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Abrupt change in forest height along a tropical elevation gradient detected using airborne lidar

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Abstract: Most research on vegetation in mountain ranges focuses on elevation gradients as climate gradients, but elevation gradients are also the result of geological processes that build and deconstruct mountains. Recent findings from the Luquillo Mountains, Puerto Rico, have raised questions about whether erosion rates that vary due to past tectonic events and are spatially patterned in relation to elevation may drive vegetation patterns along elevation gradients. Here we use airborne light detection and ranging (lidar) technology to observe forest height over the Luquillo Mountain Range. We show that models with different functional forms for the two prominent bedrock types best describe the forest height - elevation patterns. On one bedrock type there are abrupt decreases in forest height with elevation approximated by a sigmoidal function, with the inflection point near the elevation of where other studies have shown there to be a sharp change in erosion rates triggered by a tectonic uplift event that began approximately 4.2 My ago. Our findings are consistent with broad geologically mediated vegetation patterns along the elevation gradient, consistent with a role for mountain building and deconstructing processes.

Keywords: ecology; vegetation; geology; active remote sensing; erosion; tectonics; ^{10}Be; critical zone observatory; long-term ecological research; three-dimensional structure.

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1. Introduction

1.1. Aims

Mountain ranges are often used as ecological laboratories for climate change research [1-3], but elevation gradients are also the result of tectonics and erosion. Erosion rates are important correlates of variation in vegetation cover in mountainous landscapes [4,5]. Differences in erosion patterns can produce soil heterogeneity that influences spatial patterns of vegetation [5]. However, disentangling the relationships between erosion rates and plants requires understanding the root cause of variation in erosion rates. Here we examine vegetation patterns on a tropical elevation gradient where spatial patterns of erosion rates have been directly linked to tectonic uplift history [6,7], providing a novel scenario for understanding vegetation spatial patterns on a tropical elevation gradient.

1.2. Vegetation Observations

Airborne light detection and ranging (lidar) is the state-of-the-art method for observing three-dimensional structural properties of forests at landscape spatial scales [8]. Of all vegetation metrics that can be derived from lidar datasets, maximum height of first returns (e.g. forest height) can be derived most consistently across sensor systems [9]. Forest height is also considered a key ecosystem variable for earth observation [10]. Within sensors systems, forest height correlates strongly with other vegetation metrics such as relative heights (e.g. RH50) and metrics describing the shape of the point cloud or waveform such as the height of maximum laser return density (or height of maximum laser energy) [e.g. 9]. We used lidar-derived forest height to study vegetation patterns at landscape scales in a tropical mountain range.

1.3. Tectonic Uplift and Erosion

The Caribbean Plate underwent tilting approximately 4.2 My ago resulting in the conversion of low elevation islands into high mountaintops [11]. Studies of platform surfaces across Puerto Rico suggest contemporary Puerto Rico was once a paleoisland chain much like the modern Virgin Islands. One platform occurs in the Luquillo Mountains, Puerto Rico [6]. The platform is likely the remnant of a paleoisland, "El Yunque Island", with the paleoshoreline near 600 m elevation [6-7].

The platform is most prominently visible on one of the two main bedrock types, the quartz diorite [6]. Stream longitudinal profiles on the quartz diorite bedrock exhibit sharp changes in gradient, referred to as knickpoints. The knickpoints are clustered at similar elevations across drainage networks. These knickpoints do not coincide with lithological discontinuities, but instead represent the front to an upstream migrating wave of incision that originated at the paleoshoreline [7]. Incision into the surrounding stream slopes has occurred, resulting in steep hillslopes below the knickpoints elevation, but shallow hillslopes above the knickpoints.

Spatially explicit measurement of erosion rates has been conducted on the quartz diorite bedrock both above and below the knickpoints using sampling of quartz grains obtained from stream sediments and measurement of the cosmogenic isotope ^{10}Be [6-7]. The concentration of ^{10}Be in quartz grains depends on the duration of time that the quartz grain was near the soil surface and exposed to cosmic rays, so the concentration of ^{10}Be in quartz together with modeling assumptions can be used to estimate erosion rates. When ^{10}Be is measured in quartz grains sampled from stream sediments, erosion rates for catchments, with the output of the catchment at the sampling location, can be estimated. Data on ^{10}Be in quartz grains sampled above and below knickpoints across drainage networks on the quartz diorite indicate that catchment scale erosion rates change abruptly at the knickpoint elevation, where higher erosion rates occur below the knickpoints than above.

Because erosion causes removal of surface soils at a higher rate below the knickpoints than above, depth to the saprolite is intimately linked to location on the elevation gradient relative to the knickpoints [6,12]. Soils below the knickpoints are shallow with saprolite replenishing minerals that supply nutrients near the soil surface. In contrast, above the knickpoints the soils are generally deep so minerals from the saprolite are far from the surface. Weatherable minerals (e.g. feldspar) are depleted above the knickpoints on the quartz diorite whereas below the knickpoints soils are rich in weatherable minerals [6]. Cations below the knickpoints are at some of the highest concentrations across the entire mountain range, whereas above the knickpoints cation concentrations of soils are relatively low [9]. The consequence is two soil domains on the quartz diorite governed by erosional patterns set in place by tectonic uplift beginning around 4.2 My ago.

1.4. Additional Information From Stream Longitudinal Profiles

Our analysis is focused on the quartz diorite bedrock type, but we also present results from the other main bedrock type, volcaniclastics. Estimates of erosion rates using cosmogenic isotopes are unavailable for the volcanclastics. The primary factor preventing estimating erosion rates on the volcaniclastic bedrock is the very low amount of quartz grains in the rock. Because of this, we emphasize the results from the quartz diorite portion of the mountains. However, the stream longitudinal profiles indicate that erosion rates are likely spatially diffuse along the elevation gradient on the volcaniclastic bedrock [6]. Specifically, the elevation of the knickpoints on the quartz diorite represents a zone where catchment scale erosion rates abruptly decrease over a short range of elevations [6-7]. The absence of prominent knickpoints in stream longitudinal profiles on the volcaniclastic bedrocks together with the overall shallower stream longitudinal profiles suggest that erosion rates on the volcaniclastic bedrock are likely more spatially diffuse across the elevation gradient [6]. Specifically, the absence of knickpoints over the same elevations as on the quartz diorite indicates that the wave of incision moved up the mountain more rapidly, likely due to differences in both physical and chemical properties of the volcaniclastic bedrock [6-7,12]. Including the volcaniclastic bedrock may therefore act as a control for forest height – elevation patterns that result primarily from climate variation in relation to elevation.

1.5. Hypotheses

We expected that forest height would decrease abruptly on the quartz diorite bedrock near the elevation of the knickpoints if mountain building and deconstructing processes are important to influencing spatial patterns of vegetation on the elevation gradient. Overall we expected that forest height would decline with increasing elevation on both bedrock types. We expected that since the volcaniclastics lack knickpoints we would not observe abrupt changes in forest height near the same elevation of the quartz diorite knickpoints, regardless of whether or not plants are responding to edaphic (e.g. soil) properties that covary with erosion on the quartz diorite bedrock. Our approach to testing these hypotheses was to consider different functional forms for the forest height - elevation patterns.

2. Materials and Methods

2.1. Study Area

Over a distance of < 20 km, the Luquillo mountains rise from sea level to > 1,050 m elevation. Mean annual precipitation (MAP) ranges from 2,300 mm yr^{-1} to > 4,500 mm yr^{-1} and mean annual temperature (MAT) declines from 23°C to 19°C. Geologic maps and field observations were used to assign areas of the landscape to quartz diorite or volcaniclastic bedrock [6-7,12]. The area covered corresponds with the extent of the lidar coverage and area of closed canopy forest since 1936 (based on aerial photographs). Lidar coverage was initially planned for the entire mountain range but due to inclement weather on multiple occasions a central portion of the range was not flown. We focused on the elevation interval of 400 m to 800 m that is centered on the quartz diorite knickpoints elevation of approximately 600 m [6-7]. The elevation interval examined included data for 38.95 km^2 with 16.31 km^2 on quartz diorite and 22.64 km^2 on volcaniclastic bedrock. Figure 1 shows a map of the study area.

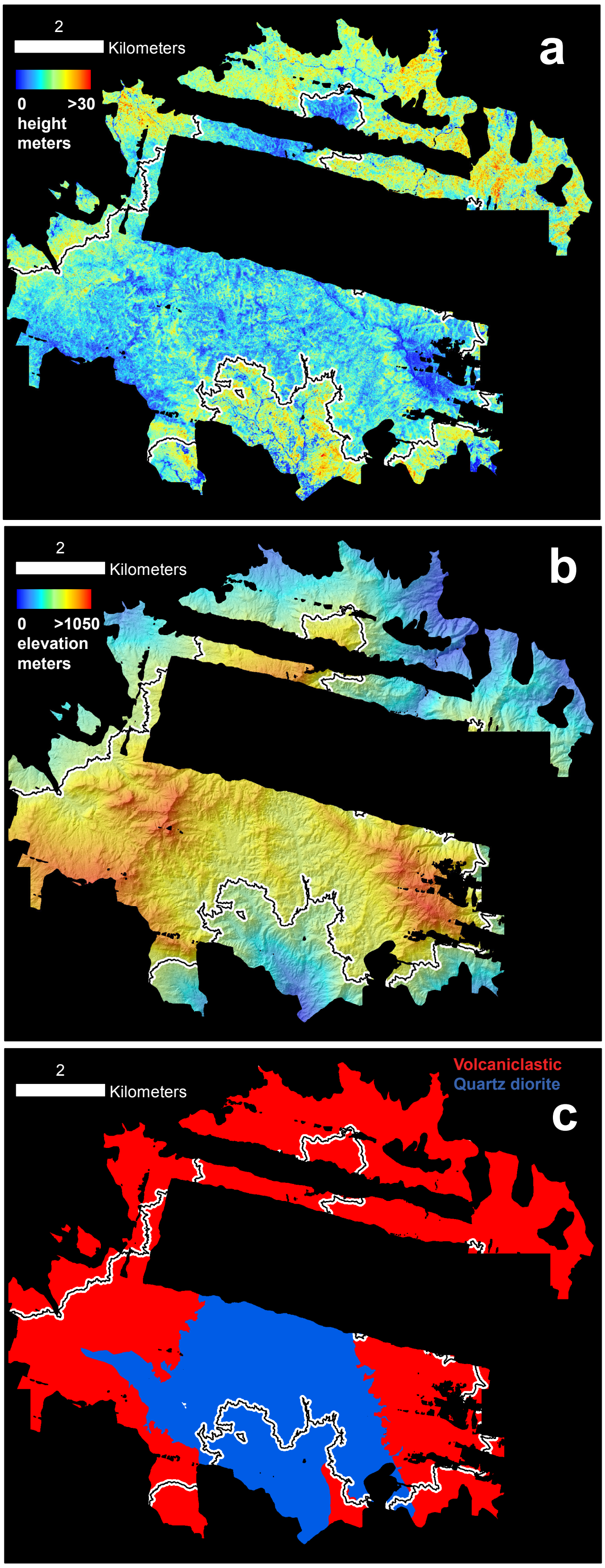

Figure 1. Study Area. (**a**) Forest height at 1-m^2 spatial resolution. (**b**) Elevation at 1-m^2 spatial resolution. (**c**) Map of quartz diorite (blue) and volcaniclastic bedrock (red). The black curve underlain by white illustrates the 600 m contour interval representing the approximate elevation of the paleoshoreline and contemporary elevation of the regional knickpoints on quartz diorite. The study area is restricted to portions of the Luquillo Mountains with airborne lidar data and forest cover in 1936.

2.2. Dataset

Airborne lidar data were collected by the National Center for Airborne Laser Mapping (NCALM) with an Optech GEMINI ALTM (Telodyne Optech, Ontario, Canada) and Applanix POS/AV 510 OEM with embedded BD950 12 channel 10 Hz GPS receiver (Applanix Corp., Ontario, Canada) onboard a Cessna Skymaster (Cessna, Witchita, KS). Data used here are from flights in May 2011. The laser wavelength was 1047 nm, laser pulse frequency was set to 100 Hz, beam divergence was 0.25 mrad (1/e), scan frequency was set to 55 Hz, scan angle was set to ±15°, and scan cutoff was ±2°. Flights were at an altitude of 600 m and speed of 60 m/s. The swath width was 277.04 m with 50% swath overlap. Point density was approximately 14 points m^{-2}. Discrete-returns were horizontally referenced to NAD 1983 UTM Zone 20 N (EPSG: 26920) and vertically referenced to NADV 1988 (EPSG: 5703). Data are available online through OpenTopography (www.opentopography.org).

2.3. Data Processing

Discrete laser returns were rasterized at 1-m^2 spatial resolution into a digital surface model (DSM) and a digital elevation model (DEM). Maximum z-value of the first returns at 1-m^2 spatial resolution were used for the DSM while minimum z-values of the last-return ground classified points were used for the DEM. Elevations for DEM pixels without ground returns were estimated by triangulation of the point cloud. A digital canopy model (DCM) representing forest height was made by taking the difference of the DSM and DEM. Stand-level height was measured using the 1-m spatial resolution DCM through averaging all forest height measurements at 1-ha scale. Resampling was done with Geospatial Data Abstraction Library (GDAL) (www.gdal.org).

2.4. Statistical Analysis

All datasets were analyzed at the hectare scale resulting in sample sizes of 1631- ha on quartz diorite and 2264 - ha on volcaniclastic bedrock. Statistical analyses were done using the R Statistical Computing Environment (R Core Development Team, 2016). Hectare scale data were also aggregated into 10 m elevation bins to statistically summarize aggregated hectare scale data at discrete elevation intervals.

We tested a series of functional forms to model stand-level forest height in relation to elevation. We evaluated a linear functional form $H=\beta_0+\beta_1 x$ (1) and quadratic functional form $H=\beta_0+\beta_1 x+\beta_2 x^2$ (2) where H is height and β_i is the coefficient for elevation x to the power i; and sigmoid (logistic) functional form,

$$H = \frac{1}{1+e^{k(x-x0)}} \times m + b, \quad (1)$$

where k is a rate parameter, $x0$ is the elevation where the inflection point in the height-elevation relationship occurs, while both m and b are scaling factors. We considered models with common parameters for both bedrock types and models with separate bedrock parameters. We also considered models with separate functional forms for the two bedrocks. Model fit was evaluated with Akaike Information Criteria (AIC) with no corrections for sample size because samples sizes were large (e.g. min. N = 1631 ha on quartz diorite). We used least-squares fits for linear and quadratic models, which result in maximum likelihood estimates. The sigmoid model was fit by maximum likelihood using simulated annealing. The optimization procedure was run 1,000 times from a random selection of different starting parameters.

3. Results

Abrupt changes in stand-level forest height occur on the quartz diorite bedrock but not on volcaniclastic bedrock (Fig. 2, Table 1). Models with separate parameters describe forest height-elevation responses across the two bedrock types far better than models with the same parameters for each bedrock type (Table A1-A2). Bedrock-specific parameters using the same functional form provided worse fits to the data than using separate functional forms for each bedrock type (Table A2). The best-fit model included a sigmoidal functional form for quartz diorite bedrock and either linear (AIC = 19407.06) or quadratic functional forms for volcaniclastic bedrock (AIC = 19405.23). Because ΔAIC was small (e.g. < 2) between the two best fit models while ΔAIC was at least > 100 for all other model contrasts (Table A2), there is strong evidence for different functional forms characterizing forest height changes with elevation on quartz diorite relative to volcaniclastic bedrock. At the stand-level, rates of change in forest height with elevation were abrupt on quartz diorite near the knickpoints elevation (k_{QD} = -0.0539 ± 0.0056, $x0_{QD}$ = 621.8 ± 2.142 m; Table 1). The decline in forest height happened over a narrow range of elevations (< 100 m) on the quartz diorite terrain. The inflection point occurred near the elevation of the pronounced knickpoints. On volcaniclastic bedrock, forest height decreased by -0.0182 ± 0.0006 m/m using the linear model (Table 1). Appendix A includes summaries of all other height-elevation models that were tested (Tables A3-A11).

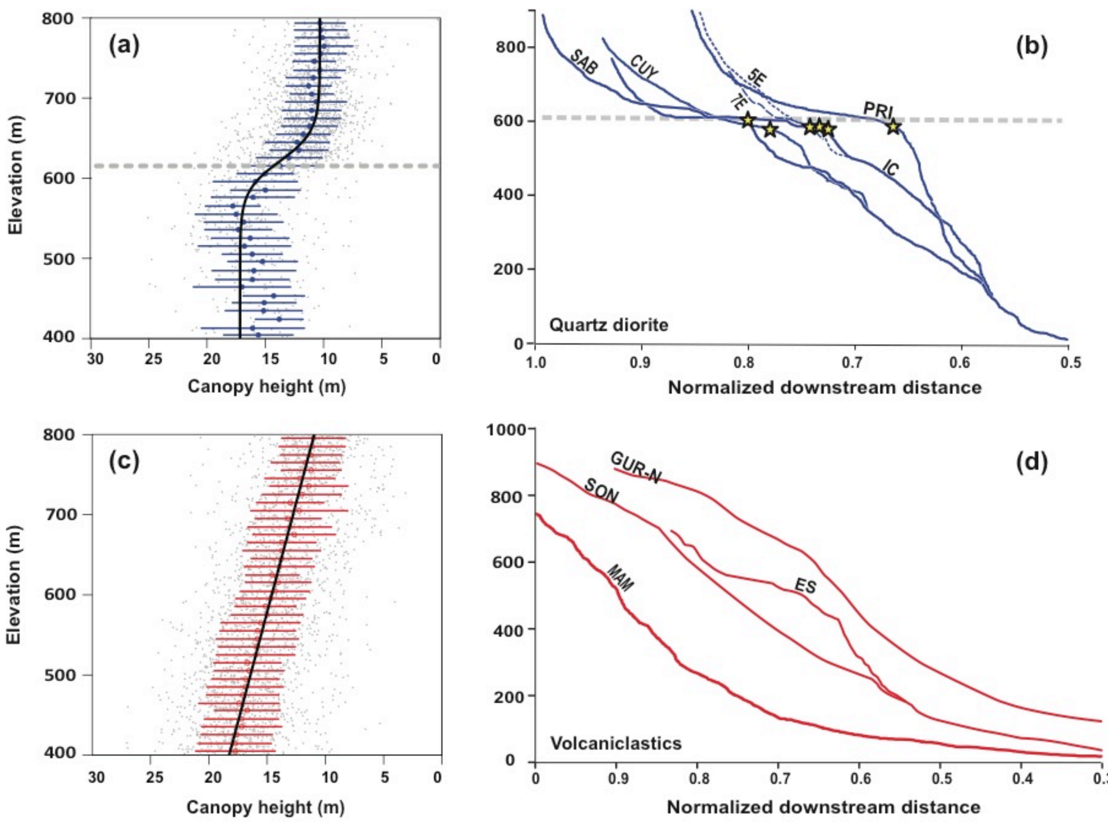

Figure 1. Forest height – elevation patterns are best described using different functional forms for quartz diorite and volcaniclastic bedrock types. (**a**) Sigmoid model of forest height and elevation with inflection point located at 621.8 ± 2.142 m (mean ± S.E.) near the elevation of the (**b**) knickpoints in stream profiles. Stars show the location of the knickpoints. (**c**) A line approximates the forest height - elevation pattern over the same elevation range on volcaniclastics where (**d**) knickpoints are absent from stream profiles. Within (**a**) and (**c**) points indicate means and lines indicate S.D. within 10 m elevation intervals.

Table 1. Model of forest height against elevation. Height-elevation was modeled using a scaled logistic function on quartz diorite (QD) and a linear model on volcaniclastic (VC) bedrock. The model is for the elevation interval between 400 m and 800 m (AIC = 19407.06). All estimates are significant at P < 0.0001 based on z-scores.

Parameter	Estimate	S.E.
L_{QD}	6.805	0.1566
k_{QD}	-0.0539	0.0056
$x0_{QD}$	621.8	2.142
b_{QD}	10.31	0.1093
$\beta0_{VC}$	25.54	0.3350
$\beta1_{VC}$	-0.0182	0.0006

4. Discussion

4.1. Aims revisted

We set out to test whether there were changes in forest height that occur as a result of the tectonic uplift and erosional patterns across a mountain range, to gain insights into the processes that influence vegetation patterns on a tropical elevation gradient. What we found is that forest height changes abruptly near the elevation of knickpoints that demarkate portions of the elevation gradient where erosion rates are high (e.g. lower elevations) from portions of the elevation gradient where erosion rates are low (e.g. higher elevations) on the quartz diorite bedrock type. We also compared results from the quartz diorite bedrock where erosion rates have been measured directly using cosmogenic isotopes and where pronounced knickpoints are present, to the bedrock without directly measured erosion rates, but that lacks the knickpoints. Our results show that on the bedrock without the pronounced knickpoints, presumably where there are not sharp changes in erosion rates occuring over similar elevations, the forest height – elevation patterns are well approximated as linear. Forest height on the quartz diorite could vary abruptly due to sharp decreases in productivity without a change in species composition or may result from abrupt changes in species composition.

4.2. General Importance

These findings may have general importance for understanding vegetation patterns in mountain ranges. Climate is often viewed as the primary driver of vegetation patterns in mountains and elevation gradients are correctly assumed to be climate gradients [1]. Nevertheless, elevation gradients are also edaphic gradients, in part due to climate, but also due to geological reasons, including spatial variation in bedrock types [13-14], but also due to the land surface dynamics that depend on tectonics and erosion. Soil variation is generally important to understanding vegetation patterns in tropical forests [15-18], but the role of soils along elevation gradients is not well understood.

One of the most general patterns in biogeography is the mass-elevation effect [19-20] where rates of change in forest properties vary as a function of mountain size and proximity to other mountains or large water bodies. Large mountains have slower rates of change in forest properties than do smaller mountains. Hypotheses to explain the mass-elevation effect fall into two categories: (1) direct climate hypotheses and (2) indirect climate hypotheses. The primary indirect climate hypothesis is that increasing cloud cover at lower elevations in small mountains near large water bodies results in decreased rates of organic matter mineralization in soils, thereby decreasing rates of nutrient cycling and nutrient supply for plants, with plant productivity and species distributions along elevation gradients limited by nutrient availability. These hypotheses have been difficult to test, but we suggest that using natural experiments where geological factors cause variation in soil nutrient availability could provide important insights into understanding the role of bottom-up controls on phenomena such as the mass-elevation effect.

5. Conclusions

The geological processes that build and deconstruct mountains play a prominent role in spatial patterns of vegetation in relation to elevation in the Luquillo Mountains.

Supplementary Materials: The following are available online at www.mdpi.com/link, Supplementary Results.

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Conflicts of Interest: The authors declare no conflict of interest.

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