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LETTER

Geomorphic transience moderates topographic controls on tropical canopy foliar traits

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Abstract

Tropical ecosystems that exist on mountainous terrain harbour enormous species and functional diversity. In addition, the morphology of these complex landscapes is dynamic. Stream channels respond to mountain uplift by eroding into rising rock bodies. Many local factors determine whether channels are actively downcutting, in relative steady-state, or aggrading. It is possible to assess the trajectory of catchment-level landscape evolution utilising lidar-based models, but the effect of these trajectories on biogeochemical gradients and organisation of canopy traits across climatic and geochemical conditions remain uncertain. We use canopy trait maps to assess how variable erosion rate within catchments influence hillslope controls on canopy traits across Mt. Kinabalu, Borneo. While foliar nutrient content generally increased along hillslopes, these relationships were moderated by catchment responses to changing erosion pressure, with active downcutting associated with greater turnover in canopy traits along hillslopes. These results provide an understanding of geomorphic process controls on forest functional diversity.

Keywords

Foliar traits, imaging spectroscopy, landscape evolution, rock derived nutrients.

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INTRODUCTION

The structure, organisation and function of tropical ecosystems across complex terrain is contingent on geomorphological and hydrological processes at local and regional scales (Council 2010; Troch 2015). However, relating geomorphic processes of landscape growth and decay to ecosystem metrics such as canopy foliar trait distributions remains challenging. Local-scale topographic gradients condition species turnover and variation in foliar chemistry in tropical forest ecosystems (Phillips *et al*. 2003; Kraft *et al*. 2008; Laurance *et al*. 2010; Asner *et al*. 2015). Underlying these topographic associations, hillslope processes drive biogeochemical redistribution of nutrients in soil and vegetation (Takyu *et al*. 2002, 2003; Vitousek *et al*. 2003; Weintraub *et al*. 2015). While some studies link these patterns to hillslope form, position and relative erosion pressure (Porder *et al*. 2005, 2015; Chadwick & Asner 2016b; Osborne *et al*. 2017), we lack a systematic, spatially explicit understanding of how geomorphic processes, including active downcutting, steady-state erosion and hillslope decay, produce differences in the strength and directionality of relationships between hillslope position and biogeochemical gradients. Developing these linkages in a way that supports scaling to regional predictions of interactions between hillslope processes and nutrient supply is important as we seek to represent landscape biogeochemistry in Earth System models (Clark *et al*. 2015; Reed *et al*. 2015; Wieder *et al*. 2015; Fan *et al*. 2019).

Foliar characteristics of tree canopies, such as leaf mass per area (LMA) and nutrient concentrations (which we refer to collectively as foliar traits), are indicative of life strategies, biochemical processes and environmental conditions (Wright *et al*. 2004; Reich *et al*. 2009). For example LMA is an indicator of leaf longevity and foliar nitrogen (N) concentration is associated with increased photosynthetic capacity (Wright *et al*. 2004). Phosphorus (P) is essential for energy transfer and a building block of phospholipids (Niklas *et al*. 2005; Reich *et al*. 2009). Ratios of foliar N:P in the tropics have been shown to shift at the community level in response to changes in soil P availability (Townsend *et al*. 2007; Cleveland *et al*. 2011), although there are strong taxonomic controls on many foliar traits (Asner & Martin 2011). Humid tropical regions where chemical weathering has depleted rock derived nutrient (RDN) concentrations in soil profiles often have decreased P content in leaves, and species have been found to organise based on their tolerance for low P conditions (John *et al*. 2007; Condit *et al*. 2013). There is also growing recognition that beyond P, other RDNs play important roles in large-scale regulation of ecosystem processes (Townsend *et al*. 2011; Kaspari & Powers 2016). For example calcium (Ca) is essential in cell wall development (Demarty *et al*. 1984; McLaughlin & Wimmer 1999), and depressed foliar concentrations are observed in continental tropical forests where soils have low available Ca (Vitousek 1984; Asner & Martin 2011; Baribault & Kobe 2012). Spatial distributions of foliar traits can provide insight into underlying biogeochemical and geomorphological processes at the scale of landscapes (Chadwick & Asner 2018).

In areas where tropical soils are stable or have low erosion rates, deep chemical weathering leads to RDN depletion (Cuevas & Medina 1988; Townsend *et al*. 2011; Baribault & Kobe 2012; Augusto et al. 2017). A combination of large- and small-scale studies indicate increased erosion rates increase the pace at which fresh, weatherable material is advected through the soil column, and thereby the availability of RDN to ecosystems (Hilley *et al*. 2010; Porder & Hilley 2011). This removal of highly weathered surface soils and advection of less weathered material soil profiles is sometimes referred to as rejuvenation, and can be a critical source of RDN in tropical ecosystems (Vitousek *et al*. 2003; Porder & Hilley 2011). In the lowland Peruvian Amazon, hillslope processes dictate spatial patterns of physical erosion and chemical release of RDNs into available forms, which in turn drive hillslope gradients in foliar traits (Chadwick & Asner 2018). In Puerto Rico, a wave of incision has resulted in hillslopes above and below knickpoints having divergent minerology, soil nutrient status and tree height (Brocard *et al*. 2015; Porder *et al*. 2015; Wolf *et al*. 2016). These studies point to the importance of determining distributions of erosion regimes when considering landscape-scale biogeochemical processes.

Geomorphic theory predicts that landscapes evolve towards steady-state, where uplift is countered by lowering rate, erosion rates are constant across hillslopes and hillslopes have predictable morphology (Fig. 1a and 1c) (Gilbert 1909; Roering *et al*. 2001; Roering 2008). At steady-state, soil across hillslopes is predicted to have uniform residence time, and with a uniform thickness, would be expected to have uniform properties (though hydrological and biological processes could introduce variability) (Nikiforoff 1959; Yoo *et al*. 2006, 2011; Amundson *et al*. 2015). However, when uplift or lowering rates change, landscapes enter a transient state, deviating from steady-state morphology in predictable ways as hillslopes evolve toward a new steady-state form (Hurst *et al*. 2012, 2013; Mudd 2017). Steepening catchments, which have increased erosion rates propagating through the channel network, whereas upper portions of the hillslopes are still experiencing the original rate (Fig. 1b) (Hurst *et al*. 2013), should have shorter soil residence times at low slope positions. Conversely, in decaying catchments erosion has slowed at the channel network, whereas upper portions of the hillslopes still experienced the original erosion rate (Fig. 1d) (Hurst *et al*. 2013), increasing soil residence times at low slope positions. While increased erosion rates at low slope position may rejuvenate soils, they may also increase the rate at which nutrient-rich surface soils are removed from the system, potentially depleting nutrients such as N, that are accumulated over time.

Remote sensing platforms, such as the Global Airborne Observatory (GAO), that integrate airborne LiDAR and imaging spectrometers open the possibility of seamlessly linking geomorphic processes and ecosystem patterns. High resolution light detection and ranging (LiDAR) data allow us to interpret landscape morphology underlying forested catchments and assess if they are responding to transient perturbations (Grieve *et al*. 2016; Mudd 2017). This is possible through a framework utilising catchment-level relationships between quantitative, LiDAR-derived hillslope metrics from modern topography to explore recent changes in prevailing erosion rates and variation in erosion rates across hillslopes (Roering *et al*. 1999, 2001; Roering 2008). In addition, it is now possible to produce highly resolved, spatially extensive maps of foliar traits in tropical systems using airborne imaging spectroscopy (Chadwick & Asner 2016a; Martin *et al*. 2018). Imaging spectrometers capture surface reflectance data in the visible to shortwave infrared at high spectral resolution and, when calibrated with high quality ground data, can be used to map vegetation characteristics, including species identity and traits (Ustin *et al*. 2004; Asner *et al*. 2007; Asner & Martin 2009). These advances are paving the way for characterisation of environmental drivers of foliar trait distributions across landscapes and regions (Asner *et al*. 2015, 2016). However, assessments of landscape transience utilising this framework have yet to be combined with ecosystem-level patterning in foliar traits.

In this study, we examine the role of landscape transience in dictating distributions of canopy foliar traits LMA, N, P and Ca across over 1000 ha of humid tropical forests on Mt Kinabalu in Malaysian Borneo. Catchment-scale maps of foliar traits, combined with high-resolution topographic data, allow us to uncover the role hillslope critical zone processes play in organising foliar traits. Here, we assess the geomorphic state of 32 catchments with high-resolution, LiDAR-derived digital elevation models (DEMs). We then identify patterns in canopy foliar traits across these same catchments using foliar trait maps derived from imaging spectroscopy data (Martin *et al*. 2018). The variation in catchment morphologies across the Mt. Kinabalu study area, combined with rock types with distinct geochemical compositions, allowed us to examine the role these patterns in hillslope erosion rates play in organising canopy foliar traits. Using these high-resolution datasets, we ask: Are there systematic ways that hillslope distributions of canopy foliar traits respond to catchment steepening or decaying, across variations in rock type and elevation? This powerful methodological combination provides insight into the role of landscape evolution in ecosystem organisation.

METHODS

Study area

Mt. Kinabalu is a well-known tropical mountain in northern Malaysian Borneo. Its base lies in the biodiverse lowland tropical forests of Southeast Asia and its summit extends above tree line to 4200 m above-sea-level (Fig. 2). The area is estimated to have experienced exhumation rates, the rate at which a unit of buried rock approaches the surface, as rapid as 7 mm/year during the late Miocene and Early Pliocene and exhumation has continued at an estimated long-term rate of 0.5 mm/year (Hutchinson 2005; Hall *et al*. 2009; Sperber 2009; Cottam *et al*. 2013). However, this is likely to be an upper bound for the geological substrates surrounding the granite intrusive that comprises the summit and upper flanks of the mountain (Braun *et al*. 2014). The geology on the flanks of Mt. Kinabalu is primarily composed of ultramafic rock, predominantly serpentinised peridotite and Tertiary sedimentary rock, consisting of shale and sandstone derived from the Trusmadi and Crocker formations (Jacobson 1970; van der Ent *et al*. 2016a). These rock types have distinct geochemistry, with ultramafic and sedimentary having atomic elemental compositions of 3.15% and 0.8% Ca, 0.2% and 0.9% K, 19.4% and 4.1% Mg, 44 $\mu g\ g^{-1}$ and 171 $\mu g\ g^{-1}$ P and 13% and 24 % Si, respectively, based on rocks collected across the Kinabalu elevation gradient and Trusmadi formation by van der Ent et al. We note, however, that since these rock samples were taken from the bottom of soil pits, it is possible that they have undergone some level of chemical alteration (van der Ent *et al.* 2016a).

In addition to the differences in elemental composition between rock types, ultramafic soils have low P and N concentrations, lower quartz content, low Ca:Mg ratios, high concentrations of toxic metals and low water holding capacity when compared with soils that form on sedimentary rock (Kitayama *et al.* 1998, 2000; Kitayama & Aiba 2002; Proctor 2003; van der Ent *et al.* 2018b, a). In addition, at mid elevations soluble P concentrations increase down slope on sedimentary hillslopes, but not on ultramafic hillslopes (Takyu *et al.* 2002).

Plot studies aimed at characterising and assessing the relationship between soil characteristics and foliar traits at four points along the elevation gradient on each substrate found that LMA is higher and foliar N and P concentrations are lower on ultramafic rock (Kitayama & Aiba 2002). In addition, with increasing elevation, these studies found LMA increases and foliar N and P concentrations remain constant (Aiba & Kitayama 1999). The finding of no trend in foliar N and P with elevation was inconsistent with other tropical elevation gradient studies, which have found that elevational trends are contingent on inferred soil quality (Tanner *et al.* 1998; Asner & Martin 2016). Overall, these studies of Mt Kinabalu ecosystems have presented significant evidence to support the theory that variations in soil P availability play a role organising ecosystems across this study area (Kitayama & Aiba 2002; Takyu *et al.* 2002, 2003; Aiba *et al.* 2015; Hidaka & Kitayama 2015). These plot-level, localised studies give us a basis on which to build our understanding of this system. However, their inherent spatial limitation prevents them from capturing the extent of variability that is likely present in complex, mountainous terrain. Here, we analysed 32 catchments across the Mt. Kinabalu gradient, half on ultramafic and half on sedimentary rock, that range in elevation from 700 to 2800 m in order to better represent this variability (Fig. 1, Table S2).

Foliar trait modelling

The foliar trait models used here were developed and documented by Martin *et al.* 2018, after the crown-level methodology described in Chadwick & Asner, 2016. A further summary of these methods and associated field data, as well as details of airborne data collection, are provided in the supplementary information and Figs S1–S3. Briefly, spectrometer data were used to identify crowns visible in the imagery in the field, across this study area, as well as three other lowland sites across Sabah, Malaysia. Leaf samples from crowns in Kinabalu Park were sampled in May 2016 for foliar chemistry and LMA, using protocols documented by the Spectranomics program (https://gao.asu.edu/spectranomics-protocols). The average and range of trait values from foliage sampled at three points along the Kinabalu elevation gradient on both substrates are reported in Table S1 and Fig. S2 for reference. Partial Least Squares Regression (PLSR) models were developed to predict foliar trait values from VSWIR data using calibration and validation crowns, and the final models were

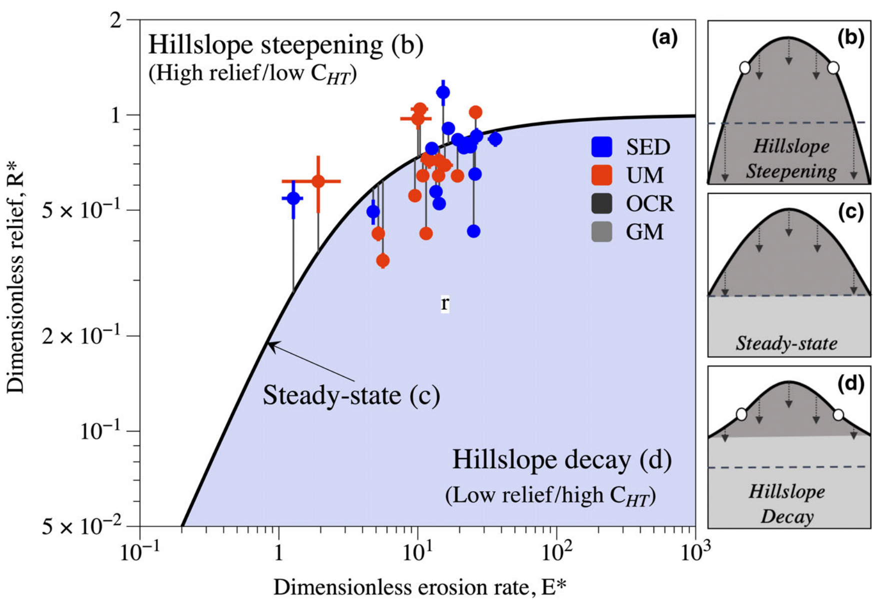


Figure 1 Catchment transience on Mt. Kinabalu. (a) Catchment-level dimensionless erosion rate (E^*) and dimensionless relief values (R^*) plotted relative to the steady-state relationship between E^* and R^* (black curve). Catchment rock type is denoted by colour, with sedimentary and ultramafic in blue and orange, respectively, and error bars show the standard error. Light grey lines connecting catchment points to the steady-state curve indicate the metric of hillslope disequilibrium (*HD*). (b–d) Conceptual diagrams depict different hillslope morphologies corresponding to varying levels of disequilibrium depicted in the main figure, ordered vertically to match the occurrence in (a). (c) steady-state hillslope with the same erosion rate (as depicted by relative length of downward arrows) across all points of the hillslope. (b) steepening hillslope where erosion rates are higher closer to the stream, with transition point indicated with white circles. This hillslope has the same hilltop curvature (C_{HT}) as the steady-state case, but greater relief, in the dimensionless framework it would fall above the steady-state line. (d) decaying hillslope with lower erosion rates closer to the stream, with the transition point indicated with white circles. This hillslope has the same C_{HT} as the steady-state case, but less relief, in the dimensionless framework it would fall below the steady-state line

evaluated against a test hold-out set of crowns which yielded R^2 values of 0.54, 0.65, 0.49 and 0.81 for mass-based foliar N, P, Ca and LMA respectively.

The PLSR models for mass-based foliar N, P, Ca and LMA were applied to spectrometer data collected across the study areas where pixels met the criteria for inclusion. These pixels had NDVI greater than 0.75 and were unshaded at the time of overflight. Pixel shading was determined by a ray tracing algorithm which utilises the sun angle at time of flight and DSM from the LiDAR to determine local inter- and intra-crown, as well as topographic shading (Asner *et al.* 2007). In steep portions of the southern face of Mt. Kinabalu, this resulted in sometimes significant portions of the west facing aspects being excluded due to morning shading unavoidable during the VSWIR survey. We acknowledge this has the potential to introduce bias into our analyses. However, a study examining spatial organisation of dominant species was conducted at 1500 m on the south face of Mt. Kinabalu found that *c.* 50% of dominant species had topographic associations, and while they did not explicitly test the role of aspect, the species maps provided do not provide evidence to support strong association with aspect (Aiba *et al.* 2004). We document the area within each catchment with suitable VSWIR data in Table S2.

Geomorphic analysis

We conducted catchment level geomorphic analysis on the 2 m ground DEM utilising LSDTopoTools software (Mudd et al. 2019). With these tools, we determined that 15 m length scale was the appropriate distance over which to calculate geomorphic parameters (Fig. S4) (Roering *et al.* 2010; Hurst *et al.* 2012). We then identified channel heads, stream networks and delineated second- and third-order catchments (Clubb *et al.* 2014, 2017). We utilised third-order catchments for our analyses when possible, but in some cases selected second-order catchments so they would fall solely within either sedimentary or ultramafic rock (Fig. 2, Table S2). We then used the hillslope trace method in LSDTopoTools to calculate median and standard error values for hilltop curvature (C_{HT}), hillslope length (L_H), relief (R) and slope (S) for the catchments, where hilltops are defined as portions of divides with slopes less than 0.4 (Hurst *et al.* 2012; Grieve *et al.* 2016). We used iterative critical slope (S_c) fitting to estimate the unitless critical slope angles for sandstone (0.9) and ultramafic (0.78) rock types independently (Grieve *et al.* 2016). The median values of L_H, C_{HT} and R, as well as the estimated S_c values for each substrate were used to calculate the observed dimensionless erosion rate (E^*):

$$E^* = \frac{-2C_{HT}L_H}{S_c}$$

and dimensionless relief (R^*):

$$R^* = \frac{R}{S_c L_H}$$

for each catchment and standard error values were propagated through these calculations. For each catchment we used the E^* value to calculate the expected R^* that would be observed if that catchment was in steady-state. We used the difference between the catchment observed R^* value and the expected steady-state R^* as an indicator of landscape transience in catchments, which we refer to as hillslope disequilibrium (*HD*) (Hurst *et al.* 2013; Mudd 2017). We calculate this as the difference in R^* relative to the steady-state prediction because as a catchment moves away from steady-state, the first effect is at the drainages, which changes R, but not C_{HT} (Fig. 1). These values allow us to assess how the observed characteristics of these catchments relate to steady-state expectations of morphology and provide an indicator of hillslope transience.

Within each catchment we calculated relative slope position (RSP) in order to consider the effect of hillslope position while controlling for differing length of hillslopes across and within the study catchments. These calculations were performed using the System for Automated Geoscientific Analyses GIS (SAGA-GIS) software (Conrad *et al.* 2015), implemented in QGIS (QuantumGIS 2018). RSP is unitless and we inverted the standard output values such that ridges have a value of zero and streams or accumulation areas a value of one. This inversion eases the interpretation of results.

Catchment-level trait analyses

For each catchment, foliar trait and RSP values were extracted. Values outside the range of tropical foliar trait values reported in Asner & Martin (2016) were removed (*c.* 1%). From these trait values we calculated the foliar N:P for all pixels. Because LMA and foliar nutrients have been found to be correlated, we extracted the residuals from linear regressions between LMA and foliar nutrient concentrations ($P < 0.01$ in all cases) to assess trends in residual nutrient content. We calculated the relationship between catchment-level mean elevation and mean foliar trait values using ordinary least squares linear regression in R (Team 2014) to determine trends in trait values with elevation.

In order to maintain consistent sample sizes across RSP, for each catchment we randomly selected 100 pixels across five equal RSP contours, and averaged the trait value for each contour bin. All catchments included in these analyses had at least 150 pixels within each contour, for a minimum of 600 m^2 of foliar trait estimates per contour, though most greatly exceeded this minimum and the average number of pixels per catchment was over 28 000 (Table S2). We repeated this process 1000 times. Using the iteratively calculated mean trait values, we determined the slope of the relationship between each binned foliar trait and RSP for each catchment. This determined the average rate of change for each foliar trait from the ridge to valley for each study catchment. We report the rate of change in both trait units as well as in units of standard deviation.

We then assessed the relationship between catchment-level geomorphic characteristics and the rate of change in foliar trait values along hillslopes. We considered the role of catchment level geomorphic characteristics: hillslope disequilibrium, along slope distance and median slope. We used Akaike Information Criterion to select significant predictors in a weighted least squares regression using inverse weighting of the

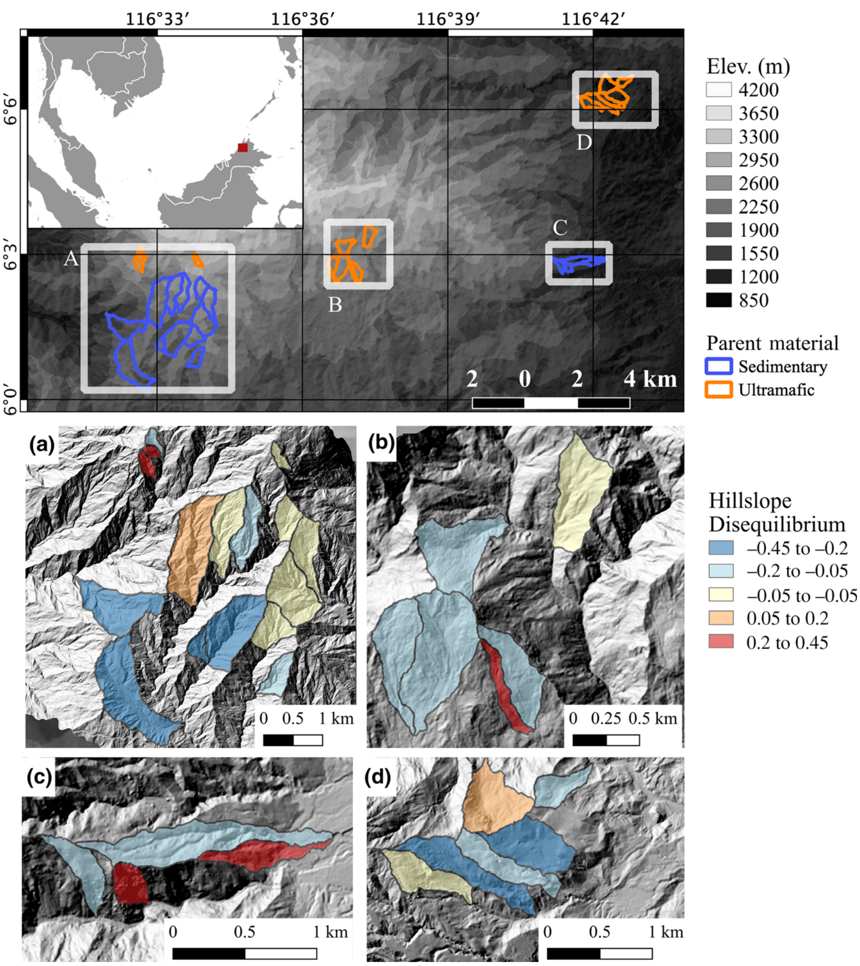


Figure 2 Map of Mt. Kinabalu study area. Primary map displays elevation data with hillshade. Catchments are outlined based on parent material, sedimentary in blue and ultramafic in orange. Catchment inset maps (a–d) show delineated catchments over a LiDAR-derived hillshade. Catchments are coloured by the hillslope disequilibrium (calculation described in Methods), where negative values (cool colours) indicate decaying hillslopes and positive values (warm colours) indicate steepening hillslopes

standard error. Through this process we assessed the relationship between geomorphic characteristics of a catchment and the strength of the relationship between hillslope position and foliar traits.

RESULTS

Catchment average trends in foliar traits

Imaging spectroscopy-based maps showed that catchment-level averages of most foliar traits varied with elevation, but trends were moderated by parent material (Fig. 3). LMA increased with elevation and was higher in catchments underlain by ultramafic rock, though the difference was greater in lower elevation forests. Foliar N and P concentrations declined, on average, with increasing elevation on both substrates, though on ultramafic rock these changes level out at elevations above 2000 m. Ultramafic catchments at the bottom of the elevation gradient had lower foliar N and P concentrations than sedimentary catchments, but concentrations converged between substrates at higher elevations. Foliar Ca decreased with elevation in sedimentary catchments but did not vary with elevation in ultramafic catchments. Rock type consistently exerted a stronger effect on catchment-averaged foliar traits of lowland forests than higher elevation forests (Fig. 3). Within catchment variation in foliar traits was quite high across substrates and elevations, supporting a role for local environmental conditions and species in driving their variability. Our study catchments do not represent elevations from 1000 to 1500 m, and that this gap precludes us from being able to clearly assess where a slope break in the trait–elevation relationships may occur.

Catchment transience

Hillslope morphology suggests that the majority of our study catchments along the Mt. Kinabalu elevation-substrate matrix are in the process of responding to local changes in erosion rate. Catchments across the elevation gradient and on both rock types deviated from the steady-state assumption, with individual catchments either steepening or decaying (Fig. 1, 2, S6). There was not a significant relationship between *HD* and either elevation or average catchment relief (Fig. 2, Fig. S6), suggesting the transience is due to processes other than elevation driven changes in *HD*. Furthermore, *HD* did not systematically vary based on rock type, though sedimentary catchments had sharper hilltop curvatures, and therefore greater estimates of *E**, on average (Fig. S5).

Within catchment trends in foliar traits

In our parameter selection, *HD* was the only significant predictor of the relationship between RSP and foliar traits in all cases where relationships were found (Fig. 4). Catchment

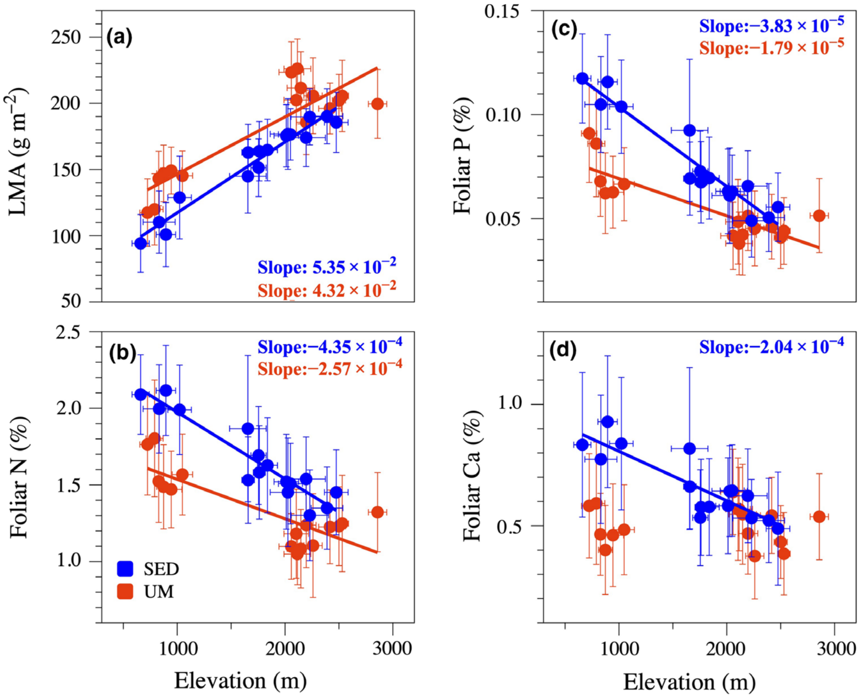


Figure 3 Catchment-level relationships between mean foliar traits and mean elevation, with sedimentary catchments in blue and ultramafic in orange. Foliar nutrient contents are mass based. Error bars indicate standard deviations. Solid lines indicate linear regressions significant at $P < 0.01$

average slope and along slope length were not found to be significant predictors. Foliar N concentrations, on average, increased along hillslope from ridge to valley (positive rate of change values); however, the rate of change was greater in steepening catchments for both rock types (Fig. 4b). LMA decreased from ridge to valley for most catchments, and on both rock types the strength of that relationship increased when moving from decaying to steepening catchments (Fig. 4a). Because LMA and foliar N are widely found to be correlated (Wright *et al*. 2004), we also examined the rate of change of residual foliar N, after accounting for the correlation with LMA (Fig. S4). While catchment-level relationships between *HD* and residual foliar N concentrations decreased on both rock types, the relationship remained significant at the $P = 0.02$ level for catchments on sedimentary rock and was not significant for catchments on ultramafic rock (Fig. S3B).

The rate of change of foliar P concentrations from ridge to valley was positive for the majority of catchments, regardless of rock type or *HD* (Fig. 4c–d, 5). Across both rock types, foliar P increased along slope more strongly in steepening catchments, although rates of change were generally higher on sedimentary rock (Fig. 4c). These trends remained consistent when accounting for the relationship between foliar P and LMA, though the strength of the relationship decreased for residual foliar P (Fig. S4c). Foliar N:P ratios decreased approximately one standard deviation along hillslopes on average, though in catchments on sedimentary rock there was no systematic change associated with *HD* (Fig. S7). Steepening catchments on ultramafic rock had larger shifts in N:P along slope and decaying catchments had lower or no change in N:P ratios along slope.

Finally, while foliar Ca concentrations also tended to increase along hillslope, only catchments on sedimentary rock had increased rates of change in steepening catchments, whereas catchments on ultramafic rock did not show systematic variability in the rate of change of foliar Ca with *HD* (Fig. 4d). The patterns for foliar Ca remained consistent when accounting for the relationship with LMA (Fig. S4d).

DISCUSSION

The role of transient morphology on within-catchment trends in foliar traits

The presence of catchments that range from steepening to decaying within our study region allowed us to determine that these geomorphic states have implications for the distribution of ecosystems characteristics across Mt Kinabalu's complex terrain. We found that geomorphic transience mediates the relationship between hillslope position and spatial organisation of foliar traits. These effects are observed across an elevation gradient and differing rock types in complex, mountainous terrain. Generally, along hillslopes, from ridge to valley, foliar nutrient concentrations increase and LMA decrease (Fig. 4), consistent with other studies of tropical forest variation along topographic gradients (Takyu *et al*. 2002, 2003; Vitousek *et al*. 2003; Chadwick & Asner 2018; Jucker *et al*. 2018). However, it has not been previously possible to put these patterns in the context of geomorphic process at spatial extents and resolutions to understand what drives the strength of these relationships and the consistency of this effect within landscapes or across the tropics. Here, we find that the transient response of hillslope morphology provides evidence that differential erosion across hillslopes alters the correlation between RSP and foliar traits.

Canopies in the majority of catchments close to steady-state had foliar nutrient concentrations that increased from ridge to

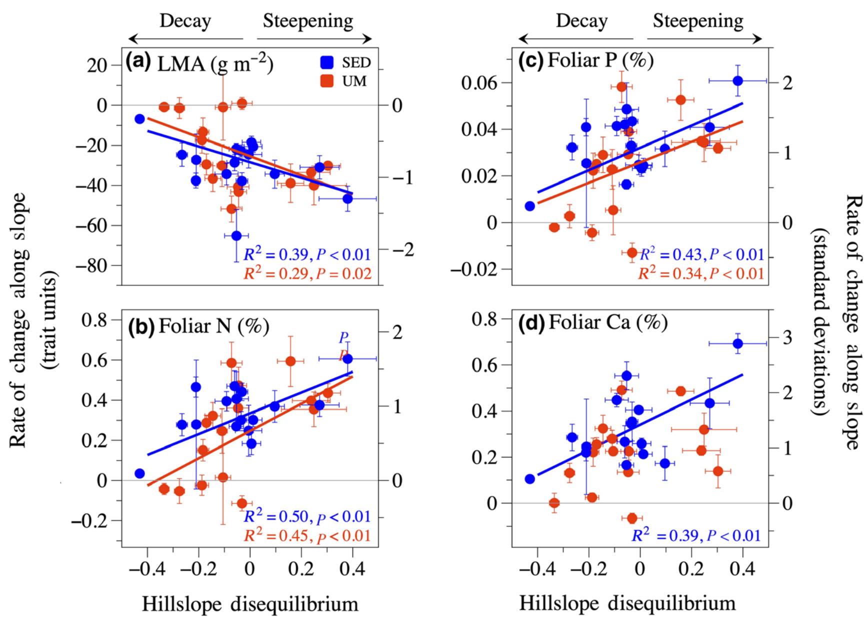
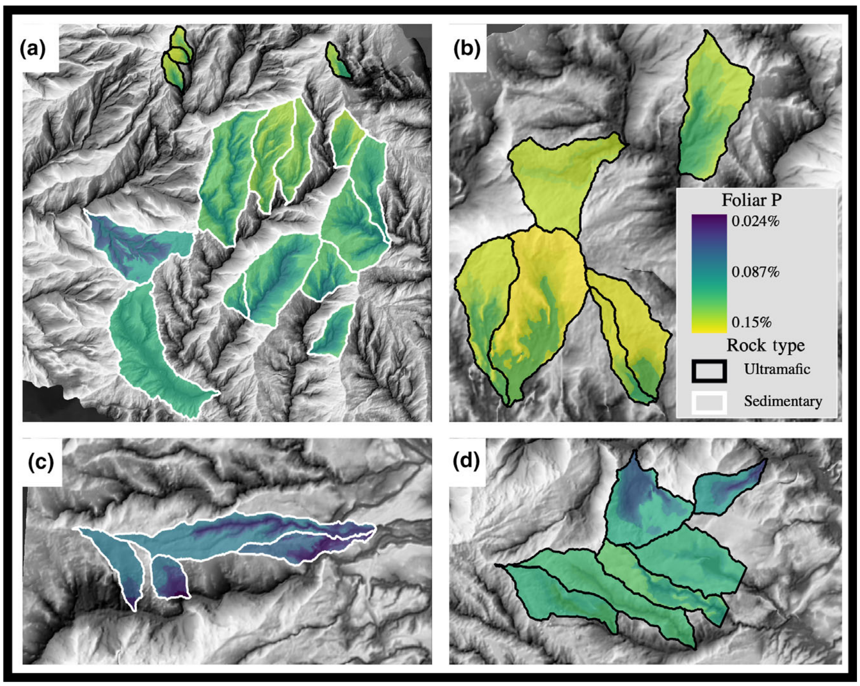


Figure 4 Scatterplots comparing the catchment level hillslope disequilibrium with the rate of change of each foliar trait in units of that trait (right-axis) or standard deviation units for cross comparability (left-axis), with relative slope position (from ridge to valley) within the catchment. Blue and orange indicate catchments in sedimentary and ultramafic rock types respectively. Error bars are standard error. Solid lines indicate regressions with $P < 0.05$. Grey lines are at zero, indicating where there is zero slope in the relationship between the foliar trait and relative hillslope position. Values above this line indicate that the trait increases from ridge to valley and values below indicate the foliar trait declines. Interpretation of (a), for example is the most strongly decaying hillslopes show almost no change in LMA values from ridge to valley (left), and moving along the x-axis, the amount of change in LMA increases, with strongly steepening hillslopes have LMA that decreases from ridge to valley by *c.* 1 standard deviation of the full range of LMA values on the elevation gradient (right). These are mapped out by catchment in Fig. 5 and S9

Figure 5 Maps of the iteratively calculated mean value for foliar P at each contour of relative slope position, similar maps for LMA, Ca and N are provided in supplementary materials. Catchment rock type is indicated by the outline colour: black and white indicate ultramafic and sedimentary respectively. The background is a relative slope position map overlain with a semi-transparent hillshade. These subset areas are indicated on the study area map in Fig. 2



valley (Fig. 4). These increases could be driven by soil creep, transport of litter and dissolved nutrients via overland flow, throughflow and groundwater subsidies to vegetation downslope. It is beyond the scope of this study to untangle the role that each of these processes plays in the downslope accumulation of nutrients in steady-state systems. In steady-state catchments erosion is acting to introduce nutrients into the system at the prevailing rate and this rate is evenly distributed from ridge to valley. Therefore, in theory, erosion should not contribute to nutrient status differentially across hillslopes, though there may be differential chemical vs physical weathering, which could also drive these patters. However, in steepening catchments, foliar traits showed greater shifts in their distributions with changing hillslope position and, conversely, in decaying catchments the foliar traits correlated less with RSP and did not significantly vary in many cases (Fig. 4). These results highlight the importance of erosion as a source of fresh nutrients to ecosystems via the advection of new material into the soil profile. This finding provides insight into the processes that underpin observed topographic variation in vegetation traits and their associated ecosystem functioning that would not be possible from ground-based studies.

Effects of rock type

Our findings suggest that local increases in erosion rate cause greater flux of RDN through the soil column, either enhancing downslope variability in foliar nutrient content in the case of steepening catchments or dampening these patterns in decaying catchments (Fig. 4). Steepening catchments show greater along-slope increases in foliar N and P on both rock types, possibly due to the higher rates of material flux through the soil column in low slope positions causing greater differentiation in soil P availability from primary minerals. In addition, along-slope changes in foliar N:P ratios are moderated by *HD* on ultramafic rock, but not on sedimentary (Fig. S7), suggesting that erosion is particularly important for introducing new weatherable material on ultramafic rock types, which have over three times less rock P and lower soil P availability. These trends in foliar concentrations are consistent with findings that suggest that N and P use is modulated by soil P availability (Hidaka & Kitayama 2015), and further indicate that landscape evolution plays an important role in the spatial distribution of P availability.

Examining patterns in residual foliar N, after accounting for the expected LMA-N relationship suggests that rock N from sedimentary rocks may also play a role in foliar trait distributions. Steepening catchments on sedimentary rocks had greater shifts in residual N along hillslope than their decaying counterparts (Fig. S4b), which may suggest a role for nutrient supplement from rock sources. Increasing numbers of studies have found that rock-derived N, found in sedimentary rocks, plays an important role in meeting the N demand of ecosystems (Morford *et al.* 2011; Houlton *et al.* 2018). This is an interesting area for future work to establish how geomorphological processes influence our growing understanding of the role rock N plays in terrestrial biogeochemistry.

Elevation gradient

The majority of catchment-averaged foliar traits had significant trends with elevation that were generally consistent with previous plot-based findings Fig. 3. Increases in LMA with elevation have been widely observed in tropical regions, including on Mt. Kinabalu (Kitayama & Aiba 2002). Declining foliar N and P concentrations are sometimes observed, especially in association with low nutrient availability (Tanner *et al.* 1998; Asner & Martin 2016). While these trends differ some from previous results across this study area, when focusing on catchments above 1700 m, elevational trends become less pronounced, mirroring previously reported observations (Kitayama & Aiba 2002). This may be attributed to climate playing a stronger role than geology in determination of foliar traits at high elevations. At mid-elevation, our foliar N concentrations, foliar P concentrations and N:P ratios are in keeping with values recently reported from plot work in the area (Hidaka & Kitayama 2015). Foliar Ca shows no catchment-average trend with elevation on ultramafic rock. While on average rock Ca is higher in ultramafic rock, at low elevations it drops to 0.3%, half that of sedimentary rocks, possibly due to increased weathering, which may drive this elevational pattern (van der Ent *et al.* 2016a). Generally, variation between our results and previous studies may be due to greater sampling size and representation of all hillslope positions afforded by airborne data.

Scaling and future directions

While this study provides new insight into linkages between geomorphic process and ecosystem assembly, we were unable to conduct extensive evaluation of soil nutrient status or local erosion rates across these catchments. We instead utilised our understanding of transient landscape morphology and foliar trait responses to biogeochemical gradients to interpret catchment processes. This trade-off allowed us to determine large-scale trends, providing insight into ways we can utilise geomorphic theory in understanding ecological and biogeochemical pattern in tropical mountainous landscapes. The ability to assess these patterns broadly is essential when seeking generalised patterns, as naturally occurring stochasticity within complex terrain could mask large-scale trends.

Despite large variation in foliar traits within catchments across the elevation gradient and between rock types, we nonetheless found significant and consistent effects of landscape transience on hillslope distributions of foliar traits. The catchments we examined span a large elevation gradient with substantial species turnover and high levels of endemism due in part to the geochemical composition of ultramafic rock (Aiba & Kitayama 1999; Proctor 2003; Aiba *et al.* 2015; Merckx *et al.* 2015; van der Ent *et al.* 2016b; Galey *et al.* 2017). Many of the patterns we observed are driven by these shifts in species composition. However, the systematic variation across these 32 catchments is notable and suggests these hillslope level trends are likely general responses of ecosystems to landscape evolution, via organisation of biogeochemical processes across landscapes.

An important next step is to explore the role of geomorphic transience in ecosystem assembly in other tropical systems and to devise methods for scaling hillslope and catchment-level nutrient dynamics across regions. This will be especially valuable in systems, such as this one, where it is not practical or realistic to conduct field sampling at sufficient density to understand systematic spatial variation in foliar traits, soil nutrient status or local erosion rates. Through the integration of high-resolution airborne remote sensing technologies, geomorphic theory and ecological observations we are able to deepen our understanding of the role of landscape evolution in organising these critical ecosystems.

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COMPETING INTERESTS

The authors have no competing interests.

AUTHOR CONTRIBUTIONS

K. D. C. participated in the following CRediT roles: Conceptualisation, Data Curation, Formal Analysis, Investigation, Methodology, Visualisation, Validation, Writing – original draft, review and editing. G. P. A. participated in the following CRediT roles: Supervision, Investigation, Resources, Methodology, Data Curation, Project Administration, Resources, Writing – review and editing.

DATA AVAILABILITY STATEMENT

Data available from the Figshare Repository: https://doi.org/10.6084/m9.figshare.12126864.

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