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Site-specific impacts of a major hurricane on alpha and beta diversity in tropical forest seedling communities

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Abstract. Large scale disturbances are known to impact the alpha and beta diversity of communities. However, whether these disturbances increase or decrease diversity is often debated. The goal of this study was to quantify how the diversity of the seedling community was impacted within and across elevation in the El Yunque forest of Puerto Rico following a major hurricane. We tested two alternative hypotheses, that hurricanes are relatively more homogenizing or non-homogenizing forces, by quantifying changes in alpha and beta diversity of the seedling community post-hurricane. This approach highlights whether ecological mechanisms associated with community homogenization (species-specific survival, successional processes, and reduced environmental heterogeneity) or non-homogenization (resource release, increased environmental heterogeneity, and stochastic processes) structure the seedling community post-hurricane. We compared species richness, Fisher's α, Simpson's evenness, and multiple aspects of beta diversity within and among 25 seedling plots at 300, 400, and 500 m in elevation pre- and post-hurricane. We found that species richness, diversity, and evenness were higher post-hurricane, but abundance decreased 19%. Increases in alpha diversity suggest that hurricanes are non-homogenizing forces potentially linked with increases in light levels promoting colonization of early-successional species and resource release for other light-demanding species. The beta diversity results varied in their support for hurricanes as homogenizing depending upon the spatial scale of the analysis, potentially due to a combination of mechanisms including species-specific survival and site-specific differences. To fully grasp how the seedling community responds and recovers from disturbance, additional long-term monitoring will be needed to allow insight into the future of species richness, abundance, and spatial and temporal changes in community composition.

Key words: alpha diversity; beta diversity; hurricane; Puerto Rico; seedling communities; tropics.

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Introduction

Plant community dynamics are often explained in the context of local-scale disturbances (e.g., light gaps generated by tree falls; Brokaw and Busing 2000). However, rare, large scale disturbances can have major impacts in the short and long term (Flynn et al. 2010, Yee et al. 2019). Large scale alterations in plant communities can occur for various reasons including, fire, pest outbreak, anthropogenic pressures, and hurricanes (Walker 1991, Verdú and Pausas 2007, Hooper 2008, Hogan et al. 2016, Hu and Smith 2018). These types of disturbances are known to have long-lasting effects on the dynamics, structure, and function of plant communities (Brokaw and Grear 1991, Zimmerman et al. 1994, Shiels et al. 2010, Comita et al. 2018). Quantifying how communities change in the short-term following major disturbances can provide insights into these long-lasting effects.

The impact that hurricanes, in particular, can have on plant communities has been well documented (Lugo et al. 1983, Brokaw and Grear 1991, Yih et al. 1991, Basnet et al. 1992, Basnet 1993, Boose et al. 2004, Uriarte et al. 2019). In the Caribbean, hurricanes are considered an important agent of natural disturbance (Crow 1980, Walker et al. 1991, Aide et al. 1995, Lomascolo and Aide 2001). The disturbance level caused by hurricanes in this area depends on their strength, path, and frequency (Lugo et al. 1983, Boose et al. 2004, Ostertag et al. 2005). Recently, the strength and frequency of hurricanes in the Caribbean have increased and are projected to further increase due to global warming (Emanuel 2005, Balaguru et al. 2018). This has the potential to cause plant communities to be altered in ways not previously observed, making observations following recent high-intensity hurricanes imperative.

Hurricanes are known to have major effects on the canopy layer of forests, causing stems to break, defoliation to occur, and overall loss of above-ground biomass (Brokaw and Walker 1991, Basnet et al. 1992, Liu et al. 2018, Uriarte et al. 2019). While tree mortality is often low (Walker 1991, Bellingham et al. 1992), damage can be extensive, altering conditions beneath the canopy and resulting in significant impacts on seedlings in the understory (Bellingham et al. 1996, Walker et al. 2003, Comita et al. 2009). The seedling layer can be both directly and indirectly affected by hurricanes. For instance, seedlings may be directly crushed by falling woody debris or blown-down and uprooted. Indirectly, hurricanes can impact the seedling layer through increases in the depth of litter, light, and temperature due to canopy defoliation and openness (Guzmán-Grajales and Walker 1991, Walker et al. 2003). By observing the seedling community post-hurricane, there is the potential to watch the onset of the regeneration process to improve our inferences regarding the trajectory of forests following rare large disturbances (Pascarella et al. 2004, Comita et al. 2009, 2018, Flynn et al. 2010, Uriarte et al. 2018). These observations may also provide insight into both direct and indirect effects hurricanes can have on seedling communities.

Hurricanes can alter the composition of seedling communities through changes in both their alpha and beta diversities. However, the direction (increases or decreases) of these changes is often debated with hurricanes thought of as both homogenizing (Vanschoenwinkel et al. 2013, Hawkins et al. 2015) and non-homogenizing forces (Yee et al. 2019). If hurricanes are relatively more homogenizing forces, they are expected to decrease both alpha and beta diversity of communities post-disturbance. These decreases have been attributed to species-specific survival (Brokaw and Walker 1991, Zimmerman et al. 1994), successional processes (Arroyo-Rodríguez et al. 2013, Vanschoenwinkel et al. 2013, Comita et al. 2018) where dominant groups of species alter the environment and to reductions in environmental heterogeneity (Vellend et al. 2007, Hawkins et al. 2015). Conversely, if hurricanes are relatively more non-homogenizing forces, they are expected to increase alpha and beta diversity. An increase in alpha diversity could result if the original community composition was dominated by few species and the disturbance allowed resource release for previously non-dominant species (Comita et al. 2009, Vanschoenwinkel et al. 2013, Yee et al. 2019). For instance, alteration of the canopy structure post-hurricane could lead to an increase in light penetrating the understory that would promote colonization of early-successional species (Denslow 1987, Uriarte et al. 2005, Comita et al. 2009, 2018). Increased beta diversity has previously been attributed to increased environmental heterogeneity post-disturbance (Maaß et al. 2014) and stochastic processes, such as priority effects, influenced by variation in initial environmental conditions (Christensen and Peet 1984).

Understanding the mechanisms by which hurricanes affect seedling communities is important for recognizing how future disturbances will affect the trajectory of regeneration and recovery of forests. The goal of this study was to quantify how the diversity of the seedling community was impacted following a major hurricane within and across elevation in the El Yunque forest of Puerto Rico. We tested two alternative hypotheses, whether hurricanes are relatively more homogeneous or non-homogenous forces, by quantifying changes in alpha and beta diversity of the seedling community post-hurricane. Through this approach, we can highlight whether ecological mechanisms associated with community homogenization (species-specific survival, successional processes, and reduced environmental heterogeneity) or non-homogenization (resource release, increased environmental heterogeneity, and stochastic processes) structure the seedling community post-hurricane.

Methods

Study site

This study was conducted in the Luquillo Experimental Forest (LEF) in the El Yunque National Forest of eastern Puerto Rico. The LEF covers 11,330 ha with an elevational range of 100–1075 m above sea level (a.s.l.; Barone et al. 2008). This study focused on elevations from 300 to 500 m a.s.l. that are classified in the subtropical wet forest life zone (Ewel and Whitmore 1973). The forest is dominated by *Dacryodes excelsa* Vahl., *Prestoea acuminata* (Willd.) H.E. Moore var. *montana* (Graham) A. Hend. & G. Galeano, *Manilkara bidentata* (A. DC.) A. Chev, and *Sloanea berteriana* Choisy ex DC. with a closed canopy at 20–25 m (Walker 1991, Zimmerman et al. 1994). Typically, at 350 m a.s.l., September is the warmest month, with temperatures averaging 24.5°C, while January is the coolest month, with temperatures averaging 21.0°C (Barone et al. 2008); however, understory temperatures increase dramatically following defoliation during hurricanes. Mean annual precipitation increases with elevation, ranging from approximately 2500 mm/yr at lower elevations to 4500 mm/yr at higher elevations (Murphy et al. 2017). At all elevations, rainfall averages more than 100 mm every month of the year (Barone et al. 2008). Soils are derived from volcaniclastic sediments which weather to become dense clays (Huffaker 2002).

In mid-September 2017, Hurricane Maria made landfall in Puerto Rico as a Category 4 hurricane with maximum wind speeds of 250 km/h and approximately 500 mm of precipitation falling in 24 h (Pasch et al. 2018). In the LEF, this hurricane caused stems to break, uproot, or die, massive branch breaking and leaf loss, along with general loss of above-ground biomass (Uriarte et al. 2019, Hall et al. 2020).

Seedling inventories

In June 2017, prior to Hurricane Maria, 50 × 50 m adult tree plots were installed across elevation, at 300, 400, and 500, where all individuals greater than 1 cm diameter at breast height (dbh) were tagged and identified. In each of these plots, 25 1 × 1 m seedling plots were installed at regular intervals with a 10 m buffer from the adult plot edge. Following Hurricane Maria's landfall in September 2017, the seedling plots were reinstalled in June 2018 within the same 50 × 50 m adult tree plots and as close to their original locations as possible, with deviations due to fallen trees and other unmovable debris for four plots. For both sets of seedling plots, all growth forms between 4 and 50 cm in height were tagged and identified. The height of individuals was measured from the ground to the meristem, except for palm species where height was measured from the ground to the base of the eophyll. Species nomenclature followed Acevedo-Rodríguez and Strong (2012). This study included seedlings that germinated post-hurricane and seedlings that survived the hurricane. Seedling species were classified into successional stage (early, mid, late) and growth from (tree, shrub, palm, liana) based on the literature (Appendix S1: Table S1).

Alpha diversity analyses

Biodiversity metrics were calculated and compared for pre- vs. post-hurricane data, both within and across elevation plots, including species, genus, and family richness. Alpha diversity changes were measured by calculating Fisher's α and Simpson's evenness using the *vegan* package (Oksanen et al. 2017) in *R* statistical software version 3.6.1 (R Core Team 2019). Simpson's evenness was calculated by dividing the inverse Simpson index by the observed number of species (Morris et al. 2014).

Beta diversity analyses

Beta diversity was measured using two dissimilarity indices: Bray-Curtis and Raup-Crick. The Bray-Curtis index is a classic beta diversity measure that calculates variation based on differences in species abundance information, thus considering both species identity and abundance (Bray and Curtis 1957, Anderson et al. 2010). Raup-Crick dissimilarity is a probabilistic index that calculates variation based on presence–absence information (Legendre and Legendre 1998, Chase et al. 2011). We measured dissimilarity using the Raup-Crick index because it is independent of alpha diversity differences, which allows for the determination of the degree that beta diversity is influenced by variation in alpha diversity (Raup and Crick 1979, Chase et al. 2011). Observed values of Bray-Curtis and Raup-Crick indices were calculated using the vegan package (Oksanen et al. 2017) in *R* statistical software version 3.6.1 (R Core Team 2019). Independent swap null models (Gotelli and Entsminger 2001) were used to compare observed and expected values of the dissimilarity indices, with the species pool differing for each analysis, as described below. These null models randomize the community data matrix, but maintain species occurrence frequency and site richness (Gotelli and Entsminger 2001). Null models were implemented using the picante package (Kembel et al. 2010) in *R* statistical software version 3.6.1 (R Core Team 2019). We calculated standardized effect sizes (SES) from 999 iterations of the null models. Positive values indicated higher dissimilarity than expected (i.e., non-homogenization), whereas negative values indicated less dissimilarity than expected (i.e., homogenization).

Beta diversity was calculated for pre- and post-hurricane seedling communities at different spatial scales (Fig. 1). First, we determined local-scale dissimilarity by quantifying beta diversity among the 25 seedling plots found within each elevation pre-hurricane and post-hurricane (Fig. 1a). For this analysis, the species pools for the null models consisted of all species present in the selected elevation pre- and post-hurricane, respectively. Unpaired Wilcoxon tests (*W*) were used to compare levels of local beta diversity before and after the hurricane. Second, we determined spatial dissimilarity pre- and post-hurricane by quantifying beta diversity between

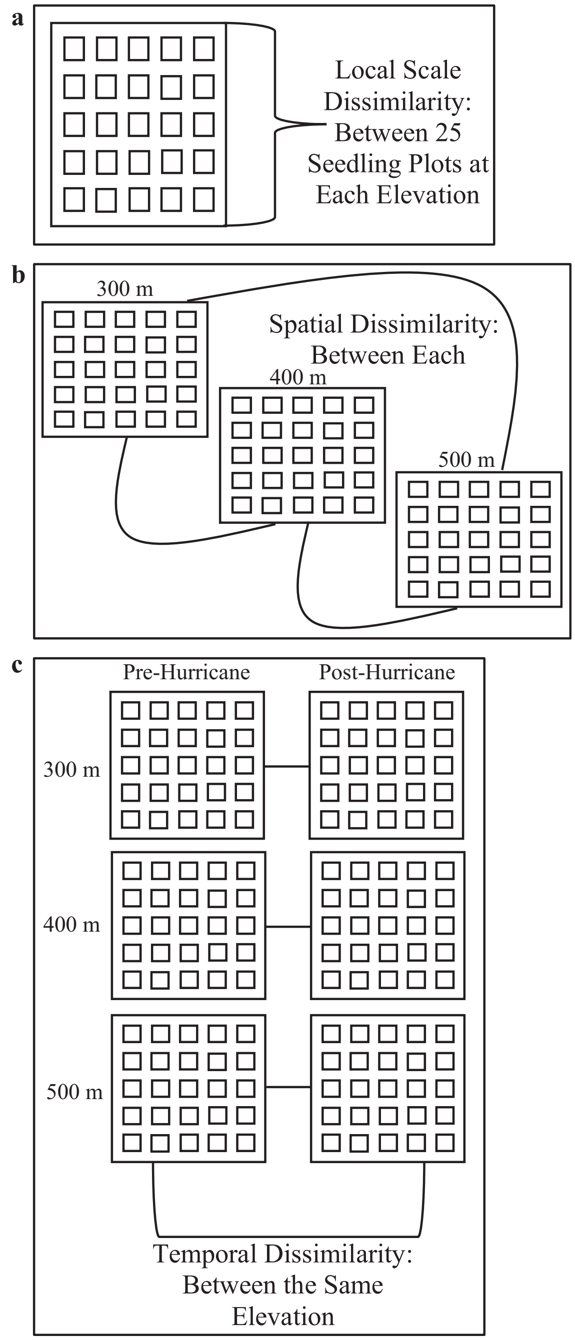

Fig. 1. Different ways in which beta diversity was assessed. (a) Local-scale dissimilarity: between the 25 seedling plots found within each elevation pre-hurricane and those same plots post-hurricane. (b) Spatial dissimilarity: between elevations (300–400 m, 400–500 m, 300–500 m) pre- and post-hurricane. (c) Temporal dissimilarity: between each elevation pre-hurricane and that same elevation post-hurricane.

elevations using the total of all 25 plots for each elevation (Fig. 1b). For this null model, the species pool consisted of all species present across the elevations pre-hurricane, then post-hurricane. Lastly, we determined local temporal dissimilarity by quantifying beta diversity between each elevation pre-hurricane and that same elevation post-hurricane (Fig. 1c). The species pool for this null model included any species present pre- and post-hurricane.

Results

Alpha diversity

Considering all seedling plots across elevation, pre-hurricane plots had 346 more individuals, which indicates a 19% decrease post-hurricane in seedling abundance (Appendix S1: Table S2). However, post-hurricane plots had eight more families, seven more genera, and nine more species than pre-hurricane plots (Table 1). Fisher's α and Simpson's evenness values followed abundance and richness trends with increases post-hurricane for all plots individually and for the community as a whole (Table 1).

Of the 61 species present, we were unable to classify nine species into a successional stage, five of which were lianas (Appendix S1: Table S1). At 300 and 400 m, we saw a shift from the highest percentage of species being late successional (42% and 43%, respectively), pre-hurricane, to early-successional, post-hurricane (41% and 38%, respectively). At 500 m, pre-hurricane, late successional species made up the largest percent of species (46%), but post-hurricane the percentages were more evenly distributed between successional stages (27% early, 30% mid, 30% late). The overall trend followed that of 300 and 400 m with a shift in species richness and abundance from late successional to early-successional species following the hurricane.

Next, we focused on how liana species richness and abundance changed post-hurricane. At 300 m, liana species richness and the percentage of individuals they constituted was similar before (six species, 31%) and after (seven species, 30%) the hurricane. At 400 m, the number of lianas species was five before and after the hurricane, but lianas made up 24% of the individuals pre-hurricane and only 10% of the individuals post-hurricane. At 500 m, the number of lianas species was three pre- and post-hurricane. However, pre-hurricane, lianas made up 40% of the individuals, while they made up only 4% of the individuals post-hurricane. In total, across all elevations, pre-hurricane there were seven species of liana making up 31% of the total abundance and post-hurricane there were nine species of liana making up 18% of the total abundance.

Beta diversity

Bray-Curtis and Raup-Crick indices were calculated to quantify the dissimilarity within and between plots pre- and post-hurricane and across elevation. To determine whether observed values were higher or lower than expected, we conducted null model analyses for all measurements of beta diversity. Local-scale dissimilarity, calculated as observed beta diversity between the 25 plots in each elevation, showed significant differences between plots pre- and post-hurricane at 300 and 500 m for both Bray-Curtis (300 m, $W = 23229$, $P < 0.0001$; 500 m, $W = 41471$, $P = 0.002$) and Raup-Crick (300 m, $W = 38491$, $P = 0.002$; 500 m, $W = 42381$,

Table 1. Values for metrics used to compare the seedling communities of 25 1 × 1 m seedling plots within and across three elevations (300, 400, and 500 m) pre- and post-Hurricane Maria in El Yunque, Puerto Rico.

	Pre-Hurricane Maria				Post-Hurricane Maria			
Metric	300 m	400 m	500 m	Total	300 m	400 m	500 m	Total
Individuals	998	470	312	1780	633	496	305	1434
Families	18	17	20	27	23	23	20	35
Genera	26	21	28	41	34	30	27	48
Species	26	21	28	44	37	32	30	53
Fisher's α	4.88	4.51	7.45	8.16	8.57	7.64	8.25	10.83
Simpson's evenness	0.24	0.29	0.19	0.21	0.30	0.36	0.25	0.33

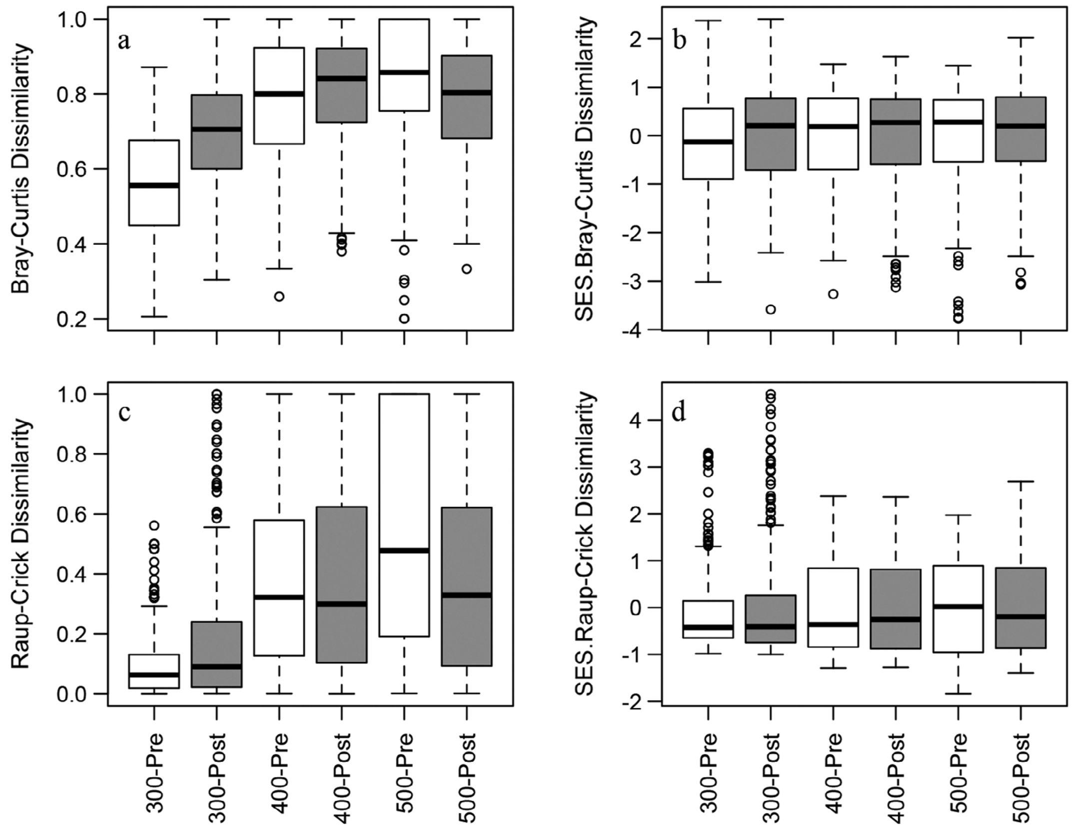

Fig. 2. Local-scale beta diversity pre- and post-Hurricane Maria within seedling plots at three elevations in the Luquillo Experiment Forest (Fig. 1a). (a) Observed Bray-Curtis dissimilarity. (b) Standardized effect sizes (SES) of Bray-Curtis dissimilarity. (c) Observed Raup-Crick dissimilarity. (d). Standardized effect sizes (SES) of Raup-Crick dissimilarity. (b, d) Positive values on the *y*-axis indicate higher than expected beta diversity (less homogenous) and negative values on the *y*-axis indicate lower than expected beta diversity (more homogenous) after null models.

$P < 0.0001$) indices (Figs. 1a, 2a, c). However, standardized effect sizes of these values showed no clear increase or decrease in local homogenization post-hurricane (Fig. 2b, d). There was no clear increase or decrease in dissimilarity between elevations following the hurricane, although some comparisons did shift idiosyncratically (Figs. 1b, 3). Both pre- and post-hurricane dissimilarity between 300 and 400 m was less than expected (i.e., more homogeneous) and dissimilarity between 400 and 500 m was greater than expected (i.e., less homogenous); these values do suggest that the two lower elevation plots are more similar to each other (Figs. 1b, 3). Beta diversity between pre- and post-hurricane seedling communities also showed no clear trend, but seemed to be driven by alpha diversity based on the decreases in beta diversity when measured using the Raup-Crick index that is independent of alpha diversity (Figs. 1c, 4a, c). Standardized effect sizes of the Bray-Curtis and Raup-Crick indices showed that turnover in composition and abundances of species was less than expected for the null expectation via community randomization (i.e., random chance alone; Fig. 4b, d).

Discussion

Forest recovery: alpha diversity

Overall, findings from this study agree with others that floristic diversity is maximized

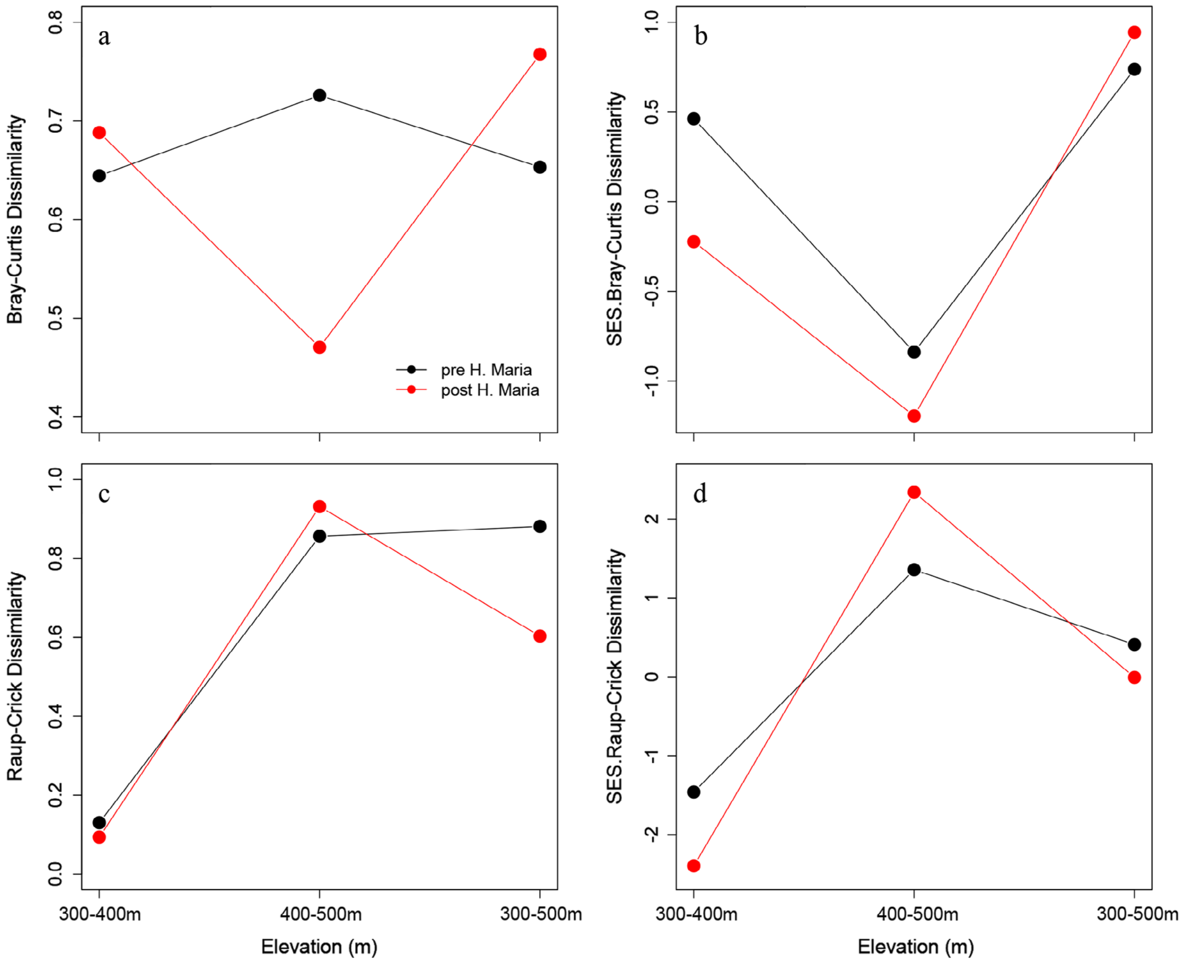

Fig. 3. Spatial beta diversity pre- and post-Hurricane Maria between elevations in the Luquillo Experiment Forest (Fig. 1b). (a) Observed Bray-Curtis dissimilarity. (b) Standardized effect sizes (SES) of Bray-Curtis dissimilarity. (c) Observed Raup-Crick dissimilarity. (d). Standardized effect sizes (SES) of Raup-Crick dissimilarity. (b, d) Positive values on the *y*-axis indicate higher than expected beta diversity (less homogenous), and negative values on the *y*-axis indicate lower than expected beta diversity (more homogenous) after null models.

shortly after disturbance when both early and mid-successional species are present and the evenness of individuals within species is increased (Crow 1980, Oatham and Ramnarine 2006, Rozendaal et al. 2019). We found that despite the severity in damage caused by Hurricane Maria, species diversity and evenness were higher post-hurricane (Table 1). Largely, the recovery of seedling species richness post-Hurricane Maria was expectedly quick (Table 1), but is it anticipated that adult tree species richness recovery will be slower (Hooper 2008).

It has been suggested and observed that increases in light due to canopy defoliation would promote colonization and growth of early-successional species (Myster and Walker 1997, Comita et al. 2009, Hogan et al. 2018, Lai et al. 2020). We can support these findings post-Hurricane Maria where we saw increases in the dominance and percentage of early-successional species across all three elevations, individually, and in the forest as a whole (Appendix S1: Table S1). For example, there was a dramatic increase in *Cecropia schreberiana* individuals, a light-demanding, early-successional species,

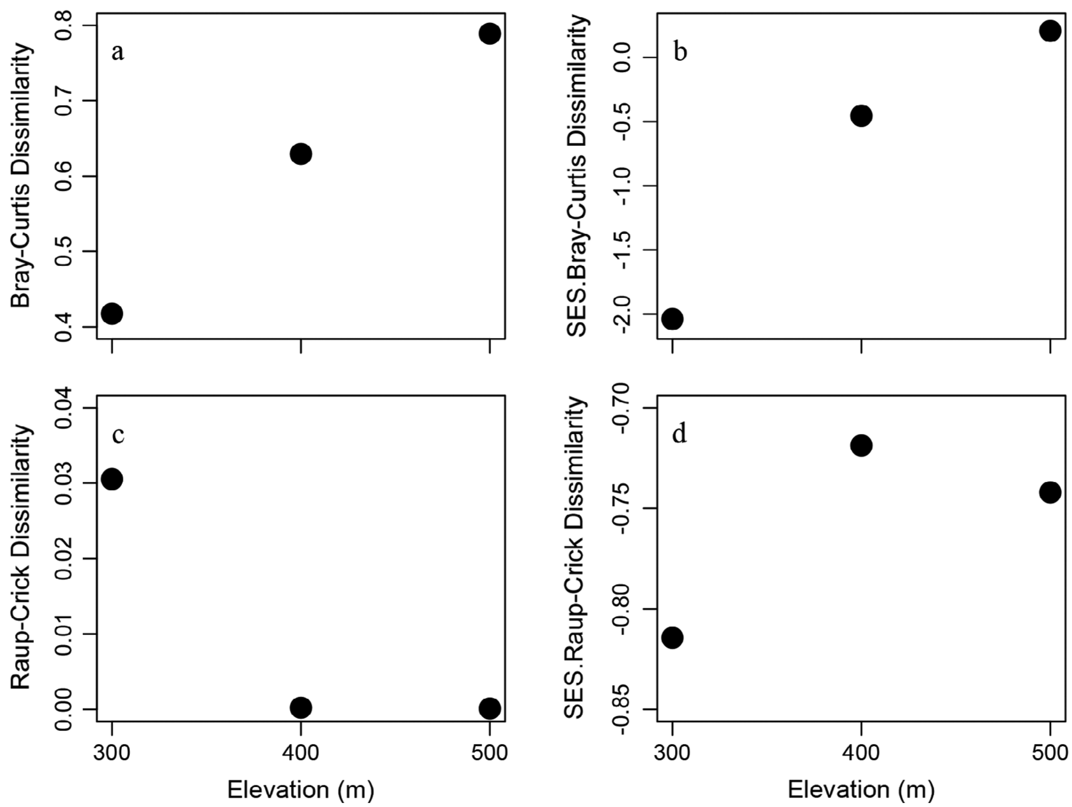

Fig. 4. Temporal beta diversity between the same elevation pre- and post-Hurricane Maria in the Luquillo Experiment Forest (Fig. 1c). (a) Observed Bray-Curtis dissimilarity. (b) Standardized effect sizes (SES) of Bray-Curtis dissimilarity. (c) Observed Raup-Crick dissimilarity. (d). Standardized effect sizes (SES) of Raup-Crick dissimilarity. (b, d) Positive values on the *y*-axis indicate higher than expected beta diversity (less homogenous), and negative values on the *y*-axis indicate lower than expected beta diversity (more homogenous) after null models.

that is the most common species in the seed bank of the LEF (Brokaw 1998; Appendix S1: Table S2). Brokaw (1998) and others have noted the widespread and abundant regeneration of *C. schreberiana* following hurricanes (Canham et al. 2010, Zimmerman et al. 2010, Comita et al. 2018). Light can also affect the frequency of species post-hurricane due to species-specific light regeneration requirements (Fernández and Fetcher 1991, Everham et al. 1996, Uriarte et al. 2005). For example, we saw a decrease in the frequency of *D. excelsa* across all elevations post-hurricane, which could be attributed to its ability to regenerate in low light levels. This was in contrast to an increase in the frequencies of *Alchorneopsis floribunda*, *Spondias mombin*, and *Schefflera morototoni*, which prefer to regenerate in high light levels (Devoe 1989, Everham et al. 1996, Oatham and Ramnarine 2006, Uriarte et al. 2012).

Due to almost complete defoliation of the forest, drought-like conditions increased following Hurricane Maria. Based on prior research, we believed this would cause increases in richness and abundance of liana species post-hurricane, given their purported demographic advantage over tree species early in ontogeny that has been associated with disturbance and drought (Rice et al. 2004, Arroyo-Rodríguez and Toledo-Aceves 2009, Hogan et al. 2017, Umaña et al. 2019). Instead, we found that despite the richness of liana species being similar pre- and post-hurricane, the total abundance of liana individuals sharply decreased post-hurricane (Appendix S1: Table S2). However, evidence has shown that lianas having significantly higher survival than tree seedlings, which could lead to their persistence and increased abundance beyond our sampling period (Umaña et al. 2019). More research should be focused on following liana species through ontogeny to better understand how they react to disturbance.

Forest recovery: beta diversity

Based on our seedling data, recovery of this forest following Hurricane Maria appears to be on trajectory with previous hurricane occurrences (Crow 1980, Guzman-Grajales and Walker 1991, Oatham and Ramnarine 2006, Hooper 2008, Comita et al. 2009). In general, we found no clear trends for increasing or decreasing beta diversity, based on observed values, following Hurricane Maria. However, we did find significant differences between pre- and post-hurricane local-scale communities at 300 and 500 m, with beta diversity increased post-hurricane. The seedling stage represents the largest demographic bottleneck in trees, so it is likely that current diversity in the seedling community will be reduced by the time surviving individuals reach adult stage (Uriarte et al. 2005, Comita et al. 2009, Muscarella et al. 2013). Many studies of hurricane effects on adult composition predict little change in long-term species composition of the forests (Walker 1991, Yih et al. 1991). It is also important to keep in mind that the recovery of structural characteristics of the forest does not indicate recovery of species composition (Hooper 2008, Hogan et al. 2016, Rozendaal et al. 2019, Yee et al. 2019).

Hurricanes: homogenizing and non-homogenizing forces

Increases and decreases in alpha and beta diversity have been found following hurricanes leaving open for debate whether hurricanes are relatively more homogenizing or non-homogenizing forces (Maaß et al. 2014, Comita et al. 2018, Yee et al. 2019). We found evidence that tends to suggests that hurricanes are relatively more homogenizing forces, based on beta diversity, and relatively more non-homogenizing forces based on alpha diversity. Measures associated with alpha diversity (Fisher's α and Simpson's evenness) were found to increase post-hurricane, despite decreases in species richness. As highlighted above, increases in alpha diversity were potentially associated with increased light levels due to canopy defoliation leading to the promotion of colonization by early-successional species along with resource release for other light-demanding species to thrive.

The beta diversity results indicated that the degree to which hurricanes homogenize the seedling community depends upon the spatial scale of the analysis. We found that when pre- and post-hurricane communities were compared, they were more similar than expected (more homogenous), especially when alpha diversity was controlled (Fig. 4). This homogenization could be due to a combination of mechanisms including species-specific survival and reductions in environmental heterogeneity. For instance, we saw a shift from low-light regenerating species to high-light regenerating species suggesting a loss of shade-tolerant species. Similar findings have been reported when investigating homogenization of a fragmented forest (Arroyo-Rodríguez et al. 2013) and a previous hurricane in Puerto Rico (Comita et al. 2018).

When comparing spatial dissimilarity (across elevation) between seedling communities, we found that the two lower elevation communities (300 and 400 m) were more homogenous than expected while the two upper elevation communities (400 and 500 m) were less homogenous than expected (Fig. 3). These findings point to site-specific differences causing some communities to become more homogenous post-hurricane, while others become less homogenous. These three seedling communities (300, 400, and 500 m) are all part of the same forest type (i.e., Tabonuco forest) that spans from lowland areas up to approximately 600 m in elevation (Weaver and Gould 2013). However, there is spatial turnover with elevation where an intermixing of species from Palo Colorado and cloud forest communities occurs between approximately 400 and 800 m that could be contributing to site-specific differences found in this study (Weaver and Gould 2013). There are other possible mechanisms driving these differences including variation in stochastic processes of species regeneration, arrival, and survival and microenvironmental differences between communities (Walker and Neris 1993, Peterson 2000, Vellend et al. 2007).

At the local scale, considering plots within elevation, we found significant increases in observed beta diversity post-hurricane (Fig. 2a, c), but these differences were neither higher or lower than expected suggesting no increase or decrease in homogenization (Fig. 2b, d). We suggest that this lack of spatial structure both pre- and post-hurricane may be attributed to stochastic processes such as priority effects, where preference is given to individuals that arrive at a site first (Fig. 2). Local site factors have been noted by others to influence species diversity post-disturbance (Reyes and Kneeshaw 2008, Rodriguez-Garcia et al. 2011, Reyes et al. 2013).

Conclusions

Following hurricane disturbance, large turnover in species is projected to occur through succession of the forest. This turnover has been linked to variation in recruitment, thinning, competitive dynamics, and other environmental impacts (Aide et al. 1996, Uriarte et al. 2005, Comita et al. 2018). However, previous work has shown that local species richness is established very early during regeneration, making immediate seedling community censuses following major disturbances important (Hubbell et al. 1999). To fully grasp how the seedling community responds and recovers from disturbance, long-term monitoring is needed that will allow insight into the future of species richness, abundance, and spatial and temporal changes in community composition. The few studies that have done this show interesting results of increased growth rates and decreased mortality for plants establishing soon after disturbances (Denslow 1987) and increased persistence of early-successional species, possibly because of their initial high seedling establishment in high-light, disturbed environments (Muscarella et al. 2013). It has been shown that it can take up to two years for temperature and humidity to return to pre-disturbance levels at the height of seedlings and anywhere from 11 to 228 yr for disturbed forest to recover to old-growth forest (Denslow and Guzman 2000, Rozendaal et al. 2019). For Puerto Rico, which has among the highest frequency of hurricanes in the North Atlantic basin, it is unlikely the forests will reach old-growth before another hurricane alters forest succession (Sanford et al. 1991, Boose et al. 2004) making post-hurricane dynamics studies imperative.

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Data Availability

Data are available from Dryad: https://doi.org/10.5061/dryad.jh9w0vtbm.
Code is available from http://doi.org/10.5281/zenodo.4671098.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3651/full