

## LETTER

# Landscape evolution and nutrient rejuvenation reflected in Amazon forest canopy chemistry

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### Abstract

*Terra firme* forests make up more than three quarters of the western Amazon basin and are often considered functionally homogeneous in regional scale mapping and modelling efforts. However, the landforms underlying these systems are subject to dynamic processes of landscape evolution occurring within an otherwise geomorphically stable terrace formation. These processes may introduce systematic variability in local nutrient status of *terra firme* ecosystems. We utilised high-resolution airborne topographic and imaging spectroscopy data, with directed field soil surveys, to reveal that active stream incision and patterns of soil rock derived nutrient availability drive foliar canopy chemistry distributions across seven catchments within a single terrace formation. These results strongly suggest that fine-scale geomorphic processes directly affect biogeochemical cycles throughout the lowland western Amazon. Furthermore, links between landscape evolution and foliar chemical distributions indicate that geomorphic processes drive the fine-scale spatial organisation of this tropical ecosystem, with implications for the functional assembly and biogeography of Amazonian forests.

### Keywords

Amazon, calcium, Carnegie Airborne Observatory, landscape ecology, rock-derived nutrients, tropical forests.

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## INTRODUCTION

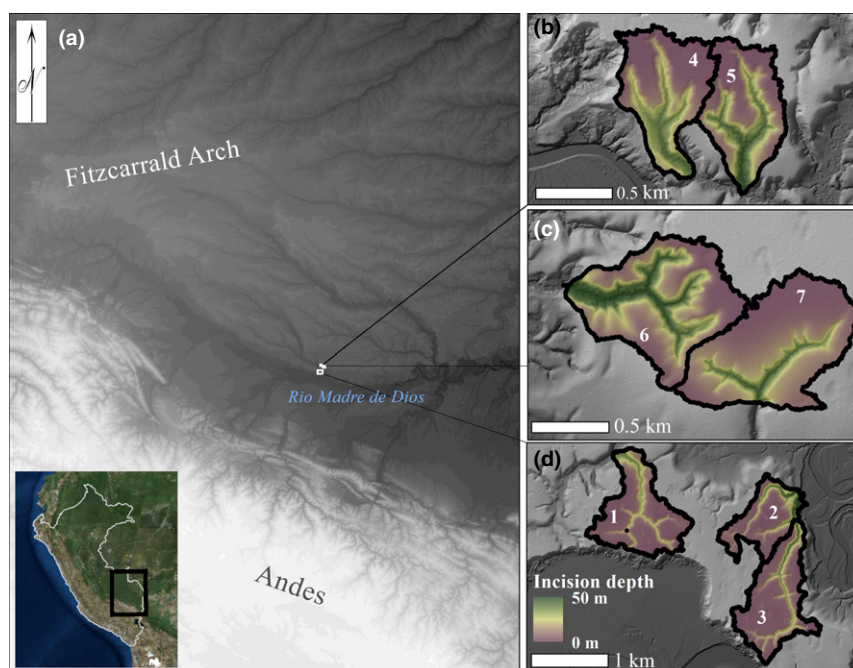
Nutrient limitation in tropical forests, particularly the lowland Amazon, plays a role in constraining ecosystem processes, including net primary productivity (NPP) of these important ecosystems (Vitousek 1984; Chapin *et al.* 1986; Townsend *et al.* 2011). Due to long-term leaching, Amazonian *terra firme* forest processes can be limited by the availability of rock-derived nutrients (RDNs) (Townsend *et al.* 2008; Kaspari & Powers 2016). Insufficient availability of phosphorus (P), calcium (Ca), magnesium (Mg) and potassium (K) have been found to constrain ecosystem processes, including decomposition and productivity, in tropical forests (Vitousek 1984; Cuevas & Medina 1988; Kaspari *et al.* 2008; Wright *et al.* 2011; Kaspari & Powers 2016).

In the western Peruvian Amazon, broad terraces and the *terra firme* ecosystems they support were created by sediment deposition during Andean uplift and have subsequently transitioned to erosional surfaces that no longer receive RDN inputs from river sediments during episodic flooding (Salo *et al.* 1986; Räsänen *et al.* 1987). Due to their location in the humid continental interior, these *terra firme* ecosystems in the western Amazon Basin receive only limited RDN inputs from dust or marine aerosols, which are the only sources to counteract intense rainfall-driven leaching (Ridley *et al.* 2012). Thus, long-term geologic and pedogenic processes act in concert to leave *terra firme* ecosystems depleted of RDNs.

However, these broad lowland terraces can be altered via subsequent downcutting by small (1–2 m wide) streams and associated hillslope formation (Vitousek *et al.* 2003; Bern *et al.* 2005; Chadwick & Asner 2016b). In the southern

Peruvian Amazon, geologic uplift that formed the Fitzcarrald Arch (Fig. 1a), and countervailing erosion pressure driven by the associated drop in baselevel, are altering terrace landscapes by making them more dynamic as they evolve in response to these pressures (Espurt *et al.* 2007, 2010). Uplift, combined with high precipitation, drive the development and maintenance of convex hillslopes through removal of eroded material from the base of hillslopes by active streams, preventing colluvial accumulation (e.g. Anderson *et al.* 2007). Enhanced erosion of highly weathered surface soils leads to rejuvenation of some RDNs through incorporation of less depleted sediments into the soil profile (Chadwick & Asner 2016b). Hydrological connectivity between hillslopes and active streams further redistributes RDNs to incised areas. This combination of rejuvenation and redistribution forms systematic patterns of soil RDN status across *terra firme* ecosystems (Chadwick & Asner 2016b).

Due to their biological importance, landscape-level distributions of RDNs in soils may contribute to spatial patterns of canopy foliar chemistry, with cascading effects on ecosystem processes such as NPP and carbon storage. While soil RDN distributions are associated with hillslope processes in *terra firme* ecosystems of the lowland Peruvian Amazon (Chadwick & Asner 2016b), these variations are small relative to the range of soil RDN content found among soil orders (Quesada *et al.* 2010), between terrace formations of different geologic ages (Laurance *et al.* 2010; Asner *et al.* 2015), or across the Amazon Basin (Quesada *et al.* 2010; Asner *et al.* 2015). We previously found that the range in available P, Ca, Mg and K content across hillslopes were 5%, 2%, 8% and 24% respectively, of the range of values reported by Quesada *et al.*



**Figure 1** Map of seven study catchments within the Los Amigos Conservation Concession, lowland Amazon basin of Peru. Digital elevation model (DEM) derived from the National Aeronautics and Space Administration Shuttle Radar Topography Mission highlighting the location of the study landscape relative to the Fitzcarrald Arch in (a). Inset map of Peru indicates region depicted in (a). Panels (b–d) display the DEM of the study area from airborne light detection and ranging, with the incision depth displayed in the catchment study areas. Based on previous work in these catchments, higher incision depths have increased concentrations of rock derived nutrient due to rejuvenation and redistribution processes. The seven study catchments are outlined in black lines.

(2010) in their basin-wide study. It is not known whether systematic variation in this magnitude in RDNs is sufficient to cause corresponding shifts in canopy chemistry at the catchment scale. Furthermore, it is not known how closely these shifts may be linked to or independent of leaf mass per area (LMA). A link between canopy chemistry and these geomorphic and pedogenic processes would indicate that RDN distributions, driven by the evolution of terrace landscapes, contribute to spatial patterning of biological processes within these ecosystems.

Over limited areas, patterns in canopy chemistry can be challenging to detect due to variability among coexisting individuals and species. While controls on concentrations of some canopy foliar chemicals and traits are underpinned by taxonomic organisation, many RDNs (including P and Ca) as well as LMA have over 50% of the variation controlled by site or individual characteristics rather than taxonomy (Asner & Martin 2016). This leaves room for landscape evolution to play an important role in controlling distributions of these canopy nutrients if sufficient sampling across the resulting gradients can be achieved. To overcome these sampling challenges, we utilised high fidelity imaging spectroscopy (HiFIS) data from the Carnegie Airborne Observatory (CAO) (Asner *et al.* 2012) to quantify canopy nutrient concentrations across seven catchments of the lowland Peruvian Amazon.

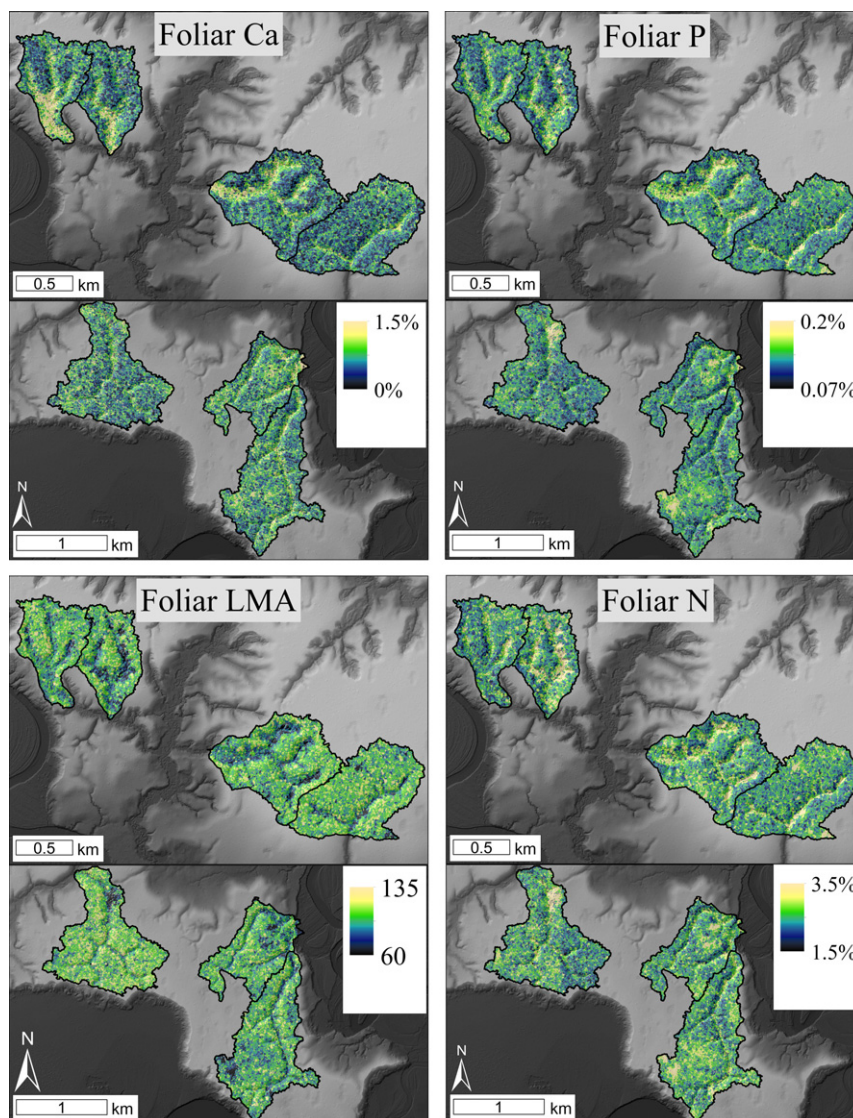
Specifically, we examine whether spatial variations in canopy foliar concentrations of five nutrients, as well as LMA, are correlated with incision depth and its associated shifts in soil RDN concentrations across seven terrace

catchments in the lowland Peruvian Amazon (Fig. 1b–d). We define incision depth as the vertical distance between the originally deposited terrace surface and the modern elevation along hillslopes, indicative of the amount of erosion that has occurred at a given location. We use maps of LMA and canopy foliar P, Ca, Mg, K and nitrogen (N) concentrations (Figs 2 and S1) derived from airborne HiFIS data (Chadwick & Asner 2016a) to assess potential links to soil RDN gradients along hillslopes created by incising streams (Chadwick & Asner 2016b). We consider LMA and foliar N, in addition to foliar RDN concentrations, because these are commonly measured traits associated with vegetation function, and may provide insights into the landscape organisation of canopy characteristics. In doing so, we ask: do concentrations of canopy RDNs increase with incision depth into terrace surfaces that have concurrent increases in soil RDNs due to redistribution and rejuvenation processes within this evolving landscape? Given the spatial dominance of these landforms and importance of RDNs in their functioning, the answer to this question has major implications for the distribution of biogeochemical processes across *terra firme* forests.

## MATERIALS AND METHODS

### Geologic setting and study area

The western Amazon Basin is distinct from the eastern Amazon, which overlies ancient cratons, because the Andean orogeny and associated Miocene wetlands and lakes have



**Figure 2** Maps of canopy foliar Ca, P, N and leaf mass per area (LMA) across the seven study catchments; nutrient concentrations are in percent and LMA is  $\text{g m}^{-2}$ . These maps are derived from airborne imaging spectroscopy. Colour scales are linear, pixels aggregated to 6 m resolution for visualisation. Digital elevation model and hillshade maps were derived from airborne light detection and ranging.

uniquely shaped the geology, topography and climate of the region. As a result, the development of western Amazonian ecosystems has been strongly influenced by tectonically driven landscape evolution (Hoorn *et al.* 2010). In the southern Peruvian Amazon, there is a region of moderate uplift within the basin, known today as the Fitzcarrald Arch (Fig. 1a) (Regard *et al.* 2009). The source of this uplift has been debated (Clift & Ruiz 2007), but is often believed to be associated with the subduction of the Nazca ridge under the South American plate (Espurt *et al.* 2007; Regard *et al.* 2009). The Fitzcarrald Arch now forms the divide between the Madeira and Ucayali drainage basins.

The Madre de Dios River, a tributary of the Madeira, 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 uplift, and countervailing erosion pressure, moving northwest onto the arch (Regard *et al.* 2009). Three

geologically distinct terrace formations have been identified in association with this portion of the Madre de Dios River (Rigsby *et al.* 2009). The oldest terrace formation is where we conducted our study, and is part of the Cerro Colorado sequence (Latrubesse *et al.* 2010). Campbell *et al.* dated the bottom of this formation at *c.* 9 Ma and the top at *c.* 3 Ma, (Campbell *et al.* 2001, 2010), though there is debate and others are only willing to constrain it to being beyond the range of radiocarbon dating ( $> 48\,000$ ) (Rigsby *et al.* 2009; Latrubesse *et al.* 2010). The transition of this terrace from a depositional surface to an erosional surface has driven stream incision into the terrace formation, resulting in the geomorphic and biogeochemical patterns we observe today.

Our study is conducted across seven catchments within the terrace described above, located within the Los Amigos Conservation Concession (LACC), at the confluence of the Madre de Dios River and the Los Amigos River, which has



headwaters on the Fitzcarrald Arch (Fig. 1). The terrace formation is *c.* 45 m thick at LACC (Rigsby *et al.* 2009), and is thought to be of Andean origin, as suggested by its unconsolidated silt and sand composition alluvial and fluvial deposits with quartzite composition (Campbell *et al.* 2010; Espurt *et al.* 2010). The dominant hillslopes found in these catchments transition from flat at the terrace surface to a slope angle of *c.* 30° when approaching the incising streams. The forest in LACC is broadleaf humid tropical forest, with canopies 30–45 m tall. The elevation is *c.* 275 m a.s.l. and mean annual precipitation is 2700 mm, with a mean annual temperature of 25.5°C (Osher & Buol 1998; Rigsby *et al.* 2009; Pitman 2010). LACC is comprised of predominantly primary forest, although the current research station was used as a mining camp prior to LACC's acquisition of the site in 2001, and a limited amount of selective logging took place within the study area during that time (Pitman 2010).

#### Airborne remote sensing data

The CAO collected both visible-to-shortwave infrared (VSWIR) imaging spectrometer and light detection and ranging data at 2 m resolution over LACC in August–September 2013. The specifications of the CAO-AToMS sensors and data collection procedures have been well documented elsewhere (Asner *et al.* 2012) and details related to the acquisition utilised in this study are included in Supporting Information.

#### Topographic analysis

We used the 2 m resolution ground digital elevation model (DEM) to delineate study catchments using Arc Hydro Tools in ArcGIS 10.2 (ESRI 2013). Portions of flat terrace surface adjacent to catchments two and three (Fig. 1d) were excluded from the study due to the presence of significant historical disturbance in the area (clearing for landing strip). These catchments were defined such that they are only comprised of stream reaches that are incised into the study terrace, excluding any portions that would incorporate younger terraces, as this would introduce confounding factors to our analysis. All catchments, with the exception of catchment four, contain hillslopes that were sampled for analysis of soil nutrient distributions (Chadwick & Asner 2016b). The results of that work are used in the analysis and interpretation of our results in this study.

To determine the extent of incision into the original terrace surface, we used the DEM to calculate incision depth, a metric of the vertical elevation difference between a point on a hillslope and the geomorphically stable surface of the study terrace (Fig. 1b–d). This metric was utilised and documented as residual relief in Chadwick & Asner (2016b). Briefly, incision depth values of 0 m are areas at the elevation of the terrace surface, whereas positive incision depth values, such as 30 m, indicate the elevation of the modern land surface at that location is 30 m below the elevation of the original terrace surface, suggesting that 30 vertical metres of originally deposited terrace material have been removed from the site since this formation began eroding. Each catchment was then divided into 5 m incision depth contour intervals, which were

used for analysis. While incision depth extends past 40 m in some study catchments, we did not extend our analysis past 40 m, because the terrace formation of interest has been observed to have a vertical height of *c.* 45 m, and we did not want to introduce effects of potentially different parent material.

#### Foliar trait mapping

The canopy scale models developed for measuring foliar traits from CAO HiFIS data within this study area were presented by Chadwick & Asner (2016a) and methods are detailed in Supporting Information. These models predicted crown-level foliar values of LMA, N, P, Ca, K and Mg with  $R^2 = 0.45, 0.49, 0.53, 0.67, 0.47$  and  $0.53$ , and normalised root mean squared error (RMSE) = 0.13, 0.14, 0.12, 0.11, 0.12 and 0.13 (Chadwick & Asner 2016a). The models were applied across the full LACC study area to generate foliar trait maps.

Across the catchments of interest, we used the mapped foliar traits to calculate ratios of foliar nutrients, as well as analyse the relationships between foliar nutrients and LMA. Ratios of foliar nutrients can be used to indicate relative availability of these nutrients to plants. N:P ratios are often employed to indicate limitation of P or N, with a ratio of *c.* 16 suggested as a transition from N to P limitation of plant productivity (Koerselman & Meuleman 1996). We calculated foliar ratios in RDNs, as well as N:P, to explore the relative rate of change in these nutrients with incision depth across these catchments. In addition, to account for interaction between LMA and foliar nutrients, we fit the relationship between each nutrient and LMA using second order polynomials. These fits were all significant at  $P < 0.001$ . We then calculated the residuals from these regressions for each pixel and divided by the 2–98 percentile range of each nutrient across the catchments and converted to a percentage, so that the residuals are related to the amount of variability that occurs across the landscape.

#### Field and laboratory methods

Foliar samples were collected at LACC in 2013 for foliar trait model calibration. These samples were collected from trees located on both terrace and floodplain substrates, using a collection method implemented for partial least squares regression (PLSR) model development (Chadwick & Asner 2016a; Supporting Information). Samples were collected from 254 canopy trees (Fig. S2) using the Spectranomics methodology (<http://spectranomics.ciw.edu>). LMA and foliar N and RDN concentrations were determined.

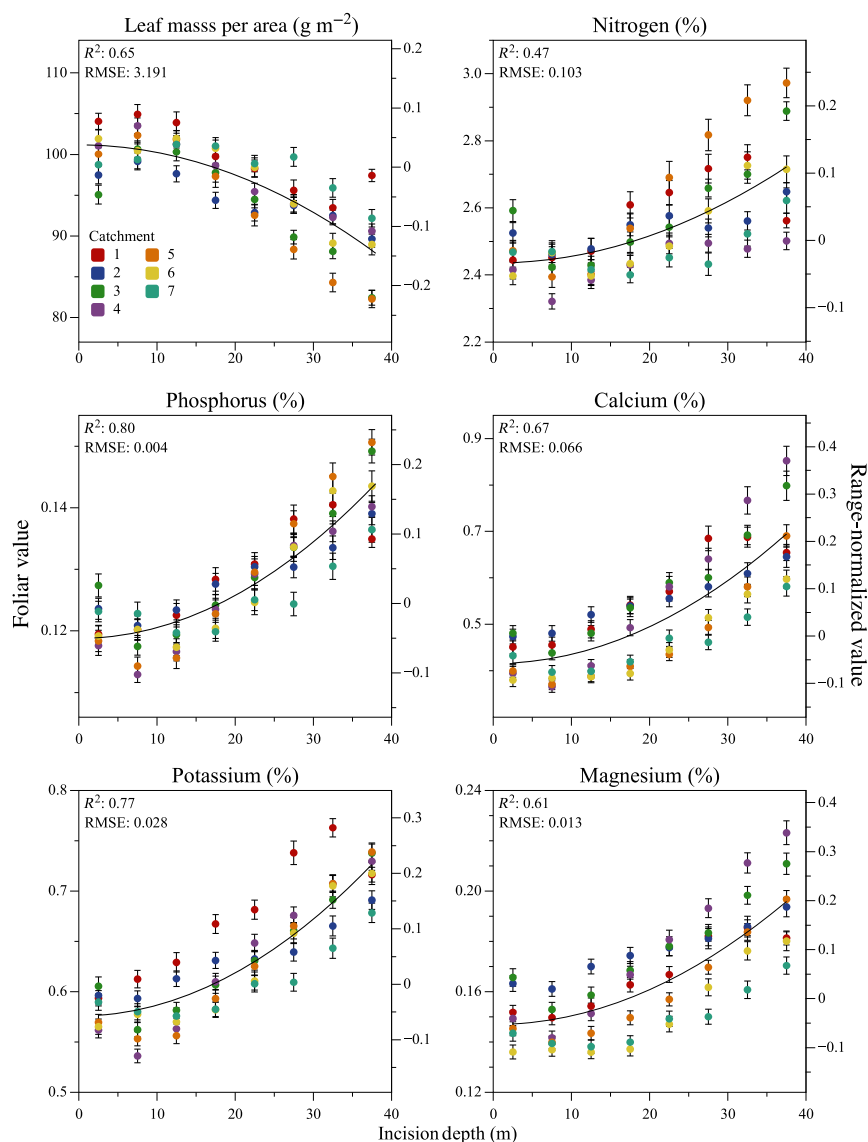
Soil samples were collected at LACC in 2013. The sampling methodology, handling and analysis were described in Chadwick & Asner (2016b), are outlined briefly here, and included in Supporting Information. Soils were collected at five to six points along eight hillslopes that terminated in incising streams. At least one hillslope was sampled within each catchment except for 4 (Fig. 1, Chadwick & Asner 2016b). Exchangeable, also referred to here as available, cation concentrations and available P were determined. We use oxalate extractable P as our metric of available P because in highly weathered soils it has been found that oxalate extractable P is

strongly correlated with the sum of the 'extractable' portions of the Hedley procedure ( $R^2 = 0.939, 0.948$ ) and is strongly related to the amount of P available to plants in a growth experiment (Guo & Yost 1999). In addition, multiple tropical studies have found after completing extensive Hedley fractionation procedures, that the sum of the extractable P fractions (not including extraction by hot concentrated acid) and total P have the strongest relationship with biomass accumulation (Kitayama *et al.* 2000; Quesada *et al.* 2012). Total element concentrations were also determined.

### Analyses

For each catchment, mean values of foliar traits, nutrient ratios, and LMA normalised nutrient values, were determined

for each 5 m incision depth contour through iterative random selection of pixels. For each contour interval up to 40 m, foliar traits from 200 pixels were randomly selected and averaged to determine a mean foliar trait value for that incision depth range (all contour intervals included in the analysis have > 750 pixels appropriate for foliar trait prediction). The random selection was repeated 500 times, and the average and standard deviation of these randomly selected means were calculated. This allowed us to create even sample sizes across each contour and decrease the incidence of multiple pixels from the same individual being included within an iteration of the analysis. Regressions were performed to determine the relationship between mean foliar trait concentrations and incision depth (taken as the midpoint of the incision depth contour) across all study catchments (Fig. 3). The best fit of



**Figure 3** Mean canopy foliar chemical values and leaf mass per area, for 5 m incision depth contour intervals by study catchment. Mean values are calculated by random selection of 200 pixel samples at each incision depth contour, calculating the mean of the sample, repeating this process 500 times, and taking the mean of the 500 mean values. Right axes display the mean-zeroed, range standardised equivalent values to provide context for the change in foliar nutrients relative to the range in observed foliar nutrient content. Solid black regression lines,  $R^2$ , and RMSE values are displayed when regressions are statistically significant at  $P < 0.01$ , dashed lines are non-significant trends.

linear or quadratic incision depth terms were determined using the Akaike information criterion to select the best model.

To relate foliar calcium (Ca), magnesium (Mg), potassium (K) and phosphorus (P) to observed patterns of these nutrients within soils across the study catchments we compared mean foliar concentrations at each contour interval to three metrics of soil nutrient content at each incision depth contour interval. We considered the following soil nutrient metrics: amount of available Ca, Mg, K and P in the top 1 m of soil, the concentration factor (CF) of available nutrient in the top 10 cm normalised against the available amount of that nutrient in the top 1 m (Jobbágy & Jackson 2004; Chadwick & Asner 2016b), and the total concentration of each nutrient in subsurface soil (defined here as 50–100 cm depth). We compared these soil nutrient metrics to their respective foliar nutrient concentrations. Pearson's correlation ( $r$ ) was calculated to assess the relationship between the foliar nutrient and each soil metric, for all RDNs.

Finally, we calculated the rate of change in foliar traits and soil RDN concentrations with incision depth contour. This was calculated as the difference between the mean nutrient value for an incision depth contour and the one above it, and dividing by the mean nutrient value between the contours. For soil nutrient metrics, this was done using the models developed in (Chadwick & Asner 2016b) to predict the nutrient value at the midpoint of a given incision depth interval and then calculating the rate of change from those values. In the case where the relationship between the soil nutrient and incision depth was not statistically significant in that study, we assume that the rate of change with incision depth is zero across the landscape.

## RESULTS

### Nutrient distributions across tropical catchments

Canopy foliar concentrations of Ca, K, Mg and P, derived from HiFIS data, increased quadratically with incision depth across the seven study catchments (Figs 2 and 3). While these increases are all statistically significant, foliar Ca and K increase the most relative to the range of foliar values found across the landscape (Fig. 3). Conversely, LMA declined with incision depth across all catchments. While on average foliar N concentrations increased with incision depth, this trend was not consistent across all catchments. The rates of change in foliar nutrient concentrations with incision depth are mostly positive after the first 5 m of incision depth, though Ca has higher rates of increase, indicating a faster rate of change for this nutrient (Fig. S4).

In order to examine the relationship between these trends in canopy foliar nutrients and soil nutrient availability, we related foliar RDN concentrations to mean concentrations of RDNs in soils sampled at corresponding incision depth intervals (Chadwick & Asner 2016b). Despite the relatively small shifts in soil RDN content, foliar Ca and K were significantly positively correlated with the amount of available nutrient in the top metre of soil ( $r = 0.88$  and  $0.99$  respectively,  $P < 0.05$ , Fig. 4). Foliar Mg was weakly correlated with available soil Mg ( $r = 0.42$ ,  $P > 0.05$ ), and foliar P was negatively

correlated with available P in the soil column ( $r = -0.78$ ,  $P < 0.05$ , Fig. 4). In addition, foliar P, K and Mg were positively correlated with the total concentration of these elements in 50–100 cm subsurface soils ( $r = 0.89$ ,  $0.91$  and  $0.93$ ,  $P < 0.05$ ). Total Ca concentrations in subsurface soils are highly depleted and showed no statistically significant correlation with foliar Ca ( $r = -0.38$ ,  $P > 0.05$ , Fig. 4).

In addition to these direct measures of available and total soil RDN concentrations, we also compared vertical profile patterns in soil RDN concentrations driven by biotic cycling, as measured by the surface CF. K and Mg foliar concentrations were negatively correlated with soil CF,  $r = -0.95$  ( $P < 0.05$ ),  $-0.56$  ( $P > 0.05$ ) respectively. P and Ca foliar concentrations were positively correlated with CF,  $r = 0.98$  ( $P < 0.05$ ),  $0.59$  ( $P > 0.05$ ).

### Nutrient ratios

In this system, N:P ratios are consistently above 16, but they decline from an average of mean value of 20.7 (average SD from iterative sampling = 0.2) near the terrace surface, to 19.3 (average SD from iterative sampling = 0.2) at the 35–40 m incision depth contour interval (Fig. S3). Nutrient ratios of foliar Ca:P, Ca:K and Ca:Mg increased with incision depth ( $R^2 > 0.5$ ,  $P < 0.01$ ), indicating that foliar Ca increased proportionally faster with incision depth than these other RDN (Fig. S3). K:P and Mg:P also showed statistically significant but weaker increases with incision depth ( $R^2 = 0.28$  and  $0.2$  respectively), while Mg:K did not have a significant relationship with incision depth.

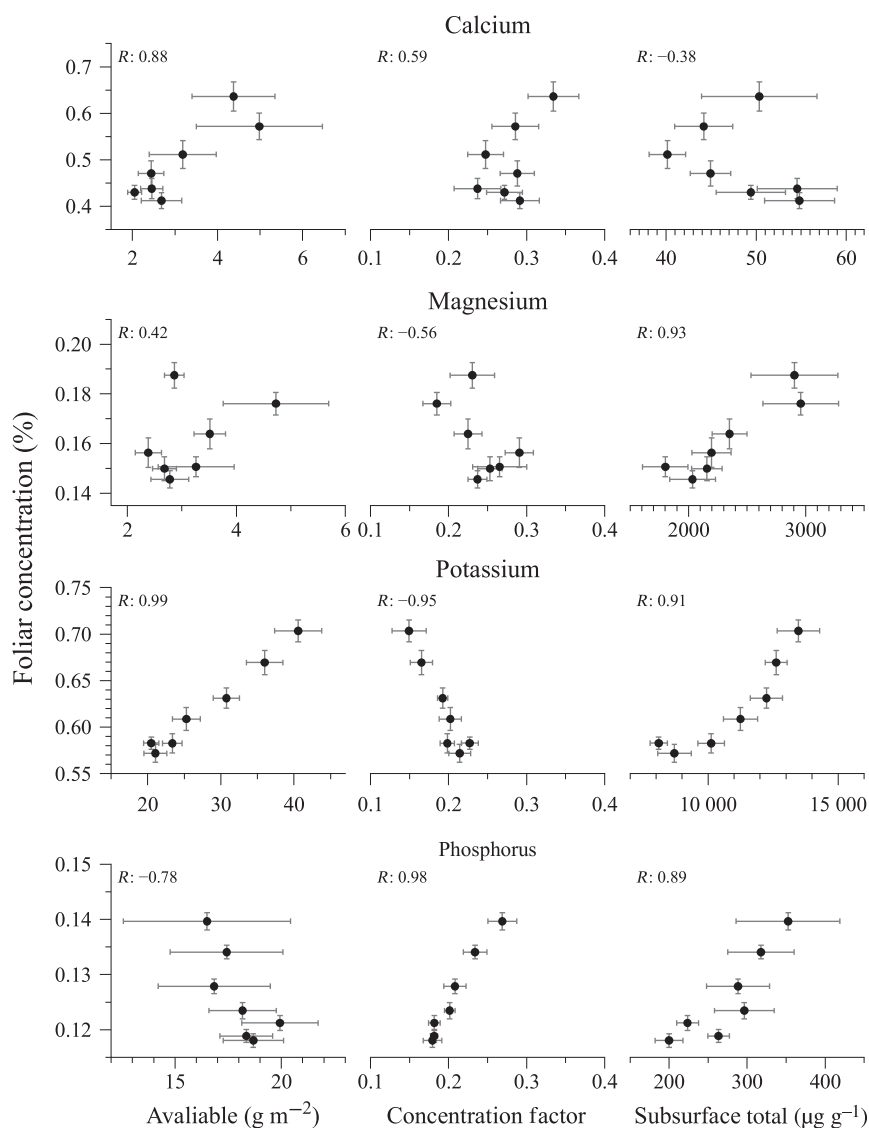
### Relation to LMA

To consider the extent to which variation in LMA was a factor in observed foliar nutrient patterns, we assessed how residuals from a regression between LMA and foliar nutrient content varied with incision depth (Fig. 5). When normalised for shifts in LMA, N concentration has no relationship with incision depth. Normalised foliar P increases statistically significantly with incision depth, however, this shift is  $< 10\%$  of the range in foliar P values in all catchments, which is unlikely to be biologically significant. By contrast, foliar Ca, Mg and K, increased from concentrations below what would be predicted based on LMA values (negative normalised residuals) on the terrace surface, to concentrations exceeding those predicted by LMA alone at high incision depths. For Ca, this increase amounts to a shift in foliar concentrations that represents 20–35% of the range of foliar Ca values found across these catchments, the highest and most consistent of the foliar RDNs.

## DISCUSSION

### Role of landscape evolution

The combination of soil and foliar nutrient data across these catchments gives us a picture of how RDN biogeochemical cycles are playing out across these terrace catchments. Our findings suggest that Ca has the lowest supply relative to

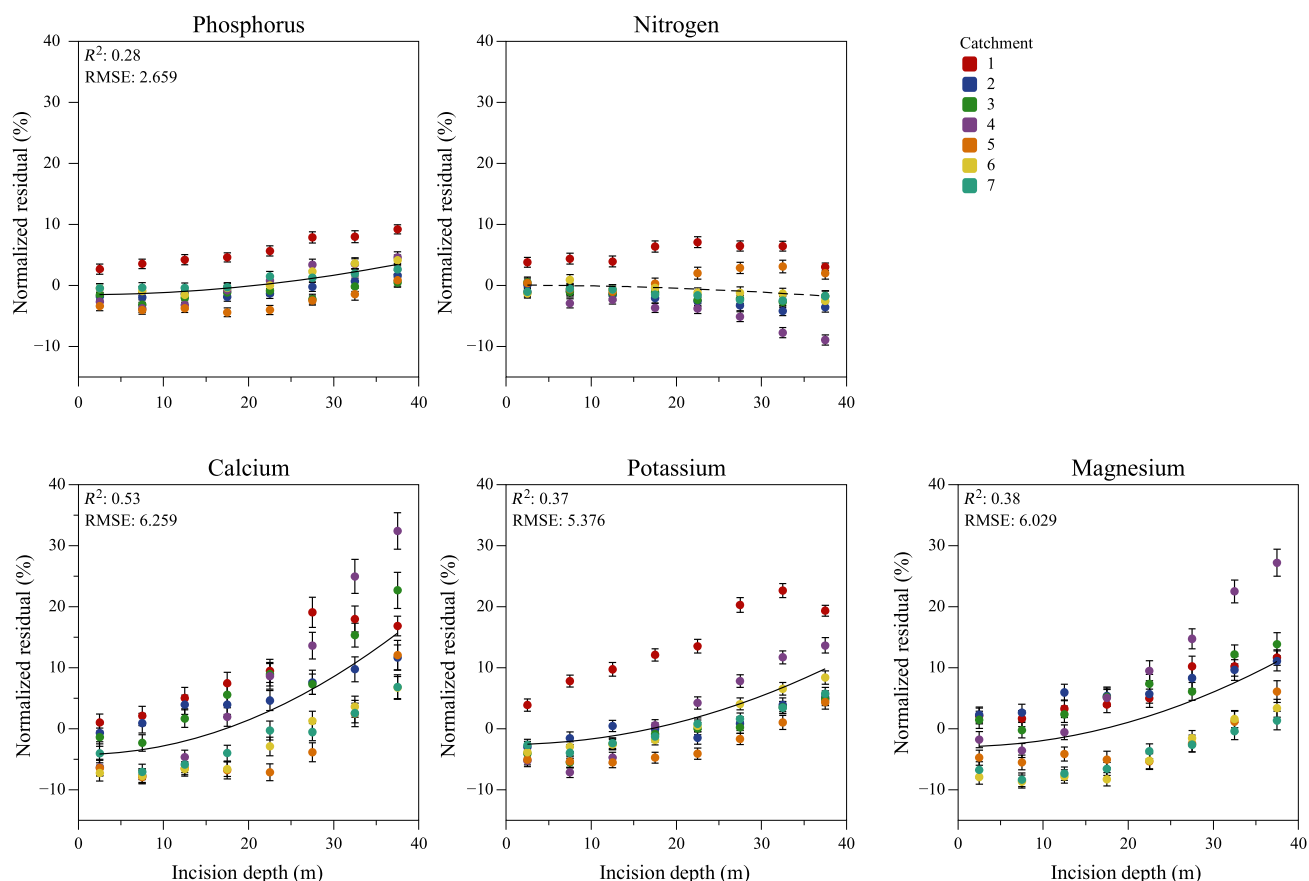


**Figure 4** Relationship between soil nutrient characteristics and foliar nutrient concentrations from high fidelity imaging spectroscopy for rock derived nutrients (RDNs) averaged for each incision depth contour interval across all catchments. Soil nutrient data are from convex hillslopes described in Chadwick & Asner (2016b). Concentration factor is the ratio of the amount of an available RDNs in the surface soil (0–10 cm) to the cumulative amount in top metre of soil (Jobbágy & Jackson 2004). Error bars display standard error and correlation values are displayed in each panel.

ecosystem demand of the RDNs we consider. Foliar Ca concentrations increase with incision depth, even when controlling for shifts in LMA (Figs 3 and 5). Similar increases in foliar Ca with relative elevation were found in Hawaiian ecosystems (Porder *et al.* 2005). This observation can be coupled with previous results indicating that Ca in soils is not being rejuvenated due to depletion across the landscape in subsurface soils, downslope increases in its availability are controlled by redistribution through movement of solutes or particulates, and the proportion of Ca retained in surface soils through biotic cycling is not changing along slope (Chadwick & Asner 2016b). These results suggest foliar Ca concentrations are increasing down slopes due to increased availability from hydrologic redistribution and biotic cycling of Ca remains strong across hillslopes.

Different patterns emerge for those nutrients being rejuvenated through landscape evolution processes. While foliar K

also increases with incision depth, its increase once accounting for LMA is less than that of Ca. Previous work demonstrated that total soil K concentrations are less depleted relative to other RDNs in soils across the catchments, and rejuvenation acts to increase total amounts of K in soils with increasing incision depth (Chadwick & Asner 2016b). Other studies in tropical ecosystems found RDN concentrations can be rejuvenated along hillslopes from erosional processes and these processes can affect foliar chemical composition (Vitousek *et al.* 2003; Porder *et al.* 2005, 2015). Furthermore, as the amount of K available in soils and its foliar concentrations increase with incision depth, the CF declines (Figs 3 and 4). The decline in K CF with incision depth suggests that as more K is available in soils through rejuvenation and redistribution processes, there is enough K present to allow for increasing foliar concentrations without tight biotic cycling, resulting in a decrease in the strength of ecosystem retention. In addition,



**Figure 5** Mean residuals of each foliar nutrient after accounting for relationship between nutrient and leaf mass per area (LMA), for 5 m incision depth contour intervals by study catchment. Residuals from second order polynomial fit between predicted foliar nutrient concentration and LMA were normalised to the range of the foliar nutrient values. Mean residual values are calculated by random selection of 200 pixel samples at each incision depth contour, calculating the mean of the sample, repeating this process 500 times, and taking the mean of the 500 mean residual values. Black error bars are standard deviation of the mean values. Solid black regression lines,  $R^2$ , and RMSE values are displayed when regressions are statistically significant at  $P < 0.01$ , dashed lines are non-significant trends.

the foliar ratio of Ca:K is increasing with incision depth (Fig. S4), indicating foliar Ca is increasing more rapidly than K, despite the fact that soil available K is much higher than Ca (Fig. 4).

Foliar patterns of Mg are similar to those of K. It is increasing with incision depth even when accounting for LMA, and Mg:K ratios do not change with incision depth. Total soil Mg is being rejuvenated and available Mg in the profile is increasing with incision depth, however, the CF does not change with incision depth (Chadwick & Asner 2016b). So, while foliar Mg is slightly positively correlated with soil availability and slightly negatively correlated with CF, neither relationship is strong (Fig. 4), with these patterns falling between those of K and Ca. This suggests that while rejuvenation is increasing the supply of Mg relative to ecosystem demand, not enough becomes available to form strong patterns of availability and consistent decrease in ecosystem retention, as is seen with K. On the other hand, the Ca:Mg ratio increases with increasing incision depth, suggesting that the vegetation uptake response is stronger for Ca than Mg.

Foliar P, the last RDN, also increases with incision depth, though only by  $< 5\%$  of the range of values, once LMA is

accounted for (Figs 3 and 5). Concentrations of total soil P also increase as the result of rejuvenation, but the profile available P do not show a corresponding increase (Chadwick & Asner 2016b). Despite this, foliar concentrations and CF increase with incision depth, suggesting that in low slope positions the ecosystem is cycling P more tightly, even in the absence of increases in the amount of soil available P. There are multiple reasons why this may occur. First, plants may be able to access a greater portion of the P pool than we have determined to be available, and the increases in foliar concentrations may consequently be a response to rejuvenation increasing total soil P concentrations. This possibility is supported by studies in tropical ecosystems that found total soil P to be more strongly associated with ecosystem responses than available P fractions (Cleveland *et al.* 2011; Quesada *et al.* 2012). Soil P chemistry is complex, and our understanding of which pools of P are accessible to plants, on what time scales, and how that varies between ecosystems is still limited (Turner 2008; Turner & Engelbrecht 2011). Second, after accounting for the correlation between LMA and foliar P, the increase in foliar P along hillslopes is small relative to the range of foliar P values ( $< 10\%$ ). This may indicate that the



foliar P is primarily adjusting to leaf economic spectrum drivers (Wright *et al.* 2004), rather than variation in the soil availability. Porder *et al.* (2005) found there was no increase in foliar P or N along slope within a single species on substrates that are unlikely to be limited in RDN, isolating to a single species in a less diverse ecosystem may have a similar effect as controlling for LMA in a diverse ecosystem.

It is interesting to note that while the N:P ratio is decreasing with incision depth, Ca:P, Mg:P and K:P are all increasing, and the Ca:P increase is the strongest. Foliar Ca:P ratios in this system vary from a mean of 3.4 near the terrace surface to 4.8 near streams (Fig. S4). These values are consistently lower than ratios from a nearby study area on the Tambopata River, where ratios of 7.6 and 6.5 were reported for floodplain and *terra firme* forests respectively (Asner & Martin 2011). The terrace examined in that study is part of a formation that extends south of the Madre de Dios river and is geologically younger than the one we consider in this study (INGEMMET 1999). Therefore, it is reasonable to expect further depletion on this terrace formation, as has been found in other studies (Phillips *et al.* 2003). This is a final indicator that vegetation is responding strongly to increases in Ca availability.

Landscape-level trends in foliar RDN concentrations are unlikely to be due to large shifts in canopy species composition, as previous work in this study area shows low  $\beta$ -diversity changes across this *terra firme* forest (F  ret & Asner 2014). This does not completely discount the possibility of these changes being associated with shifts in species composition, especially because LMA systematically declined across the study catchments (Fig. 3). However, considering the residual change in foliar nutrients after accounting for their relationship with LMA helps to assess the role of incision depth while attempting to control for some potential shifts in composition or age. In this analysis, we see that foliar N does not vary with incision depth once LMA has been accounted for (Fig. 5). This is expected because N is widely observed to be more abundant than RDNs in the lowland humid tropics (e.g. Vitousek 1984). Therefore, N limitation is unlikely to alter the negative correlation with LMA that is observed due to the tradeoff between foliar structural investment and growth (Wright *et al.* 2004; D  az *et al.* 2015). The fact that the RDNs increase even after accounting for the relationship with LMA suggests that these patterns are the result of underlying process.

Understanding catchment-level patterns of soil and foliar RDNs, which vary from nutrient to nutrient, reveals the different processes contributing to these distributions. The ability to identify the role of local to regional landscape evolution in the cycling of RDNs allows us to gain a better understanding of what nutrients are likely to be in low supply relative to ecosystem demand and how long-term, tectonic processes contribute to biogeochemical cycles at local scales.

### Scalability

This study considered the chemical assembly of canopies across multiple catchments within a single terrace formation. However, we still found evidence of these shifts being reflected in foliar chemistry. Erosion and stream incision are processes that occur within terraces across the Amazon basin,

suggesting that these patterns are widely distributed. Previous studies in this region indicate that, regardless of terrace age, there are consistently lower foliar and soil concentrations of RDN in *terra firme* ecosystems, than their adjoining floodplains (Phillips *et al.* 2003; Asner *et al.* 2015). This depletion in soil nutrients increases as a function of age of the surface (Phillips *et al.* 2003). One of these studies also suggests a pattern of declining foliar P concentration with terrace age and distance from the Andes, as the most recent source of nutrient input via sediments (Asner *et al.* 2015). These cross-basin trends suggest that landscape processes affect soil and canopy RDN patterns at the basin scale; however, these general results can mask intra-terrace complexities, driven by geomorphic evolution of these landscapes, that occur at scales commensurate with the distribution of individual canopies within these dominant Amazonian landforms.

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### AUTHORSHIP

KDC and GPA designed the study; GPA led the collection and processing of remote sensing data and foliar chemical data; KDC led the collection and processing of soil chemical data, performed analysis and wrote the manuscript; GPA provided editorial advice.

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