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EFFECTS OF TOPOGRAPHY ON TROPICAL FOREST STRUCTURE DEPEND ON CLIMATE CONTEXT

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ABSTRACT

1. Topography affects abiotic conditions which can influence the structure, function, and dynamics of ecological communities. An increasing number of studies have demonstrated biological consequences of fine-scale topographic heterogeneity but we have a limited understanding of how these effects depend on the climate context.

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2. We merged high-resolution (1 m^2) data on topography and canopy height derived from airborne lidar with ground-based data from 15 forest plots in Puerto Rico distributed along a precipitation gradient spanning ca. 800 to 3,500 mm yr^{-1}. Ground-based data included species composition, estimated above-ground biomass (AGB), and two key functional traits (wood density and leaf mass per area, LMA) that reflect resource-use strategies and a trade-off between hydraulic safety and hydraulic efficiency. We used hierarchical Bayesian models to evaluate how the interaction between topography × climate is related to metrics of forest structure (i.e., canopy height and AGB), as well as taxonomic and functional alpha- and beta-diversity.

3. Fine-scale topography (characterized with the topographic wetness index, TWI) significantly affected forest structure and the strength (and in some cases direction) of these effects varied across the precipitation gradient. In all plots, canopy height increased with topographic wetness but the effect was much stronger in dry compared to wet forest plots. In dry forest plots, topographically wetter microsites also had higher levels of AGB but in wet forest plots, topographically drier microsites had higher AGB.

4. Fine-scale topography influenced functional composition but had only weak or non-significant effects on taxonomic and functional alpha- and beta-diversity. For instance, community-weighted wood density followed a similar pattern to AGB across plots. We also found a marginally significant association between variation of wood density and topographic heterogeneity that depended on climate context.

Synthesis: The effects of fine-scale topographic heterogeneity on tropical forest structure and composition depend on the climate context. Our study demonstrates how a stronger integration of topographic heterogeneity across precipitation gradients could improve estimates of forest structure and biomass, and may provide insight to the ways that topography might mediate species responses to drought and climate change.

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INTRODUCTION

Topography profoundly affects abiotic conditions which, in turn, influence the structure, function, and dynamics of ecological communities (Janzen 1967; Ghalambor *et al.* 2006; Baldeck *et al.* 2012; Moeslund *et al.* 2013; Sundqvist *et al.* 2013; Féret & Asner 2014; Fortunel *et al.* 2018; Jucker *et al.* 2018). Over large spatial and temporal scales, topography shapes climate regimes and influences diversification processes (Molnar & England 1990; Badgley *et al.* 2017; Antonelli *et al.* 2018). At local scales, topography affects thermal, hydrologic, and edaphic conditions (Silver *et al.* 1999; Daws *et al.* 2002; Dobrowski *et al.* 2009; Moeslund *et al.* 2013; Werner & Homeier 2014; Chadwick & Asner 2016). Until recently, however, a lack of high-resolution topography data has hampered our ability to quantify the biological implications of fine-scale topographic heterogeneity. Advances in remote sensing are providing new opportunities to elucidate the influence of fine-scale topographic heterogeneity on the composition and dynamics of ecosystems (e.g., Féret & Asner 2014; Mascaro *et al.* 2014; Jucker *et al.* 2018). Although an increasing number of studies have demonstrated the biological consequences for fine-scale topographic heterogeneity, we currently have a limited understanding of how these topographical effects may depend on the climate context (Lenoir *et al.* 2016). Addressing this knowledge gap will clarify links between environmental heterogeneity and ecosystem structure and diversity, including a more nuanced understanding of ecosystem responses to climate change.

In forests, local topographic heterogeneity is linked with a broad set of abiotic conditions (e.g., soil water availability, nutrient content and soil texture, microclimate, exposure, flood regimes) that can influence stand structure, dynamics, and composition (Silver *et al.* 1999; Daws *et al.* 2002; Dobrowski *et al.* 2009; Werner & Homeier 2014; Chadwick & Asner 2016; Uriarte *et al.* 2018). Unsurprisingly, numerous studies have identified topographically-mediated habitat associations among tropical tree species (Harms *et al.* 2001; Russo *et al.* 2005; Comita & Engelbrecht 2009). In some cases, species' traits have been linked with their topographic associations, illustrating the physiological mechanisms that generate and reinforce local habitat associations (Silvertown *et al.* 2015; Cosme *et al.* 2017; Fortunel *et al.* 2018). For example, ridge-associated species often have traits enabling them to cope with drought and nutrient limitation ('conservative' resource-use traits such as high wood density and leaf mass per area, LMA), whereas species associated with the more mesic and fertile conditions of valleys tend to have traits more strongly associated with rapid growth

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(e.g., low wood density and LMA) (Johnston 1992; Paoli 2006; Cosme *et al.* 2017; Fortunel *et al.* 2018). Links between topography, abiotic conditions, and species traits can generate variation in other properties of forests including diversity patterns and biomass (e.g., Jucker *et al.* 2018).

To date, most studies that have examined the effects of fine-scale topography on forest structure and composition have focused on single plots or areas with relatively uniform climate (Baldeck *et al.* 2012; Féret & Asner 2014; Jucker *et al.* 2018). These studies provide a strong foundation for understanding the complex ways that topography influences abiotic conditions. However, the impacts of topographically-mediated abiotic gradients at the local scale may depend on the climatic context. For example, local variation in soil moisture (e.g., from valleys to ridges) is likely to represent a more biologically meaningful shift in water availability compared to average conditions in seasonally dry forests compared to aseasonal wet forests (Fig. 1, arrows 1 & 2). As a result, we may expect metrics of forest structure that are sensitive to water availability (i.e., canopy height, biomass) to respond more strongly to topographic variation in seasonally dry forests compared to aseasonal wet forests. Nonetheless, drought does occur in aseasonal rain forests and hydrological aspects of microtopography can also be important in areas that generally receive ample rainfall on an annual basis (Johnston 1992; Uriarte *et al.* 2018). In wet forests, however, topographically wet microsites can be frequently flooded and so the effects of buffered soil moisture during relatively short-term droughts may be counteracted by physiological stress of anoxia and inundation during wet periods (Silver *et al.* 1999; Peña & Duque 2013; Silva *et al.* 2013). In other words, excess moisture under typical climate conditions could exert greater selective pressure on composition of wet forests than short-term droughts.

Fine-scale topographic heterogeneity may influence local diversity patterns in ways that mirror the effects on forest structure. For example, if topographical effects on e.g. soil moisture are more biologically meaningful in dry forests than wet forests, fine-scale topographic heterogeneity may be expected to have a more pronounced effect on elevating local species diversity in dry forests compared to wet forests. Topographically-mediated diversity gradients could emerge from sorting of species based on, for example, hydrological niche differences (Silvertown *et al.* 2015). From this perspective, we might expect aspects of functional diversity that reflect hydrological niches to exhibit stronger associations with topographic conditions than species diversity, *per se*. Overall, fine-scale topographic heterogeneity may more strongly affect structure and composition of seasonally dry

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forests compared to aseasonal wet forests if the magnitude of variation in topographically-mediated abiotic conditions in dry forests constitutes a more biologically significant difference.

A contrasting prediction can be developed using a rationale parallel to Janzen's (1967) hypothesis that elevational gradients act as stronger barriers to dispersal in the tropics compared to temperate regions. The underlying rationale for his hypothesis is that tropical species are likely to have evolved narrow physiological tolerances because they occupy areas with relatively stable climatic conditions compared to temperate species that occupy areas with high degrees of seasonal and interannual climate variability (Janzen 1967; Ghalambor *et al.* 2006). A topographic corollary is that species occupying areas with highly seasonal climates might be able to tolerate a broader range of conditions whereas species that occupy areas with less seasonal (more uniform) climate regimes may be adapted to a narrower range of local conditions. As a result, topographically-mediated habitat heterogeneity could affect structure and composition of aseasonal wet forests more strongly than seasonal dry forests (Fig. 1). Janzen's hypothesis has been promoted to explain other large-scale ecological patterns (e.g. the latitudinal gradients in species range size via the 'climatic variability hypothesis' (Stevens 1989)) but, to our knowledge, it has not been evaluated in the context of fine-scale topographic associations. In general, the myriad ways that topography mediates abiotic conditions suggests likely interactions with broader scale climatic conditions but these have not yet been carefully studied.

We tested the general hypothesis that microtopography interacts with climate (i.e., total annual rainfall and its seasonality) to influence tropical forest community structure and composition. To do so, we merged high-resolution (1 m^2) data on topography and canopy height derived from airborne lidar with ground-based data from 15 forest plots located across a precipitation gradient that spans from ca. 800 to 3,500 mm yr^{-1} (Fig. 2). We evaluated how topography × climate interactions are related to aspects of forest structure including canopy height and above-ground biomass. We also included information on species diversity and functional traits to explore the implications of topography × climate interactions for the taxonomic and functional composition of forests at two spatial scales (within and among 10 m × 10 m quadrats in each plot) . We addressed the following specific questions:

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1. How does the influence of topography on forest structure (i.e., canopy height and above-ground biomass) and functional composition vary across the precipitation gradient?

(1.1) In the dry forest, we expect taller canopies and greater above-ground biomass in topographic positions with greater soil moisture (i.e., valleys). In the wet forest, we expect the same but weaker trend because water is generally less limiting. However, the opposite trend could emerge in wetter forests (i.e., taller canopies on ridges) if valleys are routinely exposed to unfavourable conditions for growth such as water-logging and anoxia.

(1.2) Based on a tradeoff between hydraulic safety and efficiency, we expect trees in topographically wet microsites to have, on average, hydraulically efficient functional strategies (i.e., lower wood density and LMA) compared to trees in topographically dry microsites. We expect this association to be stronger in dry forests due to an elevated risk of drought-induced mortality and more water-limited growth.

2. How does the influence of topography on tree diversity vary across the precipitation gradient?

(2.1) If fine-scale topography promotes species co-occurrence (e.g., via niche partitioning), we expect sites with higher topographic heterogeneity to comprise more diverse tree assemblages, in terms of both taxonomic and functional diversity.

(2.2) If the magnitude of topographically-mediated habitat heterogeneity is more biologically significant in seasonally dry forests compared to aseasonal wet forests, we expect higher within-site taxonomic and functional diversity in seasonally dry forests than in aseasonal wet forests. Alternatively, if species that occupy seasonally dry forests have broader physiological tolerances compared to species that occupy aseasonal forests, we may expect topography to more strongly mediate taxonomic and functional diversity in aseasonal forests.

MATERIALS AND METHODS

Study area, forest plot, and functional trait data

Our study is based on data from the island of Puerto Rico, which encompasses broad gradients of climate, edaphic conditions, and topography (Miller & Lugo 2009; Muscarella *et al.* 2016b). We analysed data from 15 forest plots (censused between 2012 - 2015) where all individual trees ≥2.5 cm DBH (diameter at 1.3 m above the ground) were identified, measured, and mapped into 10 m × 10

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m quadrats (Fig. 2; Table S1). All plots are located in mature forests that were not subject to major human disturbance for at least the 80 years prior to data collection based on historical records. Additionally, plots had no sign of recent natural disturbance during data collection – the most recent major hurricane prior to data collection was Georges in 1998. Most plots (12/15) measure 50 m x 50 m (0.25-ha) but we also included data from three larger plots. Specifically, we included a 5.24-ha portion of the Luquillo Forest Dynamics Plot (LFDP) classified as 'low intensity land use history' based on Thompson *et al*. (2002). We also included a 1-ha plot in the El Yunque National Forest (ELV1), as well as the 4-ha Guánica Forest Dynamics Plot (GFDP) in the dry forest. The plots vary with respect to mean annual precipitation (ranging from ca. 800 - 3,500 mm yr^{-1}) as well as precipitation seasonality (i.e., the coefficient of variation of monthly mean precipitation) (Daly *et al.* 2003) (Table S1). Overall, these two variables are negatively correlated but the relationship is decoupled for sites that receive intermediate levels of annual precipitation (Fig. 3). The plots occur across a variety of soil types derived from two main parent materials: volcanic and limestone (Muscarella *et al.* 2016b). Plots on limestone soils tend to occur at relatively low elevation and generally receive less precipitation than the typically higher elevation, volcanic soil plots (Figs 2 and 3). Water retention capacity is also lower in limestone soils compared to volcanic soils, which can exacerbate water stress in these sites (Miller & Lugo 2009). Table S1 provides additional summary data.

We focus on two traits related to plant water use and carbon acquisition strategies: wood density (g cm^{-3}) and leaf mass per area (LMA; g cm^{-2}). We combined trait data from prior work for this analysis (Swenson & Umana 2015; Muscarella & Uriarte 2016; Muscarella *et al.* 2016a; Muscarella *et al.* 2016b; Umaña *et al.* 2016). Overall, traits were measured using standard protocols (Pérez-Harguindeguy *et al.* 2013) on 1-32 individuals (mean = 9) for a total of 308 species. To incorporate a potential effect of intraspecific trait variation in our analyses, we separately measured traits on individuals in each protected area and then calculated a mean trait value for each species in each protected area where it occurred. We then calculated community-weighted mean (CWM) values for each trait in each 10 m × 10 m quadrat based on relative basal area of species in the quadrat and their site-specific species-mean trait values.

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We estimated above-ground biomass (AGB; Mg) for each stem based on its diameter and site-specific species-mean value of wood density using the equation of Chave *et al*. (2014), which integrates environmental conditions with allometric relationships (Réjou-Méchain *et al.* 2017). We used a separate approach (i.e., the allometric equation developed by Scatena *et al*. (1993)) to estimate AGB for the only common palm in our dataset, *Prestoea montana*, which represents 5% of the total stems in our full dataset and up to 30% of the individuals in the wet forest plots.

Remote sensing and data synthesis

High resolution (1 m^2) data on elevation and canopy height were derived from small footprint airborne lidar data acquired in March 2017 with NASA Goddard's Lidar, Hyperspectral, and Thermal (G-LiHT) Airborne Imager (Cook *et al.* 2013). Note that lidar data used here were collected prior to island-wide damages from Hurricane Maria. Parallel lidar transects included 30-50% overlap; total swath width was variable, depending on the allocation of flight lines to each plot location. Most plots had 3 overlapping flight lines, thereby extending the swath width to 700-800 m, but some had a single line of ~300 m width. On average, point density for the full lidar campaign was 12 pulses per m^2, with 1-3 returns per pulse. This density has been shown to be adequate to retrieve accurate topography beneath a tropical forest canopy on steep terrain (Leitold *et al.* 2015). All lidar data products used in this study, as well as metadata and additional details are available from the G-LiHT website (glihtdata.gsfc.nasa.gov).

To merge the airborne lidar data with the ground-based plot data, we recorded geographic coordinates for the corners of each plot to within ~15 cm precision using a Garmin dGPS unit (Garmin, USA). We used these points to generate a regular grid of 10 m × 10 m quadrats in each plot that correspond to quadrats in our field measured tree data. For each quadrat, we computed mean elevation and slope directly from the lidar-derived 1 m^2 digital terrain model (DTM). To better understand how topographical conditions mediate water availability for plants, we used the DTM to calculate the topographic wetness index (TWI) for each 1 m^2 grid cell using the 'dynatopmodel' R package (Metcalfe et al. 2015; 2018). The (unitless) TWI is a function of the upstream area, a, and slope, b, of a grid cell such that: $\ln a/\tan(b)$ (Beven & Kirkby 1979; Metcalfe et al. 2015). We refer especially to Metcalfe *et al*. (2015; 2018) for further details on the algorithms used to compute TWI. Two considerations when calculating TWI are the extent and grain of the input topographical data. We

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compared TWI values generated with three different buffer extents around our plots (25 m, 100 m, and 200 m) as well as three grain sizes of the DTM (1 m, 10 m, and 20 m). TWI values calculated with different buffer extents were highly correlated for a given grain size (Pearson's r > 0.88; Fig. S1). Values of TWI based on the 1 m, 10 m, and 20 m resolution DTM were also highly correlated (Pearson's r = 0.70-0.94; Table S3) and we present results using a 100 m buffer and the native 1 m DTM in order to represent fine-scale topographical effects on soil moisture. High TWI values indicate grid cells with topographical characteristics favourable for accumulating higher levels of soil moisture, and vice versa. After calculating TWI for each 1 m^2 grid cell, we used the mean and standard deviation of TWI values of grid cells in each 10 m × 10 m quadrat for comparison with ground-based data (Fig. S2). To better understand how the TWI metric relates to other commonly used topographic indices, we examined the relationships between the TWI and slope as well as the topographic position index, an index of curvature that compares the elevation of each focal grid cell to the average elevation of a neighborhood around that cell.

Statistical analyses

To address our first question about how topography and climate jointly affect forest structure and composition, we first quantified mean canopy height (m) using lidar data and above-ground biomass (AGB; Mg) using ground-based estimates. To characterize functional composition, we calculated community-weighted mean (CWM) values of wood density and LMA. These first four response variables (i.e., canopy height, AGB, and CWM wood density and LMA) describe forest structure and functional composition in each 10 m × 10 m quadrat of all plots.

To address our second question about topographic and climatic effects on diversity, we quantified taxonomic and functional diversity at two scales: α-diversity (i.e., within each quadrat) and β-diversity (i.e., pairwise variation among all quadrats in each plot). For taxonomic α-diversity, we calculated species richness using individual-based rarefaction in the 'vegan' R package (Oksanen *et al.* 2013). We used the minimum number of stems found in a single quadrat (4) as the minimum stem sample for individual-based rarefaction (results were qualitatively identical when rarefying to 10 individuals). For functional α-diversity, we calculated the standardized effect size of mean pairwise distance in trait space (i.e. SES.MPD) for each of the two focal traits using the 'picante' R package (Kembel *et al.* 2010). Specifically, SES.MPD = (r_{obs} – mean (r_{rand})) / sd (r_{rand}), where r is the mean

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distance in trait space among individuals in a quadrat. r_{obs} is the observed value of MPD while r_{rand} is a vector of MPD values based on a null model. For the null model, we generated 999 null communities for each quadrat by randomizing the plot-level community matrix and calculating r_{rand} during each iteration. This approach maintains observed species occupancy rates and quadrat-level species richness while randomizing the trait values of species found within a plot. Negative SES.MPD values indicate functional 'clustering' whereas positive values indicate functional 'evenness' (i.e., co-occurring species are more or less functionally similar than expected by chance). For taxonomic β-diversity, we used the method of Chao *et al*. (2005) from the 'vegan' R package (Oksanen *et al.* 2013), which is robust to sample size differences. Finally, for functional β-diversity, we calculated the standardized effect size of functional β-diversity (SES. β-FD) using the 'comdist' function of the 'picante' R package (Kembel *et al.* 2010) in combination with the randomization procedure described above, which helps account for differences in species richness between quadrats.

We built a 2-level hierarchical Bayesian model to examine the interactive effects of topography and climate on each response variable described above. The first level was:

$$y_{ip} \sim Normal(\alpha_{0p} + \beta_{0p} \times TOP_{ip}) \qquad \text{[eqn 1]}$$

where y_{ip} is the observed value of one of the response variables from quadrat *i* in plot *p* and TOP_{ip} is the value of the topographic covariate (*see below*) for quadrat *i* in plot *p.* Parameters α_{0p} and β_{0p} are plot-specific intercepts and slopes for plot *p*, respectively, predicted by two second-level regressions:

$$\alpha_{0p} \sim Normal(\alpha_{1.1} + \beta_{1.1} \times PPT_p + \beta_{2.1} \times soil_p) \quad \text{[eqn 2]}$$

$$\beta_{0p} \sim Normal(\alpha_{1.2} + \beta_{1.2} \times PPT_p) \qquad \text{[eqn 3]}$$

where PPT_p is the value of precipitation for plot *p* (we compared models with mean annual precipitation or precipitation seasonality; see below), and $soil_p$ is the categorical soil type for plot *p* (limestone vs. volcanic). Hyperparameters $\alpha_{1.1}$, $\beta_{1.1}$, and $\beta_{2.1}$ represent the plot-specific average value of the response variable ($\overline{y_p}$, e.g., canopy height) and its mean response to precipitation and soil type, respectively. Hyperparameters $\alpha_{1.2}$ and $\beta_{1.2}$ represent the plot-specific average effect of TOP on y and its mean response to precipitation, respectively. We did not include soil type as a predictor in Eqn 3 because of the limited number of plots within each soil type. A value of hyperparameter $\beta_{1\cdot2}$ that differs significantly from zero (i.e., 95% credible intervals do not overlap zero) indicates that the effect of TWI varies significantly along the precipitation gradient. Prior to analysis, we centred and scaled all variables within plots by subtracting the plot-specific mean and dividing by the plot-specific

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standard deviation. This approach facilitates parameter estimation and allows us to interpret the effect of topography relative to the magnitude of plot-scale variation of topography and each response variable (Gelman & Hill 2006). In other words, the standardization allowed us to quantify the effects of one unit change in local topography on one unit change in the local response variable.

To address our first question (*How does the influence of topography on forest structure and composition vary across the precipitation gradient?*), we fit the model described above using canopy height, AGB, or CWM trait values as the response variable and the corresponding values of TWI and either mean annual precipitation or plot-level precipitation seasonality as predictor variables. To address our second question (*How does the influence of topography on tree diversity vary across the precipitation gradient?*), we first fit the model above using either taxonomic or functional α-diversity as the response variable and the corresponding values of standard deviation of TWI within the quadrat and either mean annual precipitation or precipitation seasonality as the predictor variables. We then fit the same model using taxonomic or functional β-diversity as the response variable and the corresponding absolute pairwise difference of mean TWI between quadrats as the predictor variable. We completed all analyses in R v 3.5.1 (R Development Core Team 2018) and fit models with JAGS 4.3.0 (Plummer 2015) using the 'runjags' package (Denwood 2016). Details on model fit and full parameter estimates are provided in Table S2 and the JAGS model is provided in Appendix 1.

RESULTS

Across the 15 study plots, we recorded a broad range of variation in terms of canopy height (mean = 6.8 – 21.9 m; maximum = 27.1 – 49.2 m), stem density (1,471 – 10,832 stems ≥2.5 cm DBH ha^{-1}), and AGB (63.4 – 403.8 Mg ha^{-1}). Our ground-based census included a total of 62,734 individual trees ≥2.5 cm DBH belonging to 289 species. Species mean wood density ranged from 0.29 – 1.03 g cm^{-3} and LMA ranged from 15.9 – 388.0 g cm^{-2}. Across all plots, quadrat-mean values of TWI were negatively correlated with slope (Pearson's r = -0.41) and the topographic position index (an index of curvature) (Pearson's r = -0.52) (See Table S3). These relationships indicate that, on average and as expected from other studies, quadrats with more convex curvature and steeper slopes tend to have lower values for the TWI.

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How does the influence of topography on forest structure and functional composition vary across the precipitation gradient?

Across plots, lidar-derived canopy height increased with the TWI indicating that topographically wetter microsites have taller canopies across the climate gradient (Fig. 4A, D). In addition, the strength of this relationship (i.e., the magnitude of the fitted plot-specific slopes, β_{0p}) increased with precipitation seasonality. In other words, the plot with the most seasonal precipitation regime and lowest annual rainfall (the GFDP) had the largest relative increase of canopy height with TWI while the three least seasonal plots (which also receive the highest total rainfall) showed relatively modest or non-significant increases of canopy height with TWI (Fig. 4D).

Overall, canopy height was strongly correlated with AGB (Pearson's r for $\log_{10}$ AGB vs. $\log_{10}$ canopy height = 0.74) but, interestingly, the effects of topography on AGB across the rainfall gradient did not entirely mirror the results for canopy height. Specifically, only in the driest site did topographically wetter quadrats have significantly higher relative values of AGB (Fig. 4C, F). In the two wettest plots, in contrast, topographically wetter quadrats actually tended to have lower AGB, indicating a decoupling of AGB and canopy height at the local scale in some of the wetter plots.

The effect of topography on community-mean wood density of tree communities varied across the climate gradient. In particular, topographically wet microsites in the two highest rainfall plots were dominated by trees and palms with relatively low wood density (Fig. 4B, E). In the driest plot, in contrast, trees in topographically wet microsites had, on average, somewhat higher wood density than trees in topographically dry microsites although the interaction was not statistically significant for this plot. The relationship between TWI and community-mean values of LMA was less pronounced (Fig. S3). Across plots, wetter quadrats tended to comprise tree communities with relatively low values of LMA (negative intercept in Fig. S3B) but there was no significant interaction with mean annual precipitation or precipitation seasonality. Soil type did not have a significant independent effect in any of the models (Table S2).

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How does the influence of topography on tree diversity vary across the precipitation gradient? Within-quadrat topographic heterogeneity (measured as the standard deviation of TWI values within a quadrat) was significantly related to rarefied species richness in only a few plots (including the wettest two plots and the driest plot) where, surprisingly, more topographically heterogeneous quadrats tended to have lower taxonomic diversity (Fig. 5A, C). There was no significant trend in the effect of within-quadrat topographic heterogeneity on rarefied species richness across the precipitation gradient. From a functional trait perspective, quadrats in the driest plot with more heterogeneous topography tended to have less functionally diverse communities in terms of wood density (i.e., lower values of SES.MPD; Fig. 5B and E). In the three wettest plots, in contrast, quadrats with more heterogeneous topography had positive but non-significant associations between wood density diversity and topographic heterogeneity. This resulted in a marginally significant trend (i.e., 90% credible intervals did not overlap zero) across the precipitation gradient: quadrats with high topographic heterogeneity had low diversity of wood density diversity on the dry side of the gradient but high wood diversity towards the wetter end of the gradient. In part, this result was related to the distribution of the palm *P. montana* (wood density = 0.31 g cm^{-3}), which is dominant in some of the wet forest plots. Specifically, there was a positive correlation between palm abundance and wood density diversity (SES.MPD) (Pearson r = 0.24). Results for functional diversity of LMA somewhat opposed those of wood density diversity. In the driest plot, specifically, quadrats with more topographic heterogeneity contained trees with a higher diversity of LMA values. However, none of the other plots showed significant associations between topographic heterogeneity and LMA diversity, nor was there a significant trend along the precipitation gradient (Fig. 5C and F).

Within-plot topographic β-diversity (i.e., the absolute pairwise difference of mean TWI values between quadrats) was significantly related to taxonomic β-diversity in four individual plots. The relationship was negative for two plots on limestone soils with intermediate precipitation and positive for two plots on volcanic soils with intermediate to wet levels of precipitation (Fig. 6A). There was not a significant trend, however, in the slope of the relationship across the climate gradient. There was also no significant relationship between topographic β-diversity and functional β-diversity of either wood density or LMA, nor was there a significant effect for most individual plots (Fig. 6B and 6C).

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DISCUSSION

We paired high-resolution airborne lidar with ground-based data from a set of forest plots to evaluate how topography influences tropical forest structure and composition across a regional precipitation gradient. Our main findings are that: (1) across plots, topography is significantly associated with forest structure and functional composition, measured as mean canopy height, AGB, and CWM wood density, (2) the strength (and in some cases direction) of these effects varies across the precipitation gradient, and (3) fine-scale topographic heterogeneity has stronger effects on functional diversity (especially wood density) compared to taxonomic diversity. Below, we discuss these findings and argue that a stronger integration of topographic heterogeneity across precipitation gradients could improve estimates of forest biomass and provide insight to the ways that topography might mediate species and community response to climate change.

Topographical effects on forest structure and composition

Previous work on topographic effects on biodiversity has generally been conducted either with coarse resolution topography data across broad spatial extents or with fine grain topography data across small spatial extents with relatively uniform climatic conditions. For example, Yang *et al*. (2016) found strong joint effects of climate and topography on pantropical patterns of forest canopy height but their study focused on a coarse spatial resolution (0.5° grid cells), precluding inference about the interactions between climate and fine-scale topographic effects. Jucker *et al.* (2018) recently found strong effects of fine-scale (1 m resolution) topographic variation on tropical forest composition and structure but the study area has a fairly uniform climate (T. Jucker, *personal communication*). Although it was not a primary focus of their study, the plots studied by Jucker *et al.* (2018) did span a variety of edaphic conditions which appear to have interacted, at least to some extent, with the topographic effects they reported (see, for example, Fig. 5 of that paper). Similarly, Féret and Asner (2014) found topographic effects on diversity and structure of Amazonian rain forests that differed between main habitat types based on edaphic conditions (i.e., floodplain versus terra firme habitats). These studies suggest a need to consider the broader abiotic context when interpreting and predicting ways that topography may mediate the structure and diversity of tropical forests.

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Our results indicate that fine-scale topographic conditions influence the structure and composition of Puerto Rican forests, and the nature of these effects depends on the broader climatic context. For example, AGB was higher in topographically wet microsites in dry seasonal forest plots and weakly negatively related with topography in aseasonal wet rain forest plots. In seasonally dry forests, hydraulic limitation can restrict plant growth and so wet microsites can strongly facilitate growth and biomass accumulation (Ryan & Yoder 1997; Ryan *et al.* 2006). In fact, topographically wet microsites in the dry forest include relatively tall trees (also with large diameters). For example, in the driest forest plot of our study (GFDP), only 21% of the individual trees have diameters > 5 cm but these account for nearly 70% of the plot-level AGB. As a result, the association of large trees with topographically-mediated conditions has a disproportionately large effect on spatial patterns of AGB in dry forests. In the aseasonal wet forests, topographic wetness was also positively associated with canopy height but the effect was relatively weak and AGB was actually negatively related with topographic wetness. Apparently, the relatively modest gains to canopy height in wet microsites of forests on the wetter side of the gradient were offset by their lower basal area and average wood density. In wet forests of Puerto Rico, several very large, late-successional species are associated with ridge habitats (that tend to have low TWI values) including *Dacryodes excelsa*, *Sloanea berteriana*, and *Manilkara bidentata.* In the portion of the LFDP used for this study, for instance, these species account for about 55% of the stand-level AGB.

In the two wettest plots along the precipitation gradient studied here, high wood density tree species were more common in topographically dry microsites (i.e., ridges with low TWI values). This result could arise in several ways. For example, wood density may mediate a trade-off between hydraulic safety and hydraulic efficiency (Hacke *et al.* 2001; Sperry *et al.* 2008; Chave *et al.* 2009), or a trade-off between tolerance to drought and water-logging (Niinemets & Valladares 2006). Several of the dominant species in low TWI quadrats have high values of wood density compared to the plot-level average (e.g., *S. berteriana* = 0.80 g cm^{-3} and *M. bidentata* = 0.86 g cm^{-3} compared to the plot-level CWM wood density of 0.54 g cm^{-3}). The distribution of these species on ridges could also be related to a potential association between high wood density and the ability to withstand high winds typical of this study system. Alternatively, the negative association between CWM wood density and TWI in wet environments of these wet forests could emerge from faster turnover rates in response to disturbance events at low elevations, especially if water-logging exacerbates tree mortality during

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storms (e.g., Margrove *et al.* 2015). In contrast, we found a marginally significant relationship between TWI and CWM wood density in the seasonally dry forest – topographically wetter quadrats comprised tree communities with, on average, somewhat higher wood density. We believe this finding can be resolved by considering the diversity of strategies to cope with drought among dry forest tree species. Specifically, several of the most abundant (and largest diameter) tree species in the GFDP are deciduous and have unusually low values of wood density among species in this forest (e.g., *Bursera simaruba* = 0.41 g cm^{-3}, *Pisonia albida* = 0.59 g cm^{-3} compared to the plot-level CWM wood density of 0.84 g cm^{-3}). Differences between drought-avoidance and drought-tolerance strategies appears to decouple wood density and hydraulic safety in this forest thereby obscuring the link between mechanisms underlying patterns of forest composition and community-level patterns of wood density (Muscarella & Uriarte 2016).

In general, the topography × climate interactions described above appeared to be rather consistent across plots on both limestone and volcanic soils. In particular, plots on both soil types with intermediate levels of precipitation exhibited similar TWI × precipitation interactions on metrics of forest structure, and these plots also fit well within the overall trend across the precipitation gradient. Importantly, in cases where the sign of the topography × climate interaction changed along the precipitation gradient, the magnitude of these effects was muted in the 'intermediate' plots (irrespective of soil type) compared to the plots at either extreme end of the gradient. In other words, topographic effects on forest structure and composition matter most in sites with relatively extreme climate conditions.

Our analyses focus on the TWI as an integrative index of potential and relative soil moisture across our study sites. Unfortunately, we currently lack empirical data on microclimate conditions (e.g., soil moisture) with which to validate the TWI. Direct measurements of microclimatic conditions are becoming increasingly feasible with recent technological and conceptual advances (e.g., Storlie *et al.* 2014; Blonder *et al.* 2018; Wild *et al.* 2019; Zellweger *et al.* 2019). In our study, it is possible that other gradients associated with topography (besides soil moisture) influence our results. For instance, Puerto Rico is regularly exposed to hurricanes and spatial variation in disturbance can influence the metrics of forest structure and composition that we examined. We do not, however, expect spatial variation in hurricane disturbance to confound our main conclusions for two main reasons. First, prior work in Puerto Rico has shown forest structure to recover to pre-hurricane levels in a relatively short

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period (e.g., 20 years) (e.g., Zimmerman et al. 1996) and our study sites were not subject to major hurricane disturbance for >20 years prior to data collection for this study. From a longer-term perspective, spatial variation in the return interval of major hurricanes across the island (Boose et al. 2004) could affect forest structure. In particular, we would expect more frequent hurricanes to select for shorter forest canopies. However, in our study, the dry forest site has both shortest forest canopy and also the longest hurricane return interval (Boose et al. 2004). In other words, forest canopy height across the island tends to be positively associated with hurricane frequency (i.e., wetter sites with more frequently exposed to hurricane damage have the tallest canopies), suggesting that climatic factors more strongly determine canopy height across the island than variation in hurricane exposure.

Topographical effects on taxonomic and functional diversity

Until recently, much of the work investigating topographic effects on diversity patterns has focused on large (macroecological) spatial scales (Simpson 1964; Kerr & Packer 1997; Kreft *et al.* 2007; Svenning *et al.* 2010). For example, Svenning *et al*. (2010) showed a strong influence of topographic heterogeneity on the degree to which local communities represent regional species pools across the European continent. They argued that topographic heterogeneity promotes local species coexistence by providing opportunities for niche differentiation and reducing the probability of local extinction by buffering the effects of long-term climate change. But topography also affects abiotic conditions at relatively small spatial scales (Moeslund *et al.* 2013) and recent advances in remote sensing technology (e.g., lidar) are providing new opportunities to evaluate relationships between fine-scale environmental heterogeneity and plant community composition and dynamics.

In our study, with the exception of a few plots, topographic heterogeneity (i.e., the standard deviation of TWI values in 10 × 10 m quadrats) was not significantly associated with taxonomic diversity and there was no trend in the strength of the effect across the precipitation gradient. We found a marginally significant association between of topographic heterogeneity and wood density diversity, which were negatively related in the driest plot and more positively related (although not significantly so) for plots on the wetter end of the gradient. In other words, topographically diverse quadrats in the driest plot actually had lower than expected levels of wood density diversity based on the number of trees in the quadrat and the plot-wide species pool. In the wetter forests, in contrast, more topographically heterogeneous quadrats contained a somewhat higher diversity of trees in

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terms of their average wood density compared to expectations based on the pool of species that occur in those plots. It is possible that the degree of topographic heterogeneity examined at the spatial scales considered here (within 10 m × 10 m quadrats) was not sufficiently large to capture strong enough habitat differences to allow co-occurrence of many diverse species. An association between topographic wetness and topographic heterogeneity may also complicate this relationship (e.g., if topographically wet microsites also tend to be more topographically variable). In fact, these metrics were weakly correlated in most plots included in our study but the potential implications are not yet clear. We envision that future work will continue to bridge spatial scales to better address the links between topographic heterogeneity and biological diversity.

The fact that we did not find any association between topographic β-diversity and taxonomic or functional β-diversity across the climate gradient runs counter to the climatic variability hypothesis, which posits that species exposed to higher degrees of climatic variability should exhibit broader tolerances and thus wider species distributions (Janzen 1967). Applying these ideas to local scales, we predicted that dry forest species could have higher tolerance for arid conditions and, as a result, topographic effects on composition may be less pronounced in dry forests than in wet forests. Our alternative hypothesis, however, was that the range of topographically mediated habitat heterogeneity would be more biologically significant in the dry forest compared to the wet forest. As above, it is possible that the metric of topographic β-diversity we used (absolute pairwise difference of mean elevation values) does not capture the most important aspects of topographic heterogeneity in these forests.

Potential implications for plant response to climate change

By mediating how climatic change is experienced by individuals, local topographic heterogeneity can profoundly influence plant responses to environmental conditions (Daws *et al.* 2002; Loarie *et al.* 2009; Lenoir *et al.* 2016; He *et al.* 2017; Suggitt *et al.* 2018). For example, local topographic heterogeneity can buffer extreme events, provide microrefugia under climate shifts, and contribute to evolution of plasticity or adaptation to variable conditions (Diffenbaugh *et al.* 2005; Hampe & Petit 2005; Dobrowski *et al.* 2009; Lenoir *et al.* 2016). Paving a way forward for future work, Lenoir *et al*. (2016) used information on fine-scale topography to generate downscaled predictions of climate change and examine the implications of microsite heterogeneity on species responses to climate

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change. This type of work suggests that a stronger integration of microtopography in models of forest composition and dynamics can help merge processes acting at different scales (Réjou-Méchain *et al.* 2014).

We note that topographic effects on soil moisture and other edaphic properties (e.g., nutrient content and texture) may be correlated or non-linear (e.g., Schietti *et al.* 2014). This could present a challenge for uncovering the mechanisms governing species' topographically-mediated habitat associations. A functional trait perspective like the one used here can help with this issue, however, by providing links between species functional strategies and mechanistic drivers. Future work examining more detailed physiological response traits and vital rates could further clarify the mechanistic drivers of topography and forest composition.

In our study, the fact that fine-scale topography was related to variation in forest composition and structure suggests that topographic heterogeneity is likely to act as microrefugia for Puerto Rican tree species under climate change. Conservation and management initiatives would likely benefit from considering topography. For example, wet microsites of dry forests are likely to be especially important in terms of AGB. In contrast, species adapted to wet microsites in wet forests may be especially sensitive to climate change because there are likely to be fewer favourable microsites under future climate change projections (Neelin *et al.* 2006). Additionally, whether wetter microsites are more protected from tropical storms and thus suffer lower damage is an area of ongoing work. This type of interaction could confer additional importance to the local topographic variability for tropical forests with disturbance regimes similar to that of Puerto Rico.

Conclusions

Overall, our study illustrates how topographic effects on forest composition and structure can depend on the broader climate context. Topography was associated with emergent properties of forests (i.e., canopy height and AGB) in ways that varied in strength and, in some cases, direction across the precipitation gradient. Links between topographic heterogeneity and local diversity were relatively weak and not clearly related to the climate context. We argue that a stronger integration of topographic heterogeneity across precipitation gradients will improve estimates of forest composition and structure, and ultimately provide insight into ways that topography can mediate species responses to climate change.

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AUTHOR CONTRIBUTIONS

RM conceived the ideas, designed methodology. RM, MU, JKZ, and DCM collected data; RM and SK analysed data; RM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Lidar data are available from the NASA G-LiHT website (https://gliht.gsfc.nasa.gov/). Functional trait data are partially available from (https://doi.org/10.5061/dryad.j2r53). Climate data are available from (Daly *et al.* 2003). Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5rq1h6n (Muscarella *et al*. 2019).

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Figure Legends

Figure 1. Conceptual diagram showing hypothetical variation in soil moisture between topographically wet and dry microsites (blue and yellow lines, respectively) in (A) a dry seasonal forest and (B) an aseasonal wet forest. In seasonal dry forests, the difference between topographically wet and dry microsites in terms of dry season soil moisture (arrow 1) might reflect a more biologically meaningful difference for plants than the difference between microsites in aseasonal wet forests (arrow 2). We might thus expect a stronger effect of local topography on forest structure and composition in the seasonally dry forest compared to the aseasonal wet forest. Alternatively, however, seasonal variation of local conditions in wet versus dry microsites may exhibit a higher degree of overlap in the seasonal dry forest (shaded area in A) compared to the aseasonal wet forest (note lack of overlap in B). As a result, we might expect a stronger effect of topography on forest composition in the aseasonal wet forest compared to the seasonally dry forest.

Figure 2. (A) The island of Puerto Rico colored by the gradient of mean annual precipitation. Locations of 15 study plots are shown as circles or triangles for plots on limestone or volcanic soils, respectively. Lidar-derived canopy height and elevation (1 m^2 resolution) are shown for areas surrounding two example plots: (B, D) the tropical dry forest Guánica Forest Dynamics Plot (GFDP) and (C, E) the low-land use portion of the wet Luquillo Forest Dynamics Plot (LFDP). Panels (F, G) show community-weighted mean (CWM) wood density in 10 $\times$ 10 m quadrats based on forest census data and species-mean trait values. Note the different ranges of color scales in (B-E). The irregular shape of the LFDP is the 'low land-use' section of the plot used in this study.

Figure 3. (A) Average monthly precipitation (mm/month) for 15 plots in Puerto Rico based on climate data from Daly *et al*. (2003). More details on individual sites are provided in Table S1 and can be referenced by their names in (A). Colors correspond to the degree of precipitation seasonality (coefficient of variation for monthly values) where dark (blue) is least seasonal and light (yellow) is most seasonal. (B) Mean monthly precipitation (mm) versus precipitation seasonality (coefficient of variation for monthly values). Point colors correspond to precipitation seasonality as in (A). In both panels, circular and triangular symbols represent plots on limestone and volcanic soils, respectively.

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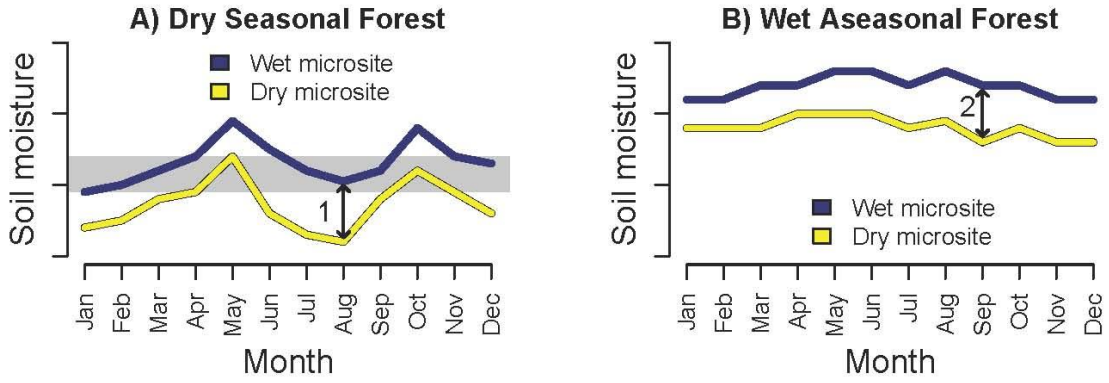
Figure 4. Relationship between the topographic wetness index (TWI) and (A) lidar-derived canopy height, (B) estimated above-ground biomass (AGB), and (C) community-weighted wood density (CWM WD) for 10 × 10m quadrats in 15 plots across a rainfall gradient. In panels (A-C), both variables were centered and scaled to unit 1 standard deviation prior to analysis. Each point represents a single 10 × 10m quadrat. The slopes of the fitted lines represent parameter b_{0p} from equations 1 and 2. Color-coding reflects a gradient of mean annual precipitation across plots (yellow=dry, blue=wet). In all panels, circular and triangular points represent quadrats in plots on limestone and volcanic soils, respectively. In panels (D-F), plot-specific slopes (again, parameter b_{0p} from equations 1 and 2 with 95% credible intervals) of corresponding panels (A-C) are plotted against either precipitation seasonality (i.e., the coefficient of variation of mean precipitation per month) or mean annual precipitation. In D-F, the bold black line (dashed if the trend was not significant) and grey shading shows the across-plot fitted relationship with 95% credible intervals (the intercept and slope of the fitted line correspond to parameters $a_{1.2}$ and $b_{1.2}$, respectively, from equation 3).

Figure 5. The relationship between topographic heterogeneity (measured as the standard deviation [σ] of TWI values within each 10 × 10 m quadrat) and (A) rarefied species richness and standardized mean pairwise distance (SES.MPD) of (B) wood density and (C) LMA for 15 plots along a precipitation gradient of precipitation seasonality. All values were centered and scaled (by subtracting the mean and dividing by the standard deviation) within each plot to facilitate comparison (see methods). In (D-F), each point represents the fitted slope (from the corresponding panel A-C) for one plot with 95% credible intervals. Points are color-coded by the plot mean annual precipitation; circles and triangles represent plots on limestone and volcanic soils, respectively. In D-F, the bold black line (dashed if the trend was not significant) shows the population-level fitted model and grey shading the simulated 95% credible interval (the intercept and slope of the fitted line correspond to parameters $a_{1.2}$ and $b_{1.2}$, respectively, from equation 3).

Figure 6. The relationship between topographic β-diversity (measured as the absolute difference of mean TWI values for each 10 × 10 m quadrat) and the taxonomic β-diversity (A) and functional β-diversity for wood density (B) and LMA (C) for 15 plots along a precipitation gradient. Points are

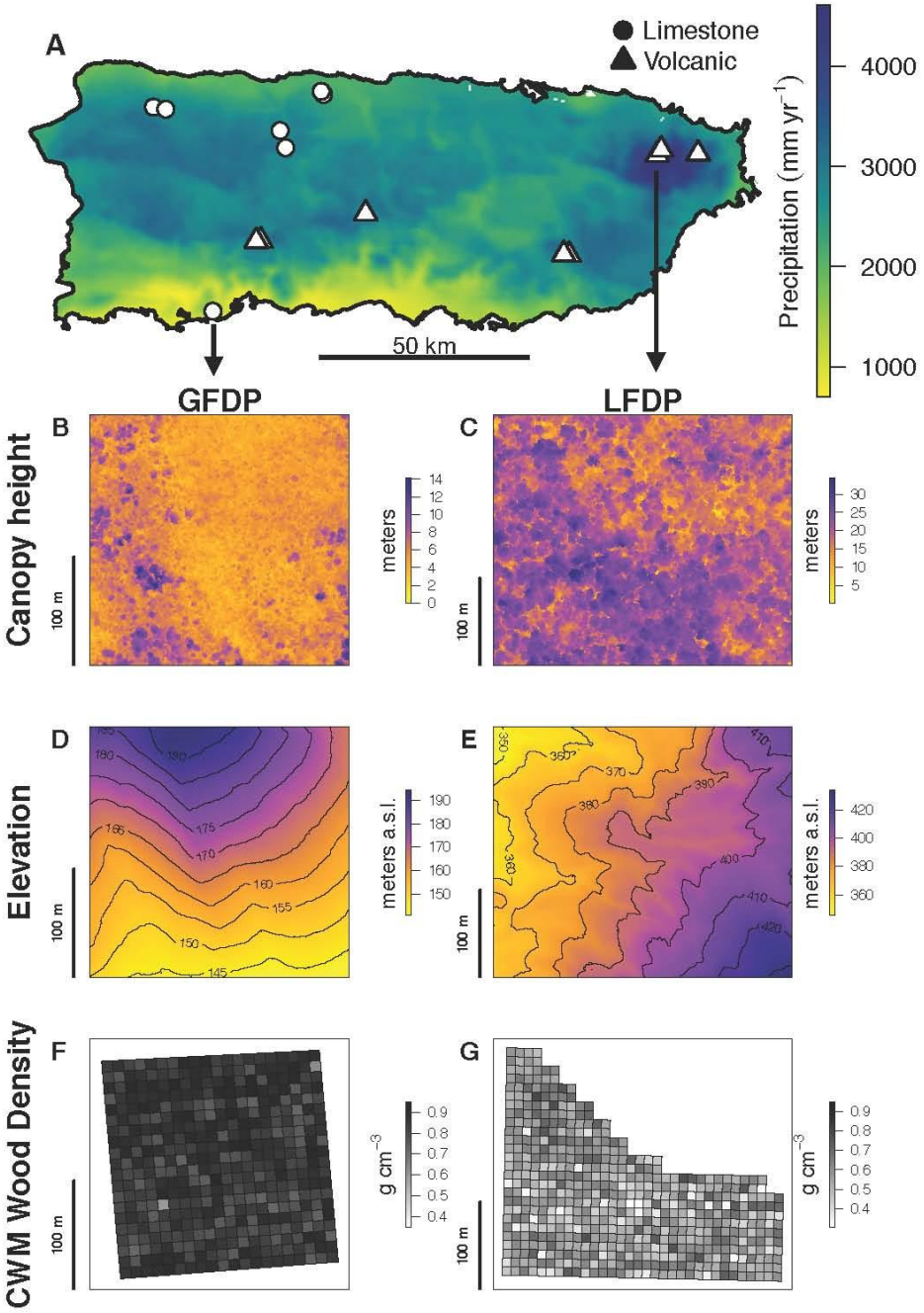
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color-coded by the plot mean annual precipitation; circles and triangles represent plots on limestone and volcanic soils, respectively. The bold black line (dashed if the trend was not significant) shows the population-level fitted model and grey shading the simulated 95% credible interval (the intercept and slope of the fitted line correspond to parameters $a_{1.2}$ and $b_{1.2}$, respectively, from equation 3).



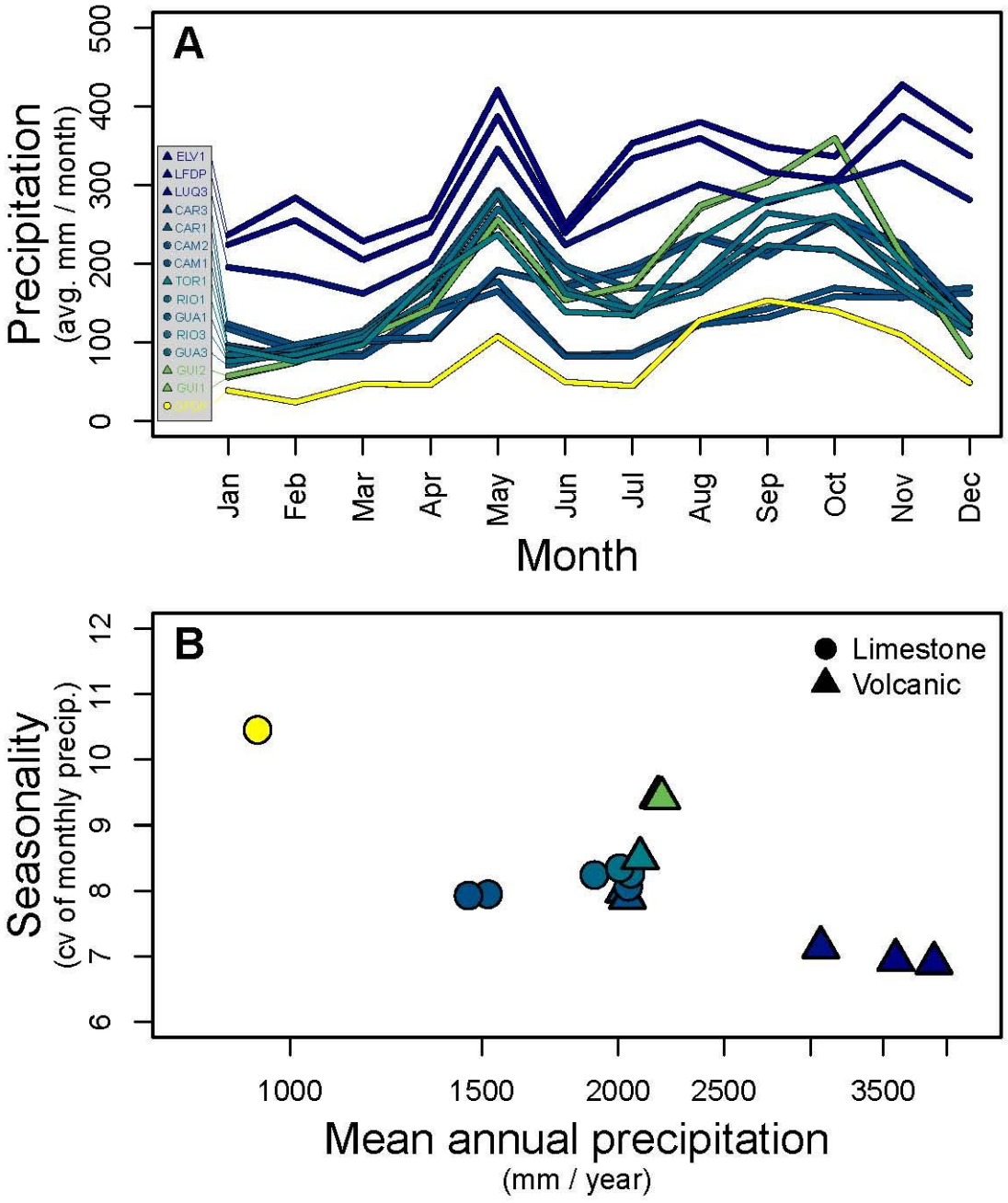
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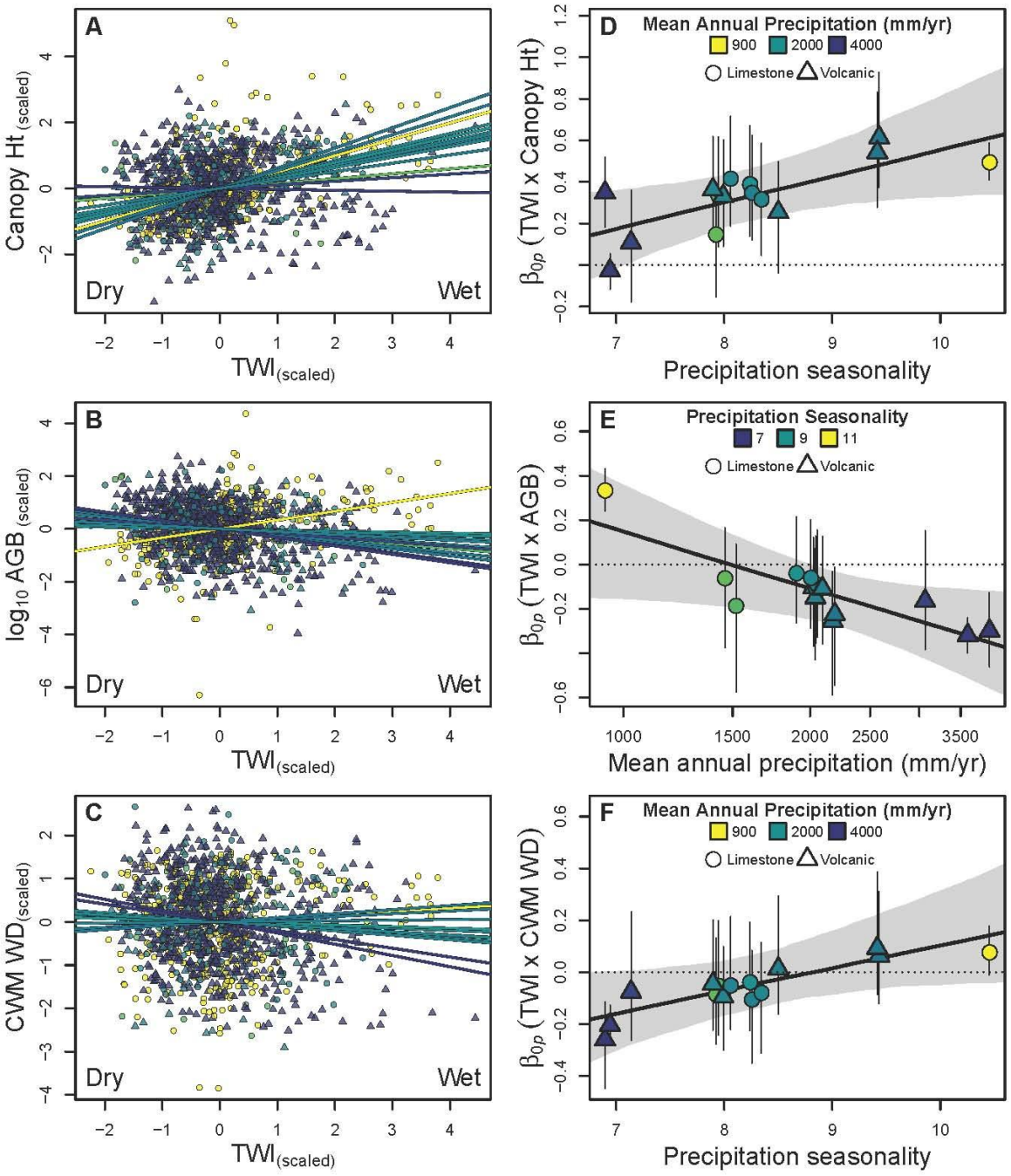
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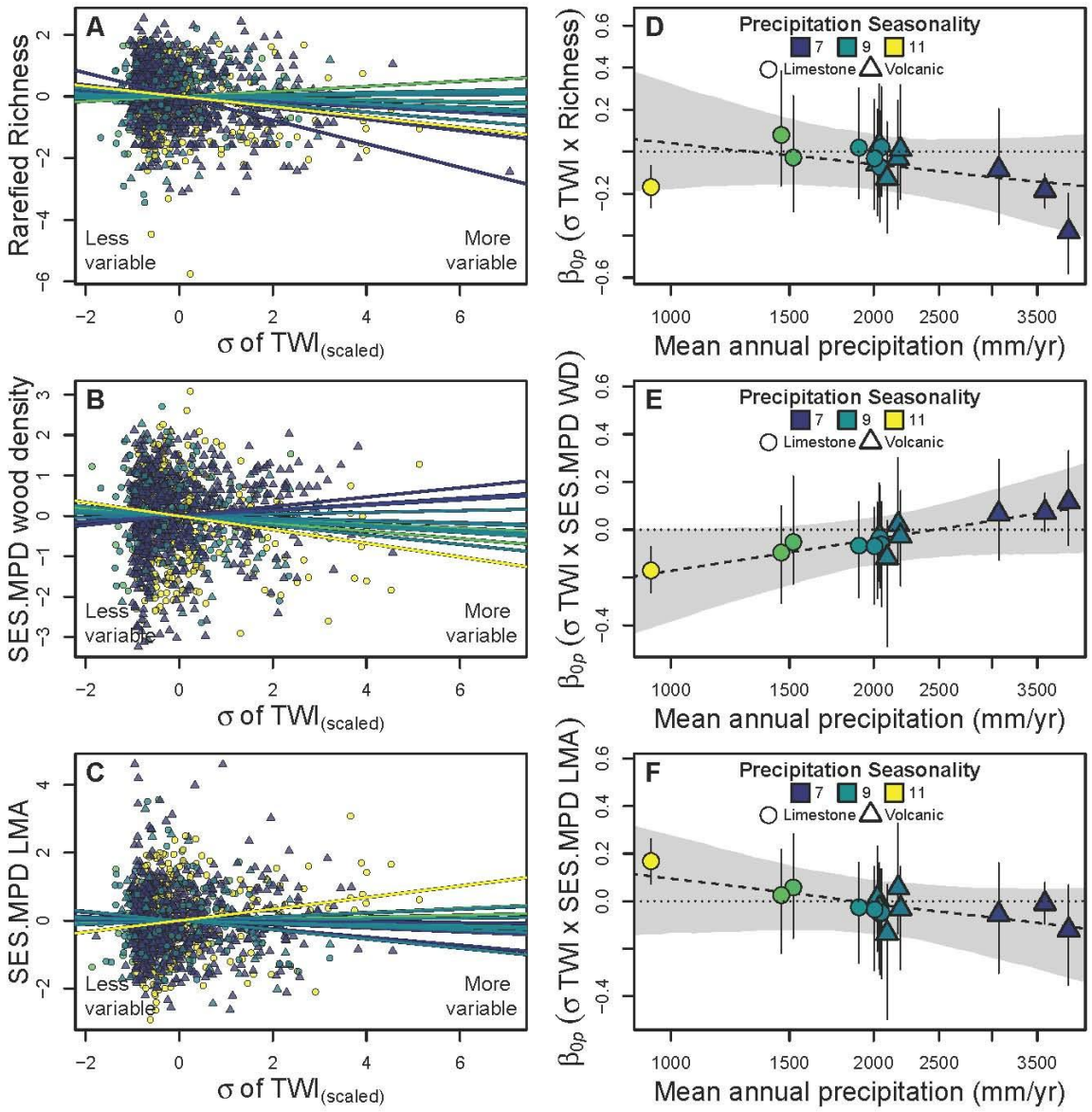
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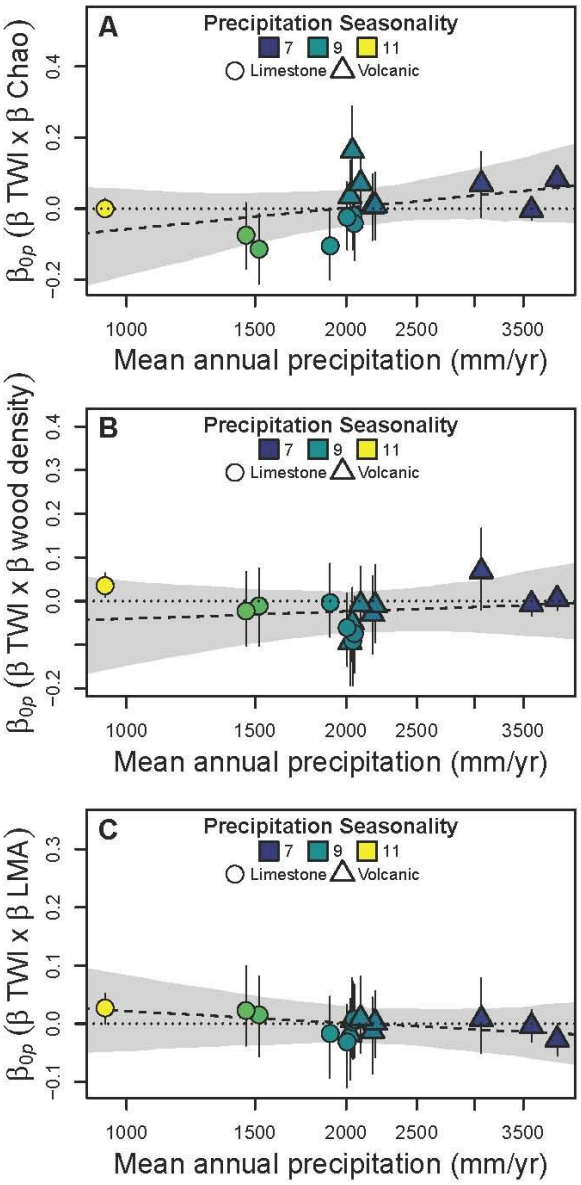
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