# Chapter 23
# Water and Nutrient Budgets of Organic Layers and Mineral Topsoils Under Tropical Montane Forest in Ecuador in Response to 15 Years of Environmental Change

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## 23.1 Introduction

The Andean tropical montane rain forest in the Ecuadorian Province of Zamora-Chinchipe on the western rim of the Amazon basin is shielded by the Andean cordillera from westerly winds during most of the time. As a consequence, westerly winds, potentially carrying polluted air from the coastal and inner Andean regions of Ecuador where most of the Ecuadorian population lives, rarely reach the east-exposed slope of the east Andean cordillera. However, westerly winds contributed to N deposition on the eastern slope of the east cordillera, where they blow during up to 40% of the time during October to December but <10% in the other months (Wilcke et al. 2013b). Westerly winds did not carry base metals (Wilcke et al. 2001; Boy and Wilcke 2008). Downwind of the dominating northeasterly trade winds to the east, the next big city is Manaus in Brazil at an aerial distance of ca. 2100 km. Although there is some local smallholder agriculture (Peters et al. 2013), it can be argued that the Ecuadorian montane rain forest on the eastern slope of the east Andean cordillera between ca. 1850 and 2200 m above sea level (a.s.l.) is still a remote ecosystem and therefore a suitable monitoring site for global change effects with minor local influence. Among the global change effects, changes in water-forest interactions and nutrient deposition with rainfall play a pivotal role for the response of the few remaining native Andean tropical montane forests.

In the north Andes, several simultaneously occurring environmental changes have been observed. For the eastern part of the north Andes, a warmer climate and

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locally variable positive and negative changes of rainfall have been predicted by model projections (Vuille et al. 2003; Urrutia and Vuille 2009). The evaluation of the available climate data of the past four decades confirmed the predicted increasing temperatures. For the city of Loja in south Ecuador an increase rate of 0.13 °C per decade was estimated (Peters et al. 2013). Moreover, Wilcke et al. (2013b) reported for the period from 1998 to 2010 an increasingly dry microclimate for the Ecuadorian tropical montane forest on the Amazon-exposed slope of the Andes, because of changing temporal rainfall distribution, while total annual rainfall did not change. Changing rainfall intensity and temporal distribution might influence nutrient cycling in the Andean forests by their impact on nutrient leaching from the canopy and thus nutrient input into the soil and by their influence on soil water fluxes. Increasing dry spells result in drier soil conditions as reflected by decreasing times of waterlogging (Wilcke et al. 2013a).

Furthermore, N deposition increases strongly in the tropical montane forests of Ecuador (Wilcke et al. 2013b), possibly shifting the Andean forest from current N and P co-limitation to pure P limitation (Homeier et al. 2012; Velescu et al. 2016). Boy et al. (2008a) additionally observed seasonal acid deposition originating from Amazonian forest fires, which was associated with a significantly elevated N and Mn deposition. Besides the increasing N and the seasonal acid deposition, episodic alkaline dust deposition, likely related with long-range Sahara dust transport during strong La Niña conditions, reaches the tropical montane forests in Ecuador (Boy and Wilcke 2008; Wilcke et al. 2013a). Changing soil acidity is an important driver of nutrient availability, because in the acid soils of the Andean tropical montane forests, increasing pH improves living conditions for microorganisms (Pepper et al. 2015) and therefore might also accelerate microbial nutrient release including P from organic matter by mineralization.

The soils of the tropical Andes are little developed and therefore shallow and rich in stones (Frei 1958; Schrumpf et al. 2001). The mineralogy reflects their young age with moderate Fe and Al concentrations and the presence of primary minerals such as mica, illites, and three-layer clay minerals (Schrumpf et al. 2001). In the absence of carbonate minerals, the soils are usually acid and thus the effective cation-exchange capacity and base saturation are low (Wilcke et al. 2017). Consequently, the nutrient supply in forests on these acid young soils strongly depends on mineralization of the thick organic layers (Grubb 1995; Wilcke et al. 2002; Dietrich et al. 2017). Thick organic layers are typical for tropical montane forests and frequently host a large part of the plant roots (Tanner et al. 1998; Wilcke et al. 2002; Soethe et al. 2006). In the humid tropical montane forests, soil organic matter mineralization is limited by episodic waterlogging contributing to the accumulation of thick organic layers (Schuur and Matson 2001; Roman et al. 2010). The increasingly drier soil conditions in response to the increasing temperatures and changing rainfall might therefore further enhance organic matter mineralization.

Nitrogen and P co-limitation is common in the forests at the rim of the Amazon basin in Ecuador and Peru (Homeier et al. 2012; Fisher et al. 2013; Velescu et al. 2016). In a fertilizer experiment, Wullaert et al. (2010, 2013) reported that N, P, and Ca added to a tropical montane forest in Ecuador on the eastern slope of the Andes at 2000–2150 m a.s.l. remained in the ecosystem and were used by the aboveground organism community. In the same forest, Wilcke et al. (2017) found that the base metal cycling (K, Ca, Mg) was strongly biotically controlled with little losses from a small water catchment. Consequently, it can be expected that deposited nutrients remain to a large part in the ecosystem and change the nutrient supply of the biota. Changing nutrient supply, particularly of N and P, might have detrimental effects on the biodiversity of the humid Andean tropical montane forests in Ecuador (Sala et al. 2000; Wassen et al. 2005), which belong to the few mega hotspots of biodiversity in the world (Barthlott et al. 2007).

Because of their immediate response to environmental changes, the aqueous ecosystem fluxes serve as early indicator of a shifting ecosystem state (Bormann and Likens 1967; Bruijnzeel 1991; Likens 2013). Consequently, budgets of whole ecosystems or ecosystem compartments such as the organic layer and the uppermost part of the mineral soil of tropical montane rain forests, where almost all roots are located (Soethe et al. 2006) and where the microbial activity is elevated, might inform about ongoing changes.

Our objective was to detect possible trends of changes in the nutrient status of a humid tropical montane rain forest on the eastern slope of the east Andean cordillera at 1850–2200 m a.s.l. in response to forest-water interaction. Therefore, we quantified the budgets of the organic layer and the uppermost 30 cm of the mineral soil, by determining all aqueous fluxes (throughfall, stemflow, litter leachate, stream flow) of macronutrients (N, P, K, Ca, Mg, S) during 15 years of naturally observed nutrient deposition and climate warming. We furthermore calculated hypothetical accumulation and depletion times of the current nutrient storages neglecting any potential changes in litterfall quantity and quality and the rate of mixing of the organic layer and the mineral soil by faunal activity. We hypothesized that (i) the increasing N deposition results in the accumulation of N in the organic layer and the mineral topsoil via N uptake by the vegetation and recycling to the soil with litterfall, (ii) the low mobility of P in soils and increasing P retention by the biota community of the ecosystem in response to increasingly stronger P limitation result in P accumulation in the organic layer and the mineral soil, (iii) the seasonal acid deposition accelerates the leaching of base metals from the organic layer and mineral topsoil particularly of K, and (iv) the increasingly dry soil conditions favor organic matter mineralization and thus S is released and leached from the organic layer and also not retained in the mineral soil because of the low anion-exchange capacity.

## 23.2 Study Site and Methods

We studied a 30–50° steep ca. 9.1 ha large microcatchment under old-growth montane rain forest between 1850 and 2200 m a.s.l. (Wilcke et al. 2001; Boy et al. 2008b). Soils are mainly shallow Dystric Cambisols developed from metamorphic rock (phyllites and metasandstones) (IUSS Working Group WRB 2014). The studied forest can be classified as “bosque siempreverde montaño” (evergreen montane forest, Balslev and Øllgaard 2002) or as lower montane forest (Bruijnzeel and Hamilton 2000). More information on the composition of the forest can be found in the work of Homeier (2004). Mean annual temperature was 14.9 °C (Wilcke et al. 2013b, 2017).

We sampled the Oi, Oe, Oa, A, and B horizons of 29 soil profiles. The studied profiles comprise nine soils at midslope position and ten soils along each of two transects near the stream and near the ridge, respectively, covering the whole extension of the study catchment. Samples were taken from the walls of soil pits and air-dried. The organic layer samples were ground with a ball mill and the mineral soil was sieved to < 2 mm. Aliquots of the sieved mineral soil samples were also ground with a ball mill for elemental analysis and total digestions. Organic horizons were separated from the underlying mineral soil at the point where there was an abrupt increase in density from about 0.1 to 0.2 g $cm^{-3}$ in the organic layer to > 1 g $cm^{-3}$ in the mineral soil. All samples were stored in closed plastic bags at room temperature until analysis. All soil samples were collected in the year 1998 at the beginning of our observation period.

To determine the bulk density of the organic horizons, we extracted organic layer samples with a metal frame (0.2 m × 0.2 m). The organic layers were separated into Oi, Oe, and Oa horizons. The Oi horizon consists of fresh, little fragmented litter, the Oe horizon contains litter fragments and many visible fungi hyphens, and the Oa horizon consists of amorphous organic matter at an advanced stage of decomposition. The volumes of the horizons were calculated by multiplying the surface area of the metal frame by the thickness of the horizon. The samples were dried to constant mass at 40 °C in an oven. We determined the bulk density at ten randomly selected profiles and used the mean density of the Oi, Oe, and Oa horizons for the calculation of the element storages in the organic layer, because of the difficulty to obtain precise measurement values at individual sites as a consequence of disturbances by larger roots and stones. In the mineral soil, we determined the bulk density at each of the 29 study sites with the help of stainless steel cylinders with a volume of 100 $cm^3$, which were driven laterally into the horizons from the wall of the pits.

We used a frequency domain reflectometry (FDR) probe to measure soil water contents in the organic layer and data were recorded hourly with a data logger. Incident precipitation was collected weekly at 2–4 gauging stations, each consisting of five Hellmann-type collectors placed in clear-cut areas. To determine internal element cycling in the forest, we set up three ca. 20 m-long measurement transects (aligned downhill), covering about 10 m in elevation, on the lower to midslope (starting at 1900, 1950, and 2000 m a.s.l., respectively). This geomorphic form represented the largest part of the catchment. The elevational gradient covered was a compromise between reasonable accessibility and representativeness of the ca. 200 m gradient of the whole catchment. At each measurement transect, we collected throughfall with 5–20 fixed-positioned funnel collectors; we started with 5 collectors in 1998 and increased the number of collectors to 8 in 2000 and to 20 in 2002. Furthermore, we collected litter leachate (three zero-tension lysimeters made of plastic boxes with a polyethylene net as collecting surface area of 0.15 m × 0.15 m, installed below the organic layer) and fine litterfall (three litter traps, 0.3 m × 0.3 m from April 1998 to October 2005 and 0.5 m × 0.5 m thereafter). Stemflow was collected with polyurethane collars at five trees. Details of tree species and properties are summarized in Fleischbein et al. (2005). Stream water was sampled above a weir, which was used to gauge stream flow

(Fleischbein et al. 2006; Boy et al. 2008b). Water level at the weir was measured hourly with a pressure transducer in the first five years, although there were several and partly longer periods when the pressure transducer did not work properly (Fleischbein et al. 2006). After 2003, water levels were recorded weekly by manual measurement.

All ecosystem solution samples were collected in weekly resolution between April 1998 and March 2013. Rainfall, throughfall, and stemflow volumes were measured with a graduated cylinder in the field. After volume measurement, the samples of the replicate collectors of each ecosystem solution type at each measurement station/transect were bulked to result in one composite volume-weighted sample per collection date, ecosystem solution type, and measurement station/transect. Litter leachates were directly bulked into one collection vessel per measurement transect to yield one individual sample per measurement site and collecting date, because zero-tension lysimeters do not collect water quantitatively (Jemison and Fox 1992). Litterfall was combined to one sample per measurement transect and sampling date and air-dried. Our hydrological year lasted from 01 April to 31 March of the following year because the experiment was established in March 1998.

The weekly litterfall samples were ground with a ball mill and composited to monthly samples. The ground litterfall and organic layer samples were digested in 8 mL concentrated $HNO_3$ and 2 mL $H_2O_2$ in a microwave oven. Ground mineral soil samples were digested with concentrated $H_2O_2$, HF, and $HNO_3$ in open Teflon vessels on a sand bath until dryness and redissolved in 5 M $HNO_3$.

We determined total N concentrations in ground litterfall, organic layer, and mineral soil samples with an elemental analyzer (EA). In the filtered 100 mL aliquots of ecosystem fluxes (pore size 4–7 μm, folded filter type 392), we determined total concentrations of N after oxidation by UV digestion with $K_2S_2O_8$ and P (in the last 10 years of the observation period) after digestion with $H_2SO_4$ with colorimetric methods in a continuous flow analyzer (CFA). Concentrations of Ca, K, and Mg in ecosystem solutions and litterfall, organic layer, and mineral soil digests were determined with a flame atomic absorption spectrometer (AAS) and those of S and P (in the digests and years 2–5 of the observation period) with an inductively coupled plasma-optical emission spectrometer (ICP-OES). Measurements of N and P were only conducted from the second year on (i.e., for the period 1999–2013) and those of S in years 1–8 (i.e., for the period 1998–2006).

For annual flux and budget calculations, weekly data of the aqueous nutrient fluxes were aggregated to monthly values to reduce the influence of outliers and the number of missing values. Monthly mean concentrations were calculated by arithmetically averaging weekly concentrations. Monthly fluxes were calculated by multiplying monthly mean concentrations with monthly water fluxes.

For the first five years (1998–2003), water fluxes through the organic layer (litter leachate) were calculated with a one-dimensional soil water budget model and taken from Boy et al. (2008b). For the later years (2004–2013), weekly litter leachate was calculated via a regression of throughfall on the modeled water fluxes of the first five observation years ($R^2 = 0.85$). In the first five years (1998–2003) we used a modeled streamflow taken from Fleischbein et al. (2006) and Boy et al. (2008b). For the later years (2004–2013) we used weekly measurements and assumed that the water level was constant during the measurement week.

The organic layer budget was calculated as the difference between the aqueous soil input (i.e., throughfall+stemflow) and the aqueous organic layer output (litter leachate) assuming that the organic layer was in steady state with respect to litterfall quantity and quality and mixing into the mineral soil. The budget of the uppermost 30 cm of the mineral soil was calculated as the difference between litter leachate and the stream flow, neglecting a possible retention of nutrients infiltrated with litter leachate by the deeper subsoil (below 30 cm) and the input of P, K, Ca, and Mg by weathering. The accumulation and depletion times were calculated by dividing the storages in the organic layer or the uppermost 30 cm of the mineral soils (element concentrations x volume x bulk density) by the mean annual budget.

The monthly time series data sets were tested for significant temporal trends with the seasonal Mann-Kendall test (Hirsch et al. 1982) as implemented in the function *SeasonalMannKendall()* from the package *Kendall* (McLeod 2011) in the statistical software R (R Core Team 2017). The seasonal Mann-Kendall test is a nonparametric trend test considering the most important autocorrelation (i.e., seasonal) which we detected. The test is not sensitive to a small number of outliers. The application of the test does not necessarily require a linear trend (Helsel and Hirsch 2002). To test, if the organic layer and mineral soil budgets of N, P, K, Ca, Mg, and S significantly differ from zero, we used a one-sample t-test as implemented in the R function *t.test ()* (R Core Team 2017). Temporal trends of the annual budget were tested with the function *zyp.trend.dataframe()* from the package *zyp()*, which uses prewhitening to account for serial correlation (Bronaugh and Werner 2015).

## 23.3 Results

From 1998 to 2013, the mean annual incident precipitation was 2320 mm ± 238 mm standard deviation of the 15 hydrological years, of which 1390 ± 199 mm reached the soil as throughfall and 30.8 ± 7.02 mm as stemflow. Of the 1420 ± 200 mm reaching the forest floor, 1160 ± 194 mm infiltrated the mineral soil as litter leachate, implying that 264 ± 114 mm were lost from the organic layer via evapotranspiration. Finally, 1060 ± 156 mm reached the stream resulting in an additional evapotranspiration loss of 100 ± 210 mm from the mineral soil (Wilcke et al. 2017). Mean annual litterfall from 1998 to 2013 was 1040 ± 115 g $m^{-2}$.

The organic layer had a mean thickness of 13.3 ± 6.85 cm ($n = 29$) and the mineral soil of 60.5 ± 18.8 cm (as far as it could be dug with a hand spade). The uppermost 30 cm of the mineral soil contained consistently more nutrients than the organic layer (Table 23.1). The nutrient storage of the organic layer accounted for 1.89 (K) to 44.4% (Ca) of the total nutrient storage in the organic layer and the uppermost 30 cm of the mineral soil.

To determine the total nutrient input to the soil via aqueous solutions, we summed the fluxes with throughfall and stemflow. The N and P fluxes in throughfall +stemflow increased significantly from 1999 to 2013 (Fig. 23.1a, b) and the S fluxes in throughfall+stemflow from 1998 to 2006 ($\tau = 0.207$, $p = 0.027$). In contrast, the

**Table 23.1** Mean storage of macronutrients in the organic layer and the uppermost 30 cm of the mineral soil in a ca. 9-ha microcatchment under tropical montane forest in Ecuador (±standard deviation, $n = 29$ soils)

| Nutrient | Organic layer | Contribution of organic layer | Uppermost 30 cm of the mineral soil |
|---|---|---|---|
| | g m$^{-2}$ | % | g m$^{-2}$ |
| N | 478 ± 283 | 42.4 ± 19.4 | 726 ± 610 |
| P | 20.3 ± 10.7 | 14.4 ± 7.41 | 131 ± 50.9 |
| K | 75.7 ± 51.2 | 1.89 ± 1.30 | 4450 ± 1720 |
| Ca | 112 ± 93.0 | 44.4 ± 16.1 | 144 ± 189 |
| Mg | 36.0 ± 23.7 | 16.1 ± 8.93 | 197 ± 92.5 |
| S | 53.3 ± 31.7 | 38.9 ± 16.2 | 81.6 ± 37.5 |

Ca fluxes with throughfall+stemflow decreased significantly (Fig. 23.1c). The K and Mg fluxes with throughfall+stemflow did not change significantly from 1998 to 2013.

On average of the 14 and 15 budgeted years, respectively, P and K accumulated significantly in the organic layer, while all other macronutrients were on average significantly leached from the organic layer ($p \leq 0.017$; Fig. 23.2). In the uppermost 30 cm of the mineral soil, all elements accumulated significantly on average of the 8 (S), 14 (N, P), or 15 (all other elements) budgeted years ($p < 0.001$).

Except for N, all element budgets showed significant temporal trends. The P (14 years) and K (15 years) budgets of the organic layer increased significantly, while those of the uppermost 30 cm of the mineral soil decreased (Fig. 23.2, inlets). The same was true for S, which was only measured during 8 years (organic layer: $\tau = 0.714, p = 0.035$; mineral soil: $\tau = -0.714, p = 0.035$). The Ca and Mg budgets showed the reverse temporal trends, i.e., negative ones in the organic layer (Ca: $\tau = -0.670$, $p = 0.001$; Mg: $\tau = -0.670$, $p = 0.001$) and positive ones in the mineral soil (Ca: $\tau = 0.538$, $p = 0.009$; Mg: $\tau = 0.780$, $p < 0.001$).

Under the current conditions, the K and P inputs would double the organic layer P and K storages in 197 and 27 years, respectively (Fig. 23.3). In contrast, the loss of N, Ca, Mg, and S could cause a depletion of the organic layer storages in 38 (Mg) to 281 years (N). In the mineral soil, all macronutrients accumulated on average at a rate which would double their current storages in the 0–30 cm layer in 57 (Ca) to 601 years (P, Fig. 23.3).

## 23.4 Discussion

The hydrological budget of the studied forest is characterized by a high annual interception loss of 587–1190 mm representing 28–50% (mean 39%) of rainfall in the 15 study years, which is at the upper end of the range reported for tropical montane rain forests with little fog influence by Bruijnzeel et al. (2011). The stemflow only accounted for 1.3 ± 0.32% of the rainfall, which was at the lower

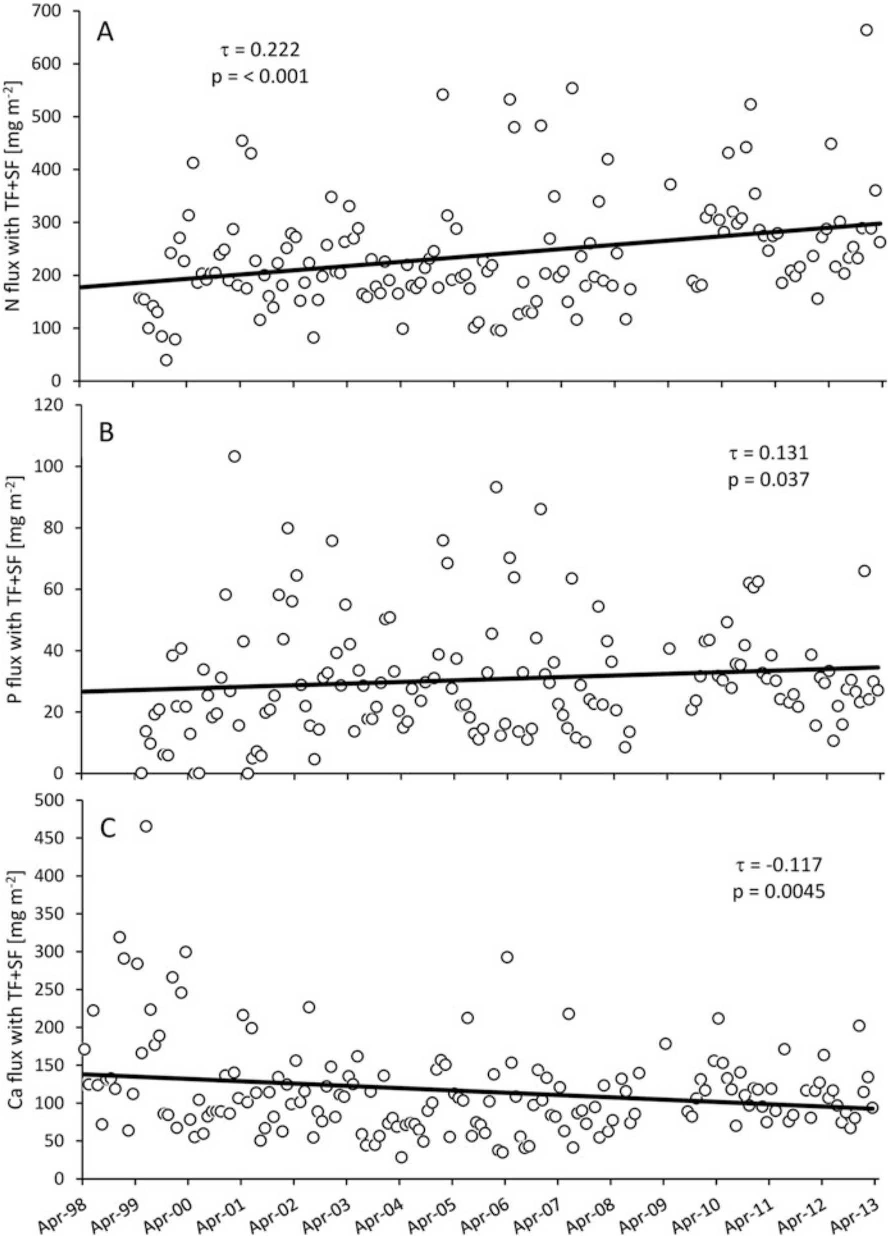

**Fig. 23.1** Temporal course of the fluxes of (**a**) N, (**b**) P, and (**c**) Ca with throughfall (TF)+stemflow (SF) from April 1998 to March 2013. The measurement of N and P started only in April 1999. Temporal trends of monthly data were statistically evaluated with the seasonal Mann-Kendall test (Hirsch et al. 1982). Regression lines are shown to illustrate significant trends but do not necessarily imply that the trend is linear

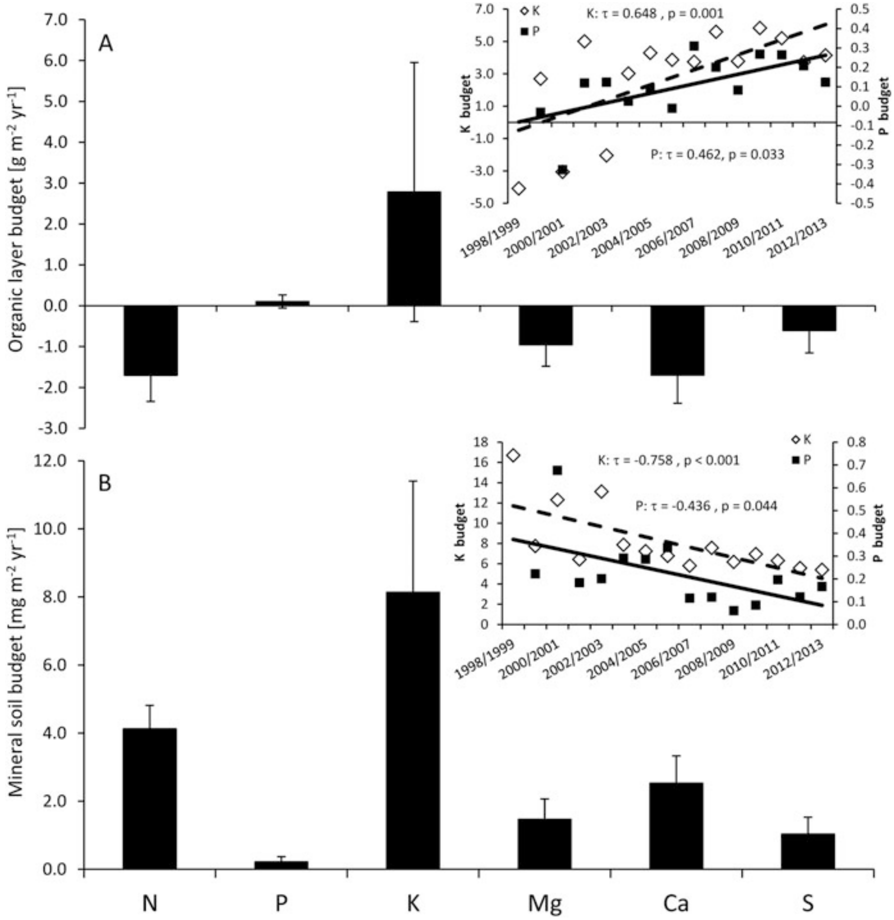

**Fig. 23.2** Mean budgets of the aqueous nutrient fluxes through (**a**) the organic layer and (**b**) the uppermost 30 cm of the mineral soil from 1998 to 2013. Negative values indicate net losses, positive ones net accumulations. Whiskers indicate standard deviations ($n = 14$ years for N and P; $n = 15$ years for K, Mg, and Ca; and $n = 8$ years for S). Mean values were significantly different from zero according to one-sample t-tests. The inlet figures show the relationships between the sampling year and (**a**) the K and P budgets of the organic layer and (**b**) the K and P budgets of the uppermost 30 cm of the mineral soil from 1998 to 2013. The units of the $y$-axes in the inlet figures are the same as of the main figures. Temporal trends of monthly data were statistically evaluated with the Mann-Kendall test (Bronaugh and Werner 2015). Regression lines are shown to illustrate significant trends but do not necessarily imply that the trend is linear

end of the range of 0.1–8.8% in Bruijnzeel et al. (2011). The annual runoff coefficient (i.e., the ratio of streamflow to rainfall) varied from 0.38 to 0.58 resulting in an evapotranspiration of 42–62% of the rainfall, which is at the lower end of the range of lower montane rain forests with little influence of fog of 50–72% (mean 62% calculated from Table V in Bruijnzeel et al. 2011). The higher water flow below

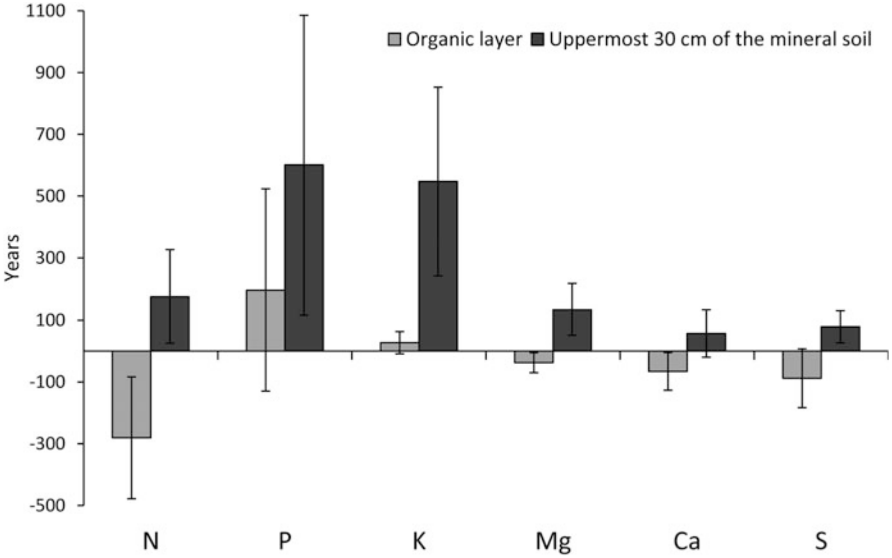

**Fig. 23.3** Time needed to double (if positive) or entirely deplete (if negative) the nutrient storage in the organic layer or uppermost 30 cm of the mineral soil considering only the mean aqueous element fluxes from 1998 to 2013 (assuming that litterfall input, organic matter decomposition, and mixing of the organic layer with the mineral soil were and remain at steady state and that erosion and soil water fluxes do not change). The error bars show standard deviations calculated considering error propagation

the organic layer (litter leachate) than streamflow suggested that the vegetation took up some of its transpiration water from the mineral soil, while we considered direct evaporation from the soil as negligible (Wilcke et al. 2017). Because there were only few roots deeper than 30 cm in the mineral soil, we assume that further water loss by plant water uptake between the 0–30 cm layer and the stream is negligible and therefore used the streamflow as water flow out of the 0–30 cm layer.

Wilcke et al. (2013b) reported a significant decrease in throughfall from 1998 to 2010 in our study catchment. Because rainfall did not change significantly in the study of Wilcke et al. (2013b), interception loss (in % of rainfall) increased significantly. The same authors reported furthermore that the relative air humidity in our study forest significantly decreased during 1998–2010. Reduced humidity could be driven by the temperature increases predicted by Vuille et al. (2003) and Urrutia and Vuille (2009) which was confirmed for the greater study area with the help of a time series since 1964 (Peters et al. 2013). The generally increasing temperatures created an increasing evaporative demand, which was further enhanced by the fact that monthly hours of extreme temperatures >25 °C increased significantly during 1998–2010 (Wilcke et al. 2013b). Moreover, Peters et al. (2013) observed an increasing number of dry periods lasting for 4–14 days from 1998 to 2010, during which evapotranspiration was pronounced.

In response to the increasingly drier microclimatic conditions, Wilcke et al. (2013b) observed significantly decreasing water contents in the Oa horizon of the organic layer at 1900 m a.s.l. during 2000–2007 and during 2007–2010 at another measurement station at 2070 m a.s.l. However, the trend of the record from 2007–2010 was not significant, possibly because of its short duration. These findings are corroborated by the report of Wilcke et al. (2013a) that the frequency of waterlogged conditions decreased during 1998–2010 in the study catchment. Wilcke et al. (2013a) recorded soil matric potentials at the 0.15 and 0.30 m mineral soil depths at measurement stations in central position of each of the three measurement transects in the study catchment with manually read tensiometers. Reduced waterlogging could potentially increase the time period during which favorable conditions for mineralization of soil organic matter prevailed and thus increase the release of organically bound N, P, and S.

The annual litterfall was greater than that reported in two other studies on north Andean montane forests (Steinhardt 1979; Veneklaas 1991) and at the upper end of the range for various tropical montane forests globally (50–1100 g m$^{-2}$ year$^{-1}$, Bruijnzeel and Proctor 1995). The forest produced as much biomass as found in tropical lowland forests (750–1330 g m$^{-2}$ year$^{-1}$; Proctor 1987) and therefore belongs to the more productive tropical montane forests.

The organic layers in the study catchment stored substantially more macronutrients than those in temperate forests from North America and Europe in the "Integrated Forest Study" (Johnson and Lindberg 1992) where the nutrient storage was on average (with ranges) 92 g m$^{-2}$ (2.8–264, N), 6.7 g m$^{-2}$ (0.3–21.3, P), 7.8 g m$^{-2}$ (0.4–19.8, K), 23 g m$^{-2}$ (0.9–66.6, Ca), 4.0 g m$^{-2}$ (0.1–8.8, Mg), and 8.5 g m$^{-2}$ (0.3–29.2, S, compare with Table 23.1). The N and P storages of the organic layer at our study site surpassed those reported by Vogt et al. (1986) for the whole organic layer in evergreen tropical broadleaf forests presumably at tropical lowland locations of 32 ± 10 g m$^{-2}$ (N) and 8.1 ± 2.3 g m$^{-2}$ (P). This underlines the strong accumulation of organic matter in tropical montane forests, mainly because of the wet conditions, which hamper organic matter mineralization in spite of the high mean annual temperature of ca. 15 °C at 1950 m a.s.l. (Rollenbeck et al. 2015) and the lack of a frost period (Schuur and Matson 2001; Roman et al. 2010).

Nitrogen storages in the uppermost 30 cm of the mineral soils at our study site fell in the range of those reported for various soil types of the Amazon of 210–1370 g m$^{-2}$ (Batjes and Dijkshoorn 1999) and of Central and Eastern Europe of 210–1520 g m$^{-2}$ (Batjes 2002; Table 23.1). Storages of other nutrients in mineral soils have rarely been determined. The only studies from the tropical climate zone with which we could compare our results originated from the Brazilian Cerrado, a savanna ecosystem on strongly weathered Ferralsols. Lilienfein and Wilcke (2003) and Wilcke and Lilienfein (2004) reported for the same non-fertilized native Cerrado soils storages of 350 ± 11 g m$^{-2}$ N, 63 ± 8.3 g m$^{-2}$ P, 8.7 ± 1.5 g m$^{-2}$ (Ca), 37 ± 5.5 g m$^{-2}$ (K), 7.5 ± 1.4 g m$^{-2}$ (Mg), and 53 ± 2.8 g m$^{-2}$ (S). These storages are considerably lower than in our study soils, particularly with respect to the base metals (K, Ca, and Mg, compare with Table 23.1). The reason is the young age of the soils at our study site associated with a low degree of weathering.

Thus, the studied tropical montane forest harbors high nutrient storages in the organic layer and the mineral topsoil, which, however, are only to a limited degree bioavailable. Wilcke et al. (2002) reported turnover times of the organic layer ranging 15–18 years (N), 12–16 years (P), 6.6–20 years (K), 5.2–10 years (Ca), 4.5–7.8 years (Mg), and 15–20 years (S) for our study area. This illustrates that particularly the elements mainly released by organic matter mineralization, i.e., N, P, and S, become only bioavailable at the decadal scale. For P, Dietrich et al. (2016) reported that on average 13% of the total P concentrations in the mineral soil were extractable with the Bray method ($HCl+NH_4F$; Bray and Kurtz 1945) thought to represent bioavailable P at a study site next to our study catchment. In the mineral topsoil, the directly bioavailable exchangeable base metal concentrations account for only 0.37 ± 0.24% (K), 8.3 ± 6.4% (Ca), and 3.9 ± 4.1% (Mg) of the total storage of these elements (Wilcke et al. 2017). Thus, the by far largest part of the base metal storage is contained in minerals, which become bioaccessible in the long term only via weathering. Weathering rates of the studied macronutrients were generally low (Boy et al. 2008b; Wilcke et al. 2017, 2019). These studies reported weathering rates of 79 ± 63 g $m^{-2}$ $year^{-1}$ for P, 0.71 ± 0.77 g $m^{-2}$ $year^{-1}$ for K, 0.14 ± 0.24 g $m^{-2}$ $year^{-1}$ for Ca, 0.33 ± 0.22 g $m^{-2}$ $year^{-1}$ for Mg, and 0.04 g $m^{-2}$ $year^{-1}$ for S. The weathering rates of P, K, Ca, and Mg were estimated with three different methods and the standard deviation was calculated from the results of these methods (see the freely accessible supplementary materials of Wilcke et al. (2017) for a detailed description of the methods). The weathering rate of S was estimated as the sum of the S export with stream water during super dry and baseflow conditions as defined in Boy et al. (2008b).

Although the uppermost mineral soil stored 56–98% of the total nutrients in the root zone, which is more than in the organic layer (Table 23.1), the latter contained with 51% (at 1900 m a.s.l.) to 61% (at 2400 m a.s.l.) the higher root length density (Soethe et al. 2006). Bruijnzeel and Veneklaas (1998) speculated about a role of Al toxicity in the mineral soil in reducing root growth and contributing to the low biomass productivity of tropical montane forests with their increasingly stunted tree growth with increasing elevation. However, in spite of the acid character of the soil (mean pH of 4.3 in the organic layer and of 4.4 in the A horizons; Wilcke et al. 2017), there were hardly any indications of Al toxicity in our study forest, particularly because of the high degree of organo-complexation of Al (Rehmus et al. 2014, 2015, 2017). Therefore, there are no indications that the reason for the lower root length in the mineral soil than in the organic layer was Al toxicity. The root length density might instead be driven by the availability of the main limiting nutrients N and P, which is higher in the organic layer than in the mineral soil. Possibly, the temporally high soil moisture might also have contributed to reduce root penetration into the mineral soil.

The increasing N fluxes with throughfall+stemflow (Fig. 23.2a) parallel similar increases in N deposition with rainfall (Wilcke et al. 2013b). Boy et al. (2008a) identified Amazonian forest fires as a major source of N deposition to our study forest. Boy et al. (2008a) used two different indices of forest fire intensity in Amazonia, a fire pixel count along the wind pathways based on satellite imagery and an integrative satellite-based index of the NO concentrations above our study area to distinguish between “fire” and “no fire” periods. They found significantly increased N concentrations in rainfall during “fire” periods relative to “no fire” periods. The N concentrations in rainfall were not or only weakly correlated with rainfall volume, indicating that the variations in concentrations could not be explained by concentration/dilution effects. Because the “fire conditions” were drier (5-year mean weekly rainfall of 34–41 mm in the study) than the “no fire” conditions (5-year mean weekly rainfall of 62–63 mm), the N deposition with rainfall was not different between the “fire” and “no fire” periods in spite of the higher N concentration in rainfall during the former than the latter periods. However, the drier conditions during “fire” periods also resulted in significantly higher dry deposition of elements related with biomass burning. Consequently, total deposition of N was higher during the “fire” than the “no fire” periods. Total P deposition also tended to be higher during “fire” than “no fire” periods, although differences were not significant. In line with our findings, the release of N and P during biomass burning in Amazonia was reported in a range of publications (Williams et al. 1997; Artaxo et al. 2002; Mahowald et al. 2005; Hoffer et al. 2006). Thus, biomass burning in Amazonia is a major driver of element deposition even to distant montane forest at the outer rim of Amazonia, such as our study site. Biomass burning intensity is linked to the El Niño-Southern Oscillation (ENSO) (e.g., Alencar et al. 2006; van der Werf et al. 2006). Thus, a proposed frequency shift of future ENSO as a consequence of global warming (Timmermann et al. 1999) as well as increased biomass burning because of growing interest in soybean cropping in the Amazon basin (Arima et al. 2017) suggests rising deposition rates of aerosols related with biomass burning to our study site in the future.

The increasing P fluxes with throughfall+stemflow reflect the accumulation of deposited P in the biological part of the study catchment and indicate that the bioavailability of P increased (Fig. 23.2b; Wilcke et al. 2019). However, in the study of Wilcke et al. (2019), the annual increase in the P cycling with throughfall +stemflow was much lower than the annual total deposition of P, which was almost entirely retained in the study catchment. Because the studied forest has reached the mature old-growth stage, there should be no net annual P accretion in wood. This suggests that most of the deposited P retained in the catchment is stored in the soil (Wilcke et al. 2019). Because only a small part of the total soil input of P is leached into the mineral soil, the soil organic layer is likely the most important storage compartment of deposited P in the studied forest (Fig. 23.3; Wilcke et al. 2019). As a consequence, the studied N+P co-limited forest did not only receive a high N deposition but also accumulated P from 1999 to 2013. If the N deposition removes the N limitation in the near future and thus P becomes the only limiting nutrient, P accumulation will increase the risk of P eutrophication with possibly detrimental consequences for the biodiversity of the study forest (Wassen et al. 2005).

The decrease in the Ca input to the soil with throughfall+stemflow is attributable to a particularly strong deposition event of alkaline dust at the beginning of our study period (in the hydrological year 1999/2000 (Fig. 23.2c). Boy and Wilcke (2008) attributed the occasionally observed alkaline dust deposition events, which are rich in Ca and Mg, to Sahara dust transport all the way over the Atlantic Ocean and the

Amazon basin during strong La Niña events. Although the Amazon basin is even wetter during such events, there are dry spells that allow for the transport of Sahara dust without being washed out of the atmosphere before the dust reaches our study site. The 1999/2000 event was particularly strong. Thereafter, we observed only one other strong event in 2010/2011, which was, however, weaker than in 1999/2000.

The increasing S deposition with throughfall+stemflow from 1998 to 2006 was not related with the Amazonian forest fires, because neither rainfall nor dry deposition of S was higher during “fire” than “no fire” periods (Boy et al. 2008a). We speculate that the increasing S return with aqueous solutions from the canopy to the soil, reflects an enhanced S uptake by the vegetation following the improved N and P supply.

The mean accumulation of P in the organic layer can be attributed to the scarcity of this nutrient in the studied forest and indicates strong biological retention (Fig. 23.3; Wilcke et al. 2019). The retention of P in the organic layer increased with time as reflected by the significant positive trend of the P budget (Fig. 23.2a, inlet). This might indicate that P becomes increasingly scarcer relative to N, because of the much higher N than P deposition from the atmosphere.

The accumulation of the highly mobile K in the organic layer is surprising, because under the acid conditions of the soils, K should be strongly leached as a consequence of its low competitiveness for cation-exchange sites. One explanation could be that the plants take up K from the K-rich mineral soil and recycle it to the organic layer to a considerable extent (Jobbagy and Jackson 2001, 2004; Wilcke et al. 2017). Alternatively, K could be accumulated in the organic layer in response to the overall higher nutrient uptake by the biota of the forest ecosystem, because of the improved supply of the two co-limiting elements N and P, which generates an additional demand of all other nutrients, particularly of the third-most needed K (Marschner 2012). The latter assumption is supported by the fact that the K budgets of the organic layer showed a significantly increasing trend (Fig. 23.2a, inlet).

The depletion of N and S from the organic layer likely reflects a higher release by mineralization from the organic matter than is needed by the plants and soil organisms so that the two nutrients are leached (Fig. 23.3). High release rates by organic matter mineralization of 63.5 g $m^{-2}$ $year^{-1}$ of N had already been reported by Wilcke et al. (2002) for our study area, which is much higher than the demand of N of the forest as approximated by the N flux with litterfall (18.7 ± 0.36 g $m^{-2}$ $year^{-1}$). The N richness is also reflected by the strong nitrification in the organic layer identified by Schwarz et al. (2011) with the help of the natural abundance of the stable N isotope ratio in nitrate. Such strong nitrification only occurs if the system is near to N saturation (Aber et al. 1998). As Homeier et al. (2012) reported that there was a N+P limitation of several ecosystem processes, the loss of N from the organic layer is surprising. Perhaps, some part of this N is quickly leached out of the organic layer by stronger rain events and can therefore not be used by the biota community.

The S release of the organic layer was identical to the S flux with litterfall (as proxy of the S demand of the vegetation) of 2.2 ± 0.08 g $m^{-2}$ $year^{-1}$ (Wilcke et al. 2002), making the S losses from the organic layer again unexpected. We speculate that the forest satisfies a part of its S demand directly from the atmospheric deposition so that some of the available S in the organic layer is not needed and can be leached or that some part of the released S in the organic layer is too quickly leached. The positive trend of the S budgets of the organic layer from 1998 to 2006 might indicate that the S supply of the vegetation is tightening so that S is increasingly accumulated in the organic layer.

The losses of Ca and Mg from the organic layer are fully expected because of the acid conditions, which favor the leaching of base metals and the smaller demand of the vegetation of these two elements than of N, P, and K. The negative trends of the Ca and Mg budgets of the organic layer might be attributable to the decreasing pH of the litter leachate from 1998 to 2013 ($\tau = 0.341$, $p < 0.001$).

The accumulation of N in the mineral soil could be attributed to its microbial immobilization, because of the sharp drop of the N concentrations from the litter leachate to the mineral soil solutions (Wilcke et al. 2013b). The accumulation of P in the mineral soil is likely mainly attributable to the sequestration of phosphate by iron (oxy)hydroxides and to the precipitation as Al-phosphates (Hinsinger 2001). The retention of the base metals (K, Ca, Mg) is likely attributable to their affiliation with the cation-exchange sites (Wilcke et al. 2017). For K, sequestration by illites, which occur in the study soils, might play an additional role (Schrumpf et al. 2001). The accumulation of S in the mineral soil can mainly be attributed to the strong retention of S-containing dissolved organic matter, because Goller et al. (2006) reported that at our study site, the contributions of dissolved organic S to the total dissolved S concentrations dropped markedly between the litter leachate (65 ± 17% of total dissolved S) and the mineral soil solution (at 30 cm depth, 18 ± 16%), while the total S concentrations did not change (0.42 ± 0.36 in the litter leachate vs. 0.43 ± 0.07 mg $L^{-1}$ in the mineral soil solution at 30 cm depth). The reason for little changing total S concentrations in the soil solution of the mineral soil relative to the litter leachate and the even higher total S concentrations in the stream flow than in rainfall is the release of $SO_4^{2-}$ by weathering in the subsoil (Goller et al. 2006; Boy et al. 2008b).

The temporal trends of the element budgets of the uppermost 30 cm of the mineral soils had generally the opposite sign than those of the organic layers, i.e., Ca and Mg were increasingly lost from the organic layer but at approximately the same rate increasingly accumulated in the mineral soil from 1998 to 2013, while for P, K, and S the contrary was true. We attribute the finding that P (1999–2013), K (1998–2013), and S (1998–2006) were increasingly less accumulated in the uppermost 30 cm of the mineral soil (Fig. 23.2b, inlet) to the increasing retention of the three nutrients in the organic layer, which resulted in reduced P, K, and S fluxes into the mineral soil. Furthermore, the increasing demand of P, K, and S in response to the high N deposition might also have stimulated the plant pump from the subsoil to the organic layer (Jobbagy and Jackson 2001, 2004). However, when discussing the temporal trend of the nutrient budgets in the organic layer and the mineral soil (Fig. 23.2a and b, inlets), it has to be borne in mind that the litter leachate and streamflow fluxes were differently determined in the early five than in the later ten years. It is therefore possible that at least a part of the apparent trend is attributable to the different determination methods. While there might be a stronger scatter in the first five years than later, we did not observe a sharp change of the slope of the regression lines or breakpoints (Fig. 23.2a and b).

Under the current conditions, the P and K inputs would double the organic layer P and K storages in 197 and 27 years, respectively, resulting in improving P and K bioavailability at the scale of a few decades (K) to a few centuries with unknown implications for the biodiversity of the studied forest, particularly with respect to P (Wassen et al. 2005). In contrast, the loss of N, Ca, Mg, and S could cause a depletion of the organic layer storages in 38 (Mg) to 281 years (N). However, the mean depletion rate of N with 1.7 g $m^{-2}$ $year^{-1}$ from the organic layer is still low relative to the increase of the bulk deposition of N of roughly 5 g $m^{-2}$ $year^{-1}$, which even does not include dry deposition (Wilcke et al. 2013b). The average losses of Ca (1.7 g $m^{-2}$ $year^{-1}$) and of Mg (0.96 g $m^{-2}$ $year^{-1}$) were similar to or even higher than the highest deposition of Ca (1.5 g $m^{-2}$ $year^{-1}$) and Mg (0.66 g $m^{-2}$ $year^{-1}$) with rainfall in the hydrological year 1999/2000. Therefore, it is unlikely that the Ca and Mg losses can be compensated by the occasional alkaline dust inputs. Consequently, these two base metals will become increasingly scarce. However, it has to be borne in mind that our organic layer budgets assume that the litterfall quantity and quality do not change significantly in the coming years, which might, however, not be the case.

The accumulation of all nutrients in the mineral soil would double their storages in the 0–30 cm layer in between 57 (Ca) and 601 years (P), again assuming no other changes such as increased leaching, erosion, or weathering. This illustrates that the nutrients are hardly lost from the whole ecosystem, which is in line with findings of Wullaert et al. (2010) for N and P, Wullaert et al. (2013) for Ca, and Wilcke et al. (2017) for the base metals (K, Ca, Mg). The shift of nutrient storages, particularly of the depleting Ca and Mg, and the already now scarce S from the organic layer into the mineral soil will, however, potentially force the plants to grow more roots into the mineral soil. Because there are indications that the currently low root density in the mineral soil is more driven by the frequent waterlogging than by other constraints including Al toxicity, the increasingly dry soils might remove this obstacle and allow for increased root growth into the mineral soil.

## 23.5 Conclusions

Contrary to our first hypothesis, N was lost from the organic layer and only accumulated in the mineral soil. This illustrated that enhanced mineralization because of the reduced soil moisture overwhelmed the accumulation of N from atmospheric deposition. Therefore, there was a shift of N storages from the organic layer into the less rooted mineral soil.

Our second hypothesis that P accumulates in the organic layer and the mineral soil was confirmed. This accumulation was particularly strong in the organic layer where it increased with time during 1999–2013. The strong retention of accumulated P in the organic layer even reduced the P input into the mineral soil during the observation period.

Surprisingly, K accumulated in the organic layer and the annual organic layer budgets even showed a positive trend in spite of the acidic soils, likely reflecting an increased K need of the biota in response to increasing N and P availability, which resulted in a tightened K cycling between the soil and the vegetation. As expected, Ca and Mg were lost from the organic layer and the budgets (i.e., losses) even increased with time during 1998–2013 in line with the observed acidification of the litter leachates. However, all three base metals accumulated in the acid mineral soil in contrast to Hypothesis iii.

The S budget of the organic layer was negative as hypothesized, although the S release by mineralization just matched the S demand of the vegetation. Thus, the vegetation must have made use of other S sources such as the deposition from the atmosphere or the mineral soil so that some of the released S in the organic layer could be leached.

Our results demonstrate that the current environmental changes enhance the internal N, P, and S cycling in the ecosystem as reflected by increasing fluxes of these nutrients with throughfall+stemflow. The enhanced N and P cycling improves the short-term availability of these two most limiting nutrients. However, the accumulation of N via deposition is stronger than that of P, possibly shifting the ecosystem from the current N+P co-limitation to pure P limitation.

Our results demonstrate that the soils of the studied tropical montane forest in Ecuador respond rapidly to the changing climate, hydrological cycle, and matter deposition, which in the long run might drive the studied remote native forest ecosystem to a new state. This new state might involve a reduced species richness, which is commonly expected in response to fertilization.

## 23.6 Future Directions

Our results illustrate how important long-term observations of the effects of water-forest interactions on the nutrient status of remote native forests are. Only at least decade-long observations can reveal trends in nutrient cycling in response to environmental change. Once such trends have been identified, their reasons can be explored by targeted experiments such as nutrient additions to simulate atmospheric deposition, litterfall manipulations to simulate changing biomass productivity, or temperature and moisture manipulations to account for climate warming. As native forest ecosystems are usually well buffered, such ecosystem manipulations must again be run for longer periods of at least a decade.

The currently observed biogeochemical changes in tropical montane forests might be detrimental for the high biodiversity existing in these forests. Therefore, in addition to the observation of water and nutrient cycles, the species composition, growth responses, and rejuvenation of individual species to the changing conditions need to be monitored and linked with specific changes by targeted manipulative experiments.

We observed indications of changing soil organic mineralization rates in response to increasingly reduced waterlogging of the soils. Increasing organic matter mineralization is also associated with the release of $CO_2$. An open question to be addressed in the future will therefore be whether the tropical montane forests with their particularly high C storages in the soil organic layer and mineral topsoil might become a future $CO_2$ source with negative feedback on climate change.

Finally, the current frequent replacement of the native tropical montane forest by pastures causes the complete loss of the living aboveground biomass and the soil organic layer, which is only partly compensated by higher C storages in the mineral topsoil under pastures than forests. This results not only in considerable nutrient losses but also in the additional release of $CO_2$ into the atmosphere. Future research should therefore address the landscape-scale element budgets including the remains of the native forests and their anthropogenic replacement systems. Besides effects on element cycles, the land-use change might also feed back on the water cycle, particularly via changed evapotranspiration, and thus on the local climate, which needs to be addressed to improve local predictions of global climate change.

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