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Response of element cycling and budgets to nutrient additions in a tropical montane forest of Ecuador

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ABSTRACT

The tropical montane forests in southern Ecuador are subject to rising nitrogen (N), low phosphorus (P), and episodic calcium (Ca) deposition. To investigate the response of the vegetation, soil organic layer and mineral soil to 0.3 m depth to increased nutrient inputs, we initiated in 2008 an interdisciplinary Nutrient Manipulation Experiment (NUMEX) at 2000 m a.s.l. We have applied N as urea at 50 kg ha^{-1} $year^{-1}$, P as NaH_2PO_4 at 10 kg ha^{-1} $year^{-1}$, combined N and P at 50 + 10 kg ha^{-1} $year^{-1}$, and Ca (as $CaCl_2$), at 10 kg ha^{-1} $year^{-1}$. From 2008 to 2012, we set up annual budgets by calculating net fluxes of N, P, Ca and Na for the canopy, the organic layer and the mineral soil and determined $\delta^{15}N$ values in the foliage of the four most abundant tree species, litterfall and organic layer. The addition of P and N + P increased P leaching from the canopy, suggesting a reduced retention of deposited P by canopy organisms. All added nutrients were largely retained in the soil organic layer and tightly cycled between the organic layer and the vegetation via litterfall and throughfall. The small leaching losses of N, P, Ca and Na from the organic layer were retained in the upper mineral soil. The retention of the added nutrients in the ecosystem indicated a strong nutrient demand. Nevertheless, the ^{15}N enrichment in the organic layer was an early indicator of beginning N losses from the ecosystem by leaching and volatilization, which could not yet be detected by our flux-based budgeting approach.

1. Introduction

The tropical montane forests of southern Ecuador on the eastern slopes of the Andes, at the western edge of the Amazon basin, are subject to climate change, particularly more frequent and longer dry phases (Peters et al., 2013). In these perhumid forests receiving > 2000 mm of annual precipitation, increasing dryness reduces soil waterlogging, which enhances organic matter mineralization and thus increases nutrient availability, particularly of N and P (Schuur and Matson, 2001; Wilcke et al., 2020a). Moreover, these forests receive increasing nitrogen (N) inputs by deposition from the atmosphere, mainly originating from Amazonian forest fires (Boy et al., 2008; Wilcke et al., 2013), steady, low phosphorus (P) inputs with the NE trade winds (Fabian et al., 2009; Wilcke et al., 2019, Prospero et al., 2020) and episodic calcium (Ca) deposition with Saharan dust during strong La Niña events (Boy and Wilcke, 2008). As a consequence, nutrient availability increases in the Ecuadorian montane forests. An increased nutrient availability, particularly of N and P, can generally be detrimental to plant diversity in natural ecosystems (Matson et al., 1999; Sala et al., 2000; Wassen et al., 2005; Phoenix et al., 2006; Hietz et al., 2011). Therefore, it can pose a threat to the species-rich, Ecuadorian tropical montane forests which belong to the Tropical Andes hotspot of biodiversity (Myers et al., 2000; Barthlott et al., 2005) and can negatively affect stream water quality (Cunha et al., 2011; Cameron et al., 2013; McDowell et al., 2025).

Nutrient manipulation experiments have been widely used to identify nutrient limitations and explore the response of ecosystems to increasing nutrient availability (Vitousek and Farrington, 1997; Tanner et al., 1998; Elser et al., 2007; Cunha et al., 2022). In such experiments, mass balances of nutrient fluxes for the canopy, the soil organic layer and the root zone of the mineral soil allow to identify nutrient retention and losses (Christ et al., 1995; Adams et al., 1997; Yanai et al., 2013; Magill et al., 2000; Likens, 2004, Shao et al., 2016). The response of

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nutrient cycling to global change is highly variable (Cusack et al., 2016), while the number of fertilization experiments in tropical forests is low (Cleveland et al., 2011; Wright, 2019). Consequently, more experiments and long-term observations are needed to predict global change effects on tropical montane forests. One such experiment is the Nutrient Manipulation Experiment (NUMEX) in the southern Ecuadorian tropical montane forest, which began in 2008 (Martinson et al., 2010; Wullaert et al., 2010; Homeier et al., 2012). NUMEX showed that forest growth in the studied ecosystem was co-limited by N and P (Homeier et al., 2012). The joint addition of N + P influenced microbial activity (Krashevska et al., 2010), nutrient cycling (Wullaert et al., 2010; 2013), biomass production (Homeier et al., 2012; Báez and Homeier, 2018), gaseous N fluxes (Martinson et al., 2013; Müller et al., 2015), seedling performance (Cárate-Tandalla et al., 2018), phosphatase activity (Dietrich et al., 2016), dissolved organic matter and N leaching (Velescu et al., 2016) and wood anatomical traits (Spannl et al., 2016).

In forest ecosystems, nutrient deposition from the atmosphere first interacts with the tree canopy, where nutrients can be retained or leached (Ulrich, 1983; Staelens et al., 2008). Retention of deposited nutrients or nutrient leaching from the canopy depend on the kind of growth limitation of the vegetation and the needs of the canopy organisms (Pardo et al., 2011; Van Langenhove et al., 2020; Guerrieri et al., 2021). In NUMEX, additions of N reduced N retention by the canopy after 1.5 experimental years and accelerated aboveground N fluxes (Wullaert et al., 2010). Additions of P to this tropical montane forest increased P concentrations in throughfall and reduced the canopy retention of deposited P from the atmosphere after 1.5 experimental years (Wullaert et al., 2010), while the P use efficiency and most likely the P resorption efficiency of the vegetation decreased (Homeier et al., 2012). However, after two years of Ca additions to this forest, the canopy budget of Ca calculated as the difference between the Ca inputs from the atmosphere by bulk and dry deposition and the Ca loss from the canopy via throughfall was not significantly changed (Wullaert et al., 2013). After five years, the addition of N and P increased the Ca fluxes with throughfall and indicated an enhanced availability of Ca in soil solution (Velescu et al., 2021).

Tropical montane forests can have thick organic layers (Wilcke et al., 2020b), which is attributed to prolonged waterlogging restricting the decomposition of organic material (Tanner et al., 1998; Schuur and Matson, 2001). Because the poor aeration of the mineral soil decreases rooting depth (Jackson et al., 1996), most of the root biomass of the studied forest in south Ecuador is found in the organic layer (Soethe et al., 2006; Moser et al., 2010). In NUMEX, after one year of nutrient additions, fertilized N, P and Ca were retained in the organic layers of the study site with minor leaching losses to the mineral soil (Wullaert et al., 2010; 2013). Although an enhanced NO_3^- mobility may be associated with cation losses from the root zone (Currie et al., 1999; Cusack et al., 2016), increasing NO_3^- leaching after five years of N additions to the studied forest did not increase Ca and Na leaching (Velescu et al., 2016; 2021).

Because biological processes change the stable N isotope ratios by fractionation, temporal trends of the $\delta^{15}N$ values in leaves, sediments or tree rings typically indicate a changing N cycling (Hietz et al., 2011; Holtgrieve et al., 2011, McLauchlan et al. 2013). Increasing foliar $\delta^{15}N$ values can reveal shifts towards N saturation (Pardo et al., 2006) and resulting N losses to water bodies and the atmosphere (Aber et al., 1998; Högberg and Johannisson, 1993). The $\delta^{15}N$ values can therefore serve as an early, sensitive indicator of N losses before these can be detected by a budgeting approach, in which the uncertainties of all considered flux measurements accumulate. In NUMEX, N additions stimulated net nitrification (Müller et al., 2015), nitrous oxide production (Martinson et al., 2013) and increased NO_3^- leaching from the organic layer (Velescu et al., 2016).

In the mineral soil, NH_4^+ can be retained through root uptake, microbial immobilization and fixation in the clay fraction (Corre et al., 2003). In contrast, NO_3^- is prone to leaching to water bodies in soils with predominantly negative surface charges, such as those in the southern Ecuadorian Andes (Schrumpf et al., 2001), unless it is taken up by plants or microorganisms from the soil solution or removed via denitrification (Cameron et al., 2013). The main retention mechanism of P in mineral soils is sorption to charged surfaces (Rechberger et al., 2021), but P can also precipitate as little soluble Al phosphates in the acidic soils of the tropical montane forest, which are unavailable for plant uptake. Calcium and Na are primarily retained in mineral soils by adsorption to cation-exchange sites, with leaching occurring only if the retention capacity in the topsoil is exceeded (Lehmann and Schroth, 2003).

In this study, our overall objective was to determine whether and how five years of nutrient additions to a native tropical montane forest in southern Ecuador shifted this ecosystem towards nutrient saturation, as reflected by the flux budgets of the canopy, the organic layer, and the mineral topsoil. As nutrient availability approaches saturation, nutrient losses are expected to become more pronounced. Specifically, we hypothesize that (i) fertilization decreases the canopy retention – determined as the flux budget of bulk + dry deposition minus throughfall – of deposited N, P and Ca from the atmosphere, because more nutrients are taken up via the roots; (ii) after five years of nutrient additions there is still a tight nutrient cycling between the organic layer and the vegetation with limited losses to the mineral soil, although the fertilization increased nutrient concentrations; (iii) nutrient budgets of the mineral soil are little changed by fertilization as a consequence of the tight nutrient cycling between the vegetation and the organic layer and (iv) nevertheless, stable N isotope ratios in foliage, litterfall and organic layer indicate beginning N losses which cannot yet be detected with the budgeting approach.

2. Material and methods

2.1. Study area

The study area is located on the Amazon-exposed slopes of the south Ecuadorian Andes (3.58° S, 79.08 W) and belongs to the Tropical Andes hotspot of biodiversity (Myers et al., 2000; Barthlott et al., 2005). The experimental plots were established in the Reserva Biológica San Francisco (RBSF) at 2010–2128 m a.s.l. (Fig. 1) and their slope ranges between 15° and 40°, with an average of 28°.

Annual precipitation is unimodally distributed with a maximum between April and July, but without a dry season. From 2008 to 2012, precipitation averaged 2131 ± 248 mm (SD), with an interception of 41 ± 3% (Velescu et al., 2021). During the same period, mean annual temperature was 15.6 ± 0.3 °C and mean air humidity was 84.9 ± 1.1%. The warmest month was November with 16.4 ± 0.3 °C and the coldest month was July with 14.7 ± 0.9 °C. Temperature and humidity were recorded at the climate station at 1957 m a.s.l. (Rollenbeck et al., 2015).

The vegetation cover consists of an old-growth lower montane forest (Bruijnzeel and Hamilton, 2000; Homeier et al., 2008). The mean canopy height is 12–14 m and the crown radius 2–4 m, reaching up to 5–6 m. At the experimental site, *Graffenrieda emarginata* Ruiz & Pav. (Melastomaceae), *Alchornea lojaensis* Secco (Euphorbiaceae), *Myrcia* sp. *nov.* (Myrtaceae) and *Hieronyma fendleri* Briq. (Phyllanthaceae) were the most common tree species and accounted for 55.6% of the tree stems with a diameter at breast height ≥ 0.1 m, contributing 28.2%, 10.2%, 8.8% and 8.4%, respectively (Báez and Homeier, 2018). The remaining 44.4% of the tree stems belonged to about 50 different species which could not be considered. The leaf area index on the studied plots was 3.4–5.3 (Homeier et al., 2013).

The soils of the study area developed from Palaeozoic phyllites and metasandstones belonging to the Chiguinda unit of the Zamora series (Hungerbühler, 1997). They are young, shallow (< 60 cm), acidic (pH < 4) and frequently water-saturated, have a loamy texture and were classified according to IUSS Working Group WRB (2022) as Stagnic Cambisols (Hyperdystric, Chromic) **(Table S1)**. The mineral soil is covered by thick organic layers which constitute the main rooting zone

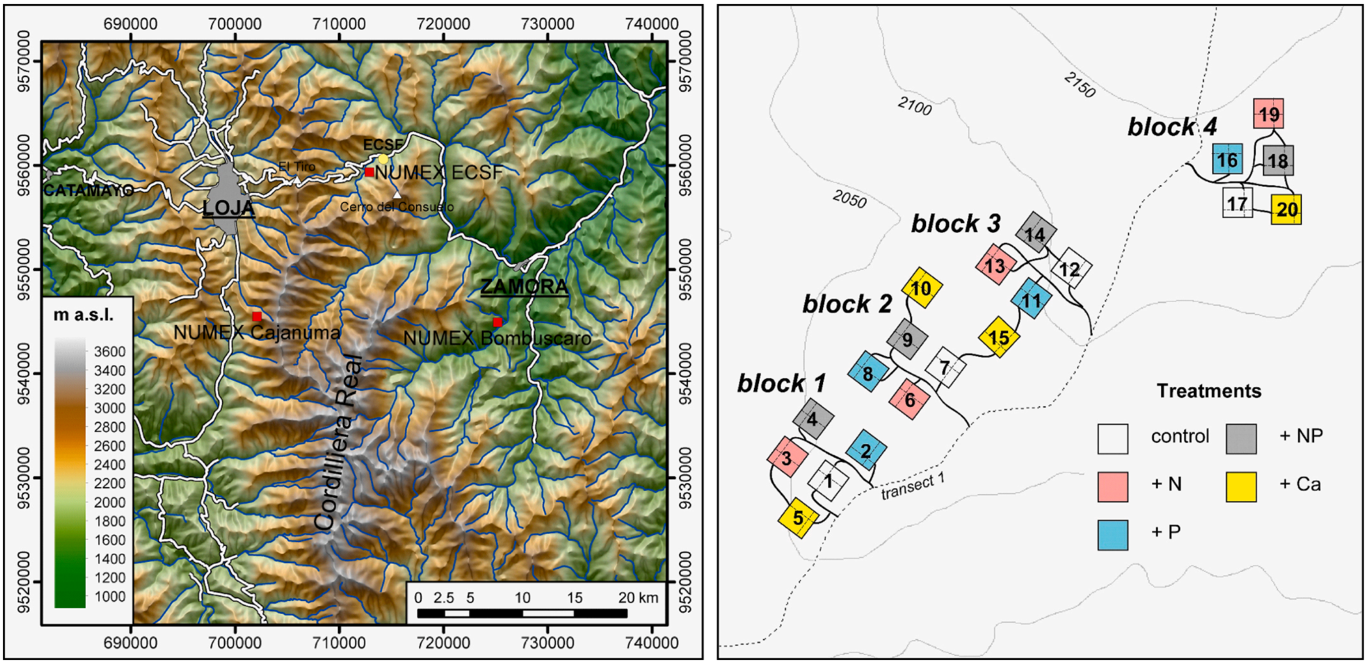

Fig. 1. Location and design of the Nutrient Manipulation Experiment (NUMEX). Our study focuses on the experimental site at 2000 m a.s.l. near the Research Station San Francisco (ECSF). Coordinate system: WGS84, UTM Zone 17 M. Cartographic data: Instituto Geografico Militar (2013).

for plants (Soethe et al., 2006; Moser et al., 2010).

2.2. Experimental design

The interdisciplinary nutrient manipulation experiment (NUMEX) consists of three experimental sites at 1000, 2000 and 3000 m a.s.l. Details on all NUMEX sites are given by Martinson et al. (2010) and Homeier et al. (2012). We focused on the experimental site at 2000 m a.s.l. in the RBSF, which consists of continuous, separate additions of N, P and Ca, a combined N + P treatment and unfertilized control plots (Fig. 1). The 20 plots (20 m x 20 m) of the experimental site are arranged in a fourfold replicated, randomized block design. To study the response of the ecosystem to increasing nutrient availability we have applied 50 kg ha^{-1} year^{-1} of N as urea (46% N, δ^{15}N value: –0.3 ± 0.1 ‰), 10 kg ha^{-1} year^{-1} of P as sodium dihydrogen phosphate ($NaH_2PO_4 \cdot H_2O$, AppliChem GmbH, Darmstadt, Germany), 50 kg + 10 kg ha^{-1} year^{-1} of N and P and 10 kg ha^{-1} year^{-1} of Ca as calcium chloride ($CaCl_2 \cdot 2H_2O$, Merck, Darmstadt, Germany). The P fertilizer included 7.4 kg ha^{-1} year^{-1} of Na. The nutrients were applied directly to the soil surface, paying particular attention to their uniform distribution on the experimental plots (Wullaert et al., 2010). Nutrient additions were split into two applications per year, amounting to a total of 10 applications for the study period 2008–2012.

2.3. Field sampling

All study plots were equipped with throughfall collectors, zero-tension lysimeters below the organic layer, suction cups at 0.15 m and 0.3 m mineral soil depth. Stem flow collectors were not included because in the studied forest stem flow accounted for < 2% of the precipitation (Fleischbein et al., 2006, Wilcke et al., 2017). The sampling and the equipment used to collect water samples is described in detail in Velescu et al. (2021). In summary, weekly precipitation was collected at two neighboring locations, each equipped with five rain collectors that sampled bulk deposition. Throughfall was sampled on the 20 experimental plots, each equipped with 20 rain collectors. Litter leachate, which is the solution percolating through the organic layer, was collected on each plot with three zero-tension lysimeters installed below the organic layer. Mineral soil solution was continuously collected with ceramic suction cups at 0.15 and 0.3 m mineral soil depth. Throughfall, litter leachate and soil solutions were sampled fortnightly from 2008 to 2012. The collected samples were transferred to the field laboratory of the Estación Científica San Francisco (ECSF) immediately after sampling, filtered through ashless filters Type 392 (Sartorius-Stedim GmbH, Göttingen, Germany) with 4–7 µm pore size and stored at –20 °C until their shipping in frozen condition to the University of Bern, Switzerland for chemical analysis.

Leaf samples of sun-exposed branches of the four most common species *G. emarginata, A. lojaensis, Myrcia* sp. *nov.* and *H. fendleri* were collected in February 2013 from a total of 109 trees on the NUMEX plots to quantify foliar nutrient concentrations and explore the response of the element cycling in plants to the added nutrients. The leaves were dried at 60 °C in a drying oven before chemical analyses.

Litterfall was collected monthly from 2008 to 2012 with six randomly placed litterfall traps (0.36 m^2) per plot, which were positioned at 1 m above ground. The collected samples were oven-dried at 60 °C before determining their dry weight. For chemical analysis, subsamples were collected one week after the monthly litterfall collection from two litterfall traps per plot, which were randomly chosen. After drying and weighing, these samples were bulked per plot and month for further analyses.

The Oi, Oe and Oa horizons which form the soil organic layer were sampled after the second annual fertilization in October 2008 and December 2012, after one and, respectively, five experimental years, at five randomly selected points within each plot. The mineral soil was sampled in August 2007, before the start of the experiment. All samples were dried at 40 °C in a drying oven. The bulk density of the organic horizons was determined by collecting two additional samples with a wooden frame (0.15 x 0.15 m), and drying them at 105 °C to constant weight in a drying oven.

2.4. Chemical analyses and quality control

Concentrations of Ca and Na in rainfall, throughfall, litter leachate and mineral soil solution were measured by flame atomic absorption spectroscopy (F-AAS, ZEEnit 700P, AnalytikJena, Jena, Germany). Total

N (TN) and total P (TP) concentrations were measured by continuous flow analysis (CFA) using UV digestion, high resolution colorimetry and photometric detection (AutoAnalyzer 3 HR, Seal GmbH, Norderstedt, Germany). Chloride (Cl^-) concentrations were also measured by CFA with an ion-selective electrode (ISE, Orion Ionplus, Thermo Scientific, Beverly, USA) optimized for low-range measurements. Average detection limits were 0.002 mg L^{-1} for Ca, 0.001 mg L^{-1} for Na, 0.042 mg L^{-1} for TN, 0.004 mg L^{-1} for TP and 0.029 mg L^{-1} for Cl^-. We analyzed certified control standards every 20 samples and accepted measurement batches if the results of the control standards deviated by < 10% from the target values.

Litterfall, leaf material and organic layer samples were ground to a fine powder in a planetary ball mill (Retsch, Haan, Germany). Aliquots of the ground samples were digested with 69% HNO_3 (Rotipuran supra, Carl Roth, Karlsruhe, Germany) and 30% H_2O_2 (Suprapur, Merck, Darmstadt, Germany) in a microwave oven (CEM, Mars 6, Kamp-Lintfort, Germany). Concentrations of Ca, Na and P were measured by inductively coupled plasma optical emission spectroscopy (Agilent Technologies, 5100 VDV ICP-OES, Waldbronn, Germany). The quantitative recovery of the target elements (100 ± 10%) was tested by including a certified reference material (SRM 1515 Apple leaves, NIST, Gaithersburg, USA) in every digestion batch (18–20 samples).

The total N concentrations and the $\delta^{15}N$ values of foliage, litterfall and of the organic layer samples were measured with an elemental analyzer (Thermo Scientific, Flash 2000 HT Plus, Bremen, Germany) coupled to an isotope-ratio mass spectrometer (Delta V Advantage IRMS, Thermo Scientific, Bremen, Germany). We referenced our measurements to $\delta^{15}N$-air scale by linear regression using the reference materials IAEA-N1, IAEA-N2 (IAEA, Vienna, Austria), USGS-61 and USGS-25 (USGS, Reston, USA). The precision of the $\delta^{15}N$ analyses determined by repeated measurements of an internal standard (homogenous leaf material from the study site) was 0.08 ‰.

2.5. Calculations and statistical evaluation

Reference evapotranspiration (ET_r) required to calculate belowground water fluxes was modeled using the Penman-Monteith equation (Allen et al., 1989, Allen et al., 1998) implemented in REF-ET 3.1.16 (Allen, 2013), based on a net balance of energy fluxes. For these calculations, we used air temperature, air humidity, wind speed and global radiation which were recorded at the ECSF climate station at 1957 m a.s.l. (Rollenbeck et al. 2015). The belowground water fluxes were calculated with a water balance model (DVWK, 1996; Leimer et al., 2014). Monthly element fluxes were obtained by multiplying monthly mean concentrations with their respective water fluxes (Velescu et al., 2021). Monthly fluxes were aggregated to annual fluxes to set up annual element budgets for the period 2008–2012. These budgets represent net fluxes through the forest canopy, the organic layer and the mineral topsoil (**Fig. S1**). Litterfall was considered an internal flux and was not included in the calculation of the ecosystem budgets.

To calculate the canopy budget (CB) of each studied element on all studied plots, we used the canopy exchange model of Ulrich (1983) to estimate the particulate dry deposition to the canopy surfaces (i.e. leaves, branches, epiphytes, epiphylls, accumulations of organic material, biological crusts). We calculated the canopy budget of an element *i* as the difference between total deposition (TD) and throughfall fluxes (TF) according to Eq. (1).

$$CB_i = TD_i - TF_i \tag{1}$$

Negative values of the CB indicate net leaching from the canopy, positive ones net retention of elements deposited from the atmosphere by the canopy (i.e. by leaf surfaces, phyllosphere organisms and accumulations of organic material). Total deposition (TD) of an element *i* was calculated with Eq. (2):

$$TD_i = BD_i + DD_i \tag{2}$$

where BD is the directly measured bulk deposition of the element *i* and DD is the fine particulate part of the dry deposition of the element *i* estimated with Eq. (3):

$$DD_i = TF_{Cl} / BD_{Cl} \times BD_i - BD_i \tag{3}$$

where TF_{Cl} represents the throughfall flux and BD_{Cl} the bulk deposition of Cl^-. The deposition ratio TF_{Cl}/BD_{Cl} can be used to estimate the DD if it is assumed Cl^- is an inert tracer in the canopy and that the ratio of TD to BD is the same for all elements (Ulrich, 1983). Previous work in the same tropical montane forest demonstrated that Cl^- could be considered a non-reactive tracer to calculate the CB (Boy and Wilcke, 2008; Boy et al., 2008; Wilcke et al., 2017; Wilcke et al., 2019). To reduce the temporal variation of the Cl^- fluxes and the influence of the measurement uncertainty of Cl^- on the CB, we calculated one deposition ratio of Cl^- for each budgeting year.

To calculate the organic layer budget (OLB) of each element *i*, we used the inputs by throughfall (TF), the outputs from the organic layer with litter leachate (LL) and the quantity of the added nutrients (A) according to Eq. (4):

$$OLB_i = TF_i - LL_i + A_i \tag{4}$$

The total soil input (TSI) of an element *i* was calculated as the sum of throughfall (TF) and litterfall (LF) reaching the surface of the soil organic layer (Eq. (5). It provides an estimation of the aboveground return fluxes from the vegetation for the given element:

$$TSI_i = TF_i + LF_i \tag{5}$$

The flux budget of the uppermost 0.3 m of the mineral soil (MSB) for each element *i* was calculated as the difference between the input to the mineral soil by litter leachate (LL) and the output flux with the soil solution (SC30) from 0.3 m mineral soil depth using Eq. (6):

$$MSB_i = LL_i - SC30_i \tag{6}$$

Total element stocks in the organic layer were calculated using bulk density, horizon thickness and element concentrations measured in each sampled organic layer horizon (Oi, Oe and Oa).

To explore the effects of the added nutrients, we compared the treatments with the controls and estimated the contribution of the fertilized elements to the nutrient budgets of each treatment. Statistical analyses were performed with the software R, version 3.5.2 (R Core Team, 2018). To detect significant treatment effects and compare effects among treatments, we used linear mixed effects models implemented in the R-package *lme4* (Bates et al., 2015) and tested for homogeneity of variances with the Levene's test and for normal distribution of the residuals using quantile–quantile plots. We specified treatments and controls as fixed effects, with the four blocks as random factor over the five years of the experiment and calculated error probabilities of the fixed effects with the functions *cftest* and *glht* in the package *multcomp* (Hothorn et al., 2008). We calculated the budget terms for each individual plot and used these values as inputs to the linear mixed effects models. The reported uncertainties reflect the variation among the replicate plots. We analyzed time series of the $\delta^{15}N$ values of litterfall using the seasonal Mann-Kendall test (Hirsch et al., 1982) included in the R-package *Kendall* (McLeod, 2011). The figures include solid lines intended to represent significant trends without implying that these trends are linear.

3. Results

3.1. Foliar nutrient concentrations, litterfall and soil organic layer

We observed significant, species-specific responses of the four studied common tree species to nutrient additions (Table 1). The N and N + P additions increased the δ^{15}N values in the leaves of all four studied species collected in 2013 after five experimental years. The P and N + P additions significantly increased foliar P concentrations of *G. emarginata, A. lojaensis* and *Myrcia* sp. *nov.*, and decreased foliar N:P ratios in all four studied species. Additionally, the P treatment led to a marginally significant increase ($p < 0.1$) in foliar P concentrations of *H. fendleri*. Calcium additions increased foliar Ca concentrations in three of the four species (*A. lojaensis, G. emarginata and Myrcia* sp. *nov.*), and decreased foliar N concentrations in *H. fendleri* and *Myrcia* sp. *nov.*

In the control, litterfall had the highest contribution to the total soil input of N (74%), P (84%) and Ca (82%), while throughfall was the main input pathway for Na (98%) to the soil organic layer. The N + P treatment increased the mean N and P fluxes with litterfall compared to the control, which was attributable to increasing N and P concentrations, while the individual additions of N or P did not significantly change the N and P fluxes with litterfall, respectively. The Ca additions marginally increased the annual mean Ca fluxes with litterfall. The δ^{15}N values of litterfall increased with time in all treatments and in the control (Fig. 2), but only the temporal trends in the N and N + P treatments were significantly different from the control. This was in agreement with significantly enriched δ^{15}N values in the fresh leaves of the studied species collected in 2013 after five experimental years in the N and N + P treatments, compared to the control (Table 1).

Table 1
Foliar nutrient concentrations, N:P ratios and δ^{15}N values of the four most common tree species in 2013. Concentrations and standard errors of the block means are given for the control treatment and the δ^{15}N values. For the other treatments, the numbers show the deviation from the control in percent. Significant differences from the control ($p < 0.05$) are shown in bold; marginally significant differences ($p < 0.1$) in italics; n is the number of sampled trees. Sodium concentrations were mostly below the detection limit and were not included.

Species	Treatment	N	P	Ca	N:P	δ^{15}N air	n
		Concentrations [mg g^{-1}] and deviation from control [%]				‰	
Alchornea lojaensis	**Control**	13.1 ± 0.9	0.84 ± 0.10	3.01 ± 0.34	16.1 ± 1.2	−3.79 ± 0.45	5
	+N	+15	+1	−28	+13	**−1.44 ± 0.70**	5
	+NP	+8	**+37**	+9	−*22*	**−0.63 ± 0.61**	6
	+P	+3	**+44**	+1	**−25**	−3.89 ± 0.48	5
	+Ca	+2	+7	**+79**	−6	−4.73 ± 0.89	4
Graffenrieda emarginata	**Control**	12.0 ± 0.7	0.49 ± 0.03	1.19 ± 0.13	24.6 ± 0.8	−2.83 ± 0.42	7
	+N	+6	+10	+3	−3	**−0.72 ± 0.19**	6
	+NP	−4	**+44**	+14	**−31**	**−0.32 ± 0.31**	6
	+P	−5	**+44**	+39	**−32**	−3.03 ± 0.31	6
	+Ca	−3	+10	**+118**	−12	−3.39 ± 0.40	5
Hieronyma fendleri	**Control**	15.0 ± 0.8	0.87 ± 0.06	2.21 ± 0.13	17.4 ± 0.6	−2.12 ± 0.70	5
	+N	−11	−19	−27	+14	**−0.33 ± 0.41**	4
	+NP	−4	+3	−18	−6	−0.87 ± 0.59	7
	+P	−9	+*14*	+10	**−21**	−3.64 ± 0.42	5
	+Ca	**−16**	−14	+20	−2	−2.94 ± 0.93	3
Myrcia sp. nov.	**Control**	13.2 ± 1.1	0.43 ± 0.02	0.77 ± 0.12	30.6 ± 2.1	−2.55 ± 0.46	7
	+N	−12	+11	−6	**−20**	−1.78 ± 0.39	6
	+NP	−13	**+21**	−21	**−27**	**−0.69 ± 0.25**	4
	+P	**−16**	**+26**	−10	**−33**	−2.40 ± 0.63	7
	+Ca	**−16**	0	**+34**	−15	−2.20 ± 0.68	6

The N and N + P treatments increased the δ^{15}N values of the organic layer compared to the control after five experimental years (Fig. 3). Additionally, the P and N + P treatments, where P was applied as NaH_2PO_4, increased the Na stocks in the soil organic layer after five years compared to the control. However, the N, P and Ca stocks in the organic layer were not significantly different from the control after five experimental years (Table 2).

3.2. *Canopy budgets*

During the study period, total N deposition ranged from 19 to 38 kg ha^{-1} year^{-1}, P deposition from 0.2 to 0.4 kg ha^{-1} year^{-1}, Ca deposition from 5 to 20 kg ha^{-1} year^{-1} and Na deposition from 6 to 9 kg ha^{-1} year^{-1} (Fig. 4). The mean annual deposition ratio of Cl$^-$ used in Eq. (3) to estimate dry deposition was 1.46 ± 0.18 over the five studied years. On average, dry deposition accounted for 33% of the N deposition, 30% of the P deposition, 29% of the Ca deposition and 30% of the Na deposition.

The canopy budget of N was consistently positive in all treatments and in the control, but this was not related with the nutrient additions during the observation period (Fig. 5A). Of the total N deposition, 43–53% were net retained in the canopy of all plots regardless of the experimental treatment. The canopy budget of P was negative in the P and N + P treatments, where P and N + P additions increased P leaching from the canopy. The canopy budgets of Ca and Na were positive in all treatments and in the control and there were no treatment effects. Of the total Ca deposited from the atmosphere, 40–62% were net retained in the canopy of all plots during the study period. Sodium retention in the canopy accounted for 30–46% of the total Na deposited from the atmosphere (**Table S2**).

3.3. *Soil organic layer budgets*

In the control, less than 6% of the total soil input of N (throughfall + litterfall, Eq. (5) reaching the surface of the soil organic layer were net lost by leaching. The inputs of P and Ca with throughfall matched the

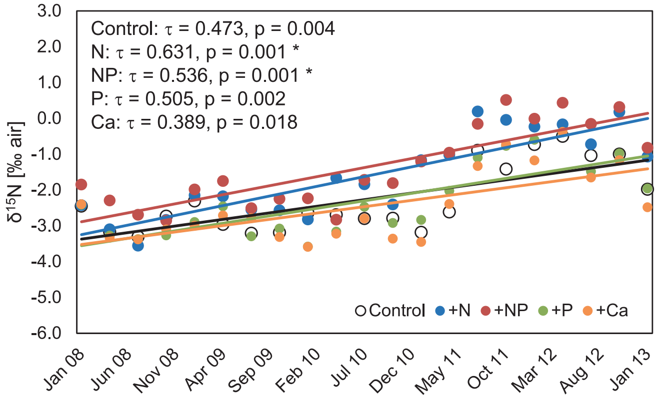

Fig. 2. Temporal course of δ^{15}N values of litterfall from 2008 to 2012. Solid lines illustrate significant trends ($p < 0.05$) as revealed by the seasonal Mann-Kendall test. Asterisks denote trends that are significantly different from the control ($p < 0.05$), as determined by linear mixed models. Nutrients were applied in February and August of each experimental year. The δ^{15}N of N-fertilizer was –0.3 ± 0.1 ‰.

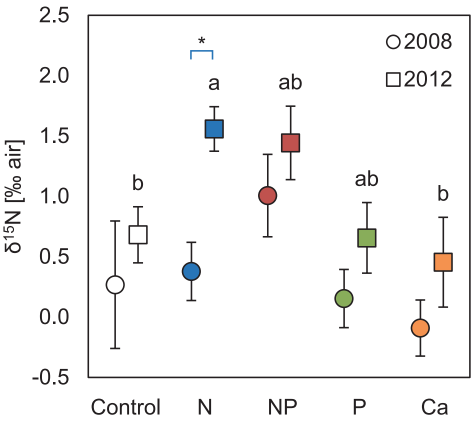

Fig. 3. $\delta^{15}N$ values in the organic layer of the experimental plots. Error bars indicate standard errors (n = 4). Values not sharing a common letter are significantly different from each other ($p < 0.05$) according to the Tukey HSD post-hoc test. Asterisks denote significant differences within the same treatment between October 2008 and December 2012. Nutrients were applied in February and August of each experimental year and the samples were taken in October 2008 and December 2012, after one and five experimental years. The $\delta^{15}N$ of N-fertilizer was –0.3 ± 0.1 ‰.

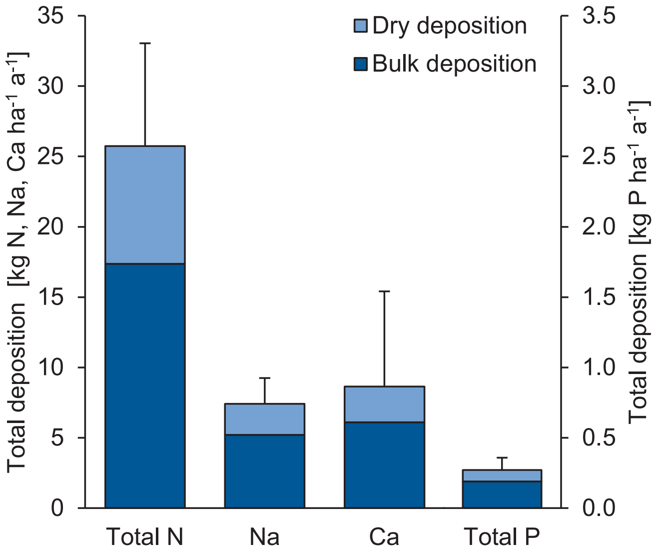

Fig. 4. Mean annual deposition at the study site from 2008 to 2012. Error bars indicate the standard deviations of the total element deposition over five observation years.

Table 2
Element stocks and $\delta^{15}N$ values in the organic layer in 2008 and 2012. The table shows the means and the standard errors (n = 4) of the element stocks and of the $\delta^{15}N$ values in the organic layer at the experimental site in October 2008 and December 2012. Values within each year not sharing a common letter are significantly different from each other ($p < 0.05$). Values in bold indicate a significant change within the same treatment between 2008 and 2012.

Year	Treatment	N	P	Ca	Na	$\delta^{15}N$ air
		Organic layer stocks [kg ha^{-1}]				‰
2008	**Control**	4063 ± 371	104.5 ± 7.0	40.1 ± 4.4	6.8 ± 0.9	0.27 ± 0.53
	+N	3364 ± 339	101.2 ± 13.9	159.2 ± 59.6	7.0 ± 1.5	0.38 ± 0.24
	+NP	4115 ± 138	113.4 ± 3.6	94.9 ± 28.9	13.9 ± 3.7	1.01 ± 0.34
	+P	3600 ± 584	96.9 ± 18.1	54.5 ± 12.1	11.1 ± 2.2	0.15 ± 0.29
	+Ca	4505 ± 782	124.8 ± 21.5	79.4 ± 15.1	8.7 ± 2.0	−0.09 ± 0.23
2012	**Control**	4437 ± 348	132.7 ± 9.2	**95.0 ± 19.2**	4.2 ± 0.1^{b}	0.68 ± 0.23^{b}
	+N	3847 ± 511	137.6 ± 19.9	95.0 ± 9.3	4.2 ± 0.4^{b}	**1.56 ± 0.18** ^{a}
	+NP	4605 ± 235	153.6 ± 6.8	117.7 ± 34.0	17.9 ± 2.8 ^{a}	1.44 ± 0.30 ^{ab}
	+P	4216 ± 675	137.2 ± 34.5	**136.1 ± 22.1**	18.7 ± 5.1 ^{a}	0.66 ± 0.29 ^{ab}
	+Ca	5297 ± 1030	157.5 ± 24.5	**152.1 ± 26.6**	5.8 ± 1.1^{b}	0.45 ± 0.37^{b}

outputs with litter leachate, while 15% of the total soil input of Na accumulated in the organic layer.

The soil organic layer budgets of N, P and Ca were positive during the studied period in the N, P, N + P and Ca treatments, respectively, and different from the control (Fig. 5B). Of the total inputs to the surface of the soil organic layer via throughfall, litterfall and fertilization, 40% of the N, 82% of the P and 33% of the Ca were retained in the organic layer. Interestingly, in the N + P and P treatments a fraction of the Na included in the P fertilizer was also retained in the organic layer, increasing the Na accumulation already observed in the control plots to 36–39% of the Na inputs via throughfall, litterfall and fertilization to the surface of the soil organic layer.

Between 6 and 10% of the added N, <9% of the added Ca, <3% of the added P and 50–55% of the added Na were leached from the organic layer into the mineral soil. Therefore, >90% of the added N, P and Ca along with roughly half of the added Na were cycled between the vegetation and the soil organic layer.

3.4. Mineral soil budgets

In all treatments and in the control, all nutrients leached from the organic layer were net retained in the upper 0.3 m of the mineral soil, which together with the organic layer constitutes the main root zone. The P and N + P additions significantly increased the net P retention in the mineral soil compared to the control (Fig. 5C). However, the N and Ca additions did not influence the mineral soil budgets significantly. The mean leaching rates with soil solution to > 0.3 m soil depth were < 1.5 kg ha^{-1} year^{-1} for all studied elements (**Table S2**). Therefore, 15–17% of the N and 8–15% of the P that leached from the organic layer were lost to soil horizons > 0.3 m soil depth. The losses of Ca to > 0.3 m soil depth accounted for 35–51% of the inputs with litter leachate. As expected, P and N + P treatments significantly increased Na losses to > 0.3 m soil depth, which represented 45–48% of the Na inputs with litter leachate, while in the control only 28% of the Na inputs with litter leachate were lost by leaching to > 0.3 m soil depth. The annual leaching losses of the added N, P and Ca with soil solution to > 0.3 m mineral soil depth accounted for 0.1–1.6% of the fertilized amounts, while losses of added Na accounted for 32–36% of the fertilized amounts.

3.5. Fate of the added nutrients

From October 2008 to December 2012 (four years and eight fertilizer applications) the annual increase of the element stock in the organic layer accounted for 59–63% of the added N, 33% of the added P, 48% of the added Ca and 25–38% of the added Na (Fig. 6). However, these increases were not statistically significant because of the strong spatial variability of element stocks in the organic layer and the relatively low fertilization inputs compared with the high background stocks. Added N and Ca were cycled to a larger extent with litterfall than with throughfall, which accounted together for 13–24% of the added N and for 50% of the added Ca. Litterfall and throughfall returned each between 6 and 12% of the added P, indicating comparable contributions of these pathways to P cycling. Sodium was predominantly cycled with throughfall, which accounted for 5–6% of the added Na. The leaching

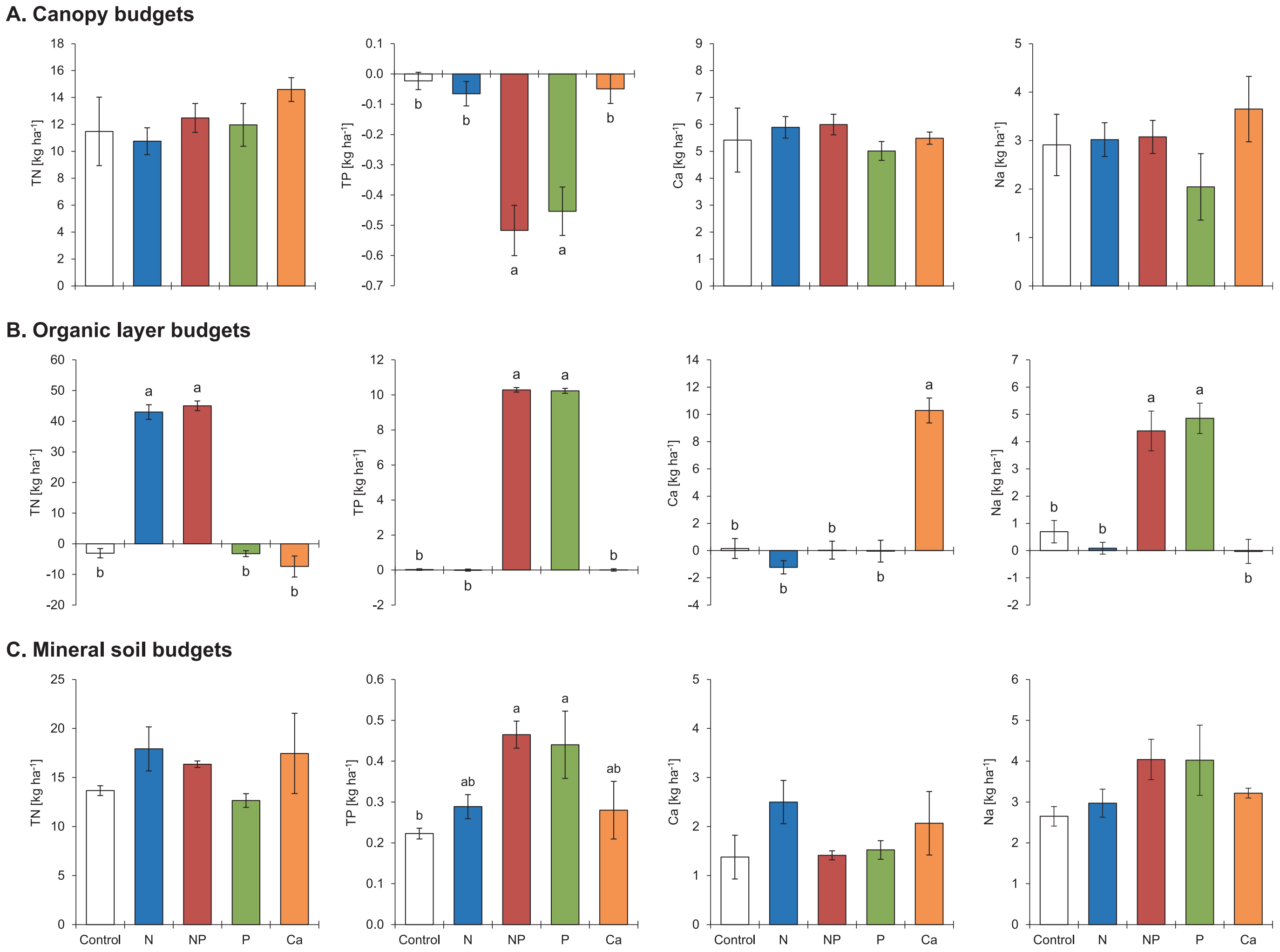

Fig. 5. Element budgets of the ecosystem from 2008 to 2012. The figures show the mean annual (A) canopy budgets (Eq. (1), (B) organic layer budgets (Eq. (4) and (C) mineral soil budgets (Eq. (6) of total nitrogen (TN), total phosphorus (TP), calcium (Ca) and sodium (Na) in the experimental plots of the nutrient manipulation experiment (NUMEX). Positive values indicate net retention, negative values denote net leaching. Error bars show standard errors (n = 4). Values not sharing a common letter are significantly different from each other ($p < 0.05$).

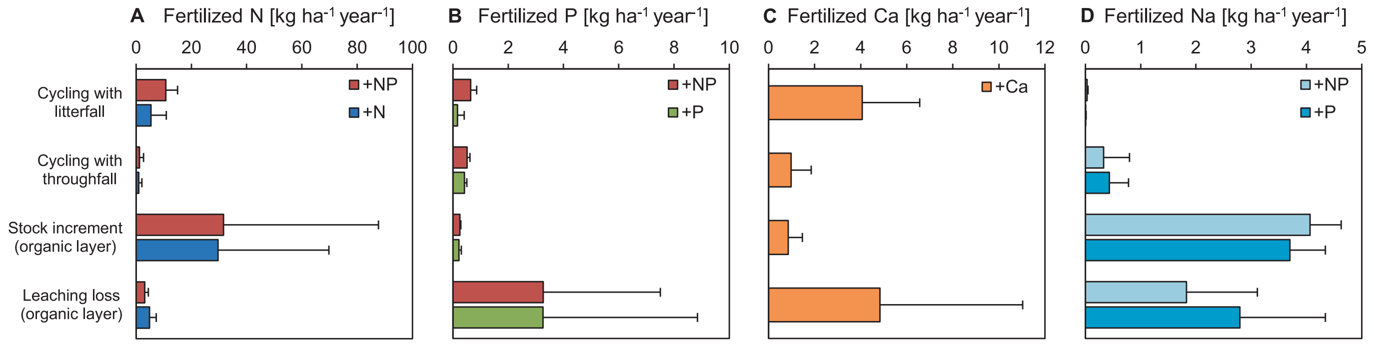

Fig. 6. Fate of the added nutrients in the experimental treatments. The figures show the mean annual cycling rates of the added (A) nitrogen, (B) phosphorus, (C) calcium and (D) sodium in the nutrient manipulation experiment (NUMEX) from October 2008 to December 2012. Error bars show standard errors (n = 4). Annual fertilization rates were 50 kg ha^{-1} $year^{-1}$ of N (urea), 10 kg ha^{-1} $year^{-1}$ of P (NaH_2PO_4), and 10 kg ha^{-1} $year^{-1}$ of Ca ($CaCl_2$). The NaH_2PO_4 fertilizer included 7.4 kg ha^{-1} $year^{-1}$ of Na.

loss of added Na to > 0.3 m mineral soil depth was similar to the increase of the Na stock in the organic layer.

4. Discussion

4.1. Effects of nutrient additions on canopy budgets

The finding that during the observation period of five years, deposited N, Ca and Na from the atmosphere were consistently net retained in the canopies of all experimental plots is in contrast to our first hypothesis. Only the P and N + P additions significantly increased leaching losses of P, shifting the P canopy budgets towards negative values in line with our expectation (Fig. 5A).

The retention of the total N deposition in the canopy (47%) falls in the range described by Lovett and Lindberg (1993), Schwarz et al. (2014) and Guerrieri et al. (2021) for several temperate and tropical forests. The finding that after five years of fertilization N additions did not change the canopy budget of N is in contrast to the earlier observations of Wullaert et al. (2010) who reported reduced canopy N retention in the N and N + P treatments after 1.5 years of fertilization. The unchanged canopy budget of N after five years is also surprising because tree seedlings showed increased foliar N concentrations in the N and N + P treatments of NUMEX (Cárate-Tandalla et al., 2018), which could increase the leaching potential of N. After the first year of fertilization in NUMEX, N + P additions increased leaf litter production significantly, but separate N additions did not have a significant effect on leaf litter production (Homeier et al., 2012). A stimulated leaf production (Homeier et al., 2012) may have favored further N uptake from the deposition in addition to the N uptake via the roots and, thus, reduced N leaching. A study by Clark et al. (2005) in a tropical montane forest in Costa Rica revealed that N retention by epiphytic bryophytes could include 61–67% of the inorganic N retained by the canopy. At our study site, N additions affected the N cycling associated with epiphytes which assimilated additional N (Matson et al., 2014) and could have additionally reduced N leaching. We therefore suggest that an increased leaf area and N uptake of epiphytes in the later phase of the five observation years reversed the early effect of the N and N + P additions on the canopy budget of N.

The negative canopy budgets of P in the P and N + P treatments confirmed earlier observations that the canopy retention of P tended to decrease after 1.5 years of fertilization (Wullaert et al., 2010). After five years, at least marginally significant increases in leaf P concentrations and consistently lower foliar N:P ratios in the leaves of the four studied species in the P and N + P treatments (Table 1) – which included the four most abundant species representing more than the half of the trees with a diameter at breast height > 0.1 m – suggested a reduced P limitation, which may have favored P leaching from the leaves. We did not study the remaining ca. 50 tree species and, therefore, their response to the P additions remains unknown.

The forest canopy retained on average 64% of the Ca deposition from the atmosphere irrespective of the treatments, which again confirmed the short term observations of Wullaert et al. (2013) at the same experimental site. The Ca concentrations in the foliage increased substantially after five years of Ca additions (Table 1), indicating that the fertilized Ca contributed to satisfying the Ca demand of the trees. At the same time the Ca uptake from deposition should have decreased. We therefore suggest that the positive canopy budgets of Ca reflected the Ca requirements of the rich epiphyte community and their associated canopy organisms (Homeier et al., 2008; Werner et al., 2012). Moreover, there was possibly a Ca immobilization by organisms living in the organic material of canopy soils (Matson et al., 2014). Apparently, the Ca demand of the canopy organisms could not be satisfied by our fertilizer application to the soil.

About 40% of the deposited Na were consistently retained in the canopy during the studied period independently of fertilization, similarly to the observations of Wilcke et al. (2017) in a neighboring catchment. At our study site, Na deposition is low during most of the time, because easterly trade winds with low Na concentrations prevail throughout the year (Makowski Giannoni et al., 2016). While Na is a beneficial but not essential element for plants, it is an essential element for animals and bacteria (Thomas and Apte, 1984). We therefore suggest that the uptake of Na by the microorganisms living in the phyllosphere and in the organic material of the canopy soils explains the net canopy retention of Na. These organisms apparently cannot benefit from the Na added to the soil.

4.2. Element cycling between the soil organic layer and the vegetation

The net retention in the organic layer of the added N, P and Ca was comparable to the short-term effects observed by Wullaert et al. (2010; 2013) after 1.5 years of nutrient additions (Fig. 5B). The low net losses of added N, P and Ca leaving the soil organic layer with litter leachate and the considerable return of the added nutrients with litterfall and throughfall emphasized the tight cycling of the added nutrients between the soil organic layer and the vegetation. This supported our second hypothesis.

Our calculation of the change in N stocks of the soil organic layer after five years of fertilization was associated with a high uncertainty, because the annual N additions accounted for only 1% of the total N pool. The average annual increase of the N stocks in the organic layer estimated at 30 kg ha^{-1} year^{-1} in the N and N + P treatments corresponded to 60% of the applied N and was probably the result of adsorption and immobilization of NH_4^+ by microorganisms and conversion to organic N forms (Arnold et al., 2009; Gerschlauer et al., 2016). The N cycling rates of the added N with litterfall and throughfall (13–24% of the added N) suggested that N and N + P additions increased the N cycling between vegetation and organic layer, in line with observations from nutrient manipulations experiments conducted in several, similarly species-rich tropical forests (Wright et al., 2018).

The retention of the added P in the organic layer with little net leaching losses to the mineral soil accompanied by increasing P concentration in foliar tissue in response to P and N + P additions indicated that a fraction of the added P was taken up by the vegetation. The calculated P stock increment in the organic layer from October 2008 to December 2012 accounted only for one third of the added P (Fig. 6) and had again a large uncertainty. We suspect that the calculated P accumulation could be substantially underestimated as a consequence of the high spatial heterogeneity of the P concentrations and stocks in the organic layers, which was difficult to sample representatively. The organic layers at our study site serve as a habitat for highly diverse microbial communities that play a crucial role in the biological retention of P (Krashevska et al., 2010). Therefore, we suggest that the main P retention process was microbial immobilization favored by elevated C:P ratios (Wullaert et al., 2010) along with mycorrhizal P uptake and transfer to plants (Camenzind et al., 2018; 2019). Additionally, added P could also be sorbed to reactive, Al-rich organo-mineral complexes (Spohn, 2024; Violante et al., 2002) in the organic layer, which contained approximately 10% of mineral material at the study site (Wullaert et al., 2010).

The annual increase in the Ca stocks of the organic layer from 2008 to 2012, which accounted for ca. 4.8 kg ha^{-1} year^{-1} (Fig. 6) and, thus, for nearly half of the added Ca, suggests that Ca additions may have had beneficial effects on soil fauna, litter decomposition and tree growth (Kaspari et al., 2008; Kaspari and Powers, 2016). Because fine-root biomass may respond to an improved nutrient supply (Nadelhoffer, 2000; Yuan and Chen, 2012), a decrease of the fine-root biomass, which was observed after one year of Ca additions (Wullaert et al., 2013), indicated improved growth conditions in response to the increased Ca availability (Gower, 1987; Fahey et al., 2016). In the Ca treatment, the percentage of the added Ca cycled with litterfall and throughfall increased from 21% after one year of Ca additions (Wullaert et al., 2013) to 50% after five experimental years. This illustrated that Ca retention in the aboveground part of the ecosystem (the vegetation and the soil organic layer) was mainly biologically controlled, in line with findings of Wilcke et al. (2017) at a nearby forest site.

The finding that 25–35% of the Na added with the P fertilizer accumulated in the soil organic layer (Fig. 6) was unexpected, given that Na is not an essential plant nutrient. Because Na should be highly mobile under the prevailing acidic conditions at our study site due to its low competitiveness for cation exchange sites (**Table S1**), we suggest that Na was biologically retained. Sodium additions were shown to be beneficial for ants and termites and enhanced decomposition in tropical forests (Kaspari et al., 2014; Clay et al., 2015). Moreover, Na was an important indicator for habitat quality of the microfauna at our study site (Krashevska et al., 2017).

4.3. Effects of nutrient addition on the mineral soil budgets

In line with our third hypothesis, the N, Ca and Na budgets of the mineral topsoil (0–0.3 m) were not significantly influenced by the nutrient additions (Fig. 5C). We attribute this to the large element stock in the mineral soil that was not changed by the small leaching losses of the added fertilizers. In contrast, fertilized P significantly accumulated in the mineral topsoil of the P and N + P treatments illustrating that the mineral soil was an important sink of the fertilized P. The main retention mechanism of P in mineral soils is sorption to positively charged surfaces (Rechberger et al., 2021). Considering the acidic pH and the high clay and Al concentrations at our study site (Wullart et , 2013), adsorption to clay, Al and Fe oxides, precipitation as Al-phosphates and occlusion in Fe and Mn concretions (Wilcke et al., 2019) likely contributed to P retention in the mineral soil. This was in contrast to our third hypothesis. We suggest that part of the fertilized P escaped the biological uptake by plants and soil organisms in the soil organic layer. This was similar to the finding that P-leaching from the leaves increased in response to P additions (Fig. 5A).

Nevertheless, the consistently positive budgets of the mineral topsoil (0–0.3 m) in all treatments and the control indicated that N and Ca accumulated in the mineral soil regardless of the treatments (Fig. 5C). Because it can be assumed that the microbial activity in the mineral soil was lower than in the organic layer (Dove et al., 2021; He et al., 2023), we expected immobilization by soil microorganisms to be less important than in the organic layer. Furthermore, N and N + P additions were reported to decrease microbial N immobilization by roughly 50% at our study site (Baldos et , 2015). The N lost from the organic layer could have been retained in the mineral soil by NH_4^+ fixation in the clay fraction (Corre et al., 2003), or by adsorption of dissolved organic N onto mineral surfaces (Bingham and Cotrufo, 2016). Some N could also have been taken up by roots that were still present in the 0–0.3 m mineral soil layer (Soethe et al., 2006; Moser et al., 2010) and some NO_3^- was leached (NO_3^- was the dominating N species in the mineral soil – Wilcke et al., 2013). For the Ca accumulation in the mineral soil, we suggest a retention by the high cation-exchange capacity of the study soils (**Table S1**), which contained three-layer clay minerals (Schrumpf et al., 2001).

Although the Na budgets of the mineral topsoil were not significantly affected by nutrient additions, the significantly increased Na leaching to > 0.3 m soil depth (**Table S2**) suggested that the Na supply with the P fertilization exceeded the assumed organismic demand for Na. It seems reasonable to assume that the Na demand decreases with increasing soil depth because of the decreasing abundance and lower activity of microorganisms (Dove et al., 2021; He et al., 2023). Additionally, more Na could have been released by weathering of the Na-rich phyllite in the mineral soil of the study area (Wilcke et al., 2017).

4.4. Effects of N amendments on the biological N cycling

The finding that the N and N + P additions increased the $\delta^{15}N$ values of litterfall (Fig. 2) and of the organic layer (Fig. 3) during the five experimental years supported our fourth hypothesis. Because we did not observe significantly increased N leaching losses from the organic layer in the N and N + P treatments, the increasing $\delta^{15}N$ values denoted subtle changes of the N cycle that could not yet be detected with our budgeting approach. Increasing $\delta^{15}N$ values either indicate that there was a ^{15}N-enriched N input into the ecosystem or that ^{14}N was preferentially lost from the organic layer by leaching and denitrification. From 1998 to 2010, Wilcke et al. (2013) observed an increasing N deposition to the study area, which had a mean $\delta^{15}N$ value of 3.4 ± 0.9 ‰ and a strong temporal variation (Alvarez et al., 2024). Therefore, the increasing $\delta^{15}N$ values of litterfall and the organic layer in all treatments and the control could be partly attributed to the deposition of ^{15}N-enriched N species. The strong temporal variation in the $\delta^{15}N$ values of bulk deposition (1.9 – 5.9 ‰ from 2013 to 2016 – Alvarez et al., 2024) could also explain why the positive trends in Fig. 2 show oscillations around the regression line. A study of the NO_3^- fluxes with ecosystem solutions and the $\delta^{15}N$ values of NO_3^- in a forest next to the NUMEX site indicated a pronounced nitrification in the soil organic layer favoring NO_3^- leaching into the mineral soil and to the stream, and found isotopic indications of denitrification in the subsoils (Schwarz et al., 2011). At the NUMEX site, the significant reduction of the soil water content in the organic layer (**Fig. S2**) and an increasing number of hours with an air temperature > 25 °C (Wilcke et al., 2020a) could have further favored soil organic matter mineralization delivering even more NH_4^+ for nitrification. Thus, besides the ^{15}N-enriched inputs, ^{15}N-depleted outputs via leaching and volatilization are likely for all NUMEX plots.

Although the N and N + P treatments had received ^{15}N-depleted urea fertilizer with a mean $\delta^{15}N$ value of –0.3 ± 0.1 ‰, the soil organic layer and the litterfall showed consistently the highest $\delta^{15}N$ values and the most pronounced positive trend, which was significantly different from the trends in all other plots. Similarly, the leaves of the N and N + P treatments showed the most enriched $\delta^{15}N$ values of all plots (Table 1). This corresponds to the expectation that $\delta^{15}N$ values of the aboveground biomass reflect the isotopic composition of the N taken up by the roots (Garten et al., 2011). Previous work at the NUMEX site had shown that N and N + P additions increased NO_3-N concentrations in litter leachate by 2–3.7 times (Velescu et al., 2016). During the same study period, N and N + P additions resulted in a tenfold increase in nitrous oxide emissions from the organic layer (Martinson et al., 2013). This indicates that N and N + P additions increased preferential losses of ^{14}N via NO_3^- leaching and denitrification, explaining the temporal change of the $\delta^{15}N$ values of litterfall and the soil organic layer. These losses have clearly altered the N isotopic composition of litterfall and the soil organic layer, but have not yet significantly influenced the organic layer budgets.

5. Conclusions

In contrast to our first hypothesis, the nutrient additions only resulted in an increased P leaching from the canopy reflecting a high nutrient demand of the organism community of the ecosystem, which was alleviated by our P additions. The majority of the added nutrients accumulated in the soil organic layer and was tightly cycled between the organic layer and the vegetation, supporting our second hypothesis. Interestingly, this was also true for the Na added with the P fertilizer, although Na is not an essential plant nutrient. We suggest that the soil fauna and the microbes, for which Na is essential, have an unmet Na demand at our study site. As expected in our third hypothesis, nutrient additions did not change the topsoil budgets significantly, although there were indications of increased N leaching in the N and N + P treatments. The latter was in line with increasing $\delta^{15}N$ values of litterfall and the soil organic layer, supporting our fourth hypothesis. Increasing $\delta^{15}N$ values could indicate upcoming N losses via leaching and volatilization earlier than the flux budgets with their inherent uncertainties.

Overall, most of the nutrients added over five years remained within the studied ecosystem, resulting in increased nutrient availability with minimal losses to the atmosphere and water bodies. This scenario can be expected to occur across the entire tropical montane forest of southern Ecuador in the long term, where an increased N, low but steady P, and episodic Ca deposition have been documented. Moreover, we observed isotopic evidence for upcoming N losses from the studied ecosystem which belongs to a headwater catchment, with possible future eutrophication risks for downstream water bodies.

CRediT authorship contribution statement

Andre Velescu: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Jürgen Homeier:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Carlos Iván Espinosa:** Writing – review & editing, Resources, Conceptualization. **Wolfgang Wilcke:** Writing – review & editing, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2026.117698.

Data availability

Data will be made available on request.

References

Aber, J., McDowell, W., Nadelhoffer, K., Magill, A., Berntson, G., Kamakea, M., McNulty, S., Currie, W., Rustad, L., Fernandez, I., 1998. Nitrogen saturation in temperate forest ecosystems: hypotheses revisited. Bioscience 48 (11), 921–934. https://doi.org/10.2307/1313296.

Adams, M.B., Angradi, T.R., Kochenderfer, J.N., 1997. Stream water and soil solution responses to 5 years of nitrogen and sulfur additions at the Fernow Experimental Forest West Virginia. For. Ecol. Manag. 95 (1), 79–91. https://doi.org/10.1016/S0378-1127(96)03990-4.

Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. Crop Evapotranspiration: Guidelines for Computing Crop Water Requirements. Food and Agriculture Organization of the United Nations, Rome.

Allen, R.G., Jensen, M.E., Wright, J.L., Burman, R.D., 1989. Operational estimates of reference evapotranspiration. Agron. J. 81, 650–662.

Allen, R.G., 2013. REF-ET: reference evapotranspiration calculation software, for FAO and ASCE standardized equations. University of Idaho.

Alvarez, P., Velescu, A., Pierick, K., Homeier, J., Wilcke, W., 2024. Sources and sinks of N in ecosystem solutions along the water path through a tropical montane forest in Ecuador assessed with δ^{15}N values of total dissolved nitrogen. J. Geophys. Res. Biogeosci. 129, e2024JG008043. https://doi.org/10.1029/2024JG008043.

Arnold, J., Corre, M.D., Veldkamp, E., 2009. Soil N cycling in old-growth forests across an Andosol toposequence in Ecuador. Forest Ecol. Manag. 257, 2079–2087. https://doi.org/10.1016/j.foreco.2009.02.014.

Báez, S., Homeier, J., 2018. Functional traits determine tree growth and ecosystem productivity of a tropical montane forest: Insights from a long-term nutrient manipulation experiment. Glob. Chang. Biol. 24 (1), 399–409. https://doi.org/10.1111/gcb.13905.

Barthlott, W., Mutke, J., Rafiqpoor, M.D., Kier, G., Kreft, H., 2005. Global centres of vascular plant diversity. Nova Acta Leopold. 92 (342), 61–83.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Soft. 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Bingham, A.H., Cotrufo, M.F., 2016. Organic nitrogen storage in mineral soil: implications for policy and management. Sci. Total Environ. 551, 116–126. https://doi.org/10.1016/j.scitotenv.2016.02.020.

Boy, J., Rollenbeck, R., Valarezo, C., Wilcke, W., 2008. Amazonian biomass burning derived acid and nutrient deposition in the north Andean montane forest of Ecuador. Glob. Biogeochem. Cycles 22, GB4011. https://doi.org/10.1029/2007GB003158.

Boy, J., Wilcke, W., 2008. Tropical Andean forest derives calcium and magnesium from Saharan dust. Glob. Biogeochem. Cycles 22, GB1027. https://doi.org/10.1029/2007GB002960.

Bruijnzeel, L.A., Hamilton, L.S., 2000. Decision Time for Cloud Forests. IHP Humid Tropics Programme Series 13, IHP - UNESCO, Paris.

Camenzind, T., Hättenschwiler, S., Treseder, K.K., Lehmann, A., Rillig, M.C., 2018. Nutrient limitation of soil microbial processes in tropical forests. Ecol. Monogr. 88 (1), 4–21. https://doi.org/10.1002/ecm.1279.

Camenzind, T., Scheu, S., Rillig, M.C., 2019. Expanding the toolbox of nutrient limitation studies: a novel method of soil microbial in-growth bags to evaluate nutrient demands in tropical forests. Funct. Ecol. 33 (8), 1536–1548. https://doi.org/10.1111/1365-2435.13352.

Cameron, K.C., Di, H.J., Moir, J.L., 2013. Nitrogen losses from the soil/plant system: a review. Ann. Appl. Biol. 162 (2), 145–173. https://doi.org/10.1111/aab.12014.

Cárate-Tandalla, D., Camenzind, T., Leuschner, C., Homeier, J., 2018. Contrasting species responses to continued nitrogen and phosphorus addition in tropical montane forest tree seedlings. Biotropica 50, 234–245. https://doi.org/10.1111/btp.12518.

Christ, M., Zhang, Y., Likens, G.E., Driscoll, C.T., 1995. Nitrogen retention capacity of a northern hardwood forest soil under ammonium sulfate additions. Ecol. Appl. 5 (3), 802–812. https://doi.org/10.2307/1941988.

Clark, L.L., Nadkarni, N.M., Gholz, H.L., 2005. Retention of inorganic nitrogen by epiphytic bryophytes in a tropical montane forest. Biotropica 37 (3), 328–336. https://doi.org/10.1111/j.1744-7429.2005.00043.x.

Clay, N.A., Donoso, D.A., Kaspari, M., 2015. Urine as an important source of sodium increases decomposition in an inland but not coastal tropical forest. Oecologia 177 (2), 571–579. https://doi.org/10.1007/s00442-014-3183-4.

Cleveland, C.C., Townsend, A.R., Taylor, P., Alvarez-Clare, S., Bustamante, M.M., Chuyong, G., et al., 2011. Relationships among net primary productivity, nutrients and climate in tropical rain forest: a pan-tropical analysis. Ecol. Lett. 14 (9), 939–947. https://doi.org/10.1111/j.1461-0248.2011.01658.x.

Corre, M.D., Beese, F.O., Brumme, R., 2003. Soil nitrogen cycle in high nitrogen deposition forest: changes under nitrogen saturation and liming. Ecol. Appl. 13 (2), 287–298. https://doi.org/10.1890/1051-0761(2003)013[0287:SNCIHN]2.0.CO;2.

Cunha, D.G.F., Dodds, W.K., do Carmo Calijuri, M., 2011. Defining nutrient and biochemical oxygen demand baselines for tropical rivers and streams in São Paulo State (Brazil): a comparison between reference and impacted sites. Environ. Manag. 48, 945–956. https://doi.org/10.1007/s00267-011-9739-8.

Cunha, H.F.V., Andersen, K.M., Lugli, L.F., Santana, F.D., Aleixo, I.F., Moraes, A.M., et al., 2022. Direct evidence for phosphorus limitation on Amazon forest productivity. Nature 608, 558–562. https://doi.org/10.1038/s41586-022-05085-2.

Currie, W.S., Aber, J.D., Driscoll, C.T., 1999. Leaching of nutrient cations from the forest floor: effects of nitrogen saturation in two long-term manipulations. Can. J. Forest Res. 29 (5), 609–620. https://doi.org/10.1139/x99-033.

Cusack, D.F., Karpman, J., Ashdown, D., Cao, Q., Ciochina, M., Halterman, S., Lydon, S., Neupane, A., 2016. Global change effects on humid tropical forests: evidence for biogeochemical and biodiversity shifts at an ecosystem scale. Rev. Geophys. 54 (3), 523–610. https://doi.org/10.1002/2015RG000510.

Dietrich, K., Spoeri, E., Oelmann, Y., 2016. Nutrient addition modifies phosphatase activities along an altitudinal gradient in a tropical montane forest in Southern Ecuador. Front. Earth Sci. 4, 12. https://doi.org/10.3389/feart.2016.00012.

Dove, N.C., Barnes, M.E., Moreland, K., Graham, R.C., Berhe, A.A., Hart, S.C., 2021. Depth dependence of climatic controls on soil microbial community activity and composition. ISME Commun. 1 (1), 78. https://doi.org/10.1038/s43705-021-00081-5.

DVWK, 1996. Ermittlung der Verdunstung von Land- und Wasserflächen. DVWK-Merkblätter zur Wasserwirtschaft 238, Deutscher Verband für Wasserwirtschaft und Kulturbau e.V., Bonn.

Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., et al., 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. Ecol. Lett. 10 (12), 1135–1142. https://doi.org/10.1111/j.1461-0248.2007.01113.x.

Fabian, P., Rollenbeck, R., Spichtinger, N., Brothers, L., Dominguez, G., Thiemens, M., 2009. Sahara dust, ocean spray, volcanoes, biomass burning: pathways of nutrients into Andean rainforests. Adv. Geo. 22, 85–94. https://doi.org/10.5194/adgeo-22-85-2009.

Fahey, T.J., Heinz, A.K., Battles, J.J., Fisk, M.C., Driscoll, C.T., Blum, J.D., Johnson, C.E., 2016. Fine root biomass declined in response to restoration of soil calcium in a northern hardwood forest. Can. J. Forest Res. 46 (5), 738–744. https://doi.org/10.1139/cjfr-2015-0434.

Fleischbein, K., Wilcke, W., Valarezo, C., Zech, W., Knoblich, K., 2006. Water budgets of three small catchments under montane forest in Ecuador: experimental and modelling approach. Hydrol. Proc. 20 (12), 2491–2507. https://doi.org/10.1002/hyp.6212.

Garten, C.T., Iversen, C.M., Norby, R.J., 2011. Litterfall ^{15}N abundance indicates declining soil nitrogen availability in a free-air CO2 enrichment experiment. Ecology 92, 133–139. https://doi.org/10.1890/10-0293.1.

Gerschlauer, F., Dannenmann, M., Kühnel, A., Meier, R., Kolar, A., Butterbach-Bahl, K., Kiese, R., 2016. Gross nitrogen turnover of natural and managed tropical ecosystems at Mt. Kilimanjaro, Tanzania. Ecosystems 19, 1271–1288. https://doi.org/10.1007/s10021-016-0001-3.

Gower, S.T., 1987. Relations between mineral nutrient availability and fine root biomass in two Costa Rican tropical wet forests: a hypothesis. Biotropica 19 (2), 171–175. https://doi.org/10.2307/2388741.

Guerrieri, R., Templer, P., Magnani, F., 2021. Canopy exchange and modification of nitrogen fluxes in forest ecosystems. Curr. For. Rep. 7, 115–137. https://doi.org/10.1007/s40725-021-00141-y.

He, L., Sun, X., Li, S., Zhou, W., Chen, Z., Bai, X., 2023. The vertical distribution and control factor of microbial biomass and bacterial community at macroecological scales. Sci. Total Environ. 869, 161754. https://doi.org/10.1016/j.scitotenv.2023.161754.

Hietz, P., Turner, B.L., Wanek, W., Richter, A., Nock, C.A., Wright, S.J., 2011. Long-term change in the nitrogen cycle of tropical forests. Science 334 (6056), 664–666. https://doi.org/10.1126/science.1211979.

Hirsch, R.M., Slack, J.R., Smith, R.A., 1982. Techniques for trend analysis for monthly water quality data. Water Resour. Res. 18, 107–121. https://doi.org/10.1029/wr018i001p00107.

Holtgrieve, G.W., Schindler, D.E., Hobbs, W.O., Leavitt, P.R., Ward, E.J., Bunting, L., et al., 2011. A coherent signature of anthropogenic nitrogen deposition to remote watersheds of the northern hemisphere. Science 334, 1545–1548. https://doi.org/10.1126/science.1212267.

Homeier, J., Hertel, D., Camenzind, T., Cumbicus, N.L., Maraun, M., Martinson, et al., 2012. Tropical Andean forests are highly susceptible to nutrient inputs – rapid effects of experimental N and P addition to an Ecuadorian montane forest. PLoS One 7 (10), e47128. https://doi.org/10.1371/journal.pone.0047128.

Homeier, J., Leuschner, C., Bräuning, A., Cumbicus, N.L., Hertel, D., Martinson, G.O., Spannl, S., Veldkamp, E., 2013. Effects of nutrient addition on the productivity of montane forests and implications for the carbon cycle. In: Bendix, J., Beck, E., Bräuning, A., Makeschin, F., Mosandl, R., Scheu, S., Wilcke, W. (Eds.), Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador. Ecological Studies 221. Springer Verlag, Berlin, Heidelberg, pp. 315–329. https://doi.org/10.1007/978-3-642-38137-9_23.

Homeier, J., Werner, F., Gradstein, R., Breckle, S.W., Richter, M., 2008. Potential vegetation and floristic composition of Andean forests in South Ecuador, with a focus on the RBSF. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F., Mosandl, R. (Eds.), Gradients in a Tropical Mountain Ecosystem of Ecuador. Ecological Studies 198, Springer Verlag, 87–100. doi:10.1007/978-3-540-73526-7_10.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. 50 (3), 346–363. https://doi.org/10.1002/bimj.200810425.

Högberg, P., Johannisson, C., 1993. ^{15}N abundance of forests is correlated with losses of nitrogen. Plant and Soil 157 (1), 147–150. https://doi.org/10.1007/BF02390237.

Hungerbühler, D., 1997. Neogene basins in the Andes of southern Ecuador: evolution, deformation and regional tectonic implications. Eidgenössische Technische Hochschule, Zürich, Switzerland. Ph.D. Thesis.

IUSS Working Group WRB, 2022. World reference base for soil resources, 4th Ed.,. International Union of Soil Sciences (IUSS), Vienna, Austria.

Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E., Schulze, E.D., 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108, 389–411. https://doi.org/10.1007/BF00333714.

Kaspari, M., Clay, N.A., Donoso, D.A., Yanoviak, S.P., 2014. Sodium fertilization increases termites and enhances decomposition in an Amazonian forest. Ecology 95 (4), 795–800. https://doi.org/10.1890/13-1274.1.

Kaspari, M., Garcia, M.N., Harms, K.E., Santana, M., Wright, S.J., Yavitt, J.B., 2008. Multiple nutrients limit litterfall and decomposition in a tropical forest. Ecol. Lett. 11, 35–43. https://doi.org/10.1111/j.1461-0248.2007.01124.x.

Kaspari, M., Powers, J.S., 2016. Biogeochemistry and geographical ecology: embracing all twenty-five elements required to build organisms. Am. Nat. 188 (1), 62–73. https://doi.org/10.1086/687576.

Krashevska, V., Maraun, M., Ruess, L., Scheu, S., 2010. Carbon and nutrient limitation of soil microorganisms and microbial grazers in a tropical montane rain forest. Oikos 119 (6), 1020–1028. https://doi.org/10.1111/j.1600-0706.2009.18169.x.

Krashevska, V., Sandmann, D., Marian, F., Maraun, M., Scheu, S., 2017. Leaf litter chemistry drives the structure and composition of soil testate amoeba communities in a tropical montane rainforest of the Ecuadorian Andes. Microb. Ecol. 74 (3), 681–690. https://doi.org/10.1007/s00248-017-0980-4.

Lehmann, J., Schroth, G., 2003. Nutrient Leaching. In: Schroth, G., Sinclair, F.I. (Eds.), Trees, Crops and Soil Fertility: Concepts and Research Methods. CABI Publishing, pp. 158–171. https://doi.org/10.1079/9780851995939.0151.

Leimer, S., Kreutziger, Y., Rosenkranz, S., Beßler, H., Engels, C., Hildebrandt, A., Oelmann, Y., Weisser, W.W., Wirth, C., Wilcke, W., 2014. Plant diversity effects on the water balance of an experimental grassland. Ecohydrology 7 (5), 1378–1391. https://doi.org/10.1002/eco.1464.

Likens, G.E., 2004. Some perspectives on long-term biogeochemical research from the Hubbard Brook Ecosystem study. Ecology 85, 2355–2362. https://doi.org/10.1890/03-0243.

Lovett, G.M., Lindberg, S.E., 1993. Atmospheric deposition and canopy interactions of nitrogen in forests. Can J. Forest Res. 23 (8), 1603–1616. https://doi.org/10.1139/x93-200.

Magill, A., Aber, J., Berntson, G.M.B., McDowell, W.H., Nadelhoffer, K.J., Melillo, J.M., Steudler, P., 2000. Long-term nitrogen additions and nitrogen aaturation in two temperate forests. Ecosystems 3, 238–253. https://doi.org/10.1007/s100210000023.

Makowski Giannoni, S., Trachte, K., Rollenbeck, R., Lehnert, L., Fuchs, J., Bendix, J., 2016. Atmospheric salt deposition in a tropical mountain rainforest at the eastern Andean slopes of south Ecuador–Pacific or Atlantic origin? Atmos. Chem. Phys. 16 (15), 10241–10261. https://doi.org/10.5194/acp-16-10241-2016.

Martinson, G.O., Corre, M.D., Veldkamp, E., 2013. Responses of nitrous oxide fluxes and soil nitrogen cycling to nutrient additions in montane forests along an elevation gradient in southern Ecuador. Biogeochemistry 112 (1), 625–636. https://doi.org/10.1007/s10533-012-9753-9.

Martinson, G.O., Werner, F.A., Scherber, C., Conrad, R., Veldkamp, E., Flessa, H., Wolf, K., Corre, M.D., Klose, M., Gradstein, S.R., 2010. Tank Bromeliads: methane producing 'canopy wetlands' in neotropical forests. Nat. Geoscience 3, 766–769. https://doi.org/10.1038/ngeo980.

Matson, P.A., McDowell, W.H., Townsend, A.R., Vitousek, P.M., 1999. The globalization of N deposition: ecosystem consequences in tropical environments. Biogeochemistry 46, 67–83. https://doi.org/10.1023/A:1006152112852.

Matson, A.L., Corre, M.D., Veldkamp, E., 2014. Nitrogen cycling in canopy soils of tropical montane forests responds rapidly to indirect N and P fertilization. Glob. Chang. Biol. 20 (12), 3802–3813. https://doi.org/10.1111/gcb.12668.

McDowell, R.W., Luo, D., Pletnyakov, P., Upsdell, M., Dodds, W.K., 2025. Anthropogenic nutrient inputs cause excessive algal growth for nearly half the world's population. Nat. Commun. 16, 1830. https://doi.org/10.1038/s41467-025-57054-8.

McLauchlan, K.K., Williams, J.J., Craine, J.M., Jeffers, E.S., 2013. Changes in global nitrogen cycling during the Holocene epoch. Nature 495 (7441), 352–355. https://doi.org/10.1038/nature11916.

McLeod, A.I., 2011. Kendall: Kendall rank correlation and Mann-Kendall trend test. R Package Version 2, 2.

Moser, G., Leuschner, C., Röderstein, M., Graefe, S., Soethe, N., Hertel, D., 2010. Biomass and productivity of fine and coarse roots in five tropical mountain forests stands along an altitudinal transect in southern Ecuador. Plant Ecol. Divers. 3 (2), 151–164. https://doi.org/10.1080/17550874.2010.517788.

Müller, A.K., Matson, A.L., Corre, M.D., Veldkamp, E., 2015. Soil N_2O fluxes along an elevation gradient of tropical montane forests under experimental nitrogen and phosphorus addition. Front. Earth Sci. 3, 58. https://doi.org/10.3389/feart.2015.00066.

Myers, N., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. https://doi.org/10.1038/35002501.

Nadelhoffer, K.J., 2000. The potential effects of nitrogen deposition on fine-root production in forest ecosystems. New Phytol. 147, 131–139. https://doi.org/10.1046/j.1469-8137.2000.00677.x.

Pardo, L.H., Fenn, M.E., Goodale, C.L., Geiser, L.H., Driscoll, C.T., Allen, E.B., et al., 2011. Effects of nitrogen deposition and empirical nitrogen critical loads for ecoregions of the United States. Ecol. Appl. 21 (8), 3049–3082. https://doi.org/10.1890/10-2341.1.

Pardo, L.H., Templer, P.H., Goodale, C.L., Duke, S., Groffman, P.M., Adams, M.B., et al., 2006. Regional assessment of N saturation using foliar and root δ^{15}N. Biogeochemistry 80 (2), 143–171. https://doi.org/10.1007/s10533-006-9015-9.

Peters, T., Drobnik, T., Meyer, H., Rankl, M., Richter, M., Rollenbeck, R., Thies, B., Bendix, J., 2013. Environmental changes affecting the Andes of Ecuador. In: Bendix, J., Beck, E., Bräuning, A., Makeschin, F., Mosandl, R., Scheu, S., Wilcke, W. (Eds.), Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador. Ecological Studies 221. Springer Verlag, Berlin, Heidelberg, pp. 19–29. https://doi.org/10.1007/978-3-642-38137-9_2.

Phoenix, G.K., Hicks, W.K., Cinderby, S., Kuylenstierna, J.C., Stock, W.D., Dentener, F.J., et al., 2006. Atmospheric nitrogen deposition in world biodiversity hotspots: the need for a greater global perspective in assessing N deposition impacts. Glob. Chang. Biol. 12 (3), 470–476. https://doi.org/10.1111/j.1365-2486.2006.01104.x.

Prospero, J.M., Barkley, A.E., Gaston, C.J., Gatineau, A., Campos y Sansano, A., Panechou, K., 2020. Characterizing and quantifying African dust transport and deposition to South America: implications for the phosphorus budget in the Amazon Basin. Glob. Biogeochem. Cycles 34, e2020GB006536. https://doi.org/10.1029/2020GB006536.

R Core Team, 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria http://www.R-project.org.

Rechberger, M.V., Zehetner, F., Gerzabek, M.H., 2021. Phosphate sorption-desorption properties in volcanic topsoils along a chronosequence and a climatic gradient on the Galápagos Islands. J. Plant Nutr. Soil Sci. 184 (4), 479–491. https://doi.org/10.1002/jpln.202000488.

Rollenbeck, R., Peters, T., Emck, P., Richter, M., 2015. ECSF Climate station best estimate Ver. 2. Available online (http://www.tropicalmountainforest.org/data_pre.do?citid=1415) from DFG-FOR816dw.

Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Global biodiversity scenarios for the year 2100. Science 287, 1770–1774. https://doi.org/10.1126/science.287.5459.1770.

Schrumpf, M., Guggenberger, G., Valarezo, C., Zech, W., 2001. Tropical montane rain forest soils – development and nutrient status along an altitudinal gradient in the South Ecuadorian Andes. Erde 132, 43–59.

Schuur, E.A.G., Matson, P.A., 2001. Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest. Oecologia 128 (3), 431–442. https://doi.org/10.1007/s004420100671.

Schwarz, M.T., Oelmann, Y., Wilcke, W., 2011. Stable N isotope composition of nitrate reflects N transformations during the passage of water through a montane rain forest in Ecuador. Biogeochemistry 102, 195–208. https://doi.org/10.1007/s10533-010-9434-5.

Schwarz, M.T., Bischoff, S., Blaser, S., Boch, S., Schmitt, B., Thieme, L., Fischer, M., Michalzik, B., Schulze, E.D., Siemens, J., Wilcke, W., 2014. More efficient aboveground nitrogen use in more diverse Central European forest canopies. Forest Ecol. Manag. 313, 274–282. https://doi.org/10.1016/j.foreco.2013.11.021.

Soethe, N., Lehmann, J., Engels, C., 2006. The vertical pattern of rooting and nutrient uptake at different altitudes of a south Ecuadorian montane forest. Plant and Soil 286 (1–2), 287–299. https://doi.org/10.1007/s11104-006-9044-0.

Spannl, S., Homeier, J., Bräuning, A., 2016. Nutrient-induced modifications of wood anatomical traits of Alchornea lojaensis (Euphorbiaceae). Front. Earth Sci. 4, 50. https://doi.org/10.3389/feart.2016.00050.

Spohn, M., 2024. Preferential adsorption of nitrogen-and phosphorus-containing organic compounds to minerals in soils: a review. Soil Biol. Biochem. 109428. https://doi.org/10.1016/j.soilbio.2024.109428.

Shao, S., Driscoll, C.T., Johnson, C.E., Fahey, T.J., Battles, J.J., Blum, J.D., 2016. Long-term responses in soil solution and stream-water chemistry at Hubbard Brook after experimental addition of wollastonite. Environ. Chem. 13, 528–540. https://doi.org/10.1071/EN15113.

Staelens, J., Houle, D., De Schrijver, A., Neirynck, J., Verheyen, K., 2008. Calculating dry deposition and canopy exchange with the canopy budget model: review of assumptions and application to two deciduous forests. Water Air Soil Pollut. 191 (1), 149–169. https://doi.org/10.1007/s11270-008-9614-2.

Tanner, E.V.J., Vitousek, P.M., Cuevas, E., 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. Ecology 79, 10–22. https://doi.org/10.2307/176860.

Thomas, J., Apte, S.K., 1984. Sodium requirement and metabolism in N-fixing cyanobacteria. J. Biosci. 6 (5), 771–794. https://doi.org/10.1007/BF02702719.

Ulrich, B., 1983. Interaction of forest canopies with atmospheric constituents: SO_2, alkali and earth alkali cations and chloride. In: Ulrich, B., Pankrath, J. (Eds.), Effects of Accumulation of Air Pollutants in Forest Ecosystems. Springer, Dordrecht, pp. 33–45. https://doi.org/10.1007/978-94-009-6983-4_2.

Van Langenhove, L., Verryckt, L.T., Bréchet, L., Courtois, E.A., Stahl, C. Hofhansl, F., Bauters, M., Sardans, J., Boeckx, P., Fransen, P., Peñuelas, J., Janssens, I.A., 2020. Atmospheric deposition of elements and its relevance for nutrient budgets of tropical forests. Biogeochemistry 149, 175–193. doi:10.1007/s10533-020-00673-8.

Velescu, A., Homeier, J., Bendix, J., Valarezo, C., Wilcke, W., 2021. Response of water-bound fluxes of potassium, calcium, magnesium and sodium to nutrient additions in an Ecuadorian tropical montane forest. Forest Ecol. Manag. 501, 119661. https://doi.org/10.1016/j.foreco.2021.119661.

Velescu, A., Valarezo, C., Wilcke, W., 2016. Response of dissolved carbon and nitrogen concentrations to moderate nutrient additions in a tropical montane forest of South Ecuador. Front. Earth Sci. 4, 58. https://doi.org/10.3389/feart.2016.00058.

Violante, A., Pigna, M., Ricciardella, M., Gianfreda, L., 2002. Adsorption of phosphate on variable charge minerals and soils as affected by organic and inorganic ligands. In: Violante, A., Huang, P.M., Bollag, J.M., Gianfreda, L. (Eds), Developments in soil science 28, Elsevier, 279–295. doi:10.1016/S0166-2481(02)80057-5.

Vitousek, P.M., Farrington, H., 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. Biogeochemistry 37 (1), 63–75. https://doi.org/10.1023/A:1005757218475.

Wassen, M.J., Venterink, H.O., Lapshina, E.D., Tanneberger, F., 2005. Endangered plants persist under phosphorus limitation. Nature 437, 547–550. https://doi.org/10.1038/nature03950.

Werner, F.A., Homeier, J., Oesker, M., Boy, J., 2012. Epiphytic biomass of a tropical montane forest varies with topography. J. Trop. Ecol. 28 (1), 23–31. https://doi.org/10.1017/S0266467411000526.

Wilcke, W., Leimer, S., Peters, T., Emck, P., Rollenbeck, R., Trachte, K., et al., 2013. The nitrogen cycle of tropical montane forest in Ecuador turns inorganic under environmental change. Glob. Biogeochem. Cycles 27, 1194–1204. https://doi.org/10.1002/2012GB004471.

Wilcke, W., Velescu, A., Leimer, S., Bigalke, M., Boy, J., Valarezo, C., 2017. Biological versus geochemical control and environmental change drivers of the base metal budgets of a tropical montane forest in Ecuador during 15 years. Biogeochemistry 136, 167–189. https://doi.org/10.1007/s10533-017-0386-x.

Wilcke, W., Velescu, A., Leimer, S., Bigalke, M., Boy, J., Valarezo, C., 2019. Temporal trends of phosphorus cycling in a tropical montane forest in Ecuador during 14 years. J. Geophys. Res. – Biogeo. 124, 1370–1386. https://doi.org/10.1029/2018JG004942.

Wilcke, W., Velescu, A., Leimer, S., Blotevogel, S., Alvarez, P., Valarezo, C., 2020a. Total organic carbon concentrations in ecosystem solutions of a remote tropical montane forest respond to global environmental change. Glob. Chang. Biol. 26, 6989–7005. https://doi.org/10.1111/gcb.15351.

Wilcke, W., Velescu, A., Leimer, S., Valarezo, C., 2020. Water and nutrient budgets of organic layers and mineral topsoils under tropical montane forest in Ecuador in response to 15 years of environmental change. In: Levia, D.F., Carlyle-Moses, D.E., Shin'ichi, I., Michalzik, B., Nanko, K., Tischer, A. (Eds.): Forest-Water Interactions. Ecological Studies 240, Springer Nature, Basel, Switzerland, 565–586, doi:10.1007/978-3-030-26086-6_23.

Wright, S.J., Turner, B.L., Yavitt, J.B., Harms, K.E., Kaspari, M., Tanner, E.V., et al., 2018. Plant responses to fertilization experiments in lowland, species-rich, tropical forests. Ecology 99 (5), 1129–1138. https://doi.org/10.1002/ecy.2193.

Wright, S.J., 2019. Plant responses to nutrient addition experiments conducted in tropical forests. Ecol. Monogr. 89 (4), e01382. https://doi.org/10.1002/ecm.1382.

Wullaert, H., Bigalke, M., Homeier, J., Cumbicus, N., Valarezo, C., Wilcke, W., 2013. Short-term response of the Ca cycle of a montane forest in Ecuador to low experimental $CaCl_2$ additions. J. Plant Nutr. Soil Sci. 176 (6), 892–903. https://doi.org/10.1002/jpln.201300146.

Wullaert, H., Homeier, J., Valarezo, C., Wilcke, W., 2010. Response of the N and P cycles of an old-growth montane forest in Ecuador to experimental low-level N and P amendments. Forest Ecol. Manag. 260 (9), 1434–1445. https://doi.org/10.1016/j.foreco.2010.07.021.

Yanai, R.D., Vadeboncoeur, M.A., Hamburg, S.P., Arthur, M.A., Fuss, C.B., Groffman, P. M., Siccama, T.G., Driscoll, C.T., 2013. From missing source to missing sink: long-term changes in the nitrogen budget of a northern hardwood forest. Environ. Sci. Technol. 47 (20), 11440–11448. https://doi.org/10.1021/es4025723.

Yuan, Z.Y., Chen, H.Y.H., 2012. A global analysis of fine root production as affected by soil nitrogen and phosphorus. Proc. R. Soc. Lond. B Biol. Sci. 279, 3796–3802. https://doi.org/10.1098/rspb.2012.0955.