi:10.1111/j.1461-0248.2012.01775.x, 2012.
- 492 Van de Weg, M. J., Meir, P., Grace, J., Atkin, O. K., van de Weg, M. J., Meir, P., Grace, J. and
493 Atkin, O. K.: Altitudinal variation in leaf mass per unit area, leaf tissue density and foliar
494 nitrogen and phosphorus content along an Amazon-Andes gradient in Peru, *Plant Ecol. Divers.*,
495 2(3), 243–254, doi:10.1080/17550870903518045, 2009.
- 496 Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-
497 bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K. and



498 Gullias, J.: The worldwide leaf economics spectrum, *Nature*, 12, 821–827, 2004.

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

	Cluster	Altitude (masl)	Number of trees per plot	Number of species per plot	BA ($\text{m}^2 \text{ha}^{-1}$)	MTH (m)	AGC (Ton C ha^{-1})	MAT ($^{\circ}\text{C}$)	MAP (mm)	Soil parent material	Soil classification
Ecuador	1	406 \pm 10	86 \pm 13	30 \pm 2	25 \pm 3.1	18.3 \pm 1	96 \pm 19	23.7	3720	Lahars	Andisol
	2	1068 \pm 25	84 \pm 38	39 \pm 15	33 \pm 9.4	16.9 \pm 0.7	140 \pm 25	20.0	3227	Lahars	Andisol
	3	1871 \pm 79	69 \pm 11	31 \pm 2	33 \pm 11	13.5 \pm 1.3	112 \pm 57	17.5	1619	Redbed volcanoclastics	Andisol
	4	3217 \pm 21	90 \pm 25	18 \pm 2	49 \pm 11	13 \pm 1.4	161 \pm 34	10.9	1241	Granitic/acid	Andisol
Rwanda	1	1760 \pm 66	70 \pm 18	21 \pm 4	34 \pm 4	13.9 \pm 0.7	121 \pm 11	17.6	1518	Shale and Quartzite	Inceptisol/Ultisol
	2	2200 \pm 64	71 \pm 18	18 \pm 3	45 \pm 9	14.3 \pm 0.3	179 \pm 27	15.9	1628	Shale and Quartzite	Inceptisol/Ultisol
	3	2512 \pm 37	122 \pm 60	11 \pm 1	31 \pm 9	12 \pm 1	99 \pm 36	14.7	1716	Shale and Quartzite	Inceptisol/Ultisol
	4	2844 \pm 77	109 \pm 56	8 \pm 2	34 \pm 4	11.5 \pm 0.5	89 \pm 10	12.9	1835	Shale and Quartzite	Inceptisol/Entisol

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506 **Table 2** Fixed effects estimates (altitude in km masl) for the different canopy-level response
 507 variables; leaf nitrogen content (LNC), inverse C:N ratio, specific leaf area (SLA), leaf phosphorus
 508 content (LPC), N:P ratio, canopy and topsoil $\delta^{15}\text{N}$, along with the estimated marginal and
 509 conditional R^2_{adj} (sensu Nakagawa and Schielzeth (5)). The interaction term for altitude x transect
 510 was not significant in any case, and was hence not retained in any model.

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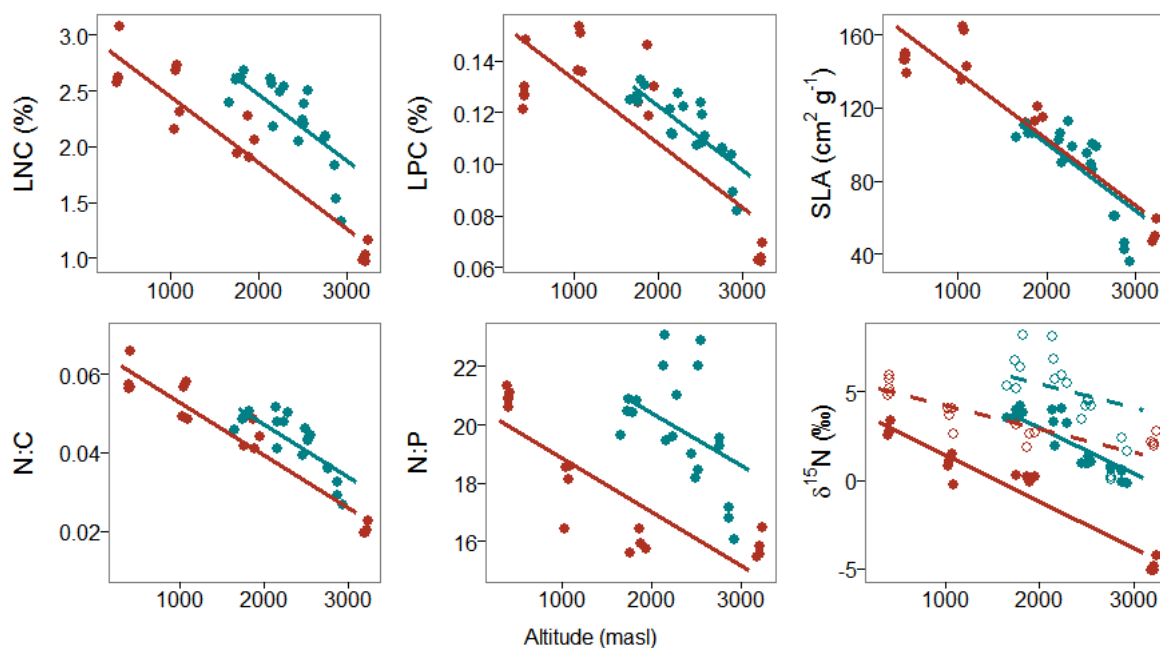
Response	Effect	Estimate	Standard Error	Marginal R^2_{adj}	Conditional R^2_{adj}
LNC (%)	Ecuador Intercept	3.04	0.11	0.83	0.85
	Rwanda Intercept	3.65	0.1		
	Altitude	-0.59	0.06		
N:C	Ecuador Intercept	0.066	0.0026	0.87	0.91
	Rwanda Intercept	0.074	0.0023		
	Altitude	-0.013	0.001		
SLA ($\text{cm}^2 \text{g}^{-1}$)	Ecuador Intercept	175.63	11.81	0.83	0.95
	Rwanda Intercept	173.06	10.41		
	Altitude	-36.47	5.91		
LPC (%)	Ecuador Intercept	0.158	0.010	0.68	0.87
	Rwanda Intercept	0.172	0.008		
	Altitude	-0.025	0.005		
N:P	Ecuador Intercept	20.67	0.87	0.60	0.71
	Rwanda Intercept	24.07	0.77		
	Altitude	-1.82	0.44		
$\delta^{15}\text{N}$ Canopy (‰)	Ecuador Intercept	4.06	0.509	0.92	0.96
	Rwanda Intercept	8.25	0.45		
	Altitude	-2.63	0.26		
$\delta^{15}\text{N}$ Topsoil (‰)	Ecuador Intercept	5.62	1.21	0.43	0.86
	Rwanda Intercept	8.11	1.07		
	Altitude	-1.34	0.61		

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