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Tropical soil nutrient distributions determined by biotic and hillslope processes

K. Dana Chadwick · Gregory P. Asner

Abstract Understanding the drivers of nutrient distributions across heterogeneous tropical landscapes, and the implication of those distributions for ecosystem processes, remains a challenge in biogeochemistry. Guided by a high-resolution digital elevation model, we determined soil chemical characteristics, including rock-derived nutrient availability and total element concentrations, along 16 hillslopes with two different morphologies on a *terra firme* landscape in the lowland Peruvian Amazon. We assessed the role of geomorphic processes in rejuvenating soils, and the role of biotic processes in retaining nutrients in surface soils along toposequences. Our results show that the chemical weathering state of subsurface soils decreases down convex slopes, suggesting a role for erosion-driven rejuvenation. Total phosphorus (P) and calcium (Ca) are less depleted in surface soils than subsurface soils, in contrast to the vertical patterns observed for total magnesium (Mg) and potassium (K). Exchangeable Ca and Mg are highly concentrated in surface soils relative to the total available in the top meter of soil, which remains true as the total amount of these nutrients available in the top meter of soil increases along convex hillslopes. The combined results suggest that Ca is especially tightly cycled by this tropical forest ecosystem, and that steep, eroding hillslopes play a major role in the distribution and rejuvenation of rock-derived nutrients in regions far from marine aerosol and dust inputs. Geomorphically-mediated distributions of these nutrients, in turn, may underpin spatial variation in tropical forest carbon dynamics.

Keywords Amazon · Calcium · Phosphorus · Rock-derived nutrients · Toposequence

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Introduction

Understanding the spatial distribution of nutrients across landscapes and their role in enabling or constraining ecosystem processes, including the fixation and storage of carbon, is critical to biogeochemistry and ecosystem ecology. Predicting nutrient distributions in tropical forest ecosystems is increasingly important as we strive to forecast the response of these systems to rising CO_2 levels. Tropical forests, and the Amazon in particular, are thought to be major

contributors to the terrestrial sink of carbon (e.g. Malhi and Grace 2000; Schimel et al. 2015), dampening the rise of atmospheric CO_2 levels throughout the industrialized era (Schimel 1995). The ability of these forests to continue this increased uptake of CO_2 is contingent upon the availability of essential nutrients required for primary production.

Despite their importance, the nutrient dynamics of terrace formations in the western Amazon Basin have been understudied. Existing studies primarily examine differences between distinct geologic surfaces, such as *terra firme* (terrace) and floodplains, or terraces of differing ages (e.g. Laurance et al. 2010; Asner and Martin 2011; Quesada et al. 2011), revealing stark differences in soil and forest characteristics. However, *terra firme* surfaces make up the majority of land area in the Peruvian Amazon, up to 88 % in southern Peru (Salo et al. 1986). Therefore, nutrient gradients on and within these particular surfaces have the potential to control ecosystem processes across large portions of the Amazon Basin.

While there have long been indications that multiple nutrients may be limiting to tropical ecosystem processes (e.g. Vitousek 1984; Cuevas and Medina 1988; Wright et al. 2011), much of the literature remains focused on the nitrogen (N) versus phosphorus (P) limitation dichotomy (e.g. Cleveland et al. 2011; Fisher et al. 2013; Sullivan et al. 2014). It may be especially important to consider the role of additional macronutrients that lack a gaseous phase in terraces of the southwestern Amazon which do not receive sediment additions by modern river activity. These forests exist on highly weathered soils, far from additional sources of nutrients such as marine aerosols and dust (Ridley et al. 2012), which can provide a significant supply of rock-derived nutrients in some systems (Chadwick et al. 1999). There is a need to broaden the discussion of nutrient dynamics to include rock-derived nutrients beyond P, as well as to develop new methods by which to consider nutrient scarcity and demand in a landscape context.

At the landscape scale, topography plays an important role in mediating soil distributions and ecosystem properties (Jenny 1941). However, the relationship between soils and topographic position can depend on the geomorphic context (Mage and Porder 2013; Porder et al. 2015), which can include the morphology along the entire hillslope and the character of channels at the base. Gaining an understanding

for the geomorphic context of hillslopes can be challenging in tropical forests. It is difficult to assess local topography in the field because of high tree density, and digital elevation models (DEM) derived from spaceborne sensors lack the necessary resolution for many hillslope studies. However, the increasing availability and quality of airborne light detection and ranging (LiDAR) sensors, which are able to detect ground elevation through forest canopy cover, is facilitating directed field campaigns to compare soil characteristics on hillslopes with different morphologies.

Topographic gradients result in nutrient losses from ecosystems through both physical erosion, which can be caused by soil creep or overland flow, and hydrologic leaching along hillslopes. However, in the tropics strong erosive processes can also remove surface soils that are highly depleted in rock-derived nutrients from convex hillslopes (hillslopes that have continuously increasing slope angles along their length), exposing less weathered material and incorporating it into the soil column. This process can rejuvenate concentrations of rock-derived nutrients in old landscapes (Vitousek et al. 2003; Porder et al. 2005). Convex hillslopes arise due to soil transport processes, coupled with constant removal of transported soil from the base of the hillslope by active channels (e.g. Gilbert 1909; Culling 1960; Furbish 2003). This shape is maintained in the presence of baselevel lowering, which causes incision into the underlying lithology and increases removal of transported soil (Mudd and Furbish 2007). In the absence of an active channel to remove transported soil from the base of the hillslope, accumulation will occur at the toe slope, and this accumulation will cause a convex to concave transition, a shift from increasing slope angle to decreasing slope angle, along the hillslope (Furbish 2003). Thus, the form of hillslopes expresses the history of erosion rates, thereby affording study of the relationship between topography and nutrient concentrations along contrasting hillslopes, and their role in mediating nutrient distributions across a landscape.

In addition to the heterogeneity caused by topographic variability within *terra firme* landscapes, the high biodiversity of lowland Amazonian forests makes the causes and consequences of variation in nutrient dynamics particularly difficult to resolve (Townsend et al. 2008). Foliar nutrient ratios are used as indicators of N or P limitation of primary production in many

ecosystems (e.g. Koerselman and Meuleman 1996; Güsewell 2004). However, recent studies in tropical systems have demonstrated that many aspects of foliar chemistry are controlled phylogenetically (e.g. Fyllas et al. 2009; Asner et al. 2014), and that foliar nutrient ratios can vary seasonally (Townsend et al. 2007). These findings complicate the interpretation of foliar ratios when seeking to identify nutrients in low supply, rendering them less useful in these regions. Another proposed indicator of ecosystem demand relative to supply is the concentration of nutrients in surface soils relative to the amount present in the soil profile (Jobbágy and Jackson 2001). These vertical distributions can be altered by biotic processes, with ecosystems uplifting and strongly cycling elements that are essential for ecosystem processes (Jobbágy and Jackson 2004). Considering these vertical distributions across a landscape allows us to assess and compare the relative retention of many essential rock-derived nutrients.

Naturally occurring gradients have often been used in studies to examine drivers of ecosystem processes. Topographic gradients are associated with changes in nutrient availability in both temperate and tropical regions (e.g. Tiessen et al. 1994; Osher and Buol 1998; Yoo et al. 2009; Weintraub et al. 2014). Notably, it has been shown that erosion along hillslopes as short as 100 m can lead to nutrient rejuvenation within an ecosystem (Vitousek et al. 2003). By pairing geomorphic and biogeochemical data, utilizing topographic gradients and vertical nutrient distributions, we consider the contribution of different processes determining nutrient distribution and availability across an Amazonian forest landscape. Focusing on the rock-derived macronutrients P, Ca, Mg, and K, we ask the following questions: Does geomorphic context influence nutrient distributions along topographic gradients? How does biotic cycling of nutrients influence these distributions? And, using these relationships, can we identify nutrients that are in low supply relative to ecosystem demand?

Conceptual framework

The nutrient distributions that we observe across the hillslopes considered in our study are the result of the interplay between geomorphic and biotic processes. Here we present a conceptual model for how these processes may interact to determine nutrient availability in a humid tropical terrace landscape (Fig. 1). At the stable terrace surface, where physical erosion rates are low, there has been long-term chemical weathering and leaching of nutrients out of the soil profile (Fig. 1a). Geomorphic and hydrologic processes act on hillslopes to remove soil mass, through soil creep and overland flow (Fig. 1b) (e.g. Kirkby 1967; Kirkby and Chorley 1967; Lewis 1974). On convex hillslopes that are responding to baselevel lowering and are connected to actively incising channels, the mass that is transported to the base of the slope is removed by streams rather than accumulating at low slope positions (Fig. 1c) (e.g. Gilbert 1909; Culling 1960; Furbish 2003). This removal of mass and stream incision will act to effectively lift less weathered material from deeper in the terrace formation into the top meter of soil (Fig. 1d) (e.g. Vitousek et al. 2003). As a result, we expect indicators of less weathered material at low slope positions on convex slopes in subsurface soils. In addition, chemical weathering and the leaching of soluble weathering products through the soil profile and downslope may cause the redistribution of nutrients to the base of convex slopes (Fig. 1e) (e.g. Schellekens et al. 2004, Boy et al. 2008). Both the raising of less weathered sediments (Fig. 1d) and the hydrologic redistribution of solutes (Fig. 1e) could increase available nutrients at high relief positions on convex hillslopes. On hillslopes that transition from convex to concave we might expect to see indicators along the convex or planar portion of the slope that subsurface soils are relatively less weathered than those found at flat, stable terrace positions, these soils would not be as fresh as those found on the convex hillslopes.

Biotic processes, such as nutrient retention through biotic cycling (Fig. 1f) and biotic uptake of nutrients from deeper soils (biotic pump) (Fig. 1g) (e.g. Jobbágy and Jackson 2001, 2004), overlay these abiotic geomorphic and pedogenic processes, and modify the patterns in nutrient availability in surface soils. On flat, stable regions of the terrace we expect that available nutrients would be low in both surface and subsurface soils, but that a relatively high proportion of available nutrients would be present in the surface soils, where they are retained through biotic cycling (Fig. 1a, f). On convex slopes, the subsurface soils should increase in total nutrient concentration downslope; this provides a
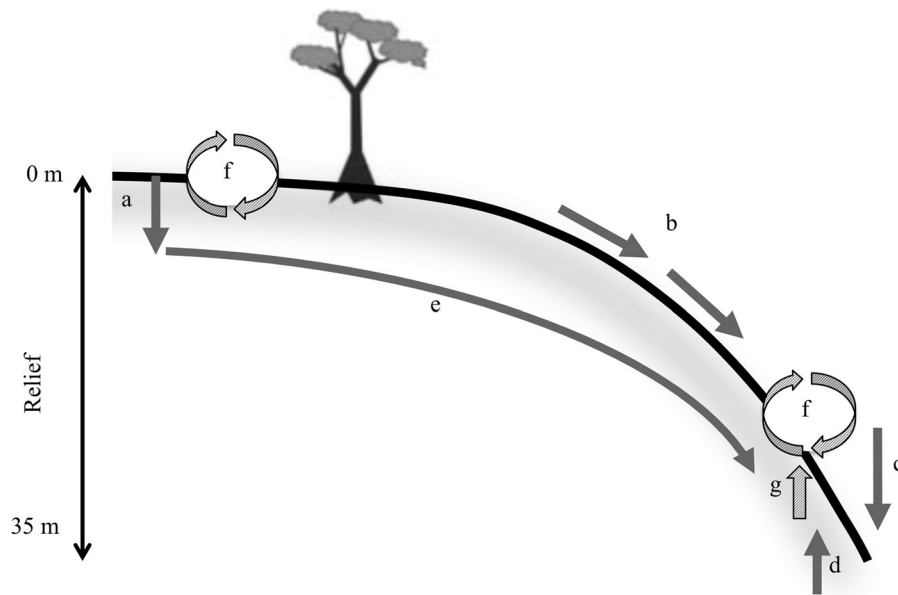
Fig. 1 A conceptual model of processes influencing nutrient distributions in humid tropical landscapes. Direction of increasing relief highlighted on *left* of figure. *Gray arrows* indicate abiotic processes involving mass or solute flux. *Striped arrows* indicate biotic processes. On long time scales, the terrace surface becomes depleted of rock-derived nutrients through chemical weathering and the leaching of solutes (*a*). On hillslopes, geomorphic and hydrologic processes act to remove nutrient content through soil creep and overland flow (*b*). Actively incising channels cut into the terrace, lowering the land surface through the removal of depleted surface soils (*c*) and the effectively raising less weathered material into the top meter of soil (*d*). Through the incorporation into the soil profile and subsequent weathering of minerals that are less weathered

(*d*) and/or the hydrologic redistribution of chemical weathering solutes downslope (*e*), more available nutrients will be available in subsurface soils at high relief positions. When this occurs, nutrients that are in low supply relative to ecosystem demand are likely to get biotically pumped to the surface horizons (*g*) where they will be tightly cycled (*f*), a combination of processes which will result in increased concentrations of these nutrients at low slope positions. Nutrients will also be tightly biotically cycled at terrace surface locations that are highly depleted of rock derived nutrients, and may have a higher topsoil concentration of nutrients relative to the total amount in the 1 m profile than are observed at other sites on the landscape (*f*). See text for detailed discussion of conceptual model

fresh source of minerals that can be weathered into available forms. Nutrients that are in low supply relative to their ecosystem demand can be biotically pumped into surface soil horizons, and maintained there through tight biotic cycling (Fig. 1f, g) (e.g. Jobbágy and Jackson 2004). This would result in nutrients that are strongly demanded by the vegetation and soil organisms to have increased concentrations in surface soils at low slope positions on convex slopes. On slopes that transition from convex to concave, we expect that surface retention of available nutrients would be higher because no new material is being actively incorporated into the soil profile from the underlying material. However, we do not necessarily expect this to vary with slope position. As we discuss the results of our study, we will refer to this conceptual model to provide context.

Methods

Study area

Our study was conducted in the Los Amigos Conservation Concession (LACC) in the southern Peruvian Amazon (Fig. 2d), at the confluence of the Madre de Dios and Los Amigos rivers (Fig. 2a). The study area has a humid tropical climate with mean annual temperature of 25.5 °C (Osher and Buol 1998) and mean annual precipitation of 2650 mm (2001–2008) (Rigsby et al. 2009). This region was acquired by LACC in 2001 and is comprised primarily of old growth forest. Prior to 2001, there was a limited amount of selective logging in the area and the current research station was the site of a mining camp, though this activity had limited impact on the terrace formation of focus in this study (Pitman 2010).
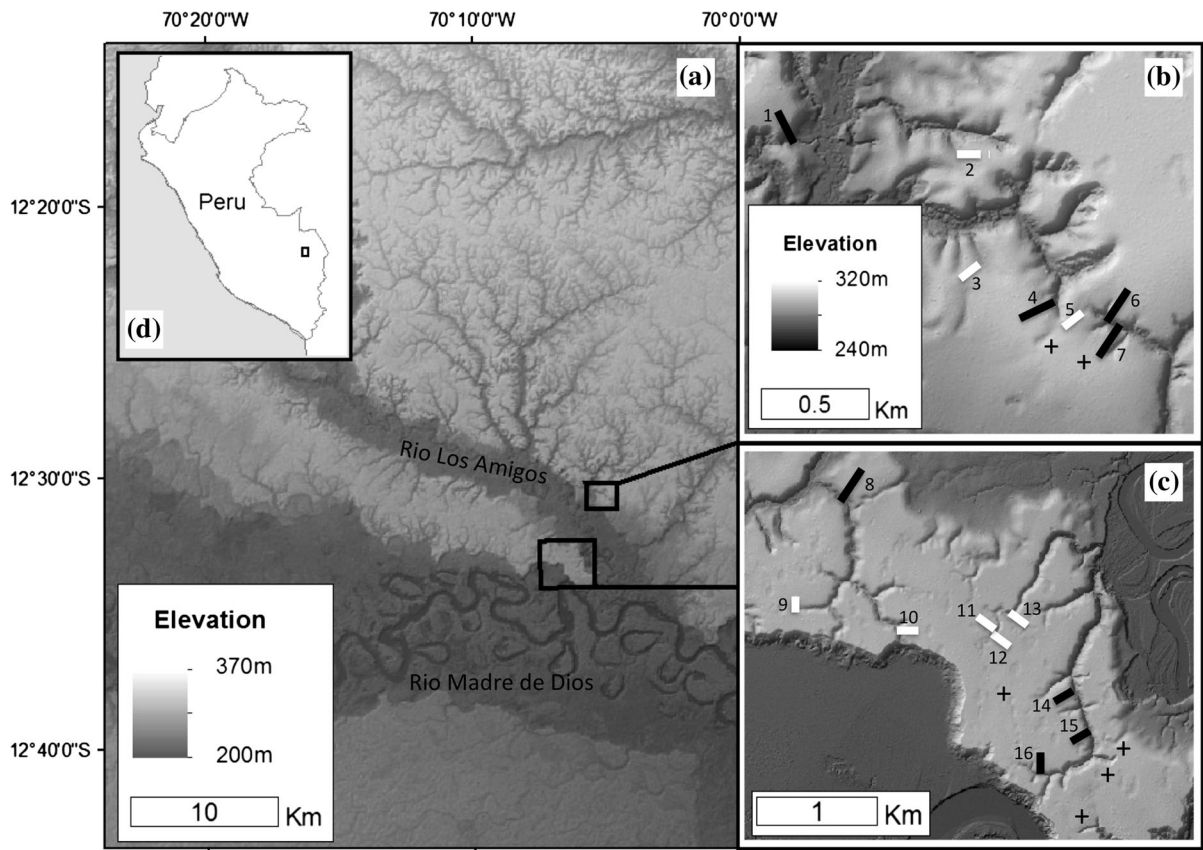
Fig. 2 Maps of the study region, including: **a** 90 m resolution shuttle radar topography mission digital elevation map of the region, including the Madre de Dios and Los Amigos rivers, **b**, **c** 2 m resolution digital elevation maps of the study area on either side of the Los Amigos river derived from the light detection and ranging sensor on the Carnegie Airborne Observatory, and **d** a line map of Peru and the South America coastline. Convex slopes (described in main text) are shown in *black*, hillslopes that are convex-concave slopes are shown in *white*, and individual sampling locations on the terrace surface are displayed with + symbols. Hillslopes are numbered to correspond with descriptions in Table S1

This region is at the southern edge of the Fitzcarrald Arch, a region of uplift within the southwestern Amazon basin (Espurt et al. 2007; Regard et al. 2009). The Madre de Dios River, flows along the southern edge of the Fitzcarrald Arch. Terraces that extend to the north of this river have been exposed to a gradient of increasing tectonic uplift moving northwest onto the Arch.

A study by Rigsby et al. (2009) identified three distinct terrace formations occurring along the Madre de Dios River. Our study focused on the oldest terrace formation at the confluence of the Madre de Dios and Los Amigos rivers (Fig. 2b, c). We use the same notation for this terrace, T3, as used by Rigsby et al. (2009). This terrace was described as part of the Cerro Colorado sequence by Latrubesse et al. (2010), and is older than ~48 ky, as revealed by failure to date it using radiocarbon methods (Rigsby et al. 2009; Latrubesse et al. 2010). This formation is 46 m thick at LACC (Rigsby et al. 2009), and is composed of coarse grain alluvial and fluvial deposits with volcanic and quartzite composition, suggesting an Andean origin (Espurt et al. 2010). Work by Espurt et al. (2010) in the Fitzcarrald Arch region suggests that this terrace may be part of the Juanjui/Corrientes formation (Fig. 6.3 from Espurt et al. (2010)), which they report as being deposited during the Pliocene (~3–4 Ma), though this is older than other estimates.

Topographic analysis

Topographic data were collected by the Carnegie Airborne Observatory (CAO) LiDAR sensor in 2013

and processed to a 2 m resolution ground DEM (Asner et al. 2012). We used this high resolution DEM to determine the fine-scale residual relief (here after referred to as relief) of the landscape by calculating the difference in elevation between a given pixel and the flat, geomorphically stable terrace surface. A relief value of 0 m indicates that a location is at a point on the terrace surface, which is unlikely to have undergone significant erosion, whereas a value of 35 m would indicate that erosion has resulted in 35 m of material loss from that location since the original deposition of the terrace surface (Fig. 1).

Field methods

Soil samples were collected in July and August 2013. Sampling was conducted along two types of hillslope transects: convex hillslopes with mean slope angle from channel to shoulder slope of >20° that terminate in active streams displaying channelization, with a maximum vertical depth of ~35 m, hereafter referred to as convex hillslopes; and hillslopes with mean slope angles of <20° that transition from convex to concave curvatures and are shallower, with a maximum vertical depth of ~25 m, and terminate in hollows that show no evidence of present connectivity to ground water, hereafter referred to as convex-concave (CC) hillslopes. Eight hillslopes of each type were sampled. Hillslopes were selected to avoid areas that had evidence of slumping, though this occurs infrequently on this landscape. Four to six sites along each hillslope were sampled: a flat site, a shoulder site, and between two and four slope sites, depending on the length of the hillslope. All sites were selected to avoid locations of significant tree throw disturbance, as well as profile or planform concavity where mass accumulation may be occurring, including avoiding concave regions of CC hillslopes. In addition six sites were sampled at flat terrace surface locations, away from hillslopes. A total of 85 sites were sampled. Global Positioning System (GPS) data were collected at each sampling site, which were used to determine the LiDAR derived relief value at the site.

Samples were collected at each site with a soil corer or auger as follows: five replicates of 0–10 cm mineral soil within a 1 m radius; four replicates of 10–20 cm soil, composited in the field; two replicates of 20–50 cm, composited in the field; two replicates of 50–100 cm, composited in the field. In addition, at

each site one bulk density sample was collected from the top of the mineral soil using a 7.5 cm diameter core to prevent compression of samples (Hao et al. 2008). This sampling strategy follows the medium intensity soil sampling protocol from Robertson (1999). This sampling intensity was chosen to achieve adequate site level information, while also allowing for the replication of hillslope types required for a landscape level analysis. All samples were air dried in the field and returned to the Carnegie Institution where they were air dried for an additional 3 days prior to analysis.

Samples of modern river sediment from the Madre de Dios River were collected in August 2014. Seven samples were collected in 2 days from the active bank when the river was low. Each sample was collected to represent the average characteristics of the bank sediments; any discolorations or unusually textured sediments were avoided. These samples were oven dried and ground using a mortar and pestle. These samples were collected to provide an approximation of total element concentrations present in the terrace parent material because the Madre de Dios River currently drains a large potion of the Andes that would have contributed to the fluvial sediments deposited to form the terrace that constitutes our study area. While these samples will differ from the true parent material values, because we are primarily interested in how relative soil chemical depletion varies for a given element with relief rather than 'true' chemical depletion since deposition, these modern river sediment samples provide a useful indexing material that is a proxy for the parent material of the terrace sediments. Thus, we do not seek to control for grain size distributions of the modern river sediments, which would be important if we were seeking to establish a true parent material composition (e.g. Bouchez et al. 2011).

Laboratory methods

Soil samples were passed through a 2 mm sieve, coarse fractions are disregarded in analyses because they constitute <1 % of mass based on bulk density samples. Exchangeable K (K^+), Mg (Mg^{2+}), Ca (Ca^{2+}) and Al (Al^{3+}) concentrations were determined by extraction in an unbuffered 0.1 M $BaCl^2$ solution (Hendershot and Duquette 1986). The concentrations of cations in extractant solution were determined by Inductively Coupled Plasma-Optical Emission

Spectroscopy (ICP-OES) using a Thermo Scientific ICAP 6300 Duo View Spectrometer at the Stanford University Environmental Measurements-1 facility (em-1.stanford.edu). All samples for a site were analyzed for exchangeable cations. The results from the 0–10 cm depth samples were averaged for site level analysis.

Oxalate extractable phosphorus (P_{ox}), iron (Fe_{ox}) and aluminum (Al_{ox}) were determined by a dark extraction in a 0.2 M ammonium oxalate and oxalic acid solution, with analysis by ICP-OES (McKeague and Day 1966; Soil Survey Staff 2014). Oxalate dissolves noncrystalline hydrous oxides of Fe and Al and releases associated phosphate; it also extracts organically bound P, Fe and Al (Loeppert and Inskeep 1996; Fransson 2001; Soil Survey Staff 2014). A subset of three of the 0–10 cm replicate samples were analyzed and averaged for site level analysis of surface soils and all subsurface soils were analyzed. The amount of P extracted using this method has been found to be a good measure of available P in highly weathered soils (Guo and Yost 1999), and the ratio of P_{ox} to the sum of Fe_{ox} and Al_{ox} has been used as a P saturation index (PSI) (Turner and Engelbrecht 2011).

Soil pH was determined in deionized water using a 1:2 soil-to-solution ratio on one sample from each depth interval, per site. Carbon (C) concentrations (%C) were determined on a subset of three of the surface samples and on 50–100 cm depth samples by combustion with a Carlo-Erba Elemental Analyzer. We make the assumption that all of the carbon measured through this method is organic because mean pH values of surface and subsurface soils across all sites are 3.8 and 4.35, respectively. Therefore, these soils are outside the range of carbonate buffering (pH ∼7+), and any carbonate that formed would be consumed through dissolution reactions (van Breemen et al. 1983). Total element concentration analysis were performed on a surface and 50–100 cm sample from each site; samples were oven dried at 105 °C for 72 h, ground, and determined by X-Ray Fluorescence (XRF) (Spectro Xepos HE XRF Spectrometer) in the Environmental Measurements-1 Facility (em-1.stanford.edu). Oxalate and $BaCl_2$ extraction results are reported based on air-dry weight, %C and total element data are reported based on weight after oven drying for analysis.

Metric calculation and statistical analysis

We calculated a pseudo chemical depletion index (τ_j) for elements of interest (j) in both surface and subsurface soils using the equation:

$$\tau_{j,w} = \left(\frac{C_{j,w}}{C_{j,p}} \times \frac{C_{i,p}}{C_{i,w}} \right) - 1$$

where i is the indexing element, w is the weathered soil material, p is the modern river sediment, and C is the concentration of specified element (Brimhall et al. 1988; Kurtz et al. 2000). We used zirconium (Zr) as the indexing element for these calculations. As discussed above, because our interest is the relative change in chemical depletion or enrichment among samples, this is useful metric even though the modern river sediment is at best an approximation of the true terrace parent material. We denote our pseudo chemical depletion index values as $^P\tau_i$.

We use two metrics to examine the relationship between the surface and subsurface soils at a given site. The first metric is the ratio of the surface soil $^P\tau$ value to the subsurface $^P\tau$ value, which we used to compare the relative level of concentration or depletion of our elements of interest in the surface versus subsurface soils at each site. We calculated the $^P\tau$ ratio (PTR) by dividing ($^P\tau_{i(0–10\ cm)} + 1$) by ($^P\tau_{i(50–100\ cm)} + 1$) for each site. One is subtracted in the initial calculation of $^P\tau$ in order to scale $^P\tau$ so positive values indicate enrichment and negative values indicate depletion, here we have reversed that part of the calculation in order for a PTR value of greater than one to indicate higher concentrations in the surface than at depth, and less than one indicate the inverse. This metric compares the relative level of surface concentration of elements while controlling for organic matter dilation that occurs in surface soils, as well as bulk density change, that can distort the relationship between concentration values of elements through soil profiles (Resner et al. 2015).

The second metric is the topsoil concentration factor (CF) considered by Jobbágy and Jackson (2001), which we used to assesses the relative retention of exchangeable cations and P_{ox} (hereafter jointly referred to as available nutrients) in surface soils versus the total profile content. For this calculation we first determined the total amount of each available nutrient in the 1 m soil profile. To do this we

transformed our data for surface and subsurface samples from gravimetric to volumetric using pedotransfer functions from the Jobbagy and Jackson (2001) meta-analysis, which are based on %C, normalizing to the average surface bulk density found in our sampling (1.12 g/cm^3). Samples from the 20–50 cm depth were normalized based on a bulk density assumed to be the average of that calculated for the surface and subsurface. We chose this method for comparability and to account for the lack of bulk density data for subsurface soils. The calculations of profile concentration and subsequent metrics can also be based on a single, proscribed bulk density estimate for each depth interval for all sites and the results do not significantly vary (data not shown). The available nutrient content of each depth interval was summed to get the total available in the 1 m profile. We then used the total profile content data to calculate the proportion of available nutrients in the 0-10 cm soil depth relative to the amount of available nutrients in the 1 m profile at each site. If the available nutrient is evenly distributed in the in the top 10 cm of soil relative to the rest of the profile, then the proportion of available nutrients would be 0.1. Concentration factor values greater than 0.1 in the surface 10 cm of soil indicate accumulation in surface soils. This metric is different from, but complimentary to, the PTR because it provides information on the distribution of the biologically available nutrients within the soil profile. In the case where the total concentration of an element in the mineral soil is high relative to the available fraction (as is the case for K), it is useful to examine the available fraction to consider biological retention processes.

Site level data and metrics were divided into convex and CC hillslope groups for analyses because the sites from these two hillslope types do not span the same range of relief values and we were interested in considering them independently. Regression analyses were performed to test the relationship between relief and the total and available nutrient concentrations, as well as the metrics described above. The best fit of linear or quadratic relationships was identified using stepwise selection based on the Akaike information criterion (AIC). The regression residuals were tested for normality using the Shapiro–Wilk test and heteroskedasticity was tested using the Breusch–Pagan test. In cases where residuals were significantly different from the normal distribution or residuals

were heteroskedastic, the dataset was transformed using the natural logarithm and, if necessary, any extreme outliers ($\pm 3 \times$ interquartile range) removed to improve the analysis. In cases where residuals are non-normal or heteroskedastic at $p < 0.01$, we report this in supplementary tables of regressions. All statistical analyses were performed using the R statistical program (R Core Team 2014).

Results

Total elements

Total concentrations of K, Mg, P, and Sr in the 50-100 cm depth range increased significantly with relief (note throughout our discussion of results and findings that increasing relief values indicate increased depth below the terrace surface, see Fig. 1 for diagram) at convex hillslope sites ($R^2 = 0.58$, 0.29, 0.14 and 0.43, respectively, $p < 0.01$), while Ca did not increase with relief (Fig. 3a, d, g, j; Table S2). CC hillslope sites did not show significant increases in total concentrations of these nutrients with relief, except in the case of K, which showed a linear and significant increase with relief ($R^2 = 0.72$, $p < 0.01$, Table S2).

Pseudo chemical depletion values for Ca, K, Mg, P, and Sr in the 50-100 cm depth showed relationships similar to their total concentrations along convex hillslopes. K, Mg, P and Sr were most depleted near the terrace surface and less depleted at high relief positions, while Ca was highly depleted at all positions, showing no relationship with relief (Table S3; Fig. 4). These trends were also reflected in the CC hillslopes (Table S3); this is expected because the flat terrace surface has undergone the longest uninterrupted period of chemical weathering and therefore should be the most depleted portion of the landscape, regardless of the type of associated hillslope. The chemical depletion calculations indicated that, on average, Si content was neither depleted nor enriched relative to modern river sediments in the 50-100 cm soils on convex hillslopes ($^P\tau \sim 0$), while Ca, K, Mg, P and Sr were all depleted ($^P\tau < 0$). Notably, Ca was extremely depleted, with $^P\tau_{Ca}$ ranging from -0.98 to -0.995. A $^P\tau$ value of -1 indicates that there is no detectable concentration of the element in question remaining. In the calculation of $^P\tau$, extreme
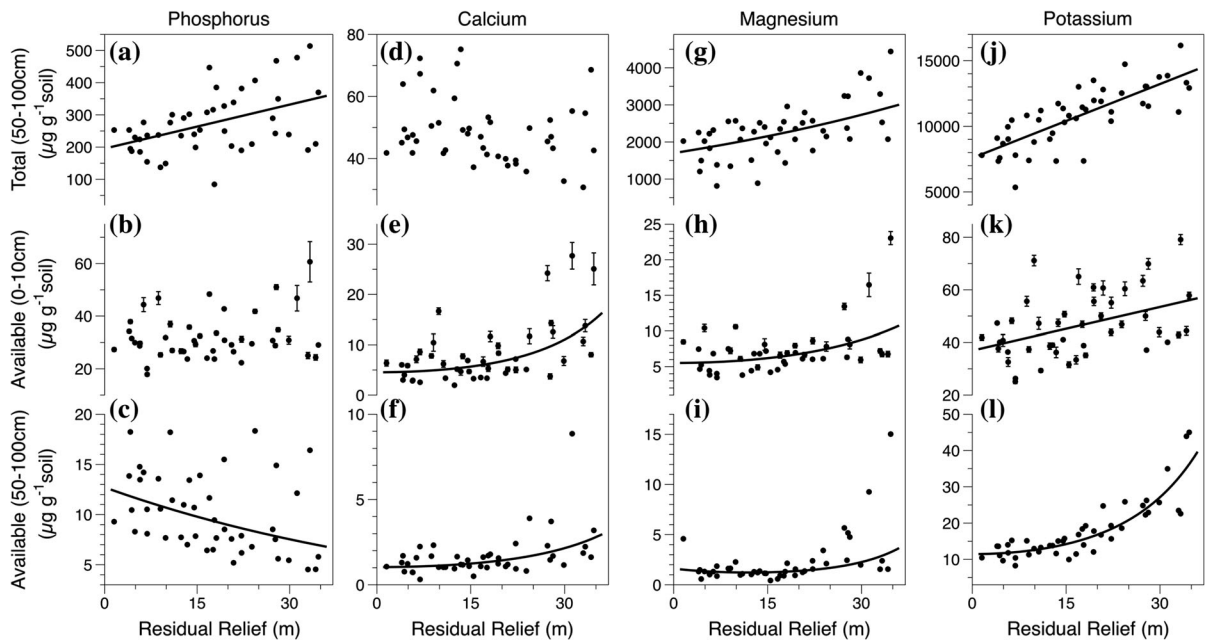
Fig. 3 Scatterplots of available and total element nutrient concentrations against relief for convex slopes. Regression lines are shown as *solid lines* when regressions are significant at the p < 0.05 level. When necessary for normality assumptions or to account for heteroskedasticity, regression analysis was performed on natural log transformed data and outliers removed (Table S2). All data and regression lines are displayed untransformed in this figure and statistical outliers that were excluded from regression analyses are displayed. *Error bars* in **b**, **e**, **h**, **k** are standard error values from averaging surface sample analyses

depletion values could be driven by abnormally high concentrations of the element in question in the indexing material; however, that is not the case for Ca. The Ca concentrations in the indexing material samples collected for this study were in the same range as those found during sediment collections by other researchers from the Madre de Dios River at LACC (Torres, unpublished data).

Available nutrients

Surface and subsurface soil concentrations, as well as total profile content of Ca^{2+}, K^+ and Mg^{2+} increased significantly with increasing relief on convex hillslopes (p < 0.05; Figs. 3, 5; Tables S2, S4). We note that, while the relationship between K^+ and relief in the subsurface was the strongest of the cations ($R^2 = 0.76$), this relationship was the weakest in the surface soil ($R^2 = 0.16$; Fig. 3j–l; Table S2). Subsurface soils at CC hillslope sites had statistically significant increases in Ca^{2+}, K^+ and Mg^{2+} concentrations; however, the fits for Ca^{2+} and Mg^{2+} had coefficients of determination of 0.1 and 0.09, respectively (Table S2). Neither surface soils nor profile concentrations of exchangeable Ca^{2+}, K^+ and Mg^{2+} had significant relationships between concentrations and relief at CC hillslope sites (Tables S2, S4).

Our measures of P availability showed somewhat different relationships with relief. Neither P_{ox} nor PSI in surface soils varied significantly with relief on CC or convex hillslopes. However, on both types of hillslopes the subsurface concentrations of P_{ox} decreased significantly with relief ($R^2 = 0.16$ and 0.15, respectively, p < 0.01; Fig. 3c; Tables S2, S6). The PSI was quite low in these soils, with the surface mean values of 0.016 and subsurface of 0.005. The PSI in subsurface soils decreased with relief along both convex and CC hillslopes ($R^2 = 0.18$ and 0.08, respectively, p < 0.05, Table S6). In addition, the profile concentration of P_{ox} did not vary with relief on convex hillslopes, but did show some decrease with relief on CC hillslopes, however, residuals in this analysis were heteroskedastic and so may interfere with the interpretation of this relationship, which does
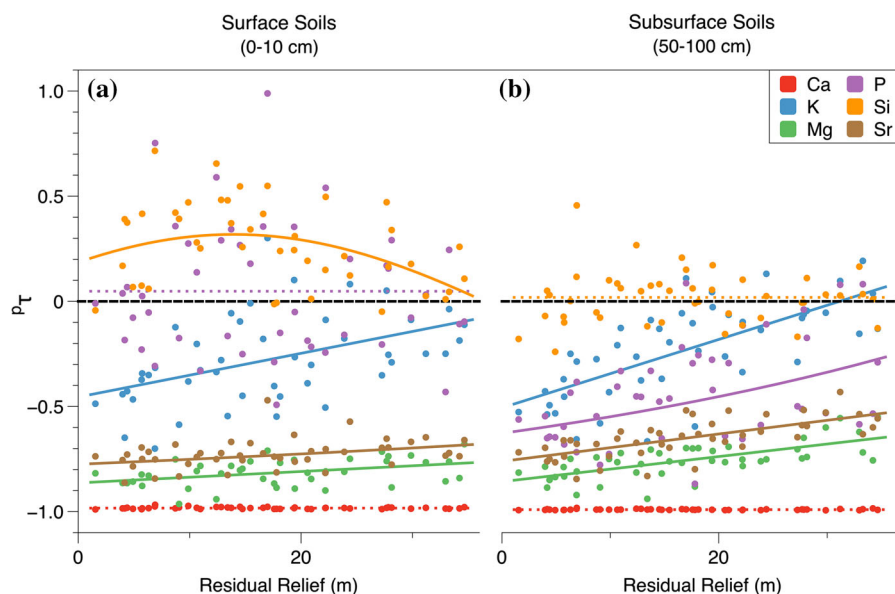
Fig. 4 Scatterplots of $^P\tau$ values against relief for surface soils (**a**) and subsurface soils (**b**) along convex hillslopes. Values were calculated using zirconium as the immobile index element. The reference material is the average element concentration found in nine sediment samples collected from the modern Madre de Dios river bank. A $^P\tau$ value of zero (*black dashed line*) indicates that the soil sample is not depleted of a given element relative to its concentration in the index material, values greater than 0 indicate relative enrichment and values less than zero indicate depletion. Regression lines are shown as *solid lines* when significant at the $p < 0.05$ level, when relationships between $^P\tau$ and relief is statistically insignificant, the mean value is plotted as a *dashed line* for visualization purposes (Table S3). When necessary for normality assumptions or to account for heteroskedasticity, regression analysis was performed on natural log transformed data and outliers removed (Table S3). All data and regression lines are displayed untransformed in this figure and statistical outliers that were excluded from regression analyses are displayed

not have strong significance ($p = 0.03$, $R^2 = 0.10$, Table S4).

Other soil characteristics

Soils in the LACC study region were highly acidic: pH values in the surface and subsurface soils had mean values across all sites of 3.81 ± 0.02 and 4.35 ± 0.01, respectively. The surface pH values did not vary with relief at either the convex or CC hillslope sites, while the subsurface values at the convex hillslope sites increased with relief ($R^2 = 0.51$; $p < 0.001$; Table S6; Fig. S1). The %C in 0-10 cm soils was 1.35 ± 0.01 and 1.27 ± 0.12 on convex and CC hillslopes, while the %C in 50–100 cm soils were 0.42 ± 0.04 and 0.40 ± 0.02, respectively. On convex hillslopes, %C in surface soils did not show significant variation with relief, while the %C decreased with relief in subsurface soils ($R^2 = 0.35$, $p < 0.01$; Fig. S1; Table S6). On CC hillslopes, %C decreased with relief in both surface and subsurface

soils ($R^2 = 0.46$, 0.39, respectively, $p < 0.01$; Table S6).

Surface versus subsurface soils

The mean PTR values for Ca, P and Si were greater than unity on both convex and CC hillslopes, indicating retention of these nutrients in surface soils. The PTR of Ca did not vary with relief, whereas the ratio of P decreased ($R^2 = 0.28$, $p < 0.01$) (Fig. 6; Table S5). The PTR of Mg and Sr across sampling sites were almost entirely less than one, indicating that these nutrients were more depleted at the surface than in the subsurface. None of the elements we considered had PTR values that varied with relief on CC hillslopes; however, PTR of K, P, Si and Sr showed decreasing relationships with relief on convex slopes.

We find that, on average across all sites, P_{ox}, Ca^{2+}, Mg^{2+}, K^+ and Al^{3+} had concentration factors of 0.19 (range 0.12–0.32), 0.32 (range 0.13–0.69), 0.26 (range 0.14–0.42), 0.20 (range 0.11–0.30), and 0.07 (range
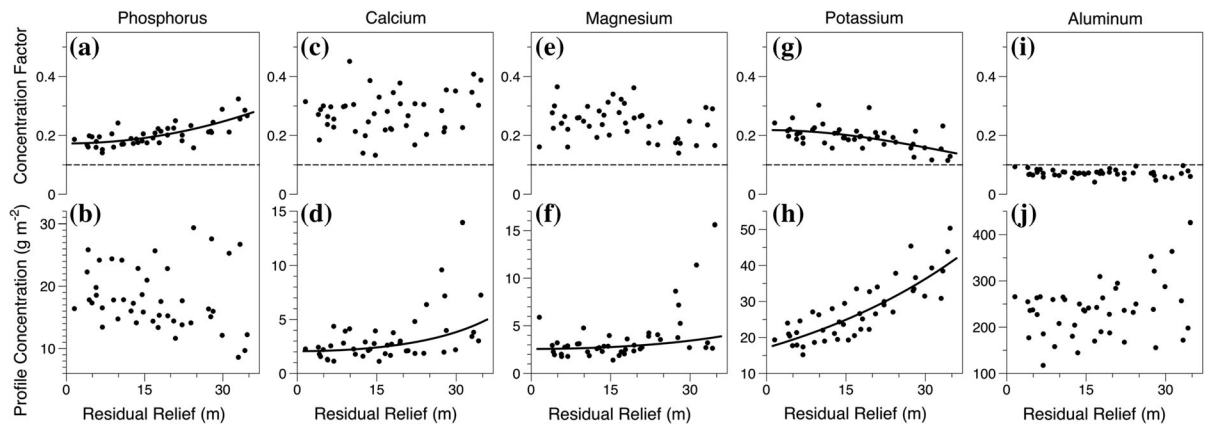
Fig. 5 Scatterplots of the concentration factors (CF) and total profile concentrations of available nutrients (and Al³⁺) against relief for convex slopes. Regression lines are shown as *solid lines* when regressions are significant at the p < 0.05 level. When necessary for normality assumptions or to account for heteroskedasticity, regression analysis was performed on natural log transformed data and outliers removed (Table S4). All data and regression lines are displayed untransformed in this figure and statistical outliers that were excluded from regression analyses are displayed. *Dashed lines* indicate expected value when there is no preferential surface retention (CF = 0.1)

0.02–0.10), respectively. The CF of these elements in the top 10 cm of soil did not change along convex hillslopes, with the exception of K^+, which showed a decrease in the CF with increasing relief, and P_{ox}, which showed an increasing CF with relief (Fig. 5a, c, e, g, j; Table S4). The CF of Ca^{2+}, Mg^{2+}, and Al^{3+} decreased with relief on CC hillslopes, while P_{ox} CF values increased (Table S4).

Discussion

Using several lines of inquiry, we found that hillslope and biotic processes are important to the distribution and maintenance of nutrient availability in this southwestern Amazonian *terra firme* landscape. Specifically we found: (1) nutrient rejuvenation is occurring as a result of geomorphic processes; (2) additional redistribution of available nutrients is occurring along convex slopes in subsurface soils; and (3) hillslope gradients and the vertical changes in nutrient distributions indicate that some rock derived macronutrients are in higher demand by the ecosystem relative to their availability than others. Nutrients that are preferentially retained through biotic cycling and pumped to the surface are likely to be elements that are in low supply relative to the amount required by a broad set of ecosystem processes and constituent species. In the Conceptual Framework section and Fig. 1 we presented

a conceptual model of processes influencing biogeochemical cycling at LACC, and next we place our results in the context of this framework.

Weathering and geomorphic processes

In our conceptual model, the subsurface soils at flat terrace locations, with low relief, have depleted total nutrient concentrations due to long-term leaching and mineral weathering (Fig. 1a). If nutrient rejuvenation is occurring, the concentration of these nutrients should increase at high relief sites on convex hillslopes. On these hillslopes, less weathered sediments are effectively raised into the top meter of the soil through actively incising channels removing surface soils (Fig. 1d). In addition, we expected that on CC slopes we would find little or no decrease in weathering state with increased relief. Results that would confirm our understanding would be an increase in the total amount of nutrient elements and their $^P\tau$ values in the 50–100 cm soils along convex hillslopes, with either less or no increase in these values on CC slopes.

We found total concentrations of P, Mg, and K in the subsurface increased with relief on convex hillslopes and their $^P\tau$ values became less depleted, while Ca did not show significant change in either total element concentration or $^P\tau_{Ca}$ (Tables S2, S3; Figs. 3a, d, g, j, 4b). On CC hillslopes, only K showed an increase in total subsurface concentrations, but when considering

$^P\tau$ values Mg and P also became less depleted with relief (Tables S2, S3). However, when comparing the mean values for convex versus CC hillslopes, the CC hillslopes all have lower $^P\tau$ values, again with the exception of $^P\tau_{Ca}$ (Table S3). While the results for P, K and Mg are consistent with our conceptual model, Ca behaves differently, with τ_{Ca} values for subsurface soils across both hillslope types of -0.99 ± 0.001, indicating that concentrations of Ca in the soils at any of these sites were depleted by approximately two orders of magnitude when indexed to the modern river sediments. It is possible that Ca shows different trends than the other nutrients considered because it is in such low concentrations. Total concentration values for Ca are closer to those of Sr than the other macronutrients being considered, which could be due to the high acidity of the system, which rapidly dissolves most Ca bearing minerals (Likens et al. 1998). Calcium aside, the results for P, K and Mg are consistent with our conceptual model and suggest that erosion along convex hillslopes that terminate in actively incising channels is exposing mineral sediments that are less weathered and have higher total concentrations of these nutrients. These trends suggest that rejuvenation of the essential macronutrients K, Mg, and P is occurring along convex hillslopes, where fresher material is being incorporated into the soil profile that can then be more readily weathered into available forms.

Available nutrient distributions along hillslopes

In our conceptual model, we also expect that there will be higher concentrations of available nutrients in subsurface soils, as well as the total available nutrient content of the profile, at high relief positions on convex hillslopes (Fig. 2). This may be due to the in situ weathering of nutrients from the fresher mineral soil into available forms or the redistribution of available nutrients along hillslopes via hydrologic transport of solutes from chemical weathering (Fig. 2d, e). We found that in subsurface soils and in the 1 m soil profile, Ca^{2+}, K^+ and, to a lesser degree, Mg^{2+} increased with relief at sites along convex hillslopes (Tables S2, S4; Figs. 3f, i, l, 5d, f, h). On CC hillslopes, we also found that there was an increase in concentration in subsurface soils with increasing relief (Table S2), but there was no significant change in the total profile content for any of the cations (Table S4). In addition, the mean subsurface concentration values
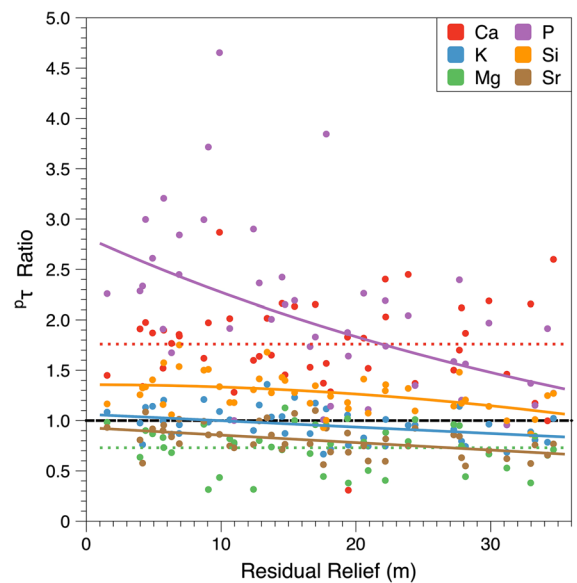

Fig. 6 Scatterplots of $^P\tau$ ratio values against relief along convex hillslopes. The ratio indicates the relative total concentration of an element in the 0–10 cm sample compared with the 50–100 cm sample from the same sampling site, indexed to the reference element Zr. A value of one (*black dashed line*) occurs when there is equal concentration of the element in the surface and subsurface soil at a site, controlling for dilating factors such as organic matter addition. Values less than one indicate that the surface soil has a relative depletion of the element, a scenario that might be expected for elements not strongly biotically cycled. Values of greater than one would be expected in cases where an element is strongly biotically cycled, retaining it in the surface horizons. Ratios for calcium (Ca), phosphorus (P) and silica fall almost entirely above one. Potassium has values that are approximately one, and magnesium and strontium have depletion in surface soils relative to subsurface soils. The decrease in surface retention of P with increasing relief is driven by increases in $^P\tau_P$ in subsurface soils as less weathered material is uncovered (Fig. 4; Table S2). Regression lines are shown as *solid lines* when significant at the $p < 0.05$ level, mean values are displayed as *dashed lines* for visual reference for those elements that do not have significant relationships with relief (Table S5). When necessary for normality assumptions or to account for heteroskedasticity, regression analysis was performed on natural log transformed data and outliers removed. All data and regression lines are displayed untransformed in this figure and statistical outliers that were excluded from regression analyses are displayed

and the total profile content were lower for all cations on CC slopes than their convex counterparts.

The increase in Ca^{2+} on convex slopes is interesting in light of the fact that the total concentration of Ca in the soil did not increase along these hillslopes. This suggests that, while weathering of newly incorporated material is likely contributing to the increased

availability of Mg^{2+} and K^+, the hydrologic redistribution of chemical weathering solutes is playing a role in the observed distribution of available nutrients along these hillslopes, since there is an increase in available Ca^{2+} without a corresponding increase in weatherable Ca content. It is worth noting that another possible mechanism responsible for the observed pattern of increased Ca^{2+} at high relief positions on convex slopes is the increase in pH levels in the subsurface soil along convex hillslopes, which could account for higher capacity to retain these cations in the subsurface at high relief sites (Fig. S1; Table S6). However, the increases in Ca^{2+}, K^+ and Mg^{2+} in subsurface soils of convex slopes cannot be explained by increasing organic matter concentrations because %C declined with relief (Fig. S1; Table S6).

These observations also support what we would expect to find based on geomorphic processes; that flat, stable locations on the terrace surface are the most depleted of available nutrients due to long term chemical weathering, and that, while there appear to be some increases in subsurface cation concentrations along CC slopes, as a whole, they have less cation nutrient availability increase than convex slopes. Another observation that suggests the incorporation of less weathered material at high relief positions on convex hillslopes is the increase in pH (Fig. S1d; Table S6). Soils acidify with increased weathering in humid regions; therefore, the increased pH values indicate the presence of less weathered material. In addition, under our assumption that all detected C is organic, declining %C suggests shorter soil residence times at low slope positions. For a given mean annual precipitation and temperature, higher levels of organic C accumulation in the soil indicate increased soil age or residence time (Amundson 2001). The accumulation of soil C is disrupted by erosive processes removing soils, making soil profiles effectively younger. It is worth noting that the %C values at high relief positions on convex slopes are approaching an average of 0.3 % (Fig. S1b), which is similar to the organic C content found in sedimentary rocks in the Madre de Dios headwaters (Clark et al. 2013), and so may not be accumulated from modern biotic processes, though our data so not allow us to assess the provenance of this carbon.

In contrast to the cation nutrients, P_{ox} concentration in the subsurface showed a significant decrease with relief on both convex and CC hillslopes, and total profile content showed a decrease on CC hillslopes

(Figs. 1c, 5b; Tables S2, S4). This trend was not associated with similar changes in Fe_{ox} and Al_{ox} on convex hillslopes, though there was a decrease in Fe_{ox} with relief on CC hillslopes (Fig. S2; Table S6), which could have indicated that this trend was due to decreasing availability of sorption sites. The PSI in 50-100 cm soils decreased with relief on both hillslope types as well (Table S6), which was driven by the change in P_{ox}. While the concentrations of Fe_{ox} and Al_{ox} did not change, the total concentrations of Fe increased with relief on both hillslope types, and total P and Al concentrations increased on convex hillslopes (Figs. 3a, S2; Tables S2, S6). These results could indicate a shift from amorphous Fe and Al oxides near the surface of the terrace to crystalline Fe and Al oxides along these hillslopes. Crystalline Fe and Al oxides can also sorb P, but are not dissolved in dark oxalate extraction, and are associated with less weathered material. This is consistent with the observations that less weathered sediments occur at low slope positions.

Other tropical hillslope studies of P distribution have reported mixed results when considering only the non-accumulating portions of hillslopes. In Hawaii, resin extractable P increased along slopes ranging in age from 150 ky to 1.4 ma (Porder et al. 2005). However, at one of the oldest sites it was found that resin P did not significantly change with increasing relief (excluding toe slope) (Vitousek et al. 2003). In addition, there were no statistically significant differences in soluble P when comparing ridge and non-accumulating slope sites on hillslopes across three different parent materials in Borneo (Takyu et al. 2002). Results in Puerto Rico were similar, where ridge and slope sites did not show significant difference in any of the measured P fractions (Mage and Porder 2013). In light of these results, our findings of decreasing available P with relief, while total and $^P\tau$ values increase in most cases, does not necessarily contradict previous findings. While these studies have been useful in furthering our understanding of these topographic relationships, many of them do not have many replicated hillslopes, which could also hinder their ability to identify landscape-level trends.

Nutrient distributions and biotic processes

Abiotic processes that might redistribute nutrients in surface soils along hillslopes are soil creep and the removal of surface material through overland flow in

heavy rain events (Fig. 1b), whereas biotic processes may act to accumulate and retain nutrients at the surface that are in low supply relative to their demand by the ecosystem (Fig. 1f, g). We found that while surface concentrations of Ca^{2+}, K^+ and Mg^{2+} increased with relief on convex hillslopes, despite the lack of a corresponding increase in %C or change in pH (Fig. S1; Table S6), the Ca^{2+} and Mg^{2+} CF values did not vary and the K^+ CF values decreased (Fig. 5c, e, f). In addition, while neither surface concentration of P_{ox} nor profile total content increased along hillslopes, CF of P_{ox} increased on convex slopes. These results contrast with CC hillslopes, which have no change in surface concentrations with relief for any of these nutrients and slightly decreasing CF of Ca^{2+} and Mg^{2+} and increasing CF of P_{ox}. When comparing the mean CF values for Ca^{2+} and Mg^{2+} between hillslope types, CC sites have higher values on average, while P_{ox} and K^+ CF are the same for both hillslope types. In addition, Ca^{2+} and Mg^{2+} have higher CF values than P_{ox} and K^+ across both slope types. Combined, these results suggest that P_{ox} and K^+ are in lower demand by the ecosystem, relative to supply, than Ca^{2+} and Mg^{2+}.

Considering these results from along convex hillslopes we find evidence for preferential biotic pumping of nutrients into surface soils, depending upon demand. While the concentration in the subsurface and total profile content of K^+ has the strongest increasing relationship with relief ($R^2 = 0.77$ and 0.68, respectively), it has the weakest positive relationship in the surface of the cations ($R^2 = 0.16$) and a negative relationship between CF and relief ($R^2 = 0.35$) (Tables S2, S4). At the highest relief sites the CF value for K^+ approaches 0.1, indicating no preferential retention at the surface (Fig. 5; Table S4). This dynamic suggests that K is not in high demand in the ecosystem relative to its supply, and as that supply is increased along convex slopes, the relative retention in the surface drops. This differs from the dynamics of Ca^{2+} and Mg^{2+}, which both show similar increases with relief in their surface and subsurface concentrations and total profile contents (Tables S2, S4). The CF values for these cations do not change significantly with relief, indicating that they are being retained at the surface in similar ratios despite increases in their total contents. These results suggest that Ca^{2+} and Mg^{2+} are biotically pumped and preferentially retained in surface soils along these hillslopes.

Another indicator of tight biotic cycling is the PTR metric. Using this ratio, which accounts for organic matter dilation and changes in bulk density, we find that Ca, P, and to a lesser degree Si, are preferentially retained in surface soils (Fig. 6; Table S5). The Si results are consistent with the findings of Lucas et al. (1993), which show that Si is retained in surface soils through biotic cycling in the Brazilian Amazon. By contrast, Mg and Sr are depleted at the surface, which is what we would expect in the absence of strong biotic cycling, and K is not significantly different than one, indicating no significant retention or depletion relative to the subsurface. This metric suggests Ca and P are being tightly cycled by this ecosystem, however, while the PTR of P is decreasing along convex hillslopes, the ratio for Ca remains constant. This suggests strong biotic cycling of Ca throughout the landscape, driven by the lack of Ca rejuvenation along convex hillslopes (Fig. 6; Table S5).

Caveats and implications

While we have replicated hillslopes within our study terrace formation, these results do not span terraces of multiple ages, and we were not able to sample across the entire extent of this landform, causing some concern about pseudo-replication—an issue present in many field-based studies of this type. As a result, we do not suggest that the regression models established in this landscape could be applied in a predictive fashion to other locations. In addition, while this study seeks to use existing gradients in soil nutrient status to understand the relative supply and demand of nutrients by the ecosystem, this is not the same as establishing nutrient limitation. Additional work, including manipulative nutrient additions, would be required to establish whether one or more of these rock-derived nutrients were limiting to productivity or other ecosystem processes. Furthermore, while we infer erosion from hillslope morphology, we are not attempting to establish actual erosion rates, nor have we attempted to date the terrace surface that is being studied. We thus cannot draw conclusions regarding the timescales over which these processes may be occurring.

Our combined data provide insight into the functioning of the biogeochemical system across this landscape. Both PTR and the relationships between total profile content and CFs suggest that Ca is being

preferentially retained by the ecosystem. Independently, PTR suggests P retention, while the relationship between profile concentration and CF suggest Mg retention. These results lend additional evidence that Ca, in addition to P, is important to consider when designing studies or modeling efforts to address the causes or implications of nutrient limitation in the tropics. This is also an important finding at the regional scale, because it contrasts with the often cited notion that the southwestern Amazon Basin is composed of young, fertile soils (Quesada et al. 2011, 2012). In a recent study of long-term plots to assess the carbon sink in the Amazon basin, plots in the southwestern Amazon showed inconsistency in their productivity trends, with many experiencing decreasing rates of carbon uptake over their monitoring periods (Brienen et al. 2015). Landscape-level heterogeneity in nutrient availability and limitation could help explain the inconsistencies in these trends (Cleveland et al. 2011), with depleted rock-derived nutrients dampening the ability of ecosystems to increase carbon stocks in response to elevated CO_2 levels. Finally, integrating the methods presented here for considering topsoil concentration through both the CF and PTR metrics in the context of topographic changes in total nutrient availability into other studies aimed at establishing nutrient limitation could help develop these relationships in a variety of systems. This would provide an indicator of nutrient limitation at a landscape scale that would be more straightforward to assess than current methods such as nutrient addition, which, by necessity, are of limited temporal duration and spatial extent. Our methods also take advantage of patterns established over time by natural processes to provide an ecosystem-level picture, rather than establishing a view of nutrient limitation using methods that may be applicable only to a minority of processes, organisms or species.

Conclusion

The sampling and chemical analysis of surface and subsurface soils along two types of topographic gradients provided us with a more complete picture of the biogeochemical processes at work across western Amazonian terrace landscapes. Geomorphic processes are contributing to the exposure of less weathered sediments in low slope positions along steep, convex hillslopes connected to active channels. These sediments, which are being effectively raised into the top meter of the soil through stream channel incision, have increased levels of many macronutrients essential for ecosystem functioning. Through what is likely a combination of in situ weathering of these rejuvenated soils and other hillslope processes, such as hydrologic redistribution of weathering products from upslope, the concentrations of exchangeable Ca^{2+}, K^+ and Mg^{2+} increase in subsurface soils downslope. These increases are mirrored in the available concentrations of these nutrients in the surface soils along the same slopes. A closer examination of the relationships between chemical depletion and retention of nutrients in surface and subsurface soils through the PTR provides us with evidence that P and Ca are preferentially retained. In addition, CF metrics indicate that Ca^{2+} and Mg^{2+} are strongly biotically cycled throughout the landscape. Multiple lines of evidence indicate that ecosystem biogeochemical processes are preferentially retaining Ca in this terrace landscape and that it is worth stronger consideration when designing nutrient limitation studies.

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