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RESEARCH

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# Landform type mediates compositional change in a hurricane-disturbed sub-tropical forest

Robert L. Spicer<sup>1</sup>, Ariel E. Lugo<sup>2</sup> and Nathan Ruhl<sup>1\*</sup>

## Abstract

**Background:** Categorization of topographical features into landform type is a long-standing method for understanding physiographic patterns in the environment. Differences in forest composition between landform types are driven primarily by concurrent differences in soil composition and moisture, but also disturbance regime. Many studies have focused on the interaction between fire disturbance, succession, and landforms, but the effects of hurricane disturbance on compositional differences between landforms are poorly understood. In the study presented here, we assess compositional and structural differences between landform types in the tree community of a young sub-tropical forest that is frequently subjected to hurricanes. Specifically, we ask whether the tree community (1) changed structurally over the study period, (2) experienced compositional change over the study period, (3) is compositionally different between landform types, and (4) exhibits compositional change mediated by landform type.

**Results:** The tree community experienced significant structural change over the course of our study, but compositional change was only significant for some landforms.

**Conclusion:** Despite large-scale, intense, and frequent hurricane disturbance to our study system, compositional change in the tree community was localized and only significant for some landform types.

**Keywords:** Hurricane, Forest, Community, Composition, Change, Succession, Landform

## Background

Topographic variation (the combination of elevation and orientation) introduces complexity to the spatial variation of a host of factors including light availability (Tateno and Takeda 2003), climate (Bader and Ruijten 2008), soil moisture (Foster 1988; Hunter and Parker 1993), drainage patterns (Nobre et al. 2011), soil depth, nutrient concentrations (Brubaker et al. 1993; Enoki et al. 1997; Schimel et al. 1985; Zak et al. 1991), and total soil nutrient accumulation (Scatena and Lugo 1995). Topographic variation, in association with climatic and geologic factors, creates physiographic patterns that invite typology (Grossman et al. 1999), so many ecological classification methods for considering

physiographic patterns relative to biota exist (reviewed by Sims and Uhlig 1992; Klijn and Udo de Haes 1994; Kent et al. 1997; Simensen et al. 2018). The common theme with all ecological classification tools is that they help us identify, manage, and appreciate patterns in the environment.

One commonly used ecological classification tool is categorization of terrestrial habitats by landform type. Landform type is in the “habitat” family of classification tools that focus on ecological classification according to the physical environment (drainage patterns and elevation in this case), which have been shown to be more repeatable than other classification methods (Hearn et al. 2011). Landform type is one of the older ecological classification tools, dating back to at least 1961 (Hills), and is often implemented as best suited to the system being studied. The combined topography/drainage pattern approach to ecological classification is powerful for its broad utility and transferability across

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habitat types but suffers from subjectivity due to a lack of strict guidelines or thresholds that define the operational units (Barnes et al. 1982; Fortin et al. 2000).

Differences in forest compositional change (successional trajectories) between landform types have been noted for some time (Host et al. 1987), and it is thought that these patterns in forests are driven primarily by concurrent differences in soil composition and moisture, but also disturbance regime (Barnes et al. 1998; White and Host 2008). Many studies have focused on the interaction between fire disturbance, succession, and landforms (e.g., Chu et al. 2017; Keeton and Franklin 2004), but few have addressed wind effects in the same context (Sinton et al. 2000) and less so in tropical latitudes. Hurricanes are the dominant vector of disturbance for many tropical and sub-tropical forests (Lugo 2008) and manifest as a combination of both wind and rain/flood disturbance, and the effects of hurricanes on successional differences between landform types are therefore poorly understood compared to other vectors of disturbance. Like fire disturbance, hurricane disturbance alters a forest community in both positive and negative ways (Lugo 2008) and the effects of disturbance interact with topography (Scatena and Lugo 1995).

It has been demonstrated that hurricane effects differ between landform types in sub-tropical forests (Bellingham 1991), but whether those effects translate into compositional change, succession, or differences in successional trajectory between landform types has not been assessed. Addressing this gap in our understanding of tropical and sub-tropical forests is important and timely because a change in intensity or frequency of hurricanes as a result of climate change (Emanuel and Sobel 2013) could have a profound influence on the structure, composition, and/or function of these forests. More generally, despite many studies taking a top-down (regional/local) perspective to succession, there is an unmet need for “bottom-up” studies that link physiographic characteristics, such as landforms, to succession (Nave et al. 2017) as a generalized process shared across many ecosystems. In the study presented here, we utilize an older dataset to assess the importance of landform type on compositional change in the tree community of a young sub-tropical forest that is frequently subjected to hurricanes. Specifically, we ask whether the tree community (1) changed structurally over the study period, (2) experienced compositional change over the study period, (3) is compositionally different between landform types, and (4) exhibits compositional change mediated by landform type.

## Materials and methods

### Study site

The Jardín Botánico and Bosque Estatal del Nuevo Milenio (JB-BN; Fig. 1) are urban moist secondary sub-tropical forest plots that together form part of the Ecological Corridor of San Juan. All plots were located on lands previously

used as an agricultural experimentation station affiliated with the University of Puerto Rico and used for a variety of science and conservation-related agricultural activities. When this study started in 1997, the forest was about 60 years old (Despiau Batista 1997), making the forest about 68 years old at the conclusion of our study in 2005 (Lugo et al. 2005).

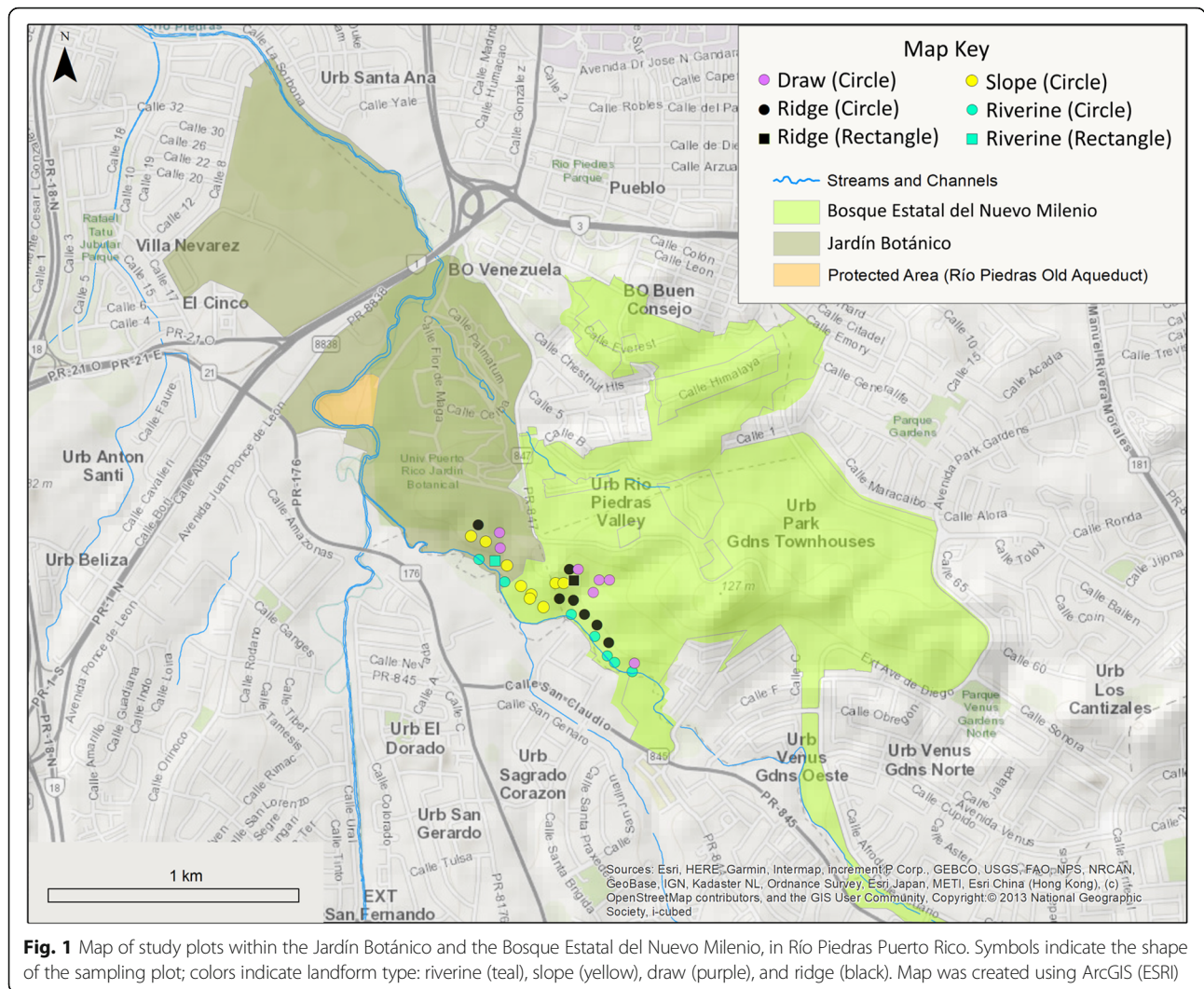
While our study site is frequently disturbed by hurricanes (Table 1), the intensity and severity of disturbance depends on the trajectory, strength, and orientation of the storm relative to the location of the study forest. Hurricane Georges struck Puerto Rico in 1998 (the year after we initiated this study) as a category three storm and caused widespread damage to infrastructure and agriculture as a result of extreme rainfall (720 mm), winds (185 km/h), and storm surge (3.05 m; Silva-Araya et al. 2018). Our study site was exposed to the strongest quadrat of hurricane Georges as it passed over the Island and hurricane Georges had the strongest visible effects of the nine hurricanes and storms in Table 1. In contrast, our site was exposed to the weakest quadrangle of hurricane Hugo, which had similar strength as Georges, but followed a trajectory north of Puerto Rico.

Storm Jeanne struck the island of Puerto Rico in 2004 (the year before the conclusion of our study) but did not have as strong an effect on the trees of JB-BN as Hurricane Georges did in 1998. Jeanne did produce significant rainfall over the 8 h it took to pass over the Island. The winds of hurricane Georges were four times more powerful than those of Jeanne because wind power is the cube of velocity. Hurricane Debby passed north of Puerto Rico, and its main effects on Puerto Rico were high rainfall with winds being less powerful because they originated on the weakest quadrangle of the hurricane. Hurricane Jose, passing north and east of Puerto Rico, and hurricane Lenny, passing south and east, were less powerful hurricanes, and despite being measurable at the San Juan Airport, their effects on JB-BN were minor.

### Field sampling

Data for this study were originally collected as part of a descriptive study of JB-BN tree biodiversity by Despiau Batista (1997). The initial data collection occurred during the months of June and July 1997 and utilized ten random plots of 254 m<sup>2</sup> for each of four landform types (40 plots total) on the same southwest aspect at an elevation of 15 to 65 m above mean sea level. Plot size was maintained across the study, but two sites were rectangular while the rest were circular (Fig. 1).

Simple landform types (slope, ridge, draw, riverine) were assigned by Despiau Batista (1997) a priori using USGS topographic maps and confirmed via ground-checking drainage patterns. Landform type was not recorded for a few sites, so the study presented here ultimately utilized 33 of the original 40 plots (8 ridge, 9 slope, 8 riverine, and 8 draw; Fig. 1; Appendix 1). Trees with a diameter at breast height (DBH) equal to or greater than 4 cm were recorded and



identified to species (after Molina and Alemañy 1997), tree height was estimated using a clinometer, and trees were marked with aluminum tags for future identification. The plots were surveyed again in 2005 between the months of June and September by Lugo et al. (2005). Tagged trees were re-measured for DBH and height while new trees

with  $DBH \geq 4$  cm were given ID's and their DBH and height were recorded.

**Statistical methods**

Structural differences (DBH and height) were compared between landforms (within each study year) using Kruskal-

**Table 1** Hurricanes and storms that struck JB-BN during our study (1997–2005) and for the 10 years prior to the study

Year	Hurricane/Storm	Station	Sustain Surface Wind (knots) <sup>1</sup>	Peak surface wind (knots)	Total Rainfall (cm)
1989	Hugo	San Juan (Carolina) Airport	67	80	7.62
1995	Marilyn	San Juan (Carolina) Airport	23	39	6.40
1996	Bertha	San Juan (Carolina) Airport	42	52	3.96
1996	Hortense	San Juan (Carolina) Airport	43	54	24.00
1998	Georges	San Juan (Carolina) Airport	69	81	13.36
1999	Jose	San Juan (Carolina) Airport	20	26	3.30
1999	Lenny	San Juan (Carolina) Airport	29	34	6.38
2000	Debby	Rio de la Plata	Missing	Missing	26.11
2004	Jeanne	San Juan (Carolina) Airport	43	62	15.19

Wallis tests with Steel-Dwass pair-wise contrasts and between years (1997 vs. 2005) using Wilcoxon tests (JMP 13) grouped by landform type. Some trees included in the PERMANOVA and NMDS procedures (below) were missing height measurements in both 1997 ( $n = 18$ ) and 2005 ( $n = 11$ ), so these trees were excluded (0.8% of pooled data) (Table 2).

Whole-forest compositional change across years (1997 to 2005) was assessed via permutational multivariate analysis of variance (PERMANOVA; Adonis function, Bray-Curtis distance, Vegan package, R 3.4). The PERMANOVA method of comparing biodiversity patterns between sites is non-parametric (distribution-free) and in the null-hypothesis family of biodiversity measures (Anderson and Walsh 2013; Magurran 2004). PERMANOVA was also used in each of 1997 and 2005 to detect differences in biodiversity attributable to landform type, but in this case, we utilized pairwise contrasts as a post hoc test to detect differences between each landform type (pair-wise ADONIS, R 3.4, Arbizu 2019). Significant  $p$  values in a PERMANOVA indicate a significant difference in a combination of centroid or spread of points in multivariate space, so non-metric multi-dimensional scaling (NMDS; Vegan package, mDS function R 3.4) with factor fitting (envfit and ordiellipse functions, Vegan package, R 3.4) was utilized to visualize biodiversity differences due to landform type. Multivariate homogeneity for PERMANOVA factors (year and landform type) were assessed using the betadisper and permutest functions in the vegan package of R (3.4).

Compositional change from 1997 to 2005 by landform type was assessed via a test for concordance between NMDS ordinations (1997 vs. 2005) using symmetric Procrustes rotation (PROTEST function, vegan package, R 3.4). Residuals were extracted from the Procrustes rotation, normalized using a Box-Cox Y-transform (JMP 13), and compared between landform types using a one-way ANOVA with post hoc Tukey HSD test (JMP 13).

## Results

### Structural change between landform types and years

During 1997, the DBH of trees at riverine sites was significantly greater than those at ridge and slope sites and marginally greater than draw sites (Tables 3 and 4). The DBH of the average tree increased significantly from 1997 to

2005 at ridge and draw sites, increased marginally at riverine sites, and did not increase significantly at slope sites (Tables 3 and 5). During 2005, DBH was still significantly greater at riverine sites compared to other landform types, but DBH at slope sites was lesser than draw and ridge sites (Table 4). Tree height was significantly higher for draw sites than slope or ridge sites in both 1997 and 2005 (Tables 3 and 4), but the mean tree height decreased significantly across all sites from 1997 to 2005 (Tables 3 and 5). The number of stems declined from 1997 to 2005 for all landform types (20.55% across the whole forest), but the decline in stems was more severe at ridge and slope sites (ridge = 34.47%, slope = 28.08%; Table 3).

### Whole-forest compositional change from 1997 to 2005

A factorial PERMANOVA of the pooled data was not possible due to heterogeneous dispersions between landform types (permutest:  $F_{3, 62} = 3.6073$ ,  $p = 0.03$ ) and unequal samples sizes between groups. A single factor PERMANOVA between years (1997 and 2005) indicated that there was no significant compositional change in the tree community between sampling periods ( $F_{1, 65} = 0.3108$ ,  $R^2 = 0.0048$ ,  $p = 0.983$ ).

### Compositional differences between landforms in 1997 and 2005

PERMANOVA of both the 1997 and 2005 forest communities (separately) indicated a significant effect due to landform type (1997:  $F_{3, 29} = 2.617$ ,  $R^2 = 0.213$ ,  $p < 0.001$ ; 2005:  $F_{3, 29} = 3.003$ ,  $R^2 = 0.237$ ,  $p < 0.001$ ). The NMDS ordinations with landform factor fitting for 1997 (stress = 0.182 in two dimensions,  $r^2 = 0.4113$ ,  $p = 0.001$ , Fig. 2a) and 2005 (stress = 0.167,  $r^2 = 0.3962$ ,  $p = 0.001$ , Fig. 2b) also indicated a significant difference in biodiversity between landform types in both years. Pairwise PERMANOVA indicated that riverine sites were significantly different than slope and ridge sites in both 1997 and 2005 (Table 2).

### Compositional change by landform type from 1997 to 2005

The landform centroids for 1997 and 2005 were similar in size, shape, and orientation but were not identical, suggesting the presence of underlying differences in

**Table 2** Pairwise PERMANOVA (ADONIS) results for between-landform differences in species diversity

Pairwise PERMANOVA	1997			2005		
	$F_1$	$R^2$	Adjusted $p$	$F_1$	$R^2$	Adjusted $p$
Draw vs. ridge	2.738	0.164	0.066	2.848	0.169	0.078
Draw vs. riverine	1.241	0.081	1.000	1.771	0.112	0.594
Draw vs. slope	1.886	0.112	0.246	2.482	0.142	0.090
Ridge vs. riverine	4.666	0.250	0.006	5.388	0.278	0.006
Ridge vs. slope	1.309	0.080	1.000	1.175	0.073	1.000
Riverine vs. slope	4.196	0.219	0.012	5.019	0.251	0.006

**Table 3** Descriptive statistics for forest structure metrics by landform type in 1997 and 2005

Variable	Year	Statistic	Draw	Ridge	Riverine	Slope	Whole forest
DBH (cm)	1997	Mean	11.66	9.81	14.45	10.24	11.06
		SD	10.72	7.47	12.67	8.49	9.57
		<i>n</i>	319	671	335	593	1918
	2005	Mean	11.96	10.69	15.18	10.26	11.70
		SD	9.57	7.74	12.70	9.10	9.80
		<i>n</i>	312	499	317	463	1591
Height (m)	1997	Mean	10.00	8.59	9.70	8.31	8.93
		SD	4.70	3.54	5.45	3.62	4.21
		<i>n</i>	317	669	333	582	1901
	2005	Mean	8.00	7.24	7.42	7.52	7.50
		SD	2.93	2.62	2.79	3.58	3.03
		<i>n</i>	311	499	317	453	1580
Tree abundance	1997	<i>n</i>	319	671	335	593	1918
	2005	<i>n</i>	312	499	317	463	1591
		% Change	− 2.24	− 34.47	− 5.68	− 28.08	− 20.55

Sample size is lower for height because of missing data points

biodiversity over the course of the study related to landform type. Procrustes rotation indicated a high degree of concordance between sampling periods ( $m^2 = 0.057$ ,  $r = 0.97$ ,  $p = 0.001$ ). Procrustes residuals differed significantly between landform types (Fig. 3; one-way ANOVA:  $DF = 3$ ,  $F_{3, 29} = 3.258$ ,  $R^2 = 0.252$ ,  $p = 0.036$ ), and post hoc tests indicated that residuals for riverine sites were significantly lower than for ridge ( $p = 0.013$ ) and draw ( $p = 0.011$ ) sites. Species centroids relative to landform ellipses are given in Appendix 2; species codes are defined in Appendix 3.

## Discussion

Over the 8-year period of our study, JB-BN was structurally altered by hurricane disturbances, but the whole-forest composition of the tree community did not change significantly. Whole-forest differences in the tree

community over time were not significant, but there were significant differences in the tree community over time attributable to landform type, suggesting differences in succession between landform types. Successional change in forests is classically considered to be a function of soil depth and acute disturbance events (e.g., fire), but succession is a complex phenomenon operating at multiple scales in space-time (Breugel et al. 2019) and can occur without a predictable trajectory (Chazdon et al. 2007), which is how we consider succession here. Also, unlike successions initiated by fires or clearcutting that homogeneously reset the system to early stages, compositional change after a hurricane resets stands to earlier stages depending on the exposure of the landform to prevailing winds and the effects of winds on trees.

Structural change to the forest was detected for both tree height (all sites) and DBH (except at slope sites).

**Table 4** Statistical tests comparing forest structural metrics between landform types

	1997 DBH		2005 DBH		1997 height		2005 height	
	$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>
<b>Kruskal-Wallis<sup>1</sup></b>								
Between landforms	26.924	< 0.001	62.538	< 0.001	36.152	< 0.001	24.458	< 0.001
<b>Steel-Dwass test</b>	<b>Z</b>	<b>p</b>	<b>Z</b>	<b>p</b>	<b>Z</b>	<b>p</b>	<b>Z</b>	<b>p</b>
Riverine—slope	4.519	< 0.001	7.419	< 0.001	2.162	0.134	1.511	0.431
Riverine—draw	2.553	0.052	2.959	0.016	− 2.462	0.066	− 2.480	0.063
Riverine—ridge	4.793	< 0.001	4.764	< 0.001	0.741	0.881	0.984	0.759
Slope—draw	− 1.549	0.408	− 4.539	< 0.001	− 6.047	< 0.001	− 4.773	< 0.001
Slope—ridge	0.180	0.998	− 3.965	< 0.001	− 2.369	0.083	− 1.080	0.702
Draw—ridge	1.756	0.295	1.400	0.499	4.563	< 0.001	4.140	< 0.001

Positive Z-scores indicate the mean of the first group (2005) is larger than the mean of the second group (1997) and vice versa for negative scores

<sup>1</sup>DF = 3

**Table 5** Statistical tests comparing forest structural metrics between years

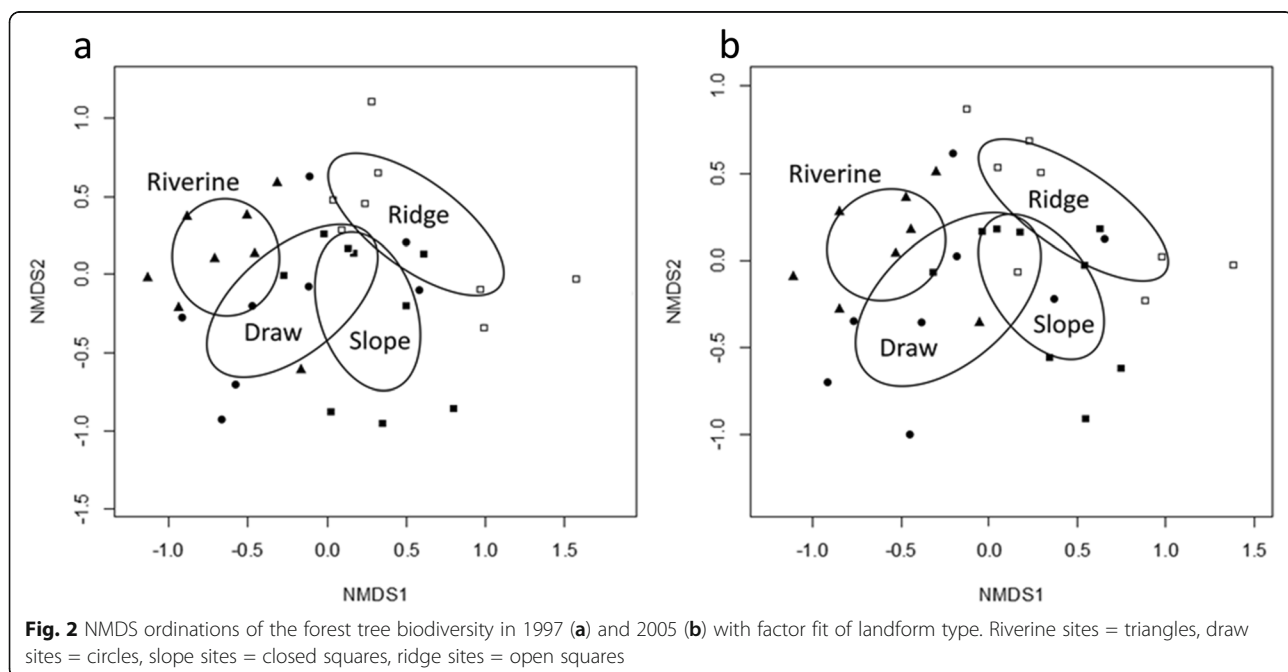
	DBH (cm) 2005–1997		Height (m) 2005–1997	
	$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>
<b>Kruskal-Wallis<sup>1</sup></b>				
Between years	14.122	< 0.001	133.283	< 0.001
<b>Steel-Dwass test</b>	<b>Z</b>	<b><i>p</i></b>	<b>Z</b>	<b><i>p</i></b>
Draw	2.036	0.042	− 5.933	< 0.001
Ridge	3.472	< 0.001	− 8.028	< 0.001
Riverine	1.915	0.056	− 4.419	< 0.001
Slope	0.797	0.425	− 5.928	< 0.001

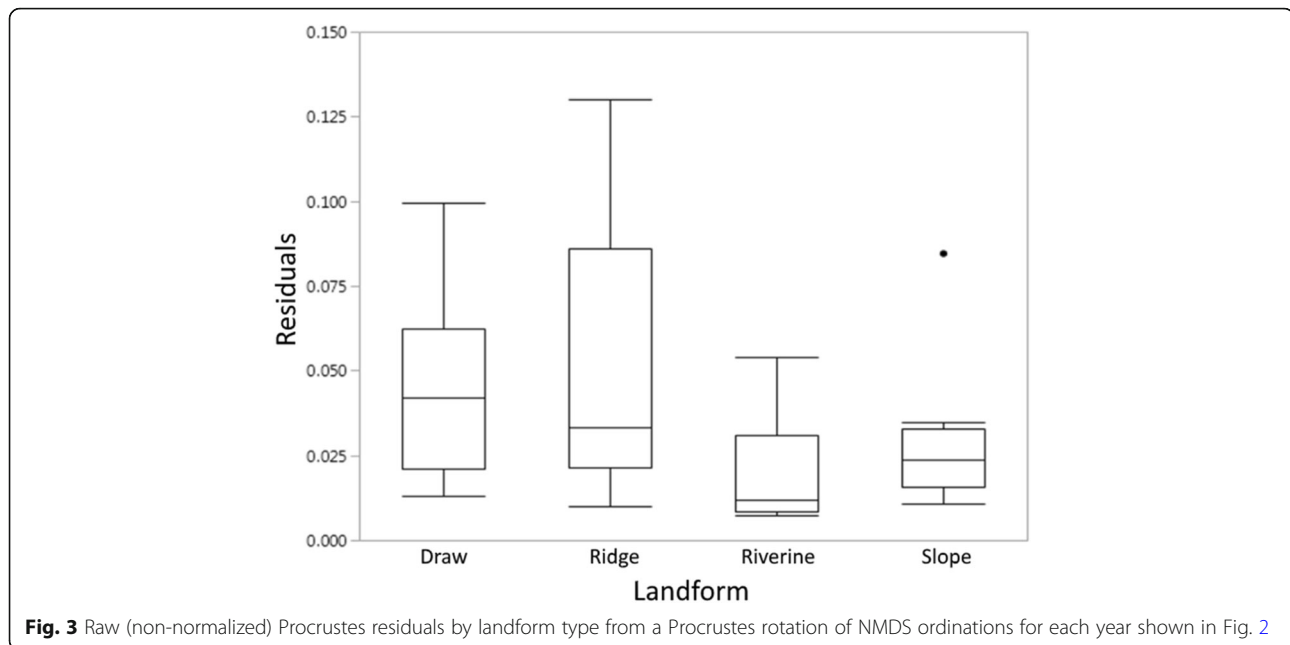
Positive Z-scores indicate the mean of the first group (2005) is larger than the mean of the second group (1997) and vice versa for negative scores  
<sup>1</sup>DF = 1

Wind power was likely responsible for the reduction in tree height via selective effects on canopy structure (Brokaw and Grear 1991; Uriarte et al. 2019). The increase in tree DBH reflects positive conditions for tree growth after the hurricane due to moisture availability, soil fertility, and light/space availability. Thus, the hurricane disturbances that affected our study site had positive (tree diameter change), negative (reduction in tree height and number of stems), and neutral effects (no overall compositional change) on the forest. It is important to note that while hurricane disturbance has an obvious and negative effect on tree mortality (Uriarte et al. 2019) and societal infrastructure, hurricanes can also have a positive effect on forests by opening canopy gaps (Brokaw 1985), which stimulate growth and productivity, increasing structural complexity (Xi et al. 2019), and redistributing soil nutrients (Gutiérrez del Arroyo and Silver 2018).

At JB-BN, tree community composition changed more at ridge and draw sites than riverine and slope sites. Normally, ridges and slopes have greater species richness than valleys (Scatena and Lugo 1995), which partially explains our results. One might expect that stands with a higher number of species are more likely to experience a change in biodiversity when disturbed compared to stands with fewer species because low diversity stands have species with greater dominance that are less likely to be lost while species in diverse stands are less dominant and have higher probability of not overcoming the disturbance. Also, slope and riverine locations are at lower elevations relative to draw and ridge sites and therefore less exposed to winds, but riverine locations are more likely to experience disturbance from flooding, which slows microbial decomposition and tree growth (Silver et al. 1999).

Differences in community composition between landform types were greatest for ridge and draw sites, but the





reduction in the number of trees between 1997 and 2005 was greatest for ridge and slope sites. There appears to be a difference in mortality between landform types that is poorly aligned with successional change in our study system, an observation that we feel is most likely attributable to the young age (68 years) of the forest we studied. Young forests have lower resistance to successional change than older/mature forests, and so, the successional trajectory and rate of change in young forests (such as ours) may differ from those of similar older forests (such as that studied by Heartsill Scalley et al. 2010).

The compositional change that we measured at JB-BN, as in other studies of succession, are the result of biotic interactions and environmental heterogeneity (Boose et al. 2004; Uriarte et al. 2012; Hogan et al. 2016). Successional dynamics that are not significant at one spatial scale (whole forest) can become significant at smaller spatial scales (landform type) because these scales are ecologically relevant to the disturbance (as in this study and that of Mollot et al. 2008) or biotic interactions. These results, while both informative and intriguing, need to be interpreted with the knowledge that the disturbance regime at JB-BN is shaped by more than just frequent hurricanes. Prior to European colonization, Puerto Rico was 100% forested (Little et al. 1974), but by the late 1940s, only 6% of the island remained forested, and only 1% of the primary forest remained (Lugo 2004; Roberts 1942). The forest at JB-BN is a relatively young forest and may respond differently to hurricane disturbance than an older forest. Likewise, disturbance via humans and hurricanes (Beard et al. 2005; Boose et al.

1994), as well as the effects of competition, is unlikely to be equally distributed across species (Batista and Platt 2003; Zimmerman et al. 1994) or the landscape (Comita et al. 2010).

### Conclusion

Collectively, our results suggest a complicated interaction between landform type and hurricane disturbance mediates successional change and ecosystem dynamics/function in JB-BN. Despite large-scale, intense, and frequent disturbance to our study system, compositional change in the tree community was localized and only significant for some landform types. In the context of a change in hurricane intensity or frequency due to global warming, our results suggest that the effects may be differentially spread across forest communities. It is our view that landform classification is most useful for studies that seek to identify generalizable patterns that might also occur in other ecosystem types composed of differing species groups (e.g., succession in a boreal forest vs. a sub-tropical forest vs. a grassland) than to compare related sets of ecosystems composed of similar species groups (e.g., succession in a sub-tropical forest vs. another sub-tropical forest) unless such studies employ strictly defined typology. In our study, we utilize a very basic landform classification scheme that can be scaled and generalized to many habitat types. The generalizable characteristics of the landform typology make it useful for ecological classification efforts based on functional classes (nonphylogenetic groupings; Duckworth et al. 2000), studies of primary succession (e.g., McKenna et al. 2019), and “bottom-up” studies of succession.



## Appendix 1

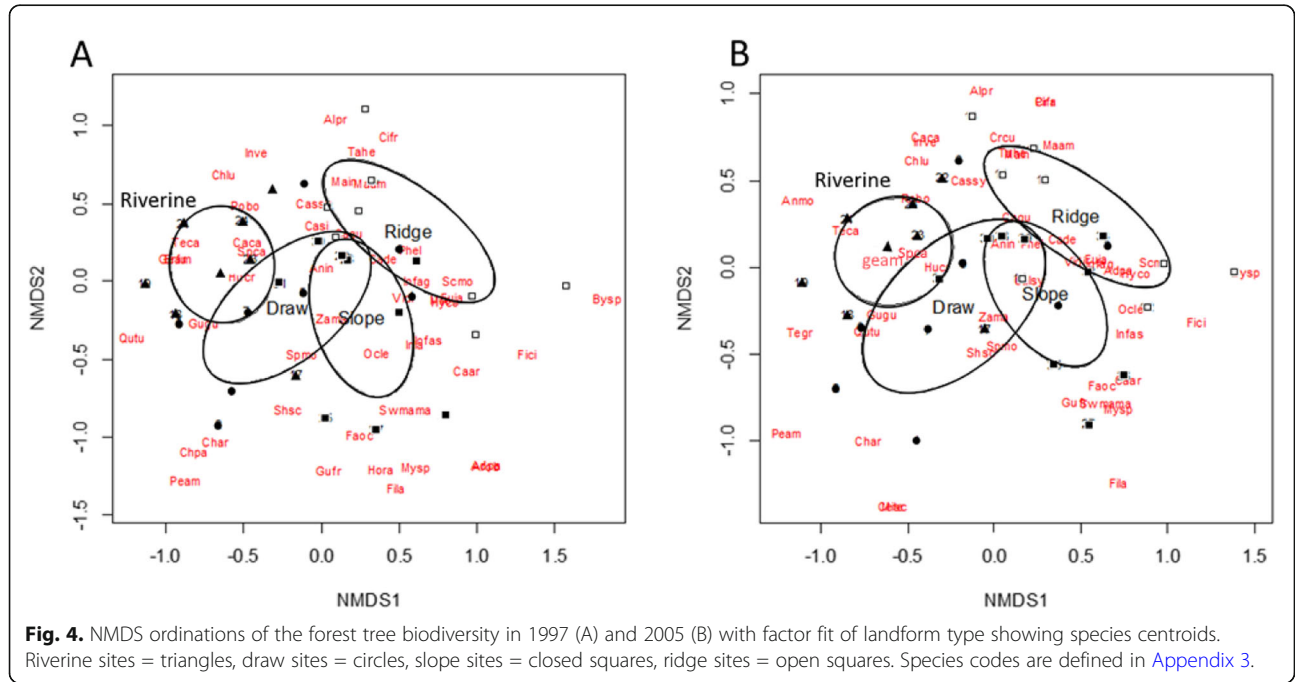
**Table 6** Sampling locations by sampling method and landform type

Site ID	Latitude	Longitude	Plot shape <sup>1</sup>	Landform type
2	18° 23' 05.20" N	66° 03' 16.10" E	Circular	Ridge
3	18° 23' 03.70" N	66° 03' 17.10" W	Circular	Slope
4	18° 23' 03.00" N	66° 03' 15.10" W	Circular	Slope
6	18° 23' 00.70" N	66° 03' 16.00" W	Circular	Riverine
7	18° 23' 00.50" N	66° 03' 13.80" W	Rectangular	Riverine
8	18° 23' 04.20" N	66° 03' 13.20" W	Circular	Draw
9	18° 23' 02.20" N	66° 03' 13.10" W	Circular	Draw
10 <sup>2</sup>	18° 22' 57.80" N	66° 03' 12.50" W	Circular	Riverine
11	18° 22' 59.90" N	66° 03' 12.20" W	Circular	Slope
13	18° 22' 57.20" N	66° 03' 10.30" W	Circular	Slope
14	18° 22' 56.10" N	66° 03' 08.90" W	Circular	Slope
15	18° 22' 55.60" N	66° 03' 09.10" W	Circular	Slope
16	18° 22' 54.50" N	66° 03' 07.30" W	Circular	Slope
17	18° 22' 57.60" N	66° 03' 05.60" W	Circular	Slope
18	18° 22' 57.60" N	66° 03' 04.50" W	Circular	Slope
19	18° 22' 59.40" N	66° 03' 03.70" W	Circular	Ridge
21	18° 22' 55.60" N	66° 03' 05.10" W	Circular	Ridge
22	18° 22' 59.40" N	66° 03' 02.50" W	Circular	Draw
23	18° 23' 00.90" N	66° 03' 01.00" W	Circular	Draw
24	18° 22' 58.00" N	66° 02' 59.70" W	Circular	Draw
25	18° 22' 56.40" N	66° 03' 00.50" W	Circular	Draw
26	18° 22' 57.90" N	66° 03' 03.10" W	Rectangular	Ridge
27	18° 22' 55.40" N	66° 03' 03.20" W	Circular	Ridge
28	18° 22' 53.60" N	66° 03' 03.50" W	Circular	Riverine
29	18° 22' 53.60" N	66° 03' 01.70" W	Circular	Ridge
31	18° 22' 52.20" N	66° 03' 00.00" W	Circular	Ridge
32	18° 22' 50.70" N	66° 03' 00.30" W	Circular	Riverine
33	18° 22' 58.00" N	66° 02' 58.30" W	Circular	Draw
34	18° 22' 48.20" N	66° 02' 58.60" W	Circular	Riverine
35	18° 22' 47.30" N	66° 02' 57.60" W	Circular	Riverine
36	18° 22' 49.90" N	66° 02' 58.40" W	Circular	Ridge
37	18° 22' 46.10" N	66° 02' 55.20" W	Circular	Riverine
38	18° 22' 47.20" N	66° 02' 54.90" W	Circular	Draw

<sup>1</sup>All sites were 254 m<sup>2</sup> (circular = radius of 9 m; rectangular = sides of 10 m and 25.4 m)

<sup>2</sup>Coordinates are approximate for this site

Appendix 2



### Appendix 3

**Table 7** Species found in JB-BN with species codes used in the Appendix 1 NMDS ordinations and found in Appendix G of the Forest Inventory and Analysis (FIA) user guide ([https://www.fia.fs.fed.us/library/database-documentation/historic/ver6/FIADB\\_User\\_Guide\\_P2\\_6-1-1\\_final.pdf](https://www.fia.fs.fed.us/library/database-documentation/historic/ver6/FIADB_User_Guide_P2_6-1-1_final.pdf)). For all species, SPGRPCD = 54 and MAJGRP = 3

Species	NMDS species code	Forest service species code #
<i>Acrocomia media</i>	ACME	6023
<i>Adenantha pavonina</i>	ADPA	6028
<i>Albizia procera</i>	ALPR	6060
<i>Andira inermis</i>	ANIN	6114
<i>Annona montana</i>	ANMO	6127
<i>Annona muricata</i>	ANMU	6218
<i>Annona reticulata</i>	ANRE	6129
<i>Ardisia obovate</i>	AROB	6164
<i>Areca catechu</i>	ARCA	6167
<i>Artocarpus heterophyllus</i>	ARHE	6173
<i>Schefflera actinophylla</i>	Brac	0888
<i>Byrsonima spicata</i>	BYSP	6313
<i>Callistemon citrinus</i>	CACI	6328
<i>Calophyllum calaba</i>	CACA	
<i>Calyptanthes sintenisii</i>	CASI	6356
<i>Calyptanthes sylvestris</i>	CASY	
<i>Cananga odorata</i>	CAOD	6370
<i>Casearia arborea</i>	CAAR	6403
<i>Casearia decandra</i>	CADE	6406
<i>Casearia guianensis</i>	CAGU	6407
<i>Casearia sylvestris</i>	CASSY	6410
<i>Cassia fistula</i>	CAFI	6415
<i>Cassia javanica</i>	CAJA	6418
<i>Cecropia sceveriana</i>	CESE	
<i>Cecropia schreberiana</i>	CESE	6443
<i>Ceiba pentandra</i>	CEPE	6449
<i>Dyopsis lutescens</i>	CHLU	6966
<i>Chrysophyllum argenteum</i>	CHAR	6539
<i>Chrysophyllum cainito</i>	CHCA	6541
<i>Chrysophyllum pauciflorum</i>	CHPA	6543
<i>Citharexylum fruticosum</i>	CIFR	0859
<i>Coccoloba uvifera</i>	COUV	6670
<i>Cocos nucifera</i>	CONU	0908
<i>Cordia sebestens</i>	COSE	
<i>Crescentia cujete</i>	CRCU	6761
<i>Cupania americana</i>	CUAM	6790
<i>Delonix regia</i>	DERE	6883
<i>Erythrina fusca</i>	ERFU	
<i>Eucalyptus robusta</i>	EURO	0514
<i>Syzygium jambos</i>	EUJA	8701
<i>Faramea occidentalis</i>	FAOC	7146

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Species	NMDS species code	Forest service species code #
<i>Ficus benjamina</i>	FIBE	7150
<i>Ficus citrifolia</i>	FICI	0877
<i>Ficus laevigata</i>	FILA	
<i>Ficus lutea</i>	FILU	7158
<i>Genipa americana</i>	GEAM	7235
<i>Grevillea robusta</i>	GRRO	7273
<i>Guaiacum officinale</i>	GUOF	7279
<i>Guapira fragrans</i>	GUFR	7285
<i>Guarea guidonia</i>	GUGU	7290
<i>Homalium racemosum</i>	HORA	7422
<i>Hura crepitans</i>	HUCR	7434
<i>Hymenaea courbaril</i>	HYCO	7442
<i>Inga fagifolia</i>	INFA	
<i>Inga fastuosa</i>	INGFA	
<i>Inga laurina</i>	INLA	7470
<i>Inga vera</i>	INVE	7474
<i>Lagerstroemia speciosa</i>	LASP	7533
<i>Mammea americana</i>	MAAM	7652
<i>Mangifera indica</i>	MAIN	0885
<i>Manilkara bidentata</i>	MABI	7662
<i>Melaleuca quinquenervia</i>	MEQU	0992
<i>Melicoccus bijugatus</i>	MEBI	7717
<i>Miconia tetrandra</i>	MITE	7822
<i>Thespesia grandiflora</i>	MOSP	8786
<i>Muntingia calabura</i>	MUCL	7867
<i>Myrcia deflexa</i>	MYDE	7887
<i>Myrcia splendens</i>	MYSF	7891
<i>Ocotea leucoxydon</i>	OCLE	7994
<i>Peltophorum pterocarpum</i>	PEPT	8121
<i>Persea americana</i>	PEAM	7211
<i>Petitia domingensis</i>	PEDO	8141
<i>Phoebe elongata</i>	PHEL	
<i>Pilocarpus racemosus</i>	PIEL	8171
<i>Pimenta racemosa</i>	PIRA	8177
<i>Psidium guajava</i>	PSGU	8356
<i>Pterocarpus indicus</i>	PTIN	8407
<i>Quararibea turbinata</i>	QUTU	8422
<i>Roystonea borinquena</i>	ROBO	8489
<i>Schefflera morototoni</i>	SCMO	8558
<i>Schoepfia schreberi</i>	Shsc	8573
<i>Spathodea campanulata</i>	SPCA	8644
<i>Spondias mombin</i>	SPMO	8650
<i>Swietenia macrophylla</i>	SWMA	8679

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Species	NMDS species code	Forest service species code #
<i>Swietenia macrophylla</i> × <i>mahagoni</i>	SWMAMA	
<i>Swietenia mahagoni</i>	SWMA	0940
<i>Syzygium malaccense</i>	SYMA	
<i>Tabebuia aurea</i>	TAAU	
<i>Tabebuia glomerata</i>	TAGL	
<i>Tabebuia heterophylla</i>	TAHE	8713
<i>Tabebuia rosea</i>	TARO	8716
<i>Hibiscus tiliaceus</i>	Tati	7412
<i>Tamarindus indica</i>	TAIN	0897
<i>Tectona grandis</i>	TEGR	8744
<i>Terminalia catappa</i>	TECA	8750
<i>Vitex divaricate</i>	VIDI	8873
<i>Zanthoxylum martinicense</i>	ZAMA	8931

**Abbreviations**

DBH: Diameter at breast height; JB-BN: Jardín Botánico and Bosque Estatal del Nuevo Milenio Study Site; NMDS: Non-metric multi-dimensional scaling; PERMANOVA: Permutational analysis of variance

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**Authors' contributions**

RLS contributed to the statistical analysis and writing of the manuscript. AEL contributed to the sampling plan, data collection, and writing of the manuscript. NR contributed to the analysis plan, statistical analysis, and writing of the manuscript, and is the corresponding author. The author(s) read and approved the final manuscript.

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