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

Running Head: Seasonally dry tropical forest on Hispaniola

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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, 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 (SPANISH)

Se reportan los resultados de estudios sistemáticos de plantas vasculares y aves en bosque seco tropical (SDTF por sus siglas en inglés) a través de gradientes de elevación de sotavento y barlovento (31-884 msnm) en la Sierra Martín García (SMG), República Dominicana. Se esperaba encontrar cambios sistemáticos y graduales de distribuciones de plantas según la elevación debido al efecto fuerte de topoclima. Al contrario, se esperaba que la composición de la comunidad de aves (predicha) estuviera relacionada débilmente a elevación, porque se esperaba que la distribución de aves estuviera fuertemente relacionada más a la estructura vegetal que a la composición de vegetación. Basado en 48 transectos de vegetación, se indentificaron siete grupos que se diferenciaron en su composición de especies, lo cual fue correlacionado con elevación y precipitación. Las comunidades de vegetación más distintas ocurren en elevaciones bajas con el clima seco y caloroso, de la ladera de sotavento, que consta de un alto número de especies indicadoras no maderables, aunque la mayoría de los árboles y arbustos en esa área están representados por especies de amplia distribución. El promedio bajo de precipitación y piedra de pizarra (en vez de caliza) podrían ser los principales factores que causan esta distinción en las parcelas del sotavento de baja elevación. En la ladera de sotavento, donde

también anotamos las aves, la comunidad de vegetación cambia gradualmente con la elevación de media- a alta elevaciones. La comunidad de aves más distinta fue asociada con el bosque del lado de sotavento de baja-elevación sobre pizarra; esta comunidad de aves fue dominada por especies de amplia distribución. En elevaciones más altas, pero aún en SDTF del lado de sotavento, las comunidades de aves tuvieron un componente más representado por especies endémicas de La Española o del Caribe en general, y el recambio de especies no correspondió a gradientes de elevación.

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

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, 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 1500-2500 m on the Pacific slope of Mexico (Manatlán Biosphere Reserve, Jalisco) that included the transition from seasonally dry forest to cloud forest (Vázguez G. & 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 3400 m of elevation on Mt. Kinabalu, Borneo, the distribution of lowland, montane, and subalpine plant formations was 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 2000m elevation gradient ranging from seasonally dry forest to cloud forest (Blundo et al. 2012). The distribution of two vegetation formations (pine woodland versus cloud forest) on the island of Hispaniola (Cordillera Central, Dominican Republic) from 1100-3100 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 0-1500 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 $<\sim$ 1800 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.*), 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 100–1074 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 and 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 (1600 to 600 BP) fossils in a cave at 1800+ 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.

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.

METHODS

Study Area and Survey Design .---

Sierra Martín García (SMG) is a small, rather isolated mountain range in southwestern Dominican Republic (Fig. 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 1350 m elevation (SEA/DED 1990). SMG 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.

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 (Fig. 1). We listed all vascular plant species' occurrences in 100-m² (50 x 2 m) plots (Braun-Blanguet 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, 1981-1996) 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 south-central windward flanks of SMG (Fig. 1); our analyses incorporate the Garcia 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, 1981–1996).

We extracted elevation and bioclimatic data (interpolated from 1960-1990 averages, 30 arc-sec grids -- about 1 km² 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 859–1081 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 = 0.99). As expected for these 48 locations, elevation had a negative relationship with MAT (r = -0.88), and a positive relationship with MAP (r = 0.67) (Fig. S1) with variation related to slope exposure. MAT and MAP were strongly negatively correlated (r = -0.88)

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).

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 six 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-minute period at each point. All point-counts were double-observer. During our first two days in the field, when we did only practice point-counts, we determined that bird activity subsided at 3 to 3.5 hours 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-minute period to avoid doublecounting. 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 zeroinflated 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'.

RESULTS

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 =0.35; F=3.61, P<0.001) based on species composition (Fig. S2). The groups (clusters) show considerable overlap in two-dimensional ordination (Fig. 2a), however, reflecting many shared species among groups. MAT (R^2 = 0.26; P <0.001) and MAP (R^2 = 0.41; P <0.001), and to a lesser extent elevation (R^2 = 0.13; P = 0.054), 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 with regard to MAP (Fig. S3A) than elevation (Fig. 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 (Fig. S3), and are also very distinct in their species composition (Fig. 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 (Fig. 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, 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 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 (Fig. 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 (Fig. 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,* and *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 or non-native species were represented (Table 2).

Birds.---

Our point-counts recorded 30 indigenous species of birds (and no nonindigenous 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 (Fig. 3) is strongly correlated (based on a posteriori fitting) with MAP (r=0.99) and MAT (r=-0.99), 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 (Figs. 3, S4), situated at low elevation (Fig. 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, Nesoctites) as an Indicator Species.

Direct ordination (Fig. S5) and zero-inflated Poisson GAM (regressiontype) models of individual bird species abundance with elevation suggest a few strong associations with elevation and many weaker ones (Table 4; Fig. S6). The strongest associations are for species preferring low elevations, such as *Columbina passerina*, *Mimus polyglottos*, *Zenaida macroura*, and *Melanerpes striatus* (Fig. 5). Two other species (*Todus subulatus*, *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).

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 guite 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 e.g., 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 (\sim 1080 mm; Fig. S3a) is well below the upper limit of precipitation (\sim 1800 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 (Vázguez G. & 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 finescale variation not explained by the elevation-climate gradient represented in our environmental data. This unexplained variation could result from spatially structured environmental factors not measured in our study (e.g., topoclimate, soil properties), human factors (land use history, 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; Figs. 2, 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 as well as 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, has 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 more labile in their habitat preferences and thus more tolerant of habitat disturbance. Two dramatic examples (are the endemic Least Paurague Siphonorhis brewsteri and the widespread Zenaida Dove Zenaida aurita), which are considered characteristic of low elevations (<1000 m) on Hispaniola today. As recently as \sim 1,000 years ago, however,

both species occurred very commonly as fossils at much higher elevations (~1820 m) in a cave called Trou 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 Trou 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.* 2006b,Blundo *et al.* 2012). Neotropical SDTF sustains a diverse flora and fauna, fueled by endemism and species turnover at multiple scales (Pennington *et al.* 2006a,Oswald *et al.* 2016,Oswald *et al.* 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.

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DATA AVAILABILITY

The data used in this study are archived at the Dryad Digital Repository (DOI doi:10.5061/dryad.v6m6454).

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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).

| | | | Indica | |
|----------------------------|--------|------|--------|-------|
| Species | Life | Stat | tor | р |
| - | Form | us | Value | - |
| Cluster 1 | | | | |
| | shrub/ | | | |
| Coccoloba flavescens | tree | HE | 0.6667 | 0.001 |
| Calliandra haematomma var. | | | | |
| haematomma | shrub | CE | 0.4966 | 0.024 |
| Scolosanthus acanthodes | shrub | HE | 0.3958 | 0.05 |
| Randia aculeata | shrub | W | 0.3599 | 0.001 |
| Maytenus buxifolia | Tree | CE | 0.3222 | 0.005 |
| Cluster 2 | | | | |
| Trichilia hirta | tree | W | 0.6127 | 0.007 |
| | shrub/ | | | |
| Ziziphus rhodoxylon | tree | CE | 0.6122 | 0.001 |
| Rauvolfia nitida | shrub | CE | 0.6061 | 0.009 |
| Tabernaemontana citrifolia | tree | CE | 0.5614 | 0.009 |
| Coccothrinax argentea | tree | W | 0.5556 | 0.021 |
| Cluster 3 | | | | |
| Callisia monandra | herb | W | 0.5000 | 0.042 |
| Celtis iguanaea | tree | W | 0.5000 | 0.042 |
| Rhynchosia pyramidalis | vine | W | 0.5000 | 0.034 |
| Centrosema pubescens | vine | W | 0.4000 | 0.043 |
| Scleria lithosperma | herb | W | 0.3261 | 0.034 |
| Cluster 4 | | | | |
| Dalea carthagenensis | herb | W | 0.6250 | 0.01 |
| Bastardia viscosa | herb | W | 0.572 | 0.017 |
| Eragrostis barrelieri | herb | W | 0.5648 | 0.016 |
| Hibiscus phoeniceus | herb | W | 0.5648 | 0.011 |
| Setaria vulpiseta | herb | W | 0.5648 | 0.014 |
| Cluster 5 | | | | |
| Chionanthus ligustrinus | tree | CE | 0.5333 | 0.019 |
| Oxandra lanceolata | tree | CE | 0.5333 | 0.005 |
| Oeceoclades maculata | herb | NN | 0.5000 | 0.009 |
| | shrub/ | | | |
| Coccoloba diversifolia | tree | W | 0.4105 | 0.044 |
| Bursera simaruba | tree | W | 0.2420 | 0.001 |
| Cluster 6 | | | | |
| Matelea viridivenia | vine | HE | 0.7500 | 0.005 |
| Pectis linearis | herb | W | 0.7500 | 0.002 |
| Tephrosia cinerea | herb | W | 0.7500 | 0.003 |
| Tribulus terrestris | herb | NN | 0.7500 | 0.003 |
| Herissantia crispa | herb | W | 0.7273 | 0.002 |
| Leptocereus paniculatus | tree | HE | 0.7273 | 0.001 |
| Melocactus lemairei | shrub | HE | 0.7137 | 0.001 |

| Species | Life Form | Stat us | Indica tor Value | р |
|---------------------------|--------------|------------|------------------------|-------|
| Stenocereus fimbriatus | tree | W | 0.6888 | 0.004 |
| Tournefortia stenophylla | shrub | CE | 0.6888 | 0.009 |
| Crossopetalum decussatum | shrub | HE | 0.6300 | 0.009 |
| Phyllostylon rhamnoides | tree | W | 0.5911 | 0.001 |
| Bothriochloa pertusa | herb | NN | 0.5625 | 0.007 |
| Mentzelia aspera | herb | W | 0.5625 | 0.006 |
| Heliotropium angiospermum | herb | W | 0.5451 | 0.003 |
| Desmodium glabrum | herb | W | 0.5000 | 0.02 |
| Cluster 7 | | | | |
| Sideroxylon horridum | tree | CE | 0.5714 | 0.008 |
| | shrub/ | | 0.4286 | 0.011 |
| Myrcianthes fragrans | tree | W | | |
| Talinum paniculatum | herb | W | 0.4286 | 0.017 |
| Capparis domingensis | shrub | HE | 0.4286 | 0.015 |
| Cordia globosa | shrub | W | 0.3983 | 0.037 |

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

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).

| | Life form | Stat | Freq | Clus |
|---------------------|-----------|------|------|------|------|------|------|------|------|------|
| Enocios | | us | (NI) | 15 | 2 | 3 | 4 | 5 | 0 | 7 |
| Species | | 14/ | | 15 | 0 | 2 | 8 | 0 | 4 | / |
| Bursera simaruba | tree | | 33 | 0.73 | 0.67 | 0.00 | 0.03 | 1.00 | 0.25 | 0.80 |
| Senna atomaria | tree | VV | 33 | 0.67 | 0.67 | 0.00 | 0.75 | 0.50 | 0.75 | 1.00 |
| Capparis | shrub/ | | 32 | | | | | | | |
| ferruginea | tree | CE | | 0.67 | 0.67 | 0.00 | 0.63 | 0.83 | 0.75 | 0.71 |
| Guaiacum | | | 30 | | | | | | | |
| officinale | tree | W | | 0.53 | 0.67 | 0.00 | 1.00 | 0.00 | 1.00 | 0.86 |
| Amyris elemifera | shrub/ | | 28 | | | | | | | |
| | tree | W | | 0.67 | 0.33 | 0.00 | 0.75 | 0.50 | 0.00 | 1.00 |
| Eugenia foetida | shrub/ | | 28 | | | | | | | |
| | tree | W | | 0.53 | 0.83 | 0.00 | 0.88 | 0.83 | 0.00 | 0.43 |
| Stigmaphyllon | | | 28 | | | | | | | |
| emarginatum | liana | CE | | 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 | shrub/ | | 26 | | | | | | | |
| caribaeum | tree | W | | 0.40 | 0.67 | 0.00 | 1.00 | 0.33 | 0.00 | 0.86 |
| Guaiacum | shrub/ | | 26 | | | | | | | |
| sanctum | tree | W | | 0.87 | 0.33 | 0.00 | 0.50 | 0.67 | 0.00 | 0.43 |
| Senegalia | | | 26 | | | | | | | |
| angustifolia | tree | CE | | 0.67 | 0.33 | 0.00 | 0.88 | 0.67 | 0.25 | 0.29 |
| Cynophalla | shrub/ | | 25 | | | | | | | |
| flexuosa | tree | W | | 0.40 | 0.17 | 1.00 | 0.88 | 0.50 | 1.00 | 0.29 |
| Tillandsia | | | 25 | | | | | | | |
| recurvata | herb | W | | 0.40 | 0.50 | 0.00 | 0.50 | 0.50 | 0.75 | 0.86 |
| Samyda | | | 24 | | | | | | | |
| dodecandra | shrub | W | | 0.60 | 0.50 | 0.00 | 0.75 | 0.00 | 0.00 | 0.86 |
| Mavtenus | | | 23 | | | | | | | |
| buxifolia | tree | CE | | 0.87 | 0.00 | 0.00 | 0.50 | 0.00 | 0.25 | 0.71 |
| Pilosocereus | | _ | 23 | | | | | | | _ |
| polvaonus | tree | w | | 0.67 | 0.33 | 0.00 | 0.00 | 0.33 | 0.75 | 0.86 |
| Eugenia rhombea | shrub/ | | 22 | | | | | | | |
| | tree | w | | 0.60 | 0.50 | 0.00 | 0.38 | 0.50 | 0.00 | 0.57 |
| Randia aculeata | shrub | Ŵ | 22 | 0.87 | 0.00 | 0.00 | 0.63 | 0.17 | 0.00 | 0.43 |
| Vachellia | | | 22 | 0.07 | 0.00 | | 0.00 | 0.17 | | |
| macracantha | Tree | W | | 0.20 | 0.83 | 0.00 | 0.75 | 0.50 | 0.00 | 0.71 |

Status categories: CE, Caribbean endemic; W, widespread (islands and continents).

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).

| | | Indicat | | | | |
|----------------------------------|------|---------|-------|--|--|--|
| Species | Stat | or | Prob | | | |
| | us | Value | | | | |
| Cluster A Low Elevation | | | | | | |
| Zenaida macroura | W | 0.5561 | 0.009 | | | |
| Mimus polyglottos | W | 0.5025 | 0.007 | | | |
| Columbina passerina | W | 0.4234 | 0.010 | | | |
| Coereba flaveola | W | 0.3868 | 0.085 | | | |
| Melanerpes striatus | HES | 0.3664 | 0.084 | | | |
| Cluster B Low-Mid-High Elevation | | | | | | |
| Turdus plumbeus | CE | 0.5400 | 0.004 | | | |
| Microligea palustris | HEG | 0.3288 | 0.066 | | | |
| Cluster C High Elevation | | | | | | |
| Zenaida asiatica | W | 0.4862 | 0.020 | | | |
| Phaenicophilus palmarum | HEG | 0.3752 | 0.015 | | | |
| Cluster D Mid-High Eleval | tion | | | | | |
| Loxigilla violacea | CE | 0.5011 | 0.012 | | | |
| Nesoctites micromegas | HEG | 0.4464 | 0.012 | | | |
| Tiaris bicolor | W | 0.4188 | 0.064 | | | |
| Vireo altiloquus | W | 0.3896 | 0.081 | | | |
| Contopus hispaniolensis | HES | 0.3333 | 0.039 | | | |

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

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 are grouped by direction of trend and listed in order of strength of the fit.

| Species | Freque | % Dev. | Prob | REML | | | |
|-----------------------------|-----------|--------|---------|-------|--|--|--|
| | ncy | Expl. | | | | | |
| Low elevation species | | | | | | | |
| Columbina passerina | 29 | 79.4 | < 0.001 | 39.21 | | | |
| Mimus polyglottos | 22 | 71.2 | < 0.001 | 26.02 | | | |
| Zenaida macroura | 19 | 43.8 | < 0.001 | 36.92 | | | |
| Melanerpes striatus | 10 | 31.2 | 0.090 | 21.65 | | | |
| Anthracothorax | 17 | 17.6 | 0.090 | 30.37 | | | |
| dominicensis | | | | | | | |
| Myiarchus stolidus | 26 | 15.6 | 0.040 | 39.97 | | | |
| Mid- and mid-high elevati | on specie | S | | | | | |
| Turdus plumbeus | 12 | 83.3 | 0.017 | 10.38 | | | |
| Vireo altiloquus | 19 | 100.0 | 0.319 | 12.25 | | | |
| High (+/- low) elevation s | pecies | | | | | | |
| Todus subulatus | 28 | 20.7 | 0.272 | 34.20 | | | |
| Coereba flaveola | 23 | 11.2 | 0.230 | 46.48 | | | |
| Weak relationship elevation | on | | | | | | |
| Mellisuga minima | 18 | 35.9 | 0.580 | 24.53 | | | |
| Zenaida asiatica | 15 | 31.8 | 0.382 | 31.82 | | | |
| Phaenicophilus palmarum | 27 | 12.8 | 0.982 | 34.11 | | | |
| Coccyzus minor | 12 | 26.7 | 0.847 | 24.10 | | | |
| Loxigilla violacea | 16 | 11.6 | 0.220 | 32.98 | | | |

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).

Fig. 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.



Fig. 2. Plant plots a) arranged by compositional similarity based on nonmetric 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), shown in geographical coordinates.



Fig. 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.



Fig. 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.



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*).



SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Fig. S1. Elevation (m) versus MAT (Mean Annual Temperature, °C) and Mean Annual Precipitation (MAP, mm) for 48 plant plot locations (Fig. 1 in main text) on Sierra Martín García.

Fig. S2. Ward's clustering cut at a similarity level of 1.3 defined seven Plant Clusters, groups of transects defined by shared plant species composition. Fig. S3. Boxplots showing the frequency distribution of (A) Mean Annual Precipitation (MAP, mm) and (B) elevation for transects in each Plant Cluster (1-7).

Fig. S4. Ward's clustering cut at a similarity level of 0.8 defined four Bird Clusters, groups of point counts defined by shared bird species composition. Fig. S5. Direct ordination of bird point counts using Canonical

Correspondence Analysis (CCA), showing the distribution of species on ordination axes that are correlated with MAP and MAT (and therefore elevation).

Fig. S6. Trend (y-axes show the log of the Poisson parameter) in bird species abundance with elevation (shown on the x-axes) calculated from zeroinflated Poisson generalized additive models (GAMs) for species showing weak association with low elevation

Table S1. Bird point count locations (geographic coordinates in decimal degrees) and nearest plant plot. (*CSV file*)

Table S2. All plant taxa recorded in 48 (50 x 2 m) plant plots at Sierra Martín García, showing life form and status. (*CSV file*)

Table S3: All species of birds recorded in the 33 point counts at Sierra Martín García in May-June 2017, in order of frequency (% Points).

Fig. S1. Elevation (m) versus MAT (Mean Annual Temperature, °C) and Mean Annual Precipitation (MAP, mm) for 48 plant plot locations (Fig. 1 in main text) on Sierra Martín García.







Fig. S3. Boxplots showing the frequency distribution of (A) Mean Annual Precipitation (MAP, mm) and (B) elevation for transects in each Plant Cluster (1-7). Thick line is median value, box encompasses 25-75%, whisker indicates 5% and 95%, circles are outliers.



Fig. S4. Ward's clustering cut at a similarity level of 0.8 defined four Bird Clusters, groups of point counts defined by shared bird species composition



Fig. S5. Direct ordination of bird point counts using Canonical Correspondence Analysis (CCA), showing the distribution of species on ordination axes that are correlated with MAP and MAT (and therefore elevation). Six letter codes indicate species (see Table S2). Position on graph indicates which species occur in lowelevation (high values on CCA1, i.e., Cho_gun= *Chordeiles gundlachii*, Geo_mon= *Geotrygon montana*, Pat_squa= *Patagioenas squamosa*, Tac_pho= *Tachornis phoenicobia*), or high-elevation (low values on CCA1, i.e., Con_his= Contopus *hispaniolensis*, Nes_mic= *Nesoctites micromegas*, Pat_ino= *Patagioenas inornata*, Vir_nan= *Vireo nanus*), or throughout the elevation transect (species in the center of graph).



Fig. S6. 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 in the main text) for species showing weak association with low elevation (*Anthracothorax dominicus*, *Myiarchus stolidus*), and mid- to high elevation (*Vireo altiloquus, Turdus plumbeus, Coccyzus minor*).



Table S1. Bird point count locations (geographic coordinates in decimal degrees) and nearest plant plot. (*Excel spreadsheet*)

Table S2. All plant taxa recorded in 48 (50 x 2 m) plant plots at Sierra Martín García, showing life form and status. (*Excel spreadsheet*)

Table S3: All species of birds recorded in the 33 point counts at Sierra Martín García in May-June 2017, in order of frequency (% Points). Status categories: HES, Hispaniolan endemic species; HEG, Hispaniolan endemic genus; CE, Caribbean endemic; W, widespread (islands and continents); NN, non-native. Points is number of point counts (out of 33) where species occurred (frequency). Total abundance is total number of birds counted. For Indicator Group see Table 3 in the main text. CCA score: low (negative) values correspond to low elevations sites with low precipitation and high temperatures, and high (positive) scores are the opposite. Elevation trend summarizes the results of GAMs in the main text (Table 4, Fig. 5), and see Fig. S5, and includes all species modelled, with low, mid-, high, and weak trend referring to elevation, and (rare) indicating to few occurrences to model.

| Species | Stat us | Point s | % Points | Total Abunda nce | Indicato r Group (elevati on) | CCA score | Elevatio n trend GAM |
|---|------------|------------|-------------|------------------------|--|-------------------|----------------------------|
| <i>Columbina passerina</i> Common Ground-Dove | W | 29 | 88 | 54 | 1 (low) | 0.21905 6 | low |
| <i>Todus subulatus</i> Broad-billed Tody | HES | 28 | 85 | 42 | | - 0.03608 7 | high +/- Iow |
| Phaenicophilus palmarum Black- crowned Palm-Tanager | HEG | 27 | 82 | 38 | 3 (mid) | - 0.05684 6 | weak trend |
| Myiarchus stolidus Stolid Flycatcher | CE | 26 | 79 | 41 | | 0.18629 5 | low |
| <i>Coereba flaveola</i> Bananaquit | w | 23 | 70 | 43 | 1 (low) | 0.14501 1 | high +/- Iow |
| <i>Mimus polyglottos</i> Northern Mockingbird | W | 22 | 67 | 32 | 1 (low) | 0.54347 3 | low |
| <i>Vireo altiloquus</i> Black-whiskered Vireo | w | 19 | 58 | 25 | 4 (mid- high) | - 0.85393 4 | mid-high |
| Zenaida macroura Mourning Dove | W | 19 | 58 | 36 | 1 (low) | 0.64708 7 | low |
| <i>Mellisuga minima</i> Vervain Hummingbird | CE | 18 | 55 | 21 | | 0.08255 | weak trend |
| Anthracothorax dominicus Hispaniolan Mango | HES | 17 | 52 | 21 | | - 0.06154 3 | low |
| <i>Loxigilla violacea</i> Greater Antillean Bullfinch | CE | 16 | 48 | 22 | 4 (mid- high) | - 0.02521 3 | low |
| Zenaida asiatica White-winged Dove | W | 15 | 45 | 22 | 3 (mid) | 0.12849 9 | no trend |
| <i>Tiaris bicolor</i> Black-faced Grassquit | W | 13 | 39 | 25 | 4 (mid- high) | - 1.08881 | (rare) |

| Species | Stat us | Point s | % Points | Total Abunda nce | Indicato r Group (elevati on) | CCA score | Elevatio n trend GAM |
|---|------------|------------|-------------|------------------------|--|-------------------|----------------------------|
| | | | | | | 7 | |
| <i>Coccyzus minor</i> Mangrove Cuckoo | w | 12 | 36 | 14 | | - 0.20188 2 | high |
| Turdus plumbeus Red-legged Thrush | CE | 12 | 36 | 13 | 2 (all) | - 0.75312 1 | middle |
| Melanerpes striatus Hispaniolan Woodpecker | HES | 10 | 30 | 13 | | 0.45495 2 | low |
| Microligea palustris Green-tailed Warbler | HEG | 7 | 21 | 10 | 2 (all) | - 0.61683 | high |
| Tyrannus dominicensis Gray Kingbird | w | 5 | 15 | 7 | | 0.50236 8 | (rare) |
| <i>Coccyzus longirostris</i> Hispaniolan Lizard- Cuckoo | HES | 4 | 12 | 4 | | - 0.86734 9 | (rare) |
| <i>Crotophaga ani</i> Smooth-billed Ani | W | 4 | 12 | 4 | | 0.38561 6 | (rare) |
| Nesoctites micromegas Antillean Piculet | HEG | 4 | 12 | 6 | 4 (mid- high) | - 1.22937 4 | (rare) |
| <i>Vireo nanus</i> Flat-billed Vireo | HES | 3 | 9 | 3 | | - 1.30962 5 | (rare) |
| <i>Zenaida aurita</i> Zenaida Dove | CE | 3 | 9 | 3 | | - 0.47245 8 | (rare) |
| Chordeiles gundlachii Antillean Nighthawk | CE | 2 | 6 | 4 | | 1.19368 5 | (rare) |
| <i>Coccyzus americanus</i> Yellow-billed Cuckoo | w | 2 | 6 | 2 | | - 0.33330 3 | (rare) |
| <i>Contopus hispaniolensis</i> Hispaniolan Pewee | HES | 2 | 6 | 2 | 4 (mid- high) | - 1.30481 5 | (rare) |
| Tachornis phoenicobia Antillean Palm-Swift | CE | 2 | 6 | 2 | | 1.22047 1 | (rare) |
| <i>Geotrygon montana</i> Ruddy Quail-Dove | W | 1 | 3 | 2 | | 1.13847 4 | (rare) |
| Patagioenas inornata Plain Pigeon | CE | 1 | 3 | 1 | | - 1.27143 6 | (rare) |
| Patagioenas squamosa Scaly-naped Pigeon | CE | 1 | 3 | 1 | | 0.79835 2 | (rare) |