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Changing ecological communities along an elevation gradient in seasonally dry tropical forest on Hispaniola (Sierra Martín García, Dominican Republic)

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Abstract

We report the results of systematic vascular plant and bird surveys in Seasonally Dry Tropical Forest (SDTF) across leeward and windward elevation gradients (31–884 masl) in the Sierra Martín García (SMG), Dominican Republic. We expected to see gradual, systematic changes in plant distributions with elevation owing to the strong effect of topoclimate. In contrast, we predicted bird community composition to be related only weakly to elevation, because we expected bird distributions to be more strongly related to vegetation structure than composition. Based on 48 vegetation transects, we identified seven groups that differed in their species composition, which was correlated with elevation and precipitation. The most distinctive vegetation community occurs in dry, warm, and low elevations on the leeward slope, featuring large numbers of non-woody indicator species (those species found frequently within one group but not in other groups) even though most of its trees and shrubs represent species that are widespread. Low rainfall and shale bedrock (rather than limestone) may be the primary drivers of distinctiveness in the low-elevation leeward plots. On the leeward slope, where we also surveyed the birds, the vegetation community changes gradually with elevation at mid- to high elevations. The most distinctive bird community also was associated with the low-elevation forest on shale bedrock and was dominated by widespread species. At higher elevations, but still within leeward SDTF, the bird communities had a stronger component of species endemic either to Hispaniola or to Caribbean islands, and species turnover did not correspond to the elevation gradient.

Abstract in Spanish is available with online material.

KEYWORDS
birds, Caribbean island, climate, community composition, Greater Antilles, plants, precipitation, turnover, windward-leeward effects

1 | INTRODUCTION

Elevational gradients on tropical mountains feature systematically decreasing temperatures and more complex changes in precipitation over short geographical distances. Precipitation and temperature regimes, along with changes in atmospheric pressure, radiation, and cloudiness, strongly affect the bioclimatic environment (water balance, humidity, thermal, and light regimes) for terrestrial ecosystems (Körner, 2007). While such patterns have long been associated with the distribution and diversity of plant and animal species and communities (von Humboldt & Bonpland, 1805; Terborgh, 1971; Gentry, 1988), there is a renewed call to study ecosystems along tropical elevation gradients as laboratories for evaluating global change (Malhi et al., 2010; Campos-Cerqueira et al., 2017).

Foundational work in plant community ecology by R.H. Whittaker and others used elevation transects to represent gradients of environmental variation (Whittaker, 1956; Whittaker & Niering, 1968), concluding that vegetation was composed of a continuum of populations—gradual turnover in species composition (rather than discontinuous assemblages)—in concordance with the individualistic model of plant communities (Gleason, 1926). These studies often used elevation in combination with topography to represent a "moisture gradient" of water available for plant growth, a key determinant of plant distributions. Whittaker also acknowledged, however, that plant community composition change is both continuous and discontinuous, with discontinuities (abrupt changes in composition) occurring where there are geographical discontinuities in environmental conditions (topography, soil parent material, and disturbance; Whittaker, 1967). In tropical mountains "individualistic" patterns of plant species turnover with elevation (staggered distributions of dominant tree species without sharp discontinuities of turnover in community composition) characterized a gradient from 1,500–2,500 m on the Pacific slope of Mexico (Manatlán Biosphere Reserve, Jalisco) that included the transition from seasonally dry forest to cloud forest (Vázquez & Givnish, 1998).

In contrast, across greater ranges of elevation, the changes in vegetation structure, life form composition, and species composition from tropical lowland forests to alpine shrublands and grasslands have been recognized as different plant formations, biomes, or life zones (Holdridge, 1947), suggesting discontinuities in species distributions. For example, spanning 3,400 m of elevation on Mt. Kinabalu, Borneo, the distribution of lowland, montane, and subalpine plant formations were associated with changes in species composition, diversity, and vegetation structure, although the rates of these changes along the gradient differed among geologic substrates (Aiba & Kitayama, 1999). (Different rates of species turnover were also found on different substrates in a temperate setting by Whittaker and Niering (1968)). In the Neotropics, differences in climatic conditions (temperature and rainfall) were the factors most strongly associated with changing plant species composition along an Andean 2,000-m elevation gradient ranging from seasonally dry forest to cloud forest (Blundo et al., 2012). The distribution of two vegetation formations (pine woodland vs. cloud forest) on the island of Hispaniola (Cordillera Central, Dominican Republic) from

1,100–3,100 m elevation was strongly determined by changes in mesoclimate, but also feedbacks between climate and the fire disturbance regimes (Martin et al., 2007; Martin & Fahey, 2014). Also for Hispaniola (Sierra de Bahoruco, Dominican Republic), plant species composition was distinct among four plant formations spanning thorn woodland to cloud forest on an elevational transect of 0–1,500 m (Fisher-Meerow & Judd, 1989).

Our study also takes place on the West Indian island of Hispaniola, focusing on Neotropical seasonally dry tropical forest (SDTF), an ecological community that is highly threatened from extensive clearing for pasture and crops (Pennington et al., 2009). SDTF is closed-canopy tropical forest typically found in frost-free areas having strongly seasonal moisture, with annual rainfall <~1,800 mm and monthly rainfall <100 mm during a 3–6 month dry season (Lugo et al., 2006). SDTF shows remarkable biogeographical patterns of tree diversity throughout the Neotropics (e.g., DRYFLOR et al., 2016), with high plant beta diversity (species turnover among disjunct regions) attributed to low dispersal ability and isolation, resulting in considerable speciation and endemism (Pennington et al., 2009). Variation in SDTF tree species composition across the West Indies is associated with large-scale gradients of temperature and precipitation, but also with biogeographical history and resulting patterns of isolation and endemism (Franklin et al., 2018). West Indian SDTF harbors unique plant (DRYFLOR et al., 2016) and bird (Prieto-Torres et al., 2018) communities. Within SDTF on Mexico's Pacific slope (Chamela-Cuixmala Biosphere Reserve, Jalisco), over an elevation range of only 48–123 m (therefore with little variation in mesoclimate), turnover in tree species composition (beta diversity) was associated with topographic factors affecting water balance—solar elevation, insolation, and slope (Balvanera et al., 2002; Segura et al., 2002). To our knowledge, no such studies of SDTF species turnover on an elevation transect have been carried out in the West Indies. A better understanding of ecological patterns and processes throughout Neotropical SDTF requires filling information gaps for little-studied areas such as the West Indies (Sánchez-Azofeifa et al., 2005).

While groups such as moths (Chen et al., 2009), ants (Longino & Colwell, 2011), and reptiles (McCain, 2010) have been studied on tropical elevation gradients (see also references cited by Guo et al., 2013), many studies of changes in animal community composition have concerned birds. In contrast with plant community studies emphasizing rate of change in species composition in relation to spatial patterns of environmental drivers, studies of tropical bird communities on elevation transects have placed a greater emphasis on determining whether competitive exclusion between species drives patterns of species turnover. These studies have broadly aimed to differentiate the direct effects of climate on physiology, the indirect effects of climate on habitat structure (e.g., vegetation changes with elevation), and the effects of competitive and other interactions among species in shaping the functional and taxonomic composition of tropical bird communities (Terborgh, 1977; Blake & Loiselle, 2000; Jankowski et al., 2013).

Only a few studies have considered the influence of both plant composition and vegetation structure on birds (Gillespie & Walter,

2001) or other vertebrate communities (Stoner, 2005) within SDTF, or in other life zones along tropical elevation gradients (Jankowski et al., 2012). In Costa Rica, for example, tropical bird community composition changed along a moisture gradient associated with habitat (forest) types, a gradient not entirely captured by elevation alone because of its complex relationship with precipitation (Jankowski et al., 2009). Some research in the West Indies has measured the vegetation characteristics associated with SDTF bird communities, although these examples contrasted bird communities between SDTF and other structurally and compositionally distinct vegetation types. In the northern Bahamas, winter bird communities occupying SDTF were distinctly different from those in pine woodlands on the same island (Franklin & Steadman, 2013). On St John, U.S. Virgin Islands, on the other hand, the differences in winter bird communities between SDTF and moist forest were minor, although species were detected more frequently in mature moist forest, and certain fruiting plant species were associated with frugivorous species of birds (Steadman et al., 2009). Also in the West Indies, a rigorous survey of birds (from 100 to 1,074 m elevation) in Puerto Rico from moist-to-very wet forest (no SDTF) revealed significant upward elevational shifts between 1998 and 2015 in 8 of the 21 species analyzed (Campos-Cerqueira et al., 2017).

Past environmental change and biogeographical factors may also shape bird community turnover on elevation gradients. Variation in SDTF bird communities on elevation gradients spanning both sides of the Andes in northwest Peru, for example, was interpreted to result at least in part from barriers to dispersal as well as the dynamic climate of the Pleistocene (Oswald & Steadman, 2015; Oswald et al., 2016; Oswald et al., 2017). The effects of past changes, including prehistoric human impacts as well as paleoclimatic fluctuations, on animal distributions are often underappreciated (e.g., Steadman, 2006; Steadman & Franklin, 2015). Pertinent to our study, there is substantial fossil-based evidence for shifts in elevation in Hispaniolan birds during pre-Columbian times (Steadman & Takano, 2013). For example, two species characteristic of lower elevation dry forest on Hispaniola today (the endemic *Siphonorhis brewsteri* and the widespread *Zenaida aurita*) occur very commonly as late Holocene (1,600–600 BP) fossils in a cave at 1,800+ m elevation in Haiti, where the modern habitat is cloud forest and pine forest (Steadman & Takano, 2013).

Here, we focus on patterns of both plant and bird species composition associated with environmental gradients within SDTF over a small geographic area (a single mountain range) on a topographically complex West Indian island. Furthermore, we include all vascular plants, not just trees. Because our study area has a single regional species pool lacking major barriers to dispersal, we expect community variation to be related to environmental variation and species interactions. Our surveys took place on Hispaniola, a large Greater Antillean island comprising Haiti and the Dominican Republic. Given the extreme level of habitat loss in Haiti at all elevations, including evidence for ongoing species-level extinction of vertebrates (Hedges et al., 2018), we chose a mountain range in nearby Dominican Republic to document ecological communities in a locality with relatively little current human impact. Essentially, all

of the Sierra Martín García (SMG) is protected as a national park. A previous vegetation survey done in 2004 focused on the eastern and southern slopes of SMG (García et al., 2007). Our field efforts took place on the northwestern (leeward) slope over a wide range of elevations, thus complementing existing data, and developing a more comprehensive analysis of the biotic communities in this tropical dry forest setting.

1.1 | Objectives of this study

By conducting coordinated plant and bird surveys along an elevation gradient on an isolated coastal mountain range, Sierra Martín García, Dominican Republic, we examined composition patterns in both plant and bird communities over a broad range of elevations occupied by SDTF. We specifically addressed these three questions:

1. Is the change in species composition of plant communities with elevation (turnover) gradual or abrupt in West Indian SDTF? We expected the turnover in species composition to be gradual within the single plant formation over this small geographical area (even though that formation occurs across an impressive elevation range).

2. Are compositional changes in the plant community related to climate? Because of the relationship between climate (temperature and precipitation regime) and elevation, the great range of elevation over which SDTF is found in the study area (31–884 m), and the association of SDTF plant species distributions with temperature and moisture gradients shown in previous studies, we expected the compositional changes in the ecological community to be related to climate.

3. Do the patterns of change differ between plant and bird communities? We expected that distributions of birds will show less turnover on the elevation/climate gradient than those of plants because of their greater dispersal ability and the general structural similarity of the SDTF habitat along the gradient (which lacks major changes in plant formations or vegetation types) and in light of previous work showing tropical bird distributions on elevation gradients to be related to habitat structure.

Understanding contemporary biotic distributions over elevation gradients, as well as how they have changed through time, is important not just for addressing these ecological questions, but also for conservation planning under a regime of climate change and human impact.

2 | METHODS

2.1 | Study area and survey design

Sierra Martín García (SMG) is a small, rather isolated, mountain range in southwestern Dominican Republic (Figure 1). Essentially, the entire SMG, including the areas that we surveyed, is within Parque Nacional Sierra Martín García, consisting of 339 km² of land from sea level to the summit at 1,350 m elevation (SEA/DED, 1990). SMG
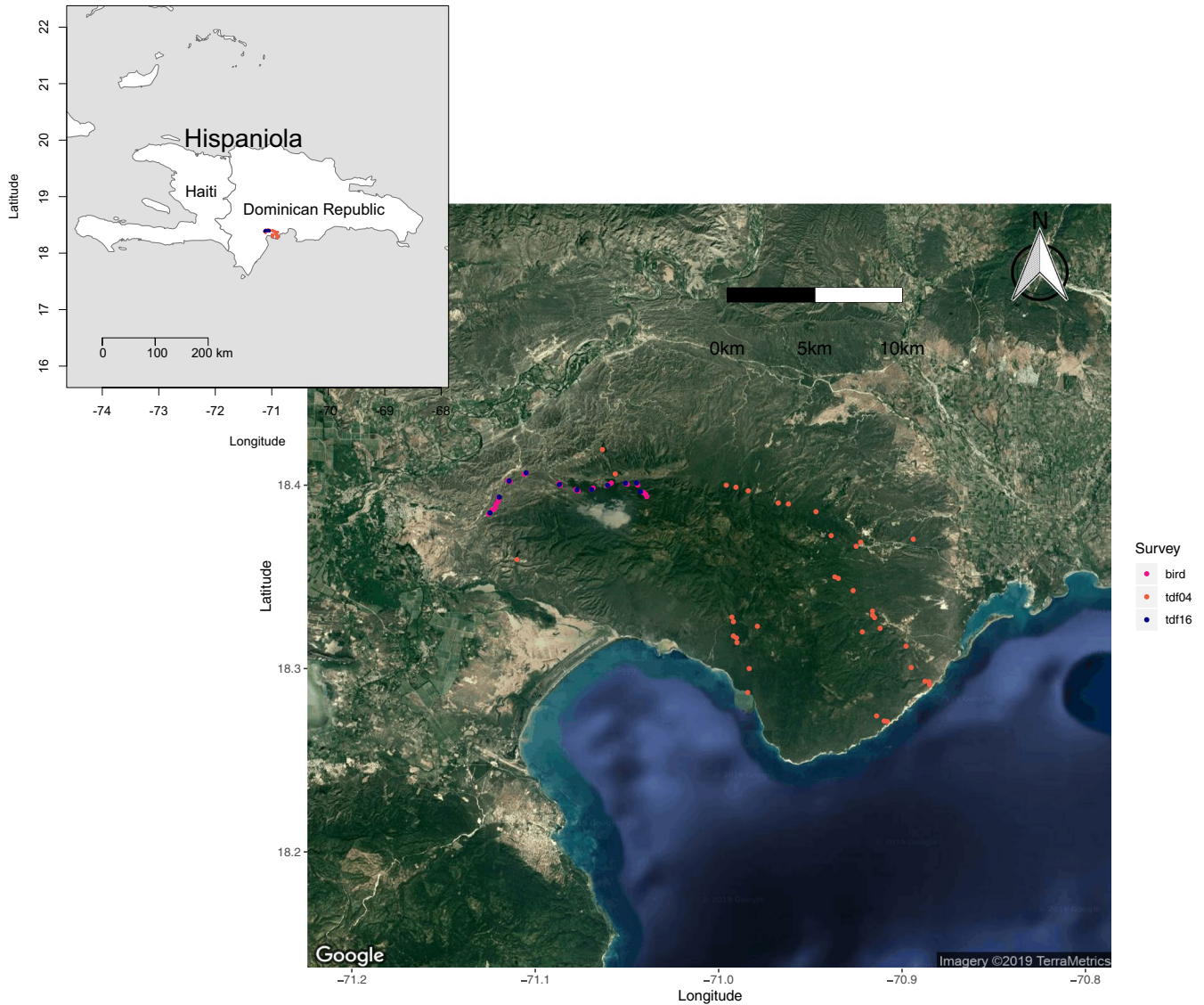
FIGURE 1 Locations of 11 vegetation plots surveyed in 2016 by the authors (tdf16), 37 vegetation plots collected by Garcia et al. (2007) in 2004 (tdf04), and bird point-counts collected by the authors in 2017 (bird) on Sierra Martín García (plot locations on Hispaniola shown in inset). Produced using ggmap (Kahle & Wickham, 2013) with Google satellite map

is surrounded entirely by arid lowlands or the Caribbean Sea. Much larger and higher mountain ranges lie to the southwest (Sierra de Bahoruco), northwest (Sierra de Neiba), and northeast (Cordillera Central). The bioclimate of the region where SMG is located is considered tropical xeric below about 800 m (Cano et al., 2012). Our coordinated surveys of plants and birds across an elevation gradient on SMG focused on one slope exposure to assure a strong relationship between elevation and precipitation, not confounded by rain shadow effects, although vegetation data were available for both exposures.

2.2 | Vegetation

From 9 to 17 November 2016, we collected data on plant community composition in Seasonally Dry Tropical Forest (SDTF) at 11 locations along the elevation gradient on the northwestern (leeward) flank of SMG (Figure 1). We listed all vascular plant species' occurrences in

100-m^2 (50 × 2 m) plots (Braun-Blanquet, 1932; Wilson, 2012) based on field identifications. We also collected all taxa encountered, and our field identifications were later confirmed in the herbarium using La Flora de la Española (Liogier, 1981, 1983, 1985, 1986, 1989, 1994, 1995, 1996) as well as comparative methods with previously collected herbarium specimens from various herbaria (FLAS, NY). Our plot-based methods were the same as those used for 37 georeferenced plots surveyed in 2004 (Garcia et al., 2007) at other areas on the eastern and southcentral windward flanks of SMG (Figure 1); our analyses incorporate the García et al. (2007) data as well, which also were compiled by DryFlor.org for trees and shrubs. We added all life forms directly from the data table in the original paper. We used a Garmin 60CSx GPS to determine the locations of our new plots (Table S1). Our list of plant species names was developed with assistance from the Taxonomic Name Resolution Service (tnrs.org) and by consulting (Acevedo-Rodríguez & Strong, 2012), as well as

recent taxonomic treatments for specific groups. Determination of plant species' distributions was carried out by consulting Acevedo-Rodriguez and Strong (2012), as well as La Flora de la Española (Liogier, 1981, 1983, 1985, 1986, 1989, 1994, 1995, 1996).

We extracted elevation and bioclimatic data (interpolated from 1960–1990 averages, 30 arc-sec grids—about 1 km^2 resolution) for all 48 plot locations from Worldclim data (worldclim.org; Hijmans et al., 2005) using the R package raster (Hijmans, 2014). Elevation values were extracted from NASA's Shuttle Radar Topography Mission (STRM) 90-m resolution data. While elevation is an indirect gradient (Austin, 2002) related to temperature (via the lapse rate) and precipitation (via orography), it can serve as a proxy for finer-scale climate variation than what is represented in the climate grids. For the 48 plant plots, elevation ranged from 31–884 m, Mean Annual Precipitation (MAP) from 859–1,081 mm, Mean Annual Temperature (MAT) from 23.0–26.0°C, and average minimum temperature of the coldest month (Tmin) from 15–18°C (but almost perfectly correlated with MAT; $r = .99$). As expected for these 48 locations, elevation had a negative relationship with MAT ($r = -.88$) and a positive relationship with MAP ($r = .67$) (Figure S1) with variation related to slope exposure. MAT and MAP were strongly negatively correlated ($r = -.88$).

Multivariate community data analysis was used to identify patterns of species composition (co-occurring species) among sites and trends in species composition along the elevation gradient for SMG dry forest. Methods were similar to those previously applied to other West Indian SDTF plot data (Franklin et al., 2015; Franklin et al., 2018). Hierarchical agglomerative clustering (Peet & Roberts, 2013) using Jaccard distance and Ward's linkage was applied to species presence/absence data for 48 sites and 750 taxa. Differences among clusters were tested using analysis of variance based on 999 permutations (permanova) (Anderson, 2001). Patterns of similarity in species composition were displayed using indirect ordination based on non-metric multidimensional scaling (NMS) (Clarke, 1993); correlation of ordination axes with climate and elevation was calculated. Indicator species analysis (Dufrêne & Legendre, 1997) was used to identify species associated with groups of plots defined by clustering. The frequencies of widespread species in all groups were calculated. We determined the amount of similarity in species composition that was associated with environment (climate variables) versus distance (geographical coordinates) by variance partitioning (Legendre, 2008) using generalized dissimilarity modeling (e.g., Fitzpatrick et al., 2013).

2.3 | Birds

We conducted bird surveys (point-counts) at SGM from 26 May to 9 June 2017, along the same elevation gradient as the 11 plant plots we had surveyed 6 months earlier. Each of the 33 point-counts for birds (GPS locations in Table S1) was performed on or within 300 m of one of the 11 plant plots, in highly similar habitat to that of the particular plant plot, yielding two to four point-counts per plant plot (Table S1). Some of the plant plots were too close to each other to allow room for more than two point-counts per plant plot. Dominant/common

tree species were identified for each point-count to confirm that the habitat represented that of the nearby plant plot. At least 200 m separated each bird point-count. All birds heard or seen within 100 m were recorded for a 10-min period at each point. All point-counts were double-observer. During our first 2 days in the field, when we did only practice point-counts, we determined that bird activity subsided at 3 to 3.5 hr after sunrise, so we did no point-counts after that time. Never were more than four point-counts done in one morning. Each point was visited a single time. Once a bird was detected, the observers kept track of its location throughout the 10-min period to avoid double-counting. In late May and early June, all of the birds recorded were resident (breeding species) rather than migrants. Nomenclature follows Chesser et al. (2018).

The bird community data, comprising species counts per point, also were analyzed using multivariate ordination methods to describe patterns of species composition and turnover on the elevation gradient. Hierarchical agglomerative clustering using Bray distance and Ward's linkage identified clusters of points with similar species composition; differences among clusters were tested using PERMANOVA. Indicator Species (IS) analysis (Dufrêne & Legendre, 1997) was used to identify species associated with groups of points defined by clustering. Correlation of ordination axes (based on NMS) with climate and elevation was calculated. In addition, generalized additive models (GAM) were used to estimate the relationship between abundance and elevation for individual bird species (Wood, 2006); a zero-inflated model with a Poisson link was used (Wenger & Freeman, 2008). Because the ecological community had far fewer species of birds than plants, it was both practical and informative to estimate responses to the elevation gradient for individual species using GAMs, providing results that are easily interpretable and complimentary to the (multispecies) ordination. All statistical analyses were done using R (R Core Team, 2018) and packages "vegan," "labdsv," and "mgcv."

3 | RESULTS

3.1 | Vegetation

There were 750 vascular plant taxa recorded in the 11 plots with 719 identified to species or variety, 30 to genus, and one to family (Table S2). Plant Clusters, defined by cutting the cluster dendrogram at a height (Ward's distance) of 1.1, divide the 48 plots into seven significantly different groups ($R^2 = .35$; $F = 3.61$, $p < .001$) based on species composition (Figure S2). The groups (clusters) show considerable overlap in two-dimensional ordination (Figure 2a), however, reflecting many shared species among groups. MAT ($R^2 = .26$; $p < .001$) and MAP ($R^2 = .41$; $p < .001$), and to a lesser extent elevation ($R^2 = .13$; $p = .054$), are correlated with ordination axes. All three show the strongest correlation with the first ordination axis (the main pattern of variation or species turnover among sites, NMS1, with plot scores ranging from −1.7 to 1.5), but little variation on the second axis of compositional variation (NMS2).

Boxplots of the frequency distribution of environmental variables also showed that the clusters are more strongly differentiated
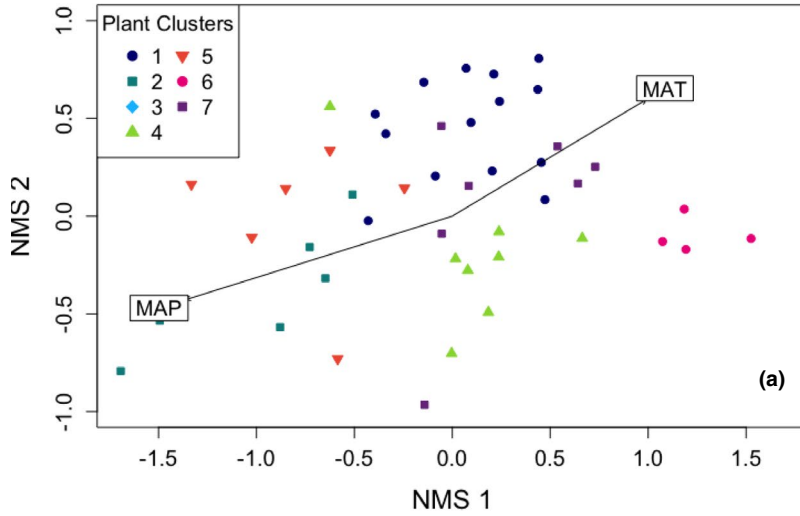
FIGURE 2 Plant plots (a) arranged by compositional similarity based on non-metric multidimensional scaling (NMDS) applied to a Jaccard distance matrix, labeled by Plant Cluster number (clustered using Ward's distance). Vectors show correlation of MAT, MAP and elevation with ordination axes; (b) locations of plant plots by Plant Cluster number (Table 1)
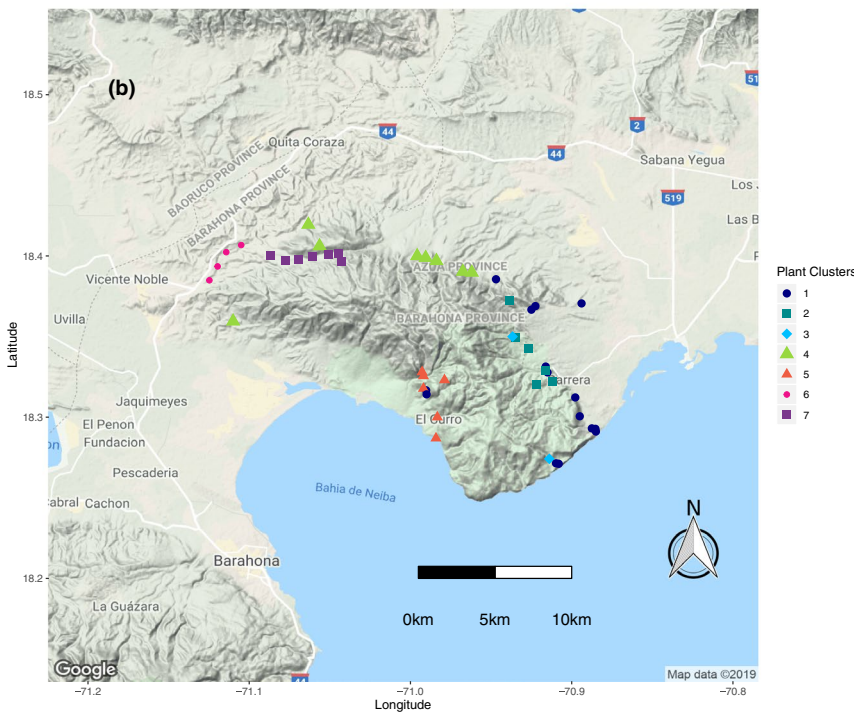
with regard to MAP (Figure S3A) than elevation (Figure S3B). This stronger relationship of MAP with species composition suggests that, although the climate data are of coarse resolution relative to the size of the study area, they nonetheless capture the rain shadow effects of prevailing ESE winds on precipitation. For example, the four leeward plots that make up Plant Cluster 6 are the driest, although not lowest in elevation (Figure S3) and are also very distinct in their species composition (Figure 2a). We note as well that the other set of leeward plots (Plant Cluster 7) has the largest range of elevation of any cluster, reflecting how gradually the plant community changed with elevation on that dry leeward slope.

While plant species composition was related to the elevation and climate gradient, clusters also show strong spatial patterns, with nearby plots typically having similar composition (Figure 2b). Variance partitioning shows that, of the 12% of explained variance in the community composition (measured by the dissimilarity matrix), most is explained

by geography, i.e., distance (6%) and the interaction of climate and distance (spatially structured climate; 4%); only 2% is explained by spatially unstructured climatic variation. (Most of the observed variance in composition, 88%, is unexplained by climate or geography.)

Our Indicator Species analysis identifies 84 species with significant indicator values for one of the clusters of plots (Table S2); those with the highest Indicator Values (IV) for each cluster are listed in Table 1. Plant Cluster 1 consists of 14 low-elevation plots sampled by García et al. (2007) predominantly on the eastern (windward) flank of SMG. Plant Cluster 2 comprises seven mid-elevation plots sampled by García et al. (2007) also on the eastern side of SMG. All five Indicator Species with the highest IVs in Plant Clusters 1 and 2 are native, primarily endemic, and woody taxa. Plant Cluster 3 consists of two lower-elevation plots sampled by García et al. (2007) on the eastern side of SMG, characterized by widespread species, with only one tree Indicator Species (*Celtis iguanaea*) identified. For Plant

TABLE 1 Top five indicator species of plants for each cluster, or all species for which indicator value >0.3, whichever is greater (*p* = probability value)

Species	Life form	Status	Indicator value	*p*
Cluster 1				
Coccoloba flavescens	Shrub/tree	HE	0.6667	.001
Calliandra haematomma var. *haematomma*	Shrub	CE	0.4966	.024
Scolosanthus acanthodes	Shrub	HE	0.3958	.05
Randia aculeata	Shrub	W	0.3599	.001
Maytenus buxifolia	Tree	CE	0.3222	.005
Cluster 2				
Trichilia hirta	Tree	W	0.6127	.007
Ziziphus rhodoxylon	Shrub/tree	CE	0.6122	.001
Rauvolfia nitida	Shrub	CE	0.6061	.009
Tabernaemontana citrifolia	Tree	CE	0.5614	.009
Coccothrinax argentea	Tree	W	0.5556	.021
Cluster 3				
Callisia monandra	Herb	W	0.5000	.042
Celtis iguanaea	Tree	W	0.5000	.042
Rhynchosia pyramidalis	Vine	W	0.5000	.034
Centrosema pubescens	Vine	W	0.4000	.043
Scleria lithosperma	Herb	W	0.3261	.034
Cluster 4				
Dalea carthagenensis	Herb	W	0.6250	.01
Bastardia viscosa	Herb	W	0.572	.017
Eragrostis barrelieri	Herb	W	0.5648	.016
Hibiscus phoeniceus	Herb	W	0.5648	.011
Setaria vulpiseta	Herb	W	0.5648	.014
Cluster 5				
Chionanthus ligustrinus	Tree	CE	0.5333	.019
Oxandra lanceolata	Tree	CE	0.5333	.005
Oeceoclades maculata	Herb	NN	0.5000	.009
Coccoloba diversifolia	Shrub/tree	W	0.4105	.044
Bursera simaruba	Tree	W	0.2420	.001

(Continues)

TABLE 1 (Continued)

Species	Life form	Status	Indicator value	*p*
Cluster 6				
Matelea viridivenia	Vine	HE	0.7500	.005
Pectis linearis	Herb	W	0.7500	.002
Tephrosia cinerea	Herb	W	0.7500	.003
Tribulus terrestris	Herb	NN	0.7500	.003
Herissantia crispa	Herb	W	0.7273	.002
Leptocereus paniculatus	Tree	HE	0.7273	.001
Melocactus lemairei	Shrub	HE	0.7137	.001
Stenocereus fimbriatus	Tree	W	0.6888	.004
Tournefortia stenophylla	Shrub	CE	0.6888	.009
Crossopetalum decussatum	Shrub	HE	0.6300	.009
Phyllostylon rhamnoides	Tree	W	0.5911	.001
Bothriochloa pertusa	Herb	NN	0.5625	.007
Mentzelia aspera	Herb	W	0.5625	.006
Heliotropium angiospermum	Herb	W	0.5451	.003
Desmodium glabrum	Herb	W	0.5000	.02
Cluster 7				
Sideroxylon horridum	Tree	CE	0.5714	.008
Myrcianthes fragrans	Shrub/tree	W	0.4286	.011
Talinum paniculatum	Herb	W	0.4286	.017
Capparis domingensis	Shrub	HE	0.4286	.015
Cordia globosa	Shrub	W	0.3983	.037

Abbreviations: CE, Caribbean endemic; HE, Hispaniolan endemic; NN, non-native; W, widespread (islands and continents).

Cluster 4, which includes 8 plots across a wide range of intermediate elevations on SMG, the five Indicator Species with the highest IVs all are "weedy" herbaceous species. Plant Cluster 5 comprises 6 mid-elevation plots surveyed by García et al. (2007) on the southwestern flank of SMG (near the park's ranger station), featuring the trees *Chionanthus ligustrinus*, *Oxandra lanceolata*, and *Coccoloba diversifolia*, and the naturalized (non-native) orchid *Oeceoclades maculata*.

Plant Cluster 6 is a distinct group consisting entirely of four plots that we surveyed in 2016 at low elevation on shale bedrock on the northwestern (leeward) side of SMG (Figure 2b), with correspondingly very low MAP and high MAT. Many Indicator Species (27) were

identified in Plant Cluster 6, but interestingly they were not predominantly tree taxa (Table S2). The tree taxa found here are shared with other clusters. The Indicator Species include five Cactaceae and many herbaceous species. Plant Cluster 7 comprises seven plots also sampled in 2016 by the authors at mid- to high elevations on the leeward side of SMG (Figure 2b); Indicator Species include the woody endemics *Sideroxylon horridum* and *Capparis domingensis*.

A number of common SDTF species occur in several clusters, and most are not Indicator Species for any single cluster. Ignoring the unusual Plant Cluster 3 with only two plots, the trees *Bursera simaruba*, *Senna atomaria*, *Capparis ferruginea*, *Guaiacum officinale*, *Senegalia angustifolia*, the shrub *Cynophalla flexuosa*, and the woody vine *Stigmaphyllon emarginatum* are found in all six other clusters and therefore represent widespread species typical of SDTF throughout the SMG elevation gradient. Other species occur in all plots at all elevations except those in the low, dry Plant Cluster 6; these are the trees *Amyris elemifera*, *Eugenia foetida*, *Eugenia rhombea*, *Exostema caribaeum*, *Guaiacum sanctum*, *Randia aculeata*, and *Vachellia macracantha* (Table 2). The 19 species that were found in 22 or more plant plots are all either Caribbean endemic (4) or widespread native (15) species; neither Hispaniolan endemics nor non-native species were represented (Table 2).

3.2 | Birds

Our point-counts recorded 30 indigenous species of birds (and no non-indigenous species), consisting of 9 Hispaniolan endemics,

9 other species endemic to the Caribbean Region, and 12 widespread species (Table S3). The mean number of species per point-count was 13.5, with no elevational trend in species richness. The first axis of the NMS ordination (Figure 3) is strongly correlated (based on a posteriori fitting) with MAP ($r = .99$) and MAT ($r = -.99$), but the smaller range of ordination scores indicates less species turnover in birds than in plants. Bird point-counts 1–11, each associated with Plant Cluster 6, form the highly distinctive Bird Cluster A (Figure 3 and Figure S4), situated at low elevation (Figure 4) on shale bedrock. Four of the five Indicator Species identified for Bird Cluster A are widespread rather than endemic species (Table 3). Furthermore, all five Indicator Species for Bird Cluster A are habitat generalists that tolerate, if not prefer, areas of secondary forest or other disturbance. At higher elevations, with plant communities developed on limestone substrate (Plant Cluster 7), the three other defined bird communities (Bird Clusters B-D) are more strongly represented by Indicator Species that are endemic either to Hispaniola or at least to the Caribbean islands (Table 3). In fact, each of Bird Clusters B-D has one of Hispaniola's endemic genera of birds (*Microligea*, *Phaenicophilus*, and *Nesoctites*) as an Indicator Species.

Direct ordination (Figure S5) and zero-inflated Poisson GAM (regression-type) models of individual bird species abundance with elevation suggest a few strong associations with elevation and many weaker ones (Table 4; Figure S6). The strongest associations are for species preferring low elevations, such as *Columbina passerina*, *Mimus*

TABLE 2 Commonly occurring species of plants, found in 22 or more (Freq = frequency) of the 48 plots, listed in order of frequency, showing the proportion of the N plots in which they are found for each Plant Cluster (Clus1-Clus7)

				Clus1	Clus2	Clus3	Clus4	Clus5	Clus6	Clus7
Species	Life form	Status	Freq (N)	15	6	2	8	6	4	7
Bursera simaruba	Tree	W	33	0.73	0.67	0.00	0.63	1.00	0.25	0.86
Senna atomaria	Tree	W	33	0.67	0.67	0.00	0.75	0.50	0.75	1.00
Capparis ferruginea	Shrub/tree	CE	32	0.67	0.67	0.00	0.63	0.83	0.75	0.71
Guaiacum officinale	Tree	W	30	0.53	0.67	0.00	1.00	0.00	1.00	0.86
Amyris elemifera	Shrub/tree	W	28	0.67	0.33	0.00	0.75	0.50	0.00	1.00
Eugenia foetida	Shrub/tree	W	28	0.53	0.83	0.00	0.88	0.83	0.00	0.43
Stigmaphyllon emarginatum	Liana	CE	28	0.93	0.50	0.50	0.50	0.33	0.25	0.43
Colubrina elliptica	Tree	W	26	0.53	0.00	0.00	0.50	0.83	1.00	0.71
Exostema caribaeum	Shrub/tree	W	26	0.40	0.67	0.00	1.00	0.33	0.00	0.86
Guaiacum sanctum	Shrub/tree	W	26	0.87	0.33	0.00	0.50	0.67	0.00	0.43
Senegalia angustifolia	Tree	CE	26	0.67	0.33	0.00	0.88	0.67	0.25	0.29
Cynophalla flexuosa	Shrub/tree	W	25	0.40	0.17	1.00	0.88	0.50	1.00	0.29
Tillandsia recurvata	Herb	W	25	0.40	0.50	0.00	0.50	0.50	0.75	0.86
Samyda dodecandra	Shrub	W	24	0.60	0.50	0.00	0.75	0.00	0.00	0.86
Maytenus buxifolia	Tree	CE	23	0.87	0.00	0.00	0.50	0.00	0.25	0.71
Pilosocereus polygonus	Tree	W	23	0.67	0.33	0.00	0.00	0.33	0.75	0.86
Eugenia rhombea	Shrub/tree	W	22	0.60	0.50	0.00	0.38	0.50	0.00	0.57
Randia aculeata	Shrub	W	22	0.87	0.00	0.00	0.63	0.17	0.00	0.43
Vachellia macracantha	Tree	W	22	0.20	0.83	0.00	0.75	0.50	0.00	0.71

Abbreviations: CE, Caribbean endemic; W, widespread (islands and continents).
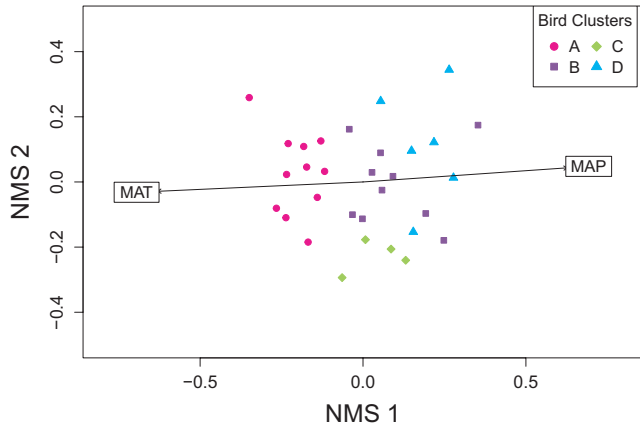
FIGURE 3 Four groups of bird point-counts (Bird Clusters A–D) defined by clustering, shown on the NMS ordination plot (axis 1 and 2) with vector indicating correlation with MAP and MAT, which are both strongly correlated with axis 1, the main variation in bird species composition

FIGURE 4 Boxplots showing frequency distribution of elevation values for groups of bird point-count locations defined by clustering (Bird Clusters). Thick line is median value, box encompasses 25%–75%, whisker indicates 5% and 95%, circles are outliers

polyglottos, *Zenaida macroura*, and *Melanerpes striatus* (Figure 5). Two other species (*Todus subulatus* and *Coereba flaveola*) seem to have bimodal elevation trends in abundance, being least common at mid-elevations. All six of these species are habitat generalists, although their feeding guilds are diverse, including granivores (the two doves), omnivores/frugivores (mockingbird, woodpecker, tody), and a nectarivore (bananaquit).

4 | DISCUSSION

We found that most changes in SDTF plant species composition along >800 m of elevation change in a single mountain range, Sierra Martín García (Dominican Republic), were gradual as we predicted, indicated by the overlapping species composition among clusters seen in ordination space and the large range of climatic conditions seen within some clusters. One cluster was quite distinct in climate (dry, warm) and species composition, but also occurred on a different geological substrate (shale) than all the others (on limestone). Plant community composition was more strongly related to climate than to elevation alone (elevation does not account for rain shadow effects on precipitation) in accordance with our second prediction. We did, however, find strong spatial patterning in plant community composition, with as much variation in composition explained by proximity as by climate. Nearby plots had similar composition, suggesting dispersal limitations, spatially structured disturbances, or both. Furthermore, much of the variation in plant species composition remained unexplained. Finally, the bird communities did show less turnover on the elevation gradient than plant communities; bird communities varied among locations, but this variation was not strongly correlated with elevation and climate, nor did the patterns of individual species reflect ordered replacement along the gradient as suggested by Terborgh (1977).

SDTF spans a large elevation range (>800 m) in Sierra Martín García. In fact, the maximum elevation (884 m) of an SDTF plot in

our study area is the highest of any Neotropical dry forest plot in the West Indies (Franklin et al., 2018), reflecting the strong rain shadow effect at SMG, which may be fueled by its steep slopes and by lying directly on the southern coast of Hispaniola. Even at this high elevation, the estimated MAP (~1,080 mm; Figure S3a) is well below the upper limit of precipitation (~1,800 m) for STDF, as put forth by Lugo et al. (2006). The only higher elevation Neotropical SDTF plots that we know of are continental, e.g., in the strong rain shadow of the inter-Andean valleys of South America (DRYFLOR et al., 2016). In spite of being represented by coarse scale maps in our study, the bioclimatic variables reflecting direct ecological gradients of moisture availability (MAP) and temperature (MAT) were more strongly related to ecological community composition than the finer-scale elevation data representing an indirect gradient. Continuous turnover in Neotropical SDTF vascular plant species composition along an elevation gradient has also been observed elsewhere (Vázquez & Givnish, 1998). Detailed examination of several plant groups in Bolivian cloud forest similarly found significant species turnover limits between, but not within, major vegetation zones (Bach et al., 2007). Systematic and gradual changes in West Indian forest composition along an elevation gradient have been shown to reflect turnover in plant functional traits, at least for rain forest trees (Swenson et al., 2010). In contrast, studies that identify abrupt discontinuities in plant community composition on tropical mountains, even in the absence of substrate differences, typically span a much greater range of elevations, encompassing multiple Holdridge life zones or vegetation formations (Hemp, 2006).

By restricting our study to a single region, we were able to identify environmental factors (MAP, MAT) affecting communities subjected to the same larger-scale biogeographical processes (Franklin et al., 2018). The SDTF plant communities in Sierra Martín García appear to be somewhat different from the SDTF flora described for nearby Sierra de Bahoruco (Fisher-Meerow & Judd, 1989), but also showed a great deal of geographically-structured fine-scale variation not explained by the elevation-climate gradient represented

TABLE 3 Top five indicator species for each bird cluster, or all for which IV >0.3, whichever is greater, showing their Indicator value and significance (*p*)

Species	Status	Indicator value	*p*
Cluster A – low elevation			
Zenaida macroura	W	0.5561	.009
Mimus polyglottos	W	0.5025	.007
Columbina passerina	W	0.4234	.010
Coereba flaveola	W	0.3868	.085
Melanerpes striatus	HES	0.3664	.084
Cluster B – low-mid-high elevation			
Turdus plumbeus	CE	0.5400	.004
Microligea palustris	HEG	0.3288	.066
Cluster C – high elevation			
Zenaida asiatica	W	0.4862	.020
Phaenicophilus palmarum	HEG	0.3752	.015
Cluster D – mid-high elevation			
Loxigilla violacea	CE	0.5011	.012
Nesoctites micromegas	HEG	0.4464	.012
Tiaris bicolor	W	0.4188	.064
Vireo altiloquus	W	0.3896	.081
Contopus hispaniolensis	HES	0.3333	.039

Abbreviations: CE, Caribbean endemic; HEG, Hispaniolan endemic genus; HES, Hispaniolan endemic species; W, widespread (islands and continents).

in our environmental data. This unexplained variation could result from spatially structured environmental factors not measured in our study (e.g., topoclimate and soil properties), human factors (land use history and other disturbance; e.g., Gillespie et al., 2000), and/or biotic factors such as dispersal limitations.

The most distinctive change in plant composition at SMG was associated with a geological boundary, namely the change from shale (Plant Cluster 6) to limestone bedrock (all other plant clusters; Figure 2 and Figure S2). This change in substrate was reflected most strongly in a unique vegetation type (Plant Cluster 6) that also was occupied by a distinctive bird community (Bird Cluster A). Shale typically weathers to a clayey soil that provides more uniform edaphic microhabitats than limestone, whereas karstic weathering provides pinnacles, pits, and crevices that can block the sun, concentrate moisture, and thus fuel microhabitat heterogeneity (Zhang et al., 2014). As noted by Whittaker (1967), discontinuous changes in plant community composition are expected when environmental conditions have strong spatial discontinuities, especially those with sharp boundaries such as disturbance (including land use) and soil parent material (geological substrate).

Bird species show a weaker relationship to elevation/climate than plants at SMG, where both plant and bird communities are rich with species endemic to Hispaniola or at least to the West Indies. Our results suggest a clear response of SDTF plants to elevation-mediated climate gradients (as also found across wetter Greater Antillean life

zones by Blake & Loiselle, 2000). The more complex (and less well understood) responses of birds may be due in part to the vegetation itself (e.g., Jankowski et al., 2009), and perhaps also to each other (interspecific interactions such as competition, e.g., Terborgh & Weske, 1975), all within a framework of past and current human impact. We did find that endemic species were largely restricted to relatively higher elevations, as has been observed for birds and other vertebrates elsewhere in the tropics (e.g., Jankowski & Rabenold, 2007).

At SMG, one suite of bird species (Bird Cluster A), characterized by habitat generalists, was confined to the lowest elevation sites with a distinctive plant community (Plant Cluster 6), although otherwise the bird species composition showed only a weak relationship to elevation. Other groups of sites with similar bird composition were detected, but species turnover was unrelated to the elevation gradient, suggesting that these patterns might be related to finer-scale environmental variation (for example, habitat structure) or to other factors. This similarity in composition within a region has been noted in other Neotropical SDTF bird communities and attributed to the dispersal ability of the species (Oswald et al., 2016). This lack of clear turnover in many STDF bird communities may reflect selection among surviving species to be flexible to dynamic conditions that include climate change and habitat disturbance, whether due to tropical storms, landslides, or human causes. It may be that forest physical structure, which is not the topic of this paper, did not vary much across our 11 plant plots on the leeward slope of SMG. Perhaps, forest structure and diversity, rather than plant species composition per se, have a stronger influence on the SMG bird community (e.g., Terborgh, 1977; Gillespie & Walter, 2001), a potentially fruitful avenue for new research.

We note that a previous bird survey in SMG (Almonte-Espinosa, 2017) included a broad range of habitats on multiple slopes of the mountain range, among which her habitat categories of BTM (*bosque de transición de áreas medias*), BS (*bosque seco*), and MES (*monte espinosa subtropical*) probably are ones that we would regard as SDTF. Of the 30 species of birds that we recorded in May-June 2017, the habitat categories of Almonte-Espinosa (2017) included 21 of the same species in BTM, 20 in BS, and 20 in MES. Without knowing the exact locations of her surveys, more detailed comparisons are not possible.

The contemporary ecological patterns observed in this study can be seen from a longer-term perspective. Paleontological evidence from across the West Indies reveals major late Quaternary changes in the abundance and distribution of birds and other vertebrates, including their inter-island distributions as well as intra-island elevation ranges (e.g., Pregill et al., 1994; Steadman & Takano, 2013; Steadman et al., 2015; Cooke et al., 2017; Soto-Centeno et al., 2017). These and other studies show that numerous species were lost on the islands at the end of the Pleistocene (a period of major glacial-interglacial change in climate and sea level) and also during the Holocene from human activities. From Hispaniola in particular, various species of rails, woodcocks, eagles, owls, and caracaras already have been lost, especially after human arrival (Olson, 1974, 1976; Steadman & Takano, 2013; Suárez & Olson, 2015; Takano & Steadman, 2015). It is likely that the surviving species of birds are

TABLE 4 Summary of zero-inflated Poisson regression generalized additive models (GAMs) for individual bird species that occurred in 10 or more point-counts with elevation as the predictor

Species	Frequency	% Dev. Expl.	p	REML
Low-elevation species				
Columbina passerina	29	79.4	<.001	39.21
Mimus polyglottos	22	71.2	<.001	26.02
Zenaida macroura	19	43.8	<.001	36.92
Melanerpes striatus	10	31.2	.090	21.65
Anthracothorax dominicensis	17	17.6	.090	30.37
Myiarchus stolidus	26	15.6	.040	39.97
Mid- and mid-high elevation species				
Turdus plumbeus	12	83.3	.017	10.38
Vireo altiloquus	19	100.0	.319	12.25
High (± low) elevation species				
Todus subulatus	28	20.7	.272	34.20
Coereba flaveola	23	11.2	.230	46.48
Weak relationship elevation				
Mellisuga minima	18	35.9	.580	24.53
Zenaida asiatica	15	31.8	.382	31.82
Phaenicophilus palmarum	27	12.8	.982	34.11
Coccyzus minor	12	26.7	.847	24.10
Loxigilla violacea	16	11.6	.220	32.98

Note: Species are grouped by direction of trend and listed in order of strength of the fit. Frequency is the number of points in which the species was recorded (out of 33), percent deviance explained (% Dev. Expl.), significance of the smoothing term (Prob), and Restricted Maximum Likelihood Estimator (REML).

more labile in their habitat preferences and thus more tolerant of habitat disturbance. Two dramatic examples are the endemic Least Pauraque *Siphonorhis brewsteri* and the widespread Zenaida Dove *Zenaida aurita*, which are considered characteristic of low elevations (<1,000 m) on Hispaniola today. As recently as ~1,000 years ago, however, both species occurred very commonly as fossils at much higher elevations (~1,820 m) in a cave called Trouing Jean Paul, which is ~100 km west of SMG (Steadman & Takano, 2013; Takano & Steadman, 2015).

Prehistoric habitat alteration (forest clearing) by people may have fueled these past upslope distributions, which may be taking place again in areas with modern habitat alteration. In fact, of the 18 non-passerine species that we recorded in 2017 at SMG, 9 (50%) of them occurred as fossils from Trouing Jean Paul; four of these species (*Zenaida aurita*, *Z. macroura*, *Columbina passerina*, and *Mellisuga minima*) are unknown from such high elevations on Hispaniola today (Keith et al., 2003; Rimmer et al., 2005).

SDTF has been widely cleared and degraded on a global scale (Gillespie et al., 2012), with species in this biome being sensitive to climate on short and long time scales (Pennington et al., 2006; Blundo et al., 2012). Neotropical SDTF sustains a diverse flora and fauna, fueled by endemism and species turnover at multiple scales (Pennington et al., 2006; Oswald et al., 2016, 2017). West Indian SDTF harbors particularly high endemism for many groups of plants and animals as a result of isolation as well as the complex historical

biogeography of the Greater Antilles (Iturralde-Vinent et al., 2000; Keith et al., 2003; Santiago-Valentin & Olmstead, 2004). The community ecology of West Indian SDTF is relatively poorly understood compared to that on the American continents (Sánchez-Azofeifa et al., 2005). Here, we addressed this knowledge gap by describing in detail a rich community of SDTF plants and birds found within a single coastal mountain range.

The protected area of SMG is critically important to preserve Caribbean SDTF and its endemic species of plants, invertebrates, and vertebrates. Other studies have shown that large protected areas can counteract the effects of human disturbance on SDTF vertebrate biodiversity (Gillespie & Walter, 2001). Our research sets a baseline to help understand how species will respond to future habitat modification and climate change on Hispaniola. With extreme levels of habitat loss already fueling considerable extinction of amphibians and reptiles in the Haitian portion of Hispaniola (Hedges et al., 2018), it is more important than ever to survey any groups of Hispaniolan organisms to learn about their biology and begin to curtail the processes underlying their declines.
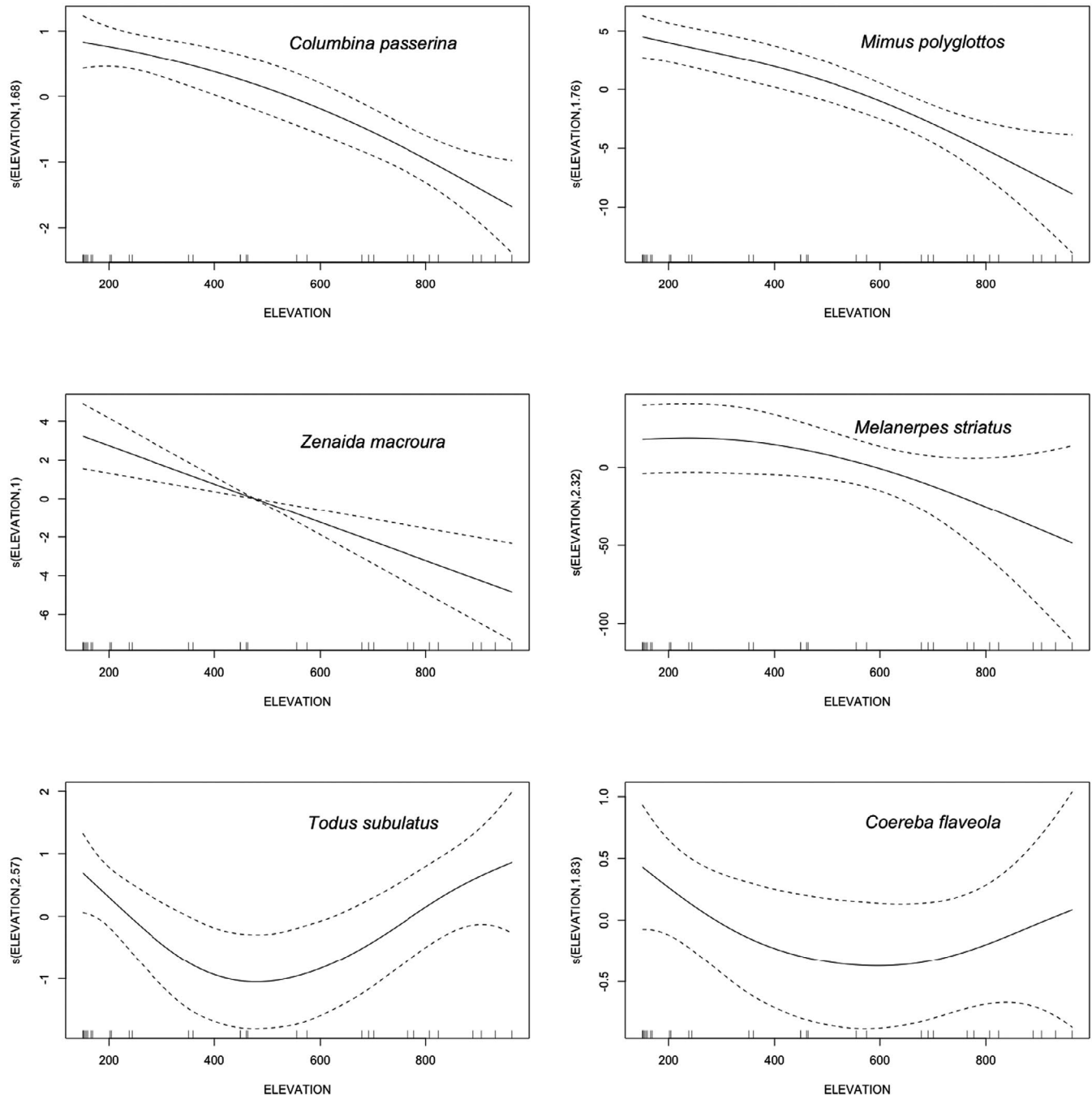
FIGURE 5 Trend (*y*-axes show the log of the Poisson parameter) in bird species abundance with elevation (shown on the *x*-axes) calculated from zero-inflated Poisson generalized additive models (GAMs; see Table 4) for four species showing association with low elevations (*Columbina passerina*, *Mimus polyglottos*, *Zenaida macroura*, *Melanerpes striatus*), and two showing bimodal pattern of low and high elevation (*Todus subulatus*, *Coereba flaveola*)

DATA AVAILABILITY STATEMENT

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