MISSING THE TREES FOR THE FOREST: POST-HURRICANE UNDERSTORY VEGETATION IN RELATION TO SPATIAL VARIATION

Nicole M. Soto-Parrilla[1,*] and Tamara Heartsill-Scalley[2,3]

[1] Department of Biological Sciences, University of Puerto Rico, Humacao.
[2] USDA Forest Service, International Institute of Tropical Forestry, Río Piedras, Puerto Rico.
[3] Department of Environmental Sciences, University of Puerto Rico.
* **Author for correspondence**: nicole.soto6@upr.edu

Abstract

Within a forest, differences in landform spatial variation (i.e., geomorphic settings: valley, slope, and ridge) could affect the species richness and distribution present at a particular site. Previous studies have confirmed that plant species richness and biomass changes after a hurricane and such values can vary among geomorphic settings. Understory vegetation, including ferns, herbs, climbers, graminoids, and shrubs, accounts for more than two thirds of flora in tropical ecosystems, but there is limited information of the effect of hurricanes on these communities. We evaluated the structure and composition of understory vegetation in a post-hurricane forest in relation to geomorphic settings. This study was conducted in El Verde Research Area in the Luquillo Experimental Forest, Puerto Rico. We established 1-m^2 plots within three geomorphic settings: riparian valley, slope, and ridge. Within each plot we identified species, estimated percent of cover and collected biomass samples. Additionally, we estimated species accumulation curves and analyzed species composition among geomorphic settings using multivariate ordination. The relative species abundance of vegetation life-forms was similar among geomorphic settings, but graminoids and climbers exhibited differences in species composition. Higher forest understory biomass and percent vegetation cover was observed at this immediate post-hurricane period than what was reported pre-hurricane. The understory of valley areas had a more distinct species composition than what was observed among ridge and slope areas. The understory vegetation patterns observed would need to be followed through time and among the landforms to confirm the hurricane disturbances effects at these understory scale.

Keywords tropical, hurricane, understory, ridge, slope, valley, species composition, biomass.

Resumen

Dentro de un bosque, las diferencias en la variación espacial de los entornos geomórficos (valles, pendientes y crestas) podrían afectar la riqueza y distribución de especies presentes en un sitio en particular. Estudios previos han confirmado que la riqueza de especies y la biomasa de plantas cambian después de un huracán y tales valores pueden variar entre entornos geomórficos. La vegetación del sotobosque, que incluye helechos, herbáceas, trepadoras, gramíneas y arbustos, representa más de dos tercios de la flora en los ecosistemas tropicales, pero aun la información sobre el efecto de los huracanes en estas comunidades es limitada. Evaluamos la estructura y composición de la vegetación del sotobosque en un bosque post-huracán en relación con los entornos geomórficos. Este estudio se realizó en el Área de Investigación El Verde, en el Bosque Experimental de Luquillo, Puerto Rico. Establecimos parcelas de 1 m^2 dentro de tres entornos geomórficos: valle ribereño, pendiente y cresta. Dentro de cada parcela

ISSN: 1940-1148

identificamos especies, porcentaje estimado de cobertura y recolectamos muestras de biomasa. Adicionalmente, estimamos las curvas de acumulación de especies y analizamos la composición de especies con ordenación multivariada en relación con entornos geomórficos. La abundancia relativa de especies por cada tipo de vida vegetal fue similar entre los entornos geomórficos, pero las gramíneas y trepadoras exhibieron diferencias en la composición de especies. Se observó una mayor biomasa del sotobosque y porcentaje de cobertura vegetal en este período inmediatamente posterior al huracán que lo que se reporto para antes del huracán por otros estudios. El sotobosque en los valles tenía una composición de especies más distinta que la observada entre las áreas de crestas y pendientes. Los patrones de vegetación del sotobosque observados deberían seguirse a lo largo del tiempo y entre los entornos geomórficos para confirmar los efectos de las perturbaciones de los huracanes a esta escala del sotobosque.

Palabras clave biomasa, composición de especies, cresta, huracán, pendiente, sotobosque, tropical, valle.

INTRODUCTION

Within a forest type there can be differences in the landforms which influence the spatial distribution of ecosystem properties, these in turn, could affect the distribution and quantity of species present at a particular site. In the tabonuco forest at the Luquillo Experimental Forest (LEF) in Puerto Rico some of these differences have been observed in the geomorphic settings (e.g., ridge, slope, and valley) that characterize its landforms and topography (Scatena and Lugo 1995). The distribution of tree species, together with their biomass, structure and composition have been associated with these geomorphic settings in this forest (Scatena et al. 1993; Heartsill Scalley et al. 2010). In addition to geomorphic settings, hurricane disturbances also have a role in shaping the structure of plant communities in the tabonuco forest. Most research conducted to assess the effects of hurricane disturbance on forest dynamics in Puerto Rico has been devoted to understanding the effects on tree species (Heartsill Scalley 2017). Previous studies in the tabonuco forest have confirmed that plant total number of species increase after a hurricane and sometimes surpasses the pre-hurricane levels (e.g., Heartsill Scalley et al. 2010; Royo et al. 2011). As found by Heartsill Scalley et al. (2010), after 15 years from Hurricane Hugo tree species richness of a tabonuco forest was significantly higher in riparian valleys than in the ridges, compared to their pre-hurricane values.

Despite the record of research on hurricane effects on forests, little is known about the effects of hurricanes on the understory, focusing on non-arborescent species. The few studies that have focused on changes in the understory plant community through time have not yet explored variation in relation to geomorphic settings. It has been shown that the understory plant community accounts for a more than two thirds of plants in tropical ecosystems and comprises the majority of tropical flora (Gentry and Dodson 1990; Chinea 1999; Royo et al. 2011). We broadly classify the species inhabiting the understory as: ferns, herbs, climbers, graminoids and shrubs, some of which have been documented to respond to the effects of a hurricane by increasing, decreasing or remaining unchanged (Royo et al. 2011). Based on previous research in this forest, we asked whether the understory plant community exhibited differences in relation to geomorphic settings six to nine months post-hurricane disturbance.

This study evaluates the structure and composition of understory vegetation (ferns, herbs, climbers, graminoids, shrubs, and tree seedlings) in the understory of the tabonuco forest in a post-hurricane environment using three different approaches: (1) identifying non-arborescent understory species; (2) estimating the percent of coverage of each species; and (3) sampling the biomass of non-tree species. We present these

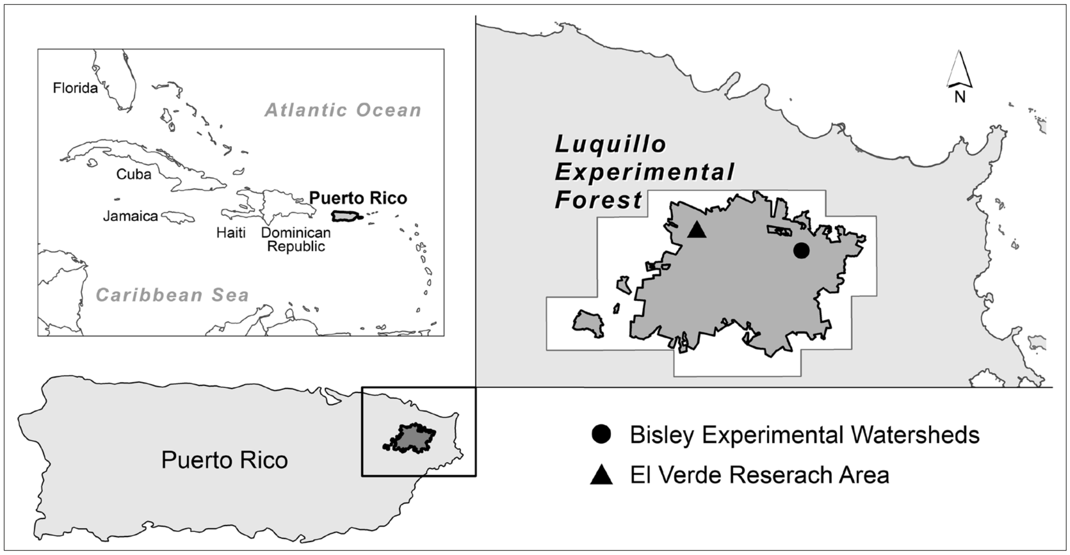

Figure 1. Study sites El Verde Research Area and Bisley Experimental Watersheds, within the tabonuco forest at Luquillo Experimental Forest, Puerto Rico.

components of the understory species community by describing them in terms of composition and number of species in relation to their location in riparian valley, slope, and ridge setting.

METHODS

Study Site

This study was conducted in the LEF located in northeast of Puerto Rico (18°32'12"N 65°81'99"W; Figure 1). The forest vegetation in the LEF is influenced by periodic disturbances such as hurricanes, tropical storms, and droughts (Harris et al. 2012). In addition, forest vegetation communities are also associated with different scales of disturbances including treefalls and landslides (Brokaw et al. 2012; González et al. 2013). Over the past three decades there have been several hurricanes that affected the LEF at different intensities with Hurricane María being the most recent and most intense (category 5; September 20, 2017) since Hurricane Hugo in 1989.

The *Dacryodes-Sloanea* forest, also known as the tabonuco forest, dominates the low elevations of the LEF (< 600 m), receives an average of 3,482 mm/yr of rainfall and encompasses 70 percent of the LEF (Harris et al. 2012). Common tree species in this forest type include the ausubo (*Manilkara bidentata*), guaraguao (*Guarea guidonia*), granadillo (*Buchenavia capitata*), laurel geo (*Ocotea leucoxylon*) and motillo (*Sloanea berteriana*) trees. Previous studies on understory non-arborescent vegetation in this forest type have found 43 species of ferns, 96 species of forbs and herbs, 28 species of vines and 20 species of shrubs (Chinea et al. 1993). Throughout the tabonuco forest, lianas (i.e., woody vines) and climbers contribute to the extent of the canopy while epiphytes tend to be most abundant in riparian areas. Ferns dominate the understory in this forest, and they can comprise up to 34 percent of total vegetation (Heartsill Scalley 2012). The geomorphic settings found in this forest type include valleys, which tend to have poorly drained soils, the least biomass, and lowest tree species richness; slopes, which receive runoff from upland areas and transmit runoff to valleys; and ridges which have well drained soils, more aboveground biomass, greater species richness and are mostly occupied with the dominant tabonuco tree species (Johnston 1992; Scatena and Lugo 1995; Heartsill Scalley et al. 2010).

For this study, we collected data at two sites in the tabonuco forest (Figure 1). The first site was the Bisley Experimental Watersheds (Bisley) on the east side of the LEF, where data were collected six months after Hurricane María. The second site was the El Verde Research Area, part of the El Verde Field Station (El Verde) on the west side of the LEF, where data were collected nine months after Hurricane María.

Non-arborescent Vegetation Sampling

At El Verde we quantified 31 1-m^2 plots in sites selected at random to include the riparian valley or valley, slope, and ridge settings. These locations were outside of permanently sampled research areas. Areas sampled were (1) the section east of Quebrada Prieta as it exits the LFDP, (2) along Quebrada Caoba, west of the main trail, and (3) south of Quebrada Sonadora west of the hanging bridge. The geomorphic settings sampled were: the ridge, which are the highest areas within the tabonuco forest; the slope, which is the steepest area located between the ridge and the valley; and the valley or riparian valley, which is the lowest part, close to stream flow or located between two slopes. For the riparian valley, the plot was established 5 m away from the stream water edge.

For each plot we identified all understory species and estimated the percent of coverage of each species. We identified species to the lowest taxonomical level possible, but for species that were difficult to identify precisely in the field, we took photos, and identified them in the laboratory, or categorized them. For species that we were unable to identify, we report them in the lowest taxonomical level possible. In addition to vegetation characterization, we estimated canopy openness above the sampled plot with a horizontal photograph at 1.5 m in height as a relative measure of light exposure condition among plots. These photographs were analyzed by placing a grid over the image and classifying grid areas as open sky or vegetation. In 9 of the 31 plots, we collected biomass (three plots per geomorphic setting). Aboveground biomass was determined by harvesting all vegetation in the plot and classifying the collected biomass per the lowest taxonomical level possible and placed in paper bags. All understory vegetation located within the space defined by vertically projecting the perimeter of the 1-m^2 plot to 1.5 m in height were sampled, regardless of whether vegetation was rooted in the plot or not (following the procedure in Royo et al. 2011). We identified tree seedlings located in the plots but did not harvest them.

Biomass Sample Processing

We took the biomass samples to the Analytical Chemistry Laboratory of the USDA Forest Service, International Institute of Tropical Forestry in Río Piedras and dried them at 65 °C to constant weight (estimated time of three days each sample). Then we weighed all the sampled vegetation to three decimal places.

Statistical Analyses

For all plots in Bisley (n = 25) and El Verde (n = 31; n = 9), species percent cover (%) and biomass (g/m^2) were calculated, along with species counts (richness). Species accumulation curves were estimated using the program EstimateS Win9.1.0 software (Colwell 2013). We also calculated richness, percent cover and biomass by vegetation life forms groups: ferns, herbs (which include forbs category), climbers (herbaceous vines and woody lianas), grasses and shrubs (i.e., multi-stemmed woody plant with mature height < 5 m, as defined in the species list by Royo et al. [2011] and USDA Plants Database). To compare understory vegetation characteristics (richness, percent cover, biomass) among geomorphic settings (ridge, slope, and riparian valley) at El Verde and among life forms at both study sites, a Kruskal-Wallis test (KW, H) was conducted. Statistics were considered significant at a level of 0.05 (Heartsill Scalley et al. 2010). All mean values for El Verde, except mean biomass, were based on 31 plots (n = 31). For biomass samples, the mean values were based on nine plots (n = 9). Based on the nine plots we calculated biomass for the most common species found (the ones

Table 1. Species per vegetation life form found in the understory of the tabonuco forest, six to nine months after Hurricane María, El Verde Research Area, Luquillo Experimental Forest, Puerto Rico.

Life Form	Species	Native Status
Fern	*Adiantum* spp.	Probably Native
	Blechnum occidentale L.	Native
	Danaea nodosa (L.) Sm.	Native
	Tectaria spp.	Probably Native
	Thelypteris deltoidea (Sw.) Proctor	Native
	Other unidentified fern species	
Graminoid	*Ichnanthus pallens* (Sw.) Munro ex Benth.	Native
	Olyra latifolia L.	Native
	Pharus latifolius L.	Native
	Poaceae	—
	Scleria canescens Boeckeler	Native
Herb	Boraginaceae	—
	Commelina diffusa Burm.f.	Native
	Euphorbia spp.	—
	Heliconia caribaea Lam.	Native
	Catopsis floribunda L.B.Sm.	Native
	Peperomia rotundifolia (L.) Kunth	Native
	Phytolacca rivinoides Kunth & C.D.Bouché	Native
	Pilea spp.	—
	Pilea inequalis	Native
	Rhynchospora radicans (Schltdl. & Cham.) H.Pfeiff.	Native
	Ruellia coccinea (L.) Vahl	Native
	Sauvagesia erecta L.	Introduced
	Spermacoce ocymifolia Willd. ex Roem. & Schult.	Native
	Tillandsia utriculata L.	Native
	Wullschlaegelia calcarata Benth.	Native
Shrub	*Urera baccifera* (L.) Gaudich. ex Wedd.	Native
	Gonzalagunia hirsuta (Jacq.) K.Schum.	Native
	Miconia racemosa (Aubl.) DC.	Native
	Microgramma piloselloides (L.) Copel.	Native
	Neurolaena lobata (L.) R.Br. ex Cass.	Native
	Piper glabrescens (Miq.) C.DC.	Native
	Piper hispidum Sw.	Native
	Piper umbellatum L.	Native
	Solanum torvum Sw.	Introduced
Tree	*Alchornea latifolia* Sw.	Native
	Andira inermis (Wright) DC.	Native
	Buchenavia tetraphylla (Aubl.) R.A.Howard	Native
	Byrsonima spicata (Cav.) Rich. ex Kunth	Native
	Casearia sylvestris Sw.	Native
	Cecropia schreberiana Miq.	Native
	Cordia borinquensis Urb.	Native
	Dacryodes excelsa Vahl	Native
	Eugenia spp.	—
	Eugenia stahlii (Kiaersk.) Krug & Urb.	Native
	Faramea occidentalis (L.) A.Rich.	Native
	Guarea guidonia (L.) Sleumer	Native
	Hirtella rugosa Thuill. ex Pers.	Native
	Inga laurina (Sw.) Willd.	Native
	Inga vera Willd.	Native
	Ixora ferrea (Jacq.) Benth.	Native
	Manilkara bidentata (A.DC.) A.Chev.	Native
	Nectandra turbacensis (Kunth) Nees	Native
	Ocotea leucoxylon (Sw.) Laness.	Native
	Psychotria berteroana DC.	Native
	Psychotria brachiata Sw.	Native
	Sapium laurocerasus Desf.	Native
	Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	Native
	Simarouba amara Aubl.	Introduced
	Sloanea berteriana Choisy ex DC.	Native
	Tabebuia heterophylla (DC.) Britton	Native
	Tetragastris balsamifera (Sw.) Oken	Native
Palm	*Prestoea acuminata* var. *montana* (Graham) A.J.Hend. & Galeano	Native
	Roystonea borinquena O.F.Cook	Native
Vine	*Cayaponia racemosa* (Mill.) Cogn.	Native
	Cissus verticillata (L.) Nicolson & C.E.Jarvis	Native
	Dioscorea polygonoides Humb. & Bonpl. ex Willd.	Native
	Dolichandra unguis-cati (L.) L.G.Lohmann	Introduced
	Heteropterys laurifolia (L.) A.Juss.	Native
	Hippocratea volubilis L.	Native
	Ipomoea alba L.	Native
	Ipomoea tiliacea (Willd.) Choisy	Native
	Marcgravia sintenisii Urb.	Native
	Mikania spp.	Probably Native
	Mikania cordifolia (L.f.) Willd.	Native
	Mikania fragilis Urb.	Native
	Paullinia pinnata L.	Native
	Philodendron hederaceum (Jacq.) Schott	Native
	Pinzona coriacea Mart. & Zucc.	Native
	Rourea surinamensis Miq.	Native
	Schlegelia brachyantha Griseb.	Native
	Securidaca virgata Sw.	Native
	Smilax domingensis Willd.	Native

found in most of the plots). All values are shown as mean ± 2 standard errors.

To explore understory vegetation community species composition among ridge, slope, and riparian valley, a non-metric multidimensional scaling (NMS) ordination analysis was conducted. An NMS ordination was used because it has been used to efficiently reduce high "dimensional" multi-variable species space (high number of species) to two dimensions, which makes it easy to plot simple two axis graphs. The NMS ordination was made for the El Verde data set in two ways; using per species biomass values and percent cover. The matrices for both ordinations were generated using Bray–Curtis distance in PC Ord-6 (McCune and Mefford 2011) in R version 3.4.0 (R Core Team 2017).

RESULTS

Distribution of Understory Vegetation Among Geomorphic Settings

A total of 95 species were found at El Verde, 85 of which belong to 49 different families. The remaining ten species were not identified, primarily because the seedlings were too small/young. From the 85 species, 8 species were identified to the genus level and 4 species were identified to the family level, with only 4 being recognized as introduced species (Table 1). Tree (> 1.5 m in height) and vine species were the greatest contributors to species richness in the understory of the tabonuco forest at El Verde. The relative species abundance of understory vegetation was also similar among all three geomorphic settings (Figure 2). However, both, vines and trees were more abundant, in terms of richness and percent cover, in ridges than in riparian valleys. Fern species exhibited a trend of decrease from riparian valleys up to ridges. Shrub species were more abundant in riparian valleys than in slopes or ridges (Figure 3). The most abundant species

Table 2. Mean values for biomass and percent cover of the most common species in the understory of the tabonuco forest six to nine months after Hurricane María, El Verde Research Area, Luquillo Experimental Forest, Puerto Rico. SE = standard error.

Life Form	Species	Mean ± 2 SE	
		Biomass g/m²	Cover (%)
Graminoid	*Ichnanthus pallens* (Sw.) Munro ex Benth.	89.57 ± 73.24	23.65 ± 10.34
Vine	*Dioscorea polygonoides* Humb. & Bonpl. ex Willd.	37.21 ± 40.86	6.65 ± 5.15
Tree/Shrub	*Psychotria berteroana* DC.	6.49 ± 11.42	2.39 ± 1.35
Vine	*Hippocratea volubilis* L.	3.55 ± 3.09	1.97 ± 1.12

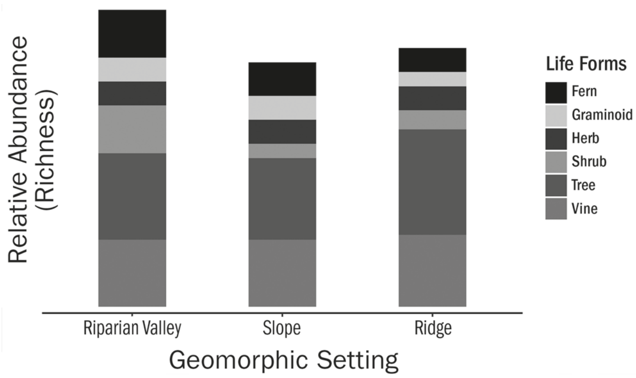

Figure 2. Differences in understory life forms patterns of relative abundance in terms of richness (number of different species) among geomorphic settings within the tabonuco forest six to nine months after Hurricane María at El Verde Research Area, Luquillo Experimental Forest, Puerto Rico.

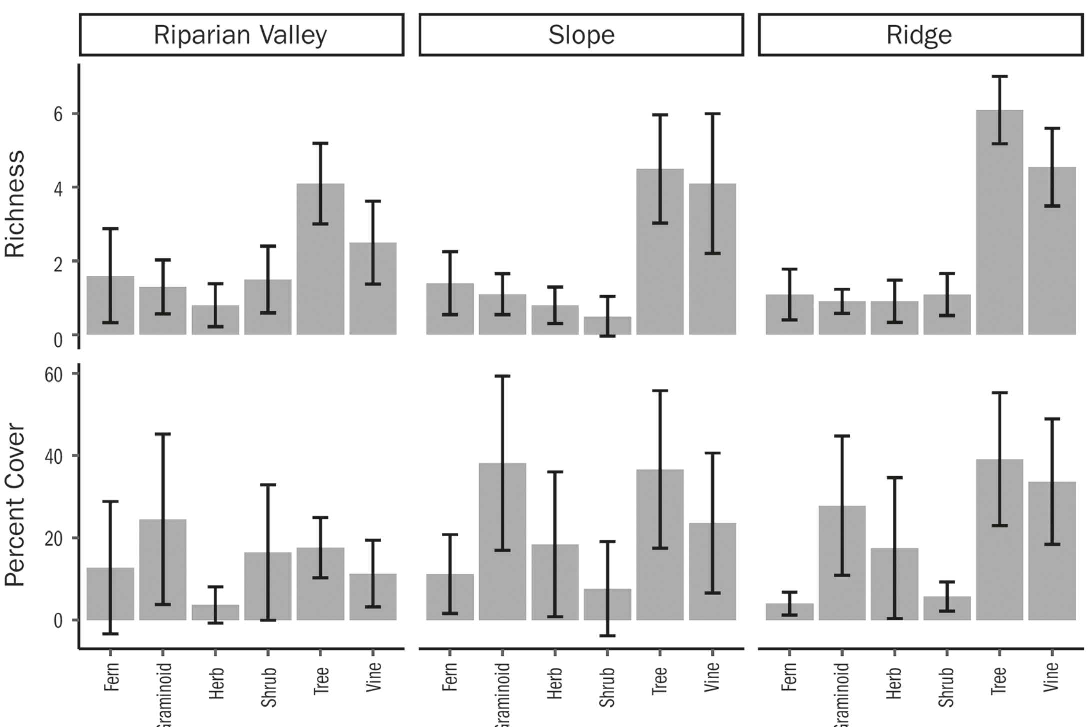

Figure 3. Mean richness (species per plot) and percent cover (%) values of understory species by life form among geomorphic settings within the tabonuco forest six to nine months after Hurricane María at El Verde Research Area, Luquillo Experimental Forest, Puerto Rico. Mean values were based on 10 plots for Riparian Valley and Slope, and 11 plots for Ridge Error bars represent two standard errors.

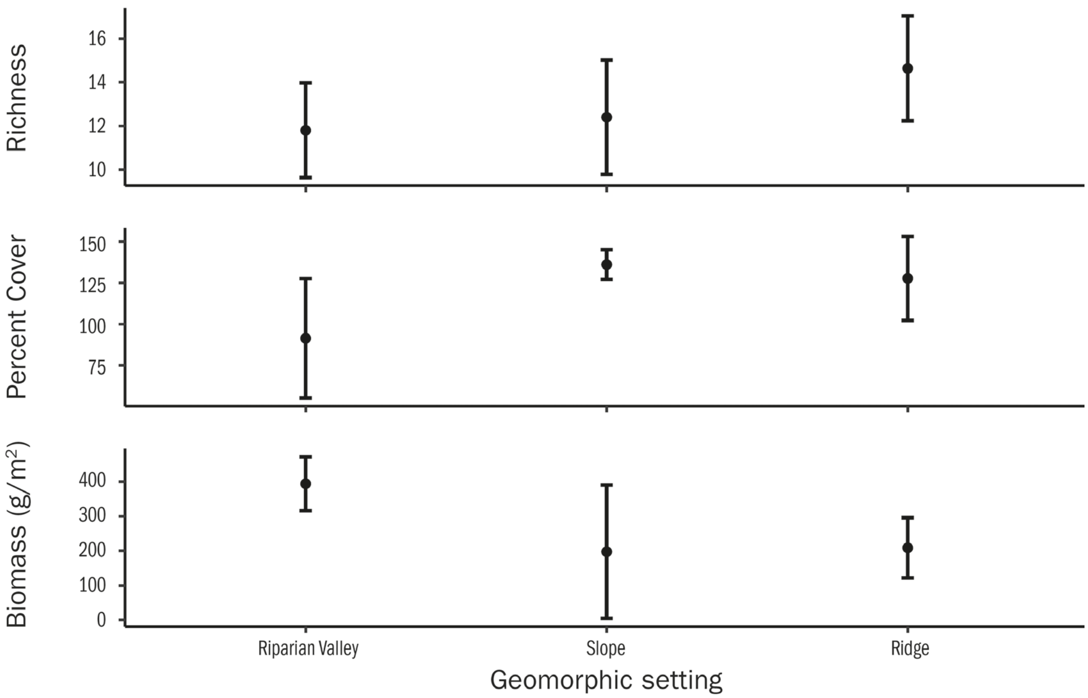

Figure 4. Mean richness (species per plot), percent cover (%) and biomass (g/m^2) values of understory species for each geomorphic setting within the tabonuco forest six to nine months after Hurricane María at El Verde Research Area, Luquillo Experimental Forest, Puerto Rico. Percent cover and richness values were Riparian Valley n = 10, Slope n = 10, and Ridge n = 11. Biomass values were Riparian Valley n = 3, Slope n = 3, and Ridge n = 3. Error bars represent two standard errors.

in terms of biomass and percent cover was a graminoid, the species *Ichnanthus pallens* (Table 2). Two vines (*Dioscorea polygonoides* and *Hippocratea volubilis)* and the tree/shrub *Psychotria berteroana* were the other top contributors to biomass and ground cover in the forest understory at El Verde.

Based on mean species richness per plot, trees seedlings and vines in the understory community at El Verde were the most abundant species among geomorphic settings (Figure 3). Tree seedling and vine mean cover exhibited a trend of increase from riparian valleys up to ridges, whereas shrub and fern cover decreased. In contrast, cover by graminoids tended to be more abundant on slopes. However, these tendencies were not statistically significant among vegetation life forms, both within the same geomorphic setting and among them (Figure 3).

Forest Understory Vegetation Characteristics in Relation to Geomorphic Setting

Within the tabonuco forest at El Verde there were no statistically significant differences in terms of richness (species per plot), percent cover, nor biomass for understory species among each geomorphic setting. A trend was observed for species richness to increase from riparian valleys up to ridges. Mean species cover was 45 percent less in riparian valley than in slopes, which had the most coverage. The aboveground biomass was comprised by every life form except tree seedlings. Riparian areas had the greatest amount of biomass and slopes the least (Figure 4). Each setting had a similar canopy cover with no significant differences among them.

Variation in Understory Vegetation Life Forms Within Tabonuco Forest Sites

The understory at El Verde had more species per plot than what was observed in Bisley (Table 3) but had similar values for percent cover (El Verde, 118.61 ± 16.19; Bisley, 161.20 ± 25.13) and biomass (El Verde, 266.75 ± 91.14; Bisley, 174.99 ± 48.03). Tabonuco forest understory vegetation had greater species richness (species per plot) for tree seedlings at Bisley, compared to species richness for other understory vegetation

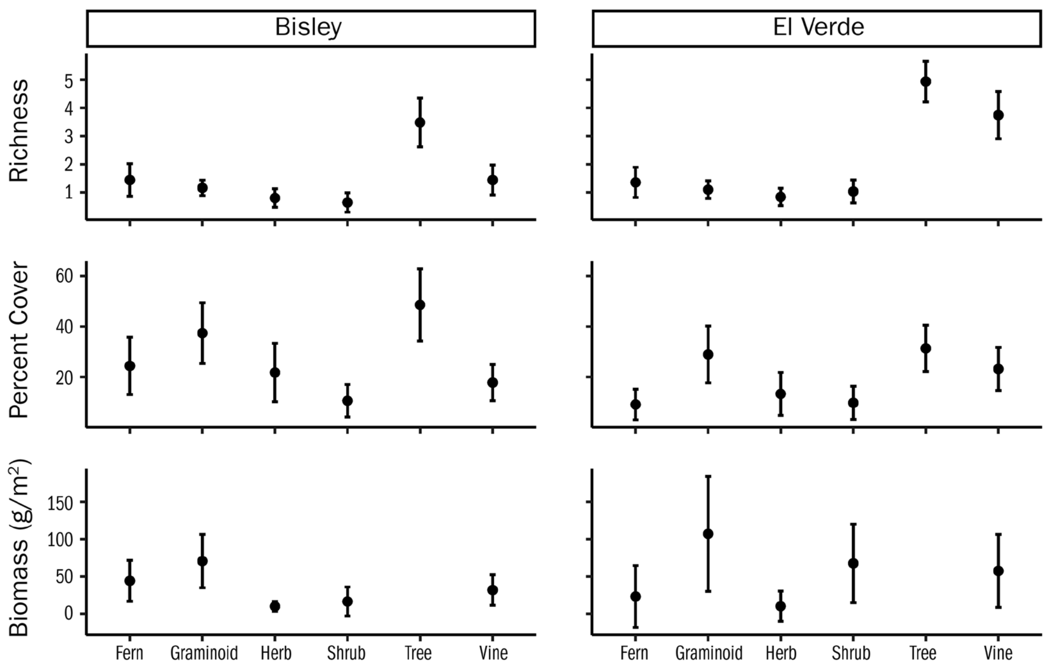

Figure 5. Mean richness (species per plot), percent cover (%) and biomass (g/m^2) values of understory species by life form within the tabonuco forest six to nine months after Hurricane María at the Bisley Experimental Watershed and at El Verde Research Area. Bisley values n = 25 plots. El Verde values n = 31 plots for percent cover and richness; biomass n = 9 plots. Error bars represent two standard errors.

life forms (KW H = 38.348, $p < 0.001$; Figure 5). At the El Verde site, the tabonuco forest understory had greater species richness for both tree seedlings and vines, compared to other vegetation life forms (KW H = 85.347, $p < 0.001$; Figure 5). In terms of percent cover tree seedlings and graminoids were the most abundant at both sites (El Verde: KW H = 44.154, $p < 0.001$; Bisley: KW H = 26.983, $p < 0.001$).

One to two species of fern, graminoid, herb, and shrub were consistently found per plot at both Bisley and El Verde. At Bisley, trees were the most abundant life form of the understory, in terms of richness and percent cover. There were significant differences in terms of biomass per vegetation life forms (El Verde: KW H = 11.331, $p < 0.023$; Bisley: KW H = 30.734, $p < 0.001$). Graminoids comprised the majority of biomass both at El Verde and Bisley, while herbs tended to have the least biomass in both sites.

Table 3. Characteristics of understory vegetation of the two tabonuco forest sites sampled six to nine months after Hurricane María in the Luquillo Experimental Forest, Puerto Rico. El Verde Research Area n = 31 for species per plot and percent cover values, n = 9 for biomass values. Bisley Experimental Watersheds n = 25 for all values. SE = standard error.

	Mean ± 2 SE	
Characteristic	Bisley	El Verde
Species/plot	9.00 (± 1.31)	13.00 (± 1.42)
Percent Cover (%)	161.20 (± 25.13)	118.61 (± 16.19)
Biomass (g/m^2)	174.99 (± 48.03)	266.75 (± 91.14)

Understory Vegetation Composition in Relation to Geomorphic Setting

Species composition of the understory vegetation in the valley plots seems to have more species in common among plots, therefore high association in their species composition, as evidenced by their close location in the multivariate species space (Figure 6). This is observed in both, the ordination based on species biomass and the one based on percent cover. Some of the species associated to valley were in contrast, species composition in the ridge and slope plots seem to be more similar, as these plots converge and are occupying an overlapping area closer together multivariate species space (Figure 6).

In the tabonuco forest at El Verde, understory species composition is richer than what we were able to capture in our sampling during this study.

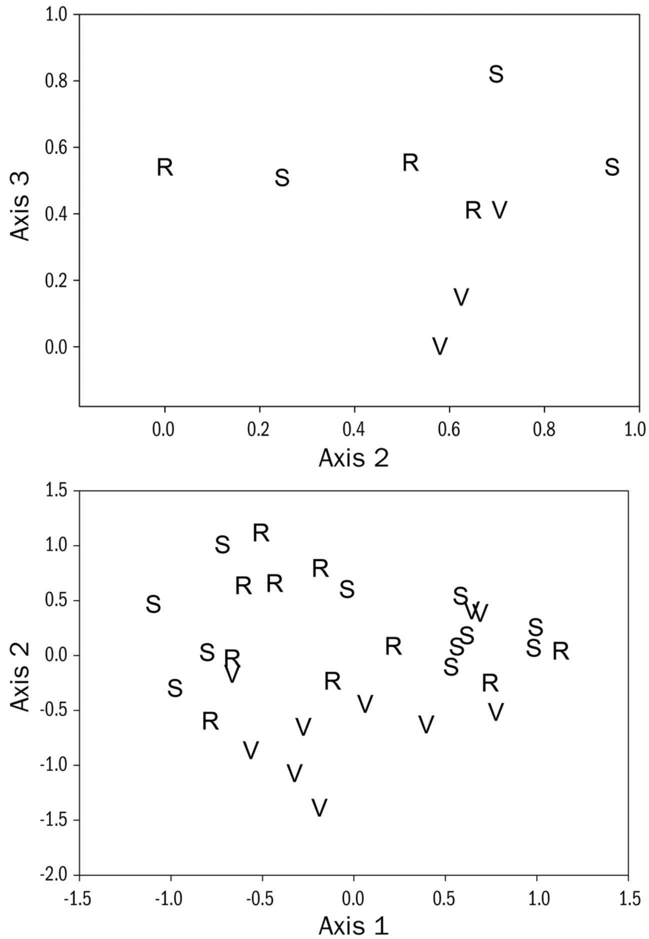

Figure 6. Ordination based on Non-metric Multidimensional Scaling (NMS) of understory vegetation community species composition among ridge, slope, and riparian valley plots six to nine months after Hurricane María in the tabonuco forest at El Verde Research Area, Luquillo Experimental Forest, Puerto Rico. Top panel ordination on species composition based on biomass (g/m^2) and bottom panel based on percent cover (%), symbols are V for riparian valley and valleys, S for slopes, and R for ridges.

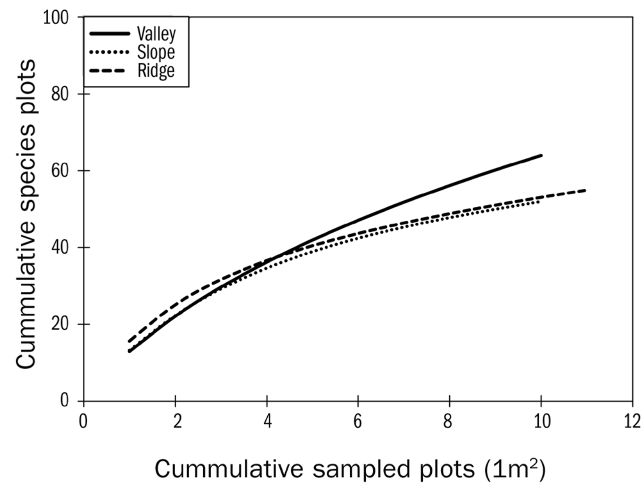

Figure 7. Species accumulation curves per geomorphic settings sampled six to nine months after Hurricane María at El Verde Research Area, Luquillo Experimental Forest, Puerto Rico. Riparian Valley n = 10, and Slope n = 10, and Ridge n = 11.

Many species found during this study occurred only once or twice in the sampled plots (Table 1). In valley plots 40 percent of species found occurred only once. This is also evidenced by the species accumulation curves generated (Figure 7). Our samples were closer to approaching a maximum number of species in plots from ridge and slope sites in comparison to plots in valleys.

DISCUSSION

Originally, we predicted that the understory community would show differences in terms of its structure and composition in relation to the geomorphic settings of the forest. Our results demonstrate that at the understory scale there could be differences in species composition among those settings. The tabonuco forest understory at both El Verde and Bisley has high biomass and percent vegetation cover at this post-hurricane period as was found by Chinea (1999) and Royo et al. (2011). However, biomass values were not representative of percent cover and richness because most species found were tree seedlings that were not collected as biomass samples. Canopy cover was similar among geomorphic settings, so we rejected it as a possible factor affecting understory vegetation characteristics, such as low biomass values found in ridges, which tend to have the greatest values according to previous observations (Scatena et al. 1992; Scatena and Lugo 1995). Nonetheless and since ridges were observed to support the greatest tree seedling relative abundance and species richness, aboveground biomass values could have been underestimated, considering that tree seedlings were not collected for destructive sampling.

The lowest species richness and highest biomass in valley areas suggests a more distinct species composition than what was observed in ridge and slope areas. The tendency of some vegetation characteristics to increase from one geomorphic setting to the other is another indicator of species composition variability in the understory. This variability in understory could be associated to differences in soil characteristics and species composition of the forest canopy dominants among geomorphic settings (Scatena and Lugo 1995). The low species richness at the Bisley site compared to the El Verde site could be associated to the different proportions of areas sampled, which in Bisley consisted mostly of slope regions. However, the overall species richness in the tabonuco forest understory is high at both sites as expected in this initial post-hurricane period (Chinea 1999; Royo et al. 2011).

Even though the tabonuco forest was in the early stages of post-hurricane dynamics at the time of our field work, there were differences in vegetation characteristics among life forms at the spatial scale of geomorphic setting. The results reflect the structure and composition of the understory community in a post-hurricane environment, which contrasts to pre-hurricane conditions as reported in previous studies in this forest (Chinea 1999; Royo et al. 2011; Kennard et al. 2020). Based on previous observations, the hurricane disturbance created opportunities for shade-intolerant graminoids and vines to thrive. Previous studies on post-hurricane disturbance effects on the understory have also found increases in certain vegetation life forms such as graminoids and lianas/vines, which have turned out to be only ephemeral increases in their biomass and ground cover that are gone after five years (Royo et al. 2011). The relative abundance of vine and graminoid in this study was significantly high, resembling the same response those previously studied post-hurricane environments.

During the post-hurricane period captured in this study, the understory of valley areas had a more distinct species composition than what was observed among ridge and slope areas which shared more species. The species composition of the understory vegetation may indeed be different among geomorphic settings, but these differences might emerge more clearly once the canopy closes over the tabonuco forest.

Acknowledgements

This research was supported by the NSF sponsored REU program of Tropical Ecology and Evolution at El Verde Field Station (NSF-grant number DBI-1062769), and the USDA Forest Service International Institute of Tropical Forestry (IITF) in collaboration with the University of Puerto Rico (UPR), and as part of IITF contributions to the Luquillo Long-Term Ecological Research Program (LTER) in the LEF. The authors thank Olga M. Ramos González (IITF Spatial Analyst) for help with the site map figure, for assistance in the field from Paul Lanctin (IITF student intern) and for laboratory work by Edgardo Valcárcel (IITF Analytical Chemistry Lab). The findings, conclusions, and views expressed in this manuscript are those of the authors and do not necessarily represent the views of the USDA Forest Service.

Literature Cited

Beard, K. H., Vogt, K. A., Vogt, D. J., Scatena, F. N., Covich, A. P., Sigurdardottir, R., and T. A. Crowl. 2005. Structural and functional responses of a subtropical forest to 10 years of hurricanes and droughts. Ecological Monographs 75:345–361.

Brokaw, N., T. Crowl, and A. Lugo. 2012. A Caribbean forest tapestry: the multidimensional nature of disturbance and response. Oxford University Press, New York, New York, USA.

Chinea, J. D., R. J. Beymer, C. Rivera, I. S. de Jeses, and F. N. Scatena. 1993. An annotated list of the flora of the Bisley Area Luquillo Experimental Forest, Puerto Rico 1987 to 1992. GTR-SO-94. USDA Forest Service, Southern Forest Experiment Station, New Orleans, Louisiana, USA.

Chinea, J. D. 1999. Changes in the herbaceous and vine communities at the Bisley Experimental Watersheds, Puerto Rico, following Hurricane Hugo. Canadian journal of forest research 29:1433–1437.

Colwell, R. K. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. http://purl.oclc.org/estimates Accessed July 2018.

Gentry, A. H., and C. Dodson. 1990. Contribution on nontrees to species richness of a tropical rain forest. Biotropica 19:149–156.

González, G., R. B. Waide, and M. R. Willing. 2013. Advancements in the understanding of spatiotemporal gradients in tropical landscape: A Luquillo focus and global perspective. Ecological Bulletins 54:245–250.

Harris, N. L., A. E. Lugo, S. Brown, and T. Heartsill-Scalley. 2012. Luquillo experimental forest: research history and opportunities. EFR-1. Washington, DC: USDA Forest Service.

Heartsill Scalley, T. 2017. Insights on Forest Structure and Composition from Long-Term Research in the Luquillo Mountains. Forests 8:204.

Heartsill Scalley, T., F. N. Scatena, A. E. Lugo, S. Moya, and C. R. Estrada Ruiz. 2010. Changes in Structure, Composition, and Nutrients During 15 Yr of Hurricane-Induced Succession in a Subtropical Wet Forest in Puerto Rico. Biotropica 42:455–463.

Johnston, M. H. 1992. Soil-vegetation relationships in a tabonuco forest community in the Luquillo Mountains of Puerto Rico. Journal of Tropical Ecology 8:253–263.

Kennard, D. K., D. Matlaga, J. Sharpe, C. King, A. M. Alonso-Rodríguez, S. C. Reed, M. A. Cavaleri, and T. E. Wood. 2020. Tropical understory herbaceous community responds more strongly to hurricane disturbance than to experimental warming. Ecology and Evolution 10:8906–8915.

Lugo, A. E., and F. N. Scatena. 1995. Ecosystem-Level Properties of the Luquillo Exerpimental Forest with Emphasis on the Tabonuco Forest. Pages 59–108 in A. E. Lugo, and C. Lowe, editors. *Tropical Forests: Management and Ecology.* Springer, New York, New York, USA.

McCune, B. and M. J. Mefford. 2011. PC-ORD. Multivariate Analysis of Ecological Data, Version 6 for Windows. MjM Software, Gleneden Beach, Oregon, U.S.A.

R Core Team. 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Royo, A. A., T. H. Scalley, S. Moya, and F. N. Scatena. 2011. Nonarborescent vegetation trajectories following repeated hurricane disturbance: ephemeral versus enduring responses. Ecosphere 2:1–18.

Scatena, F. N., and A. E. Lugo. 1995. Geomorphology, disturbance, and the soil and vegetation of two subtropical wet steepland watersheds of Puerto Rico. Geomorphology 13:199–213.

Scatena, F. N., W. Silver, T. Siccama, A. Johnson, and M. J. Sanchez. 1993. Biomass and nutrient content of the Bisley experimental watersheds, Luquillo Experimental Forest, Puerto Rico, before and after Hurricane Hugo, 1989. Biotropica 25:15–27.