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Climate warming affects spatio-temporal biodiversity patterns of a highly vulnerable Neotropical avifauna

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Abstract
Global climate change (GCC) is one of the most critical threats to biodiversity. We assessed how it might disrupt the spatio-temporal diversity dimensions of avifauna associated with endangered Neotropical seasonally dry forests (NSDF). We used ecological niche modeling estimating the geographic distributions of 151 highly vulnerable bird species (including swifts, hummingbirds, woodpeckers, and parrots) under current and future climate projections (2050s and 2070s). Then, using traditional metrics of beta-diversity for Sorensen's index, we assessed how GCC could drive alterations in both alpha and beta taxonomic, phylogenetic, and functional (through birdsong frequencies and acoustic diversity) diversity for bird assemblages across the distribution of NSDF and within current protected areas. Likewise, we estimated the relationship between the expected changes in diversity dimensions with elevation, annual temperature, and precipitation seasonality across the NSDF distribution. Under GCC, we observed a general reduction for spatial taxonomic-richness of birds across the NSDF (−7.24 ± 6.69 spp. [2050s] and − 9.40 ± 7.58 spp. [2070s]), which also implies a general reduction for alpha phylogenetic and functional (except for the acoustic space) diversities by grid-cell. We also observed changes in the potential composition of communities (increasing, on average, the dissimilarity between sites) through space and time. Our results also suggest a biotic heterogenization for NSDF bird assemblages and that protected areas are not exempt from suffering such changes in biodiversity organization. Changes in spatio-temporal diversities were related to high temperatures and low rainfall across lowlands. Our results could inform new land-use planning and beta diversity conservation efforts in NSDF.

Keywords Alpha and beta diversities · Climate change · Diversity loss · Ecological communities · Functional diversity · Species range shifts

1 Introduction

Tropical forests have lost approximately half of their original extent and continuously face the impacts of both deforestation and global climate change (GCC). These environmental disturbances promote species loss and uneven changes in the composition of species assemblages and richness levels, and may affect the ecological integrity of ecosystems (Lovejoy and

Hannah 2019; Menéndez-Guerrero et al. 2019; Peters et al. 2019). These scenarios have renewed interest in identifying interactive effects of future GCC and land use in spatio-temporal biodiversity patterns, especially for heavily threatened ecosystems (Zwiener et al. 2018; Hidasi-Neto et al. 2019). Most of these issues remain poorly understood across geographic regions and ecosystems, especially for areas highly associated with agriculture and human settlements (Strassburg et al. 2017; Peters et al. 2019). Such is the case of the endangered Neotropical seasonally dry forests (NSDF), which have an extraordinarily high species richness and endemism (Ceballos 1995; Banda et al. 2016; Prieto-Torres et al. 2019a), but have already lost 65% of their original extent. In contrast, representation of these forests in protected areas (PA) is <10% of their current extent (Portillo-Quintero and Sánchez-Azofeifa 2010; Prieto-Torres et al. 2018).

Several studies investigating how GCC could affect ecological communities across dry and lowland biomes have suggested a general decrease in alpha diversity as the most likely consequence (Prieto-Torres et al. 2016, 2020; Hidasi-Neto et al. 2019; Menéndez-Guerrero et al. 2019). Because of rapid increases in temperature and variation in annual precipitation patterns, several NSDF species may be pushed to higher elevations tracking optimal conditions (Golicher et al. 2012; Prieto-Torres et al. 2016, 2020). Climate change, therefore, may produce modifications in distributions of habitat specialists and/or gradual replacements by widely distributed habitat generalist species (Prieto-Torres et al. 2016; Hidasi-Neto et al. 2019). This is relevant because the outcome of these range shifts of species may lead to biotic simplification (i.e., homogenization) and/or augmented dissimilarity between sites (i.e., biotic heterogenization) of ecological communities over space and time (Hidasi-Neto et al. 2019; Menéndez-Guerrero et al. 2019). Such changes in biodiversity organization (i.e., beta diversity) also involve the alteration of ecosystem functioning and services provided by them (Clavel et al. 2011). Despite the importance of this topic, few studies have measured spatio-temporal species turnover and its contribution to biotic homogenization and/or heterogenization consequences across different scales in the NSDF. Given the current land-use changes and increasing impacts of climate disturbances in tropical ecosystems (Lovejoy and Hannah 2019; Peters et al. 2019), measuring the different biodiversity levels adequately across different spatio-temporal scales has never been so urgent in Latin America (Pearson et al. 2019).

During the last decade, researchers have increasingly performed integrative studies to quantify biodiversity levels and patterns, and the relationships of phylogenetic and functional structure within ecological assemblages (e.g., Devictor et al. 2010; Corbelli et al. 2015; White et al. 2018; Hidasi-Neto et al. 2019; Menéndez-Guerrero et al. 2019). These metrics are important descriptors of ecosystem-level processes and of the effects of disturbances on ecosystem services or biodiversity (Petchey and Gaston 2002, 2006; Cadotte et al. 2011; Luck et al. 2013), and are fundamental to increase knowledge of biodiversity responses to climate warning and land-use changes. By incorporating phylogenetic data, we may describe evolutionary and ecological patterns of community assemblage (Emerson and Gillespie 2008). Besides, the assessment of functional diversity allows quantifying which organismal traits (e.g., morphological, physiological, behavioral, or phenotypical traits) influence responses to both biotic and abiotic environmental conditions (Luck et al. 2013; Weiss and Ray 2019). Recently developed methods from acoustic indices allow to rapidly assess species richness and abundance across regions, as well as the prediction of habitat quality and vegetation structure, alerting on shifts in biotic assemblages (Gómez et al. 2018; Bradfer-Lawrence et al. 2020). As these measures may be unrelated to each other (Mazel et al. 2018), the combined-use of taxonomic, phylogenetic, and functional diversity maps represent an essential step for the prioritization and future establishment of new conservation areas and efforts (White et al. 2018; Hidasi-Neto et al. 2019; Menéndez-Guerrero et al. 2019).

Here we analyzed the current and future ecological conditions for the distribution of 151 NSDF bird species specialized in either nesting (swifts, woodpeckers, and parrots) or for feeding (hummingbirds), which are considered highly vulnerable to future GCC (Foden et al. 2013; Walsh et al. 2019; Prieto-Torres et al. 2020). Specifically, we describe the spatio-temporal patterns of species and assemblages across Caribbean, Mesoamerican and northern South American NSDF for the present and for 2050–2070. We focused on bird assemblages as surrogates of biodiversity because their high importance in tropical ecosystems functioning (Sekercioglu 2006), ranging from shaping the structure of communities to key ecological processes (e.g., dispersion, pollination, and plant reproduction). Therefore, by assessing how future environmental conditions may promote changes in both alpha and beta diversities across these avifaunas, we can identify vulnerable areas to guide effective conservation policies and decision-making for the long-term protection of biodiversity (Kujala et al. 2013).

From this perspective, we sought to answer the following questions: (1) are bird species, and their phylogenetic and functional trait diversities, lost across the NSDF due to future GCC?; (2) what are the frequency and incidence of future regional extinctions and immigrations among threatened and non-threatened bird species?; (3) is GCC a homogenization and/or heterogenization driver for NSDF avifaunas at taxonomic, phylogenetic, and functional biodiversity levels?; and (4) what is the relationship between changes in both alpha and beta diversities with elevation, annual temperature, and precipitation seasonality across the NSDF distribution?

2 Methods

2.1 Study area

We defined NSDF as an ecosystem typically dominated (>50%) by deciduous trees, present in frost-free areas with a mean annual temperature > 25 °C and a total annual precipitation of 700–2000 mm, with at least three dry months (precipitation <100 mm) per year (Portillo-Quintero and Sánchez-Azofeifa 2010; Banda et al. 2016). These forests encompass a total of 42 ecoregions (Olson et al. 2001) distributed discontinuously from northwestern Mexico to northern Argentina and southwestern Brazil. We here included only forests distributed throughout the so-called “northern NSDF group” (Banda et al. 2016), which involve regions of the Caribbean islands, Western Mexico, the Yucatan Peninsula, Central America, the Caribbean coast of Colombia and Venezuela, and the northern Inter-Andean valleys in Colombia (Fig. S1). This decision was based on previous studies suggesting two NSDF major groups (northern and southern) across the Neotropics, separated by significant geographical and ecological barriers, such as the Chocó and Amazon rainforests, and the Andean Cordillera (Banda et al. 2016; Prieto-Torres et al. 2019a, 2019b).

2.2 Species list, occurrences, and climate data

We focused on 151 terrestrial resident bird species (Table S1), including swifts and hummingbirds (Apodiformes; $n = 93$), woodpeckers (Piciformes; $n = 32$), and parrots (Psittaciformes; $n = 26$) inhabiting the NSDF northern group (Stotz et al. 1996; Prieto-Torres et al. 2019a, 2019b). These species were chosen because of their dependence of forested habitats for nesting (e.g., swifts, woodpeckers and most parrots are obligated cavity nesters; Lammertink et al. 2019; Walsh et al. 2019); or for their feeding specialization (hummingbirds are highly specialized on nectar as a primary food item; Arizmendi and Ornelas 1990; Fonseca et al. 2015). According to Prieto-Torres et al. (2019b), these taxa are associated (ecologically and geographically) to NSDF, showing on average more than 42% of their ranges overlapping with these forests. Also, these species are highly vulnerable to both land use and climate change (Ríos-Muñoz and Navarro-Sigüenza 2009; Buermann et al. 2011; Foden et al. 2013; Walsh et al. 2019; Prieto-Torres et al. 2020).

We built a database of available records per species from different scientific collections and online collaborative public databases (Appendix S1). Details about verification and cleaning processes (i.e., identification of problematic or imprecise occurrences with incorrect climate values affecting model performance) have been published elsewhere (Prieto-Torres et al. 2020). To avoid issues when modeling species' distributions (Stockwell and Peterson 2002), we excluded from the dataset all those species with less than nine independent records. All families and species names followed the Birdlife World List v3 (Birdlife International 2010). For each species, we also recorded the threat status based on the IUCN (2015) categories.

Potential distributions were characterized for each species based on an ecological niche modeling approach (see below), using interpolated climate data (~5 km^2 cell size resolution) from WorldClim 1.4 (Hijmans et al. 2005). Variables for future climate projections for years 2050 and 2070 were based on the IPCC Fifth Assessment Report (IPCC 2014), from which we selected four general circulation models (ACCESS 1.0, CCSM4, MIROC5 and HadGEM2-ES), and two contrasting representative concentrations pathways (RCP4.5 and RCP8.5). In general, despite both scenarios assume an increasing human population, the RCP8.5 scenario represents higher than predicted greenhouse gas emissions with absence of climate-change mitigation policies in comparison to the RCP4.5 (Riahi et al. 2011; Stocker et al. 2013). Therefore, results based on the RCP 4.5 scenario may be interpreted as "optimistic," those under the RCP8.5 scenario, as "pessimistic."

2.3 Ecological niche models and future projections

Given its high performance and suitability for presence-only data (Elith et al. 2011), we modeled climatic suitability for species using MaxEnt 3.4.1 (Phillips et al. 2006). To reduce overfitting and collinearity of environmental layers, we selected a specific set of variables for each species based on uncorrelated ($r < 0.8$; by means of a Pearson's correlation coefficient) variables and a Variance Inflation Factor value <10. This was implemented using the "*corrplot*" (Wei and Simko 2017) and "*vegan*" (Oksanen et al. 2016) libraries for R (R-Core-Team 2019). We also created an area for model calibration (or "M"), which reflects historically accessible and restriction regions (including dispersal barriers) for each species (Soberón and Peterson 2005; Barve et al. 2011). These calibration areas were individually defined for each species using a geographic mask based on the intersection of occurrence data with the WWF Terrestrial Ecoregions (Olson et al. 2001) and the Neotropical Biogeographic Provinces (Morrone 2014).

All models were run with no extrapolation to avoid artificial projections caused by extreme values of ecological variables (Owens et al. 2013). All other MaxEnt's parameters were set to default (regularization multiplier = 1; maximum number of background points = 10,000; maximum interactions = 500; convergence threshold = 0.00001; adjust sample radius = 0, and default prevalence = 0.5). Then, we converted logistic values of suitability from each model into a presence-absence map by setting a decision threshold equal to the tenth percentile training presence (TPTP), which allowed us to reduce commission errors (Liu et al. 2013). Models for species with less than 15 records ($n = 4$), were developed using all presence data and assessed using a jackknife test (Pearson et al. 2007). For species with >15 records, the models were generated using a random sampling of 80% of the locality records for model training and the remaining 20% for model evaluation. In this case, statistical performance of models was evaluated using the Partial-ROC test (Peterson et al. 2008).

For future scenarios, geographic distribution estimates were obtained by overlaying the binary projections from the four global climate models, considering only sites in which at least three predictive models coincided for each species. We obtained consensus maps of the modeled forecasts for each bird species (two-time scenarios [2050 and 2070] × two RCP scenarios [optimistic and pessimistic]). Processing of ENMs was performed in ArcMap 10.2.2 (ESRI 2010) using the "*raster calculator*" toolbox.

For all species, projections of models to future climates were performed considering a scenario of contiguous dispersal ability. From this perspective, we assumed species' ability to disperse through continuous suitable habitats and new areas (where scenopoetic conditions allow positive intrinsic growth rates for species) but not the ability to jump over barriers defined by the "M" calibration area (see Peterson et al. 2002 and Prieto-Torres et al. 2020 for a detailed explanation). This procedure allowed us to assess the hypothesis that GCC could promote the extinction of specialist species and, at the same time, range expansions of generalists, leading to a reduction in species richness and taxonomic dissimilarity (i.e., biotic homogenization) for once disparate biotas (Zwiener et al. 2018; Hidasi-Neto et al. 2019).

2.4 Presence-absence matrices and climate change effects on species' ranges

For each climate scenario, we constructed a site × species presence-absence matrix (PAM) by overlaying the estimated distribution of each species on an equal-area grid of 0.25° × 0.25° spatial resolution. This process resulted in five PAMs of 2284 sites × 151 species. We assumed species presence only if individual models predicted at least 10% of areas within the grid (approximately 30 km^2). Based on this, we categorized species' distribution size as ranging from small (occupying up to 577 sites [lower quartile]), intermediate, and large (more than 1730 sites [upper quartile]).

2.5 Phylogenetic tree and functional traits

We obtained a total of 10,000 trees from a pseudo-posterior distribution of the updated version of the bird species-level phylogeny by Jetz et al. (2012) (http://birdtree.org/, revised March 2019), based on the backbone tree by Hackett et al. (2008). To account for uncertainties in phylogenetic reconstructions, we built a maximum clade credibility tree (MCCT) using TreeAnnotator (Drummond et al. 2012; Suchard et al. 2018).

Functional diversity was assessed from traits related to resource and habitat use (Weiss and Ray 2019). We selected the following traits: maximum mass, maximum body length, sensitivity level and IUCN category, NSDF-restricted level, center of relative abundance, percentage of the distribution within NSDF, and foraging strata (Wilman et al. 2014; Gómez-Ortiz and Moreno 2017; Burgio et al. 2019; Weiss and Ray 2019). Because of its many functions in bird biology, we selected six birdsong traits thought to be describers of differences in habitat use, given sound transmission properties (Morton 1975; Wiley and Richards 1982; Slabbekoorn et al. 2002; Burivalova et al. 2019). Changes in acoustic indices values may reflect changes in species assemblages and, therefore, are useful for monitoring biodiversity and habitats quality (Gómez et al. 2018; Bradfer-Lawrence et al. 2020). Details on general methods used to obtain data for ecological and birdsong traits are included in Table S2.

2.6 Alpha and beta diversity spatio-temporal analyses

Using the PAM for each climate scenario, we calculated spatial taxonomic alpha diversity by adding to each focal cell the number of its recorded species. Then, for each of these cells, we estimated the spatial phylogenetic alpha diversity based on the mean phylogenetic distance (MPD) (Webb et al. 2002; Sobral et al. 2016; Tucker et al. 2017). For those estimations, we used the distances from the MCCT constructed for the 151 species. Additionally, we determined the mean functional distance (MFD) among all pairs of species based on a functional dendrogram (representing the ecological traits distance, Hidasi-Neto et al. 2019) generated from a distance matrix using Gower's distance and the Unweighted Pair Group Method with Arithmetic Mean (UPGMA). We calculated the standardized effects sizes of MPD and MFD to represent the structure of bird assemblages. To do this, we compared the observed results for each cell and compared them with 999 assemblages generated randomly. Positive or negative values indicate that MPD or/and MFD are higher (over-dispersion) or lower (clustering) than expected by chance, respectively (see Gotelli and Entsminger 2001).

Spatial taxonomic beta diversity was calculated as the mean turnover partition of Sorensen's index (Baselga and Orme 2012; Baselga 2013) between a focal cell and its neighbors (up to 32 cells). We used this cell size given the general dispersal ability of species (Matthysen 2005; Kim et al. 2009), discarding a greater dispersal distance because most birds associated with northern NSDF have relatively small ranges (Prieto-Torres et al. 2020). For the spatial phylogenetic and functional beta diversity estimated, we used the same process as in the taxonomic beta but implementing the turnover partition of the PhyloSor index (Baselga and Orme 2012). Then, to calculate future beta diversities (i.e., temporal beta diversities), we used corresponding PAMs to calculate the Sorensen's index (for taxonomic) and PhyloSor (for phylogenetic and functional) indices between each cell from the present and its corresponding cell in the future, i.e., difference values between future and present for each cell (see Hidasi-Neto et al. 2019). All these analyses were performed using the "*betaGrid*" and "*tempbetagrid*" functions for R (available at: http://rfunctions.blogspot.com/), both developed ad hoc and kindly provided by José Hidasi-Neto (from Universidade Federal de Goiás, Brazil). All scripts and input databases used are available at https://github.com/davidprietorres/Spatiotemporal_diversity_NSDF.

We then generated maps for both spatio-temporal alpha and beta diversities for the present and future (2050 and 2070) scenarios, calculating the values of differences between them. For the latter two, we calculated the mean values between RCP scenarios and represented them in a single map for each year, given that future climate scenarios showed qualitatively similar results.

2.7 Acoustic space, spatial comparison, and summary metrics

We used one-way ANOVA to test whether conservation status (threatened *vs.* non-threatened) and the current distributional ranges for species lead to a greater vulnerability in range contraction under future climate scenarios (i.e., increasing regional extinctions of habitat-specialists and the potential immigrations for widespread distributed species).

For each climate scenario, we calculated the acoustic space for each NSDF region considering the bird species pools counted as potentially present within them. The acoustic spaces were calculated using six birdsong traits (Table S2) and a Gaussian kernel density method as implemented in the "*hypervolume*" library for R with the default Silverman bandwidth estimator (Blonder et al. 2014, 2018). We analyzed the fraction of acoustic space overlap among regions for each region using a Jaccard similarity index following Blonder et al. (2018), assessing their statistical differences with a Kruskal-Wallis test.

We assessed the spatial congruence among the taxonomic species richness patterns and both functional and phylogenetic metrics using Pearson correlations tests in the "*stats*" R-package. In addition, we used a two-way ANOVA test to assess the proportion of change observed for spatio-temporal beta diversities among the six NSDF regions and within the current PAs. This last step allowed us to provide a complementary biogeographic interpretation of GCC on species diversity and distributional patterns, evaluating also the role of current PAs in long-term protection of NSDF biodiversity in relation to likely changes in species' distributional ranges (Zwiener et al. 2018; Medina et al. 2020). Shapefiles of PAs were downloaded from the World Database of Protected Areas (UNEP-WCMC and IUCN 2019), using the same categories considered by Prieto-Torres et al. (2018, 2020) (Table S3).

Finally, we assessed the relationship between the proportion of changes in both species richness (i.e., species loss) and beta diversity using three environmental variables (elevation, annual temperature [Bio 01], and precipitation seasonality [Bio 15]) and the interaction between them via generalized linear mixed-effect models (GLMMs) in the "*lme4*" R library (Bates et al. 2014). These variables have been defined as the most significant for NSDF in previous studies (Werneck et al. 2011; Prieto-Torres and Rojas-Soto 2016). To do this, we determined per site, the average differences values observed for both species loss and beta diversities and the environmental variables (in the case of temperature and precipitation) between the current and future climatic scenarios. Elevation was determined from a digital elevation model Hydro 1 K (USGS 2001). We carried out all calculations for spatio-temporal diversity values were done used a 10′ spatial resolution matching the PAM grid cells.

3 Results

3.1 Species distribution models and current spatial diversity patterns

Final species' distribution models were statistically better than random expectations (Table S1), indicating that models recovered adequately the ecological niches of focal species. We observed that 75.5% of species showed small potential distributional ranges within the northern NSDF, while 24.5% of the taxa showed intermediate potential range sizes. According to the IUCN (Table S1), 15 species are classified as threatened (vulnerable, endangered, critically endangered), seven as near threatened, 128 as least concern, and one as data deficient.

Overall, current NSDF assemblages showed a mean alpha taxonomic diversity of 29.01 ± 14.05, an MPD of 98.61 ± 10.42, and MFD of 1.09 ± 0.01 (Fig. 1; Table 1), without statistically significant spatial congruence among them (*r* values 0.20 to −0.45; $P > 0.05$). The region with the highest numbers of species is Central America NSDF (39.76 ± 9.43 spp.), while the Caribbean islands have the lowest values (6.69 ± 2.11

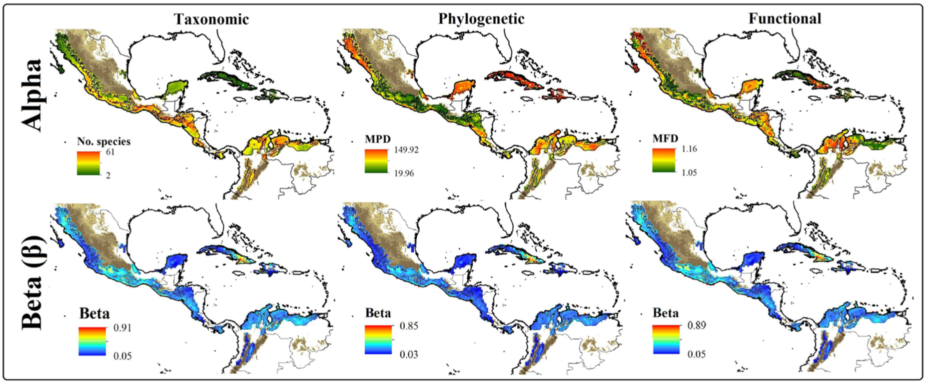

Fig. 1 Current spatial patterns for alpha and beta taxonomic, phylogenetic, and functional diversities for the 151 bird species associated to northern Neotropical seasonally dry forests

spp.). Contrarily, the NSDF region with both the highest MPD (113.07 ± 10.25) and MFD (1.090 ± 0.009) alpha values were the Caribbean islands (Table 1). The NSDF with the lowest alpha values for MPD (93.20 ± 7.99) and MFD (1.085 ± 0.006) were distributed throughout Central America and the Yucatan Peninsula, respectively. For the acoustic space analyses, all pairwise comparisons among regions resulted in highly similar acoustic spaces (Jaccard I values >0.963), showing no statistically significant differences among them (Kruskal-Wallis, $df = 5$, $P = 0.416$).

Additionally, current bird assemblages showed mean values of 0.21, 0.13, and 0.20 for the spatial taxonomic, phylogenetic, and functional beta diversity, respectively (Table 2; Fig. 1). We observed a positive correlation among these three beta diversity values (r-values ≥0.94; $P < 0.01$). The ANOVA tests showed statistically significant differences among the six NSDF regions for taxonomic ($F = 44.21$, $P < 0.01$), phylogenetic ($F = 41.79$, $P < 0.01$), and functional beta diversity ($F = 81.61$, $P < 0.01$; see Table 2). On average, the NSDF in the Yucatan Peninsula and the northern Inter-Andean valleys in Colombia were the regions with the highest similarity values for the three beta diversities indexes (Table 2).

3.2 Climate change effects on spatio-temporal diversity patterns

Model projections to the 2050 and 2070 climate scenarios showed that distribution of these taxa and their assemblages could be modified significantly in the future across the NSDF (Figs. 2 and S2). We observed that over ~85% species are predicted to see reductions in their distributional ranges (on average ~ 33%) in the future. GCC could produce potential local extirpations and/or extinctions (i.e., retraction values >95% for the potential distribution areas) for at least four species throughout the NSDF. Only ~11% of the species showed an increase (on average by ~17%) in their potential distributional areas. Species showed no statistically significant differences among them for the predicted range contraction considering their conservation status (threatened = 35.7 ± 43.9%; non-threatened = 29.0 ± 24.7%; $F = 0.90$, $P \geq 0.05$) and/or their current size of ranges (small range = 31.6 ± 29.3%; intermediate range = 24.9 ± 20.8%; $F = 1.90$, $P \geq 0.05$).

Overall, we noted decrease (−7.24 ± 6.69 spp. [2050s] and − 9.40 ± 7.58 spp. [2070s]) in the taxonomic alpha diversity in the future (Table 1; Figs. 2, S2). Only 5.99% and 5.17% of NSDF grid-cells showed increase of species richness (on average + 3.00 spp.) for the 2050 and

Table 1 Mean and standard deviation values obtained for the spatial-temporal alpha biodiversity patterns of 151 bird species associated to Neotropical seasonally dry forests (NSDF) under current and future climatic conditions

Scenario	Overall values	CIs	NMex	YP	CAm	CCV	NIAvC	Protected areas
Present								
Taxonomic	29.01 ± 14.05	6.69±2.11	26.57±11.97	19.65±4.02	39.76±9.43	35.25±10.91	35.25±4.85	31.81±14.75
Phylogenetic	98.61±10.42	113.07±10.25	95.21±9.76	103.37±9.23	93.20±7.99	100.09±6.55	97.08±3.25	97.97±10.51
Functional	1.09±0.01	1.090±0.009	1.087±0.008	1.085±0.006	1.086±0.005	1.088±0.008	1.089±0.003	1.088±0.007
Acoustic spaces	26.91±0.17	27.04	27.09	26.85	26.97	26.91	26.63	
2050								
Taxonomic	21.76±14.91	4.02±2.89	20.15±11.67	12.11±4.20	33.00±11.65	23.33±16.83	37.77±6.98	25.67±16.42
Phylogenetic	96.45±17.43	84.65±27.16	94.33±15.67	107.19±15.57	97.41±7.84	101.01±18.11	97.72±3.49	97.43±14.38
Functional	1.07±0.15	1.010±0.258	1.073±0.131	1.061±0.148	1.085±0.005	1.064±0.169	1.088±0.003	1.078±0.091
Acoustic spaces	27.83±0.49	28.37	27.85	27.39	27.50	27.89	27.98	
2070								
Taxonomic	19.61±14.94	3.48±3.06	18.40±11.72	9.64±3.95	30.48±12.37	19.91±17.08	37.22±8.20	23.54±16.56
Phylogenetic	93.13±22.98	69.63±34.41	92.36±19.25	109.56±16.36	99.09±8.06	94.74±25.00	98.49±3.64	95.48±19.56
Functional	1.03±0.21	0.836±0.341	1.049±0.181	1.061±0.149	1.087±0.005	1.023±0.230	1.089±0.005	1.048±0.156
Acoustic spaces	27.87±0.28	28.12	27.60	27.69	27.65	28.11	28.07	

Values are shown for the general and local scales, considering the six main regions herein analyzed (*CIs* Caribbean islands, *NMex* northwestern Mexico, *YP* Yucatan Peninsula, *CAm* Central America, *CCV* Caribbean coast of Colombia-Venezuela, *NIAvC* northern Inter-Andean valleys in Colombia) and current protected areas

Table 2 Mean and standard deviation values obtained for the spatial-temporal beta biodiversity patterns of 151 bird species associated to Neotropical seasonally dry forests (NSDF) under current and future climatic conditions

Scenario	Overall values	CIs*	NMex	YP	CAm	CCV	NIAvC	Protected areas
Present								
Taxonomic	0.21±0.10	0.24±0.15	0.23±0.08	0.14±0.10	0.20±0.07	0.23±0.08	0.13±0.04	0.21±0.10
Phylogenetic	0.13±0.08	0.18±0.13	0.14±0.06	0.09±0.09	0.11±0.05	0.15±0.07	0.08±0.03	0.13±0.09
Functional	0.20±0.09	0.24±0.15	0.21±0.08	0.14±0.10	0.18±0.07	0.20±0.08	0.12±0.04	0.19±0.10
2050								
Taxonomic	0.31±0.15	0.23±0.18	0.32±0.14	0.23±0.12	0.27±0.08	0.40±0.15	0.17±0.07	0.30±0.13
Phylogenetic	0.20±0.13	0.20±0.16	0.19±0.12	0.14±0.12	0.15±0.05	0.29±0.13	0.11±0.04	0.19±0.10
Functional	0.29±0.15	0.22±0.15	0.30±0.13	0.22±0.12	0.26±0.08	0.33±0.15	0.16±0.07	0.28±0.13
2070								
Taxonomic	0.34±0.16	0.24±0.17	0.35±0.16	0.26±0.12	0.30±0.08	0.44±0.15	0.20±0.10	0.33±0.14
Phylogenetic	0.23±0.15	0.21±0.16	0.23±0.15	0.15±0.13	0.17±0.06	0.34±0.15	0.12±0.07	0.22±0.13
Functional	0.33±0.16	0.23±0.16	0.34±0.16	0.25±0.12	0.28±0.08	0.43±0.15	0.19±0.10	0.31±0.14

(*) Only CIs region showed values not significantly different over time within NSDF compared present and future climate scenarios

Values are shown for the general and local scales, considering the six main regions herein analyzed (*CIs* Caribbean islands, *NMex* northwestern Mexico, *YP* Yucatan Peninsula, *CAm* Central America, *CCV* Caribbean coast of Colombia-Venezuela, *NIAvC* northern Inter-Andean valleys in Colombia) and the presently protected areas. ANOVA tests showed differences statistically significant among the six NSDF regions for the spatio-temporal beta taxonomic, phylogenetic, and functional diversity values

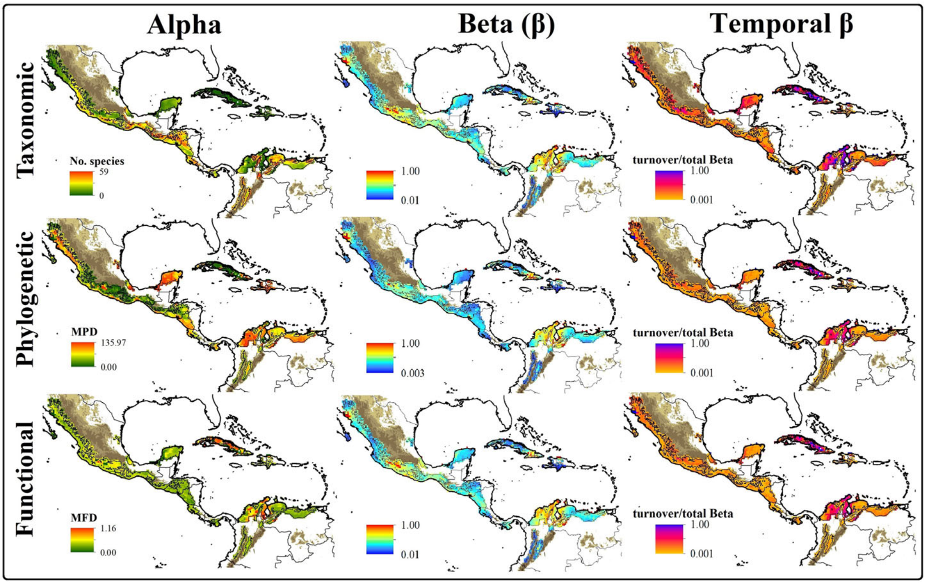

Fig. 2 Spatio-temporal patterns for the alpha and beta taxonomic, phylogenetic and functional diversities of avifauna ($n = 151$) from the northern Neotropical seasonally dry forests projected to future global climate scenarios for year 2050. Detailed results for the spatio-temporal patterns for the alpha and beta diversities of avifauna for year 2070 are available in the Fig. S2 (Supporting information)

2070 scenarios, respectively. We observed a direct relationship between changes of alpha diversities and assemblage compositions through time, with a clear tendency to increase the dissimilarity values in the future led by increasing nestedness in assemblage composition (Figs. 2, S2). Besides, an important decrease for both MPD (mean − 2.15 ± 18.50 [2050s] and − 5.47 ± 25.41 [2070s]) and MFD (mean − 0.021 ± 0.150 [2050s] and − 0.058 ± 0.209 [2070s]) values was also observed. It is important to note that ~62% and ~ 58% of grid-cells showed, on average, an increase in the phylogenetic (5.41 ± 6.19 [2050s] and 6.46 ± 6.74 [2070s]) and/or functional (mean of 0.013 ± 0.016 [2050s] and 0.013 ± 0.017 [2070s]) alpha diversity, respectively. We also observed that the diversity of acoustic spaces for each NSDF regions will persist without statistically significant differences across time, despite being lower or higher than at present (Table 1). All values in Jaccard index ranged between 0.960 and 0.977, and size changes (increase or reduction) in the acoustic space were not significant ($P > 0.05$ for all regions) for 2050s and 2070s.

Our beta diversity analyses predicted an increase (indicating biotic heterogenization) in spatial diversity across bird assemblages (Table 2). Results showed on average a positive proportion of change for the taxonomic (0.09 ± 0.12 [2050s] and 0.13 ± 0.14 [2070s]), phylogenetic (0.07 ± 0.11 [2050s], and 0.10 ± 0.14 [2070s]), and functional (0.09 ± 0.13 [2050s] and 0.13 ± 0.14 [2070s]) beta diversities in the future. Spatial positive correlation values ($R > 0.99$; $P < 0.001$) were recorded only between phylogenetic and functional diversities. In addition, we observed that ~11% sites may decrease (indicating biotic homogenization) their values for beta taxonomic (−0.08 ± 0.10 [2050s] and − 0.10 ± 0.11 [2070s]), but decrease of phylogenetic (−0.07 ± 0.10 [2050s] and − 0.09 ± 0.11 [2070s]) and functional (−0.09 ± 0.10 [2050s] and − 0.10 ± 0.10 [2070s]) diversities occurs in a different ~10% of NSDF grids.

3.3 Diversity patterns within NSDF regions and PAs

The alpha and beta diversities obtained from projections to future climate scenarios were highly variable for the six NSDF regions. However, we observed a clear tendency toward decreased richness patterns for the three dimensions by site (Figs. 2, S2), with statistically significant differences ($P < 0.001$) among five regions (except for the Caribbean Islands; Table 2) across time for the three taxonomic (region: $F = 52.01$; scenario: $F = 538.66$), phylogenetic (region: $F = 46.15$; scenario: $F = 1600.10$), and functional (region: $F = 26.58$; scenario: $F = 903.14$) beta diversity.

PAs also showed assemblages reorganization (tending to increase dissimilarity between sites) as a consequence of future GCC (Tables 1, 2). Currently, PAs showed on average alpha values of 31.81 ± 14.75 taxonomic species, 97.97 ± 10.51 MPD, and 1.088 ± 0.007 MFD. However, we observed that PAs could present a generalized decrement (mean − 6.14 ± 6.22 spp. [2050s] and − 8.27 ± 7.33 spp. [2070s]) in the potential number of species by cells in the future, as well as a decrease for both phylogenetic (mean − 0.54 ± 16.75 [2050s] and − 2.49 ± 22.75 [2070s] MPD) and functional (mean − 0.009 ± 0.092 [2050s] and − 0.039 ± 0.157 [2070s] MFD) diversity values. Likewise, bird assemblages within PAs in the future could show an increase in the spatial dissimilarity values among sites for the taxonomic (mean increase of 0.09 ± 0.12 [2050s] and 0.12 ± 0.14 [2070s]), phylogenetic (0.06 ± 0.11 [2050s] and 0.20 ± 0.14 [2070s]), and functional (0.001 ± 0.109 [2050s] and 0.138 ± 0.139 [2070s]) beta diversity.

3.4 Relationship between beta diversity changes and environmental variables

The GLMMs (Fig. 3) showed that potential changes in beta diversities tend to be higher (increasing the species loss and dissimilarity for diversity dimensions) and statistically significant ($P < 0.001$) across lowlands, as well as in those sites where temperatures will be warmer (mean = +2.1 °C [2050s] and + 2.8 °C [2070s]) and with a more intense precipitation seasonality (mean = +0.50 [2050s] and + 1.17 [2070s]). In sites with species loss and biotic heterogenization, we observed that environmental variables will show, on average, values of 26.0 °C (Bio 01) and 78.80 (Bio 15) in the future. Contrarily, sites where species loss and beta spatial diversities suggested a potential biotic homogenization process showed mean values of 24.9 °C (Bio 01) and 72.93 (Bio 15).

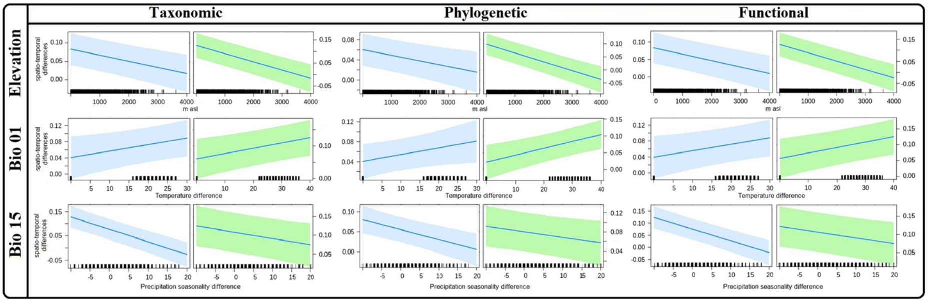

Fig. 3 Generalized linear models (GLM) and the relationship between proportional changes observed for future scenarios (2050 [blue] and 2070 [light-green] years) in beta taxonomic, phylogenetic, and functional diversities with the three environmental variables: elevation, annual mean temperature, and precipitation seasonality

4 Discussion

The potential effects of GCC on spatio-temporal diversity patterns in highly-vulnerable and ecologically specialized Neotropical bird groups detected herein provide a first guide to translate such environmental modifications and species' range shifts into changes in three alpha and beta dimensions. Overall, our results support that environmental heterogeneity (e.g., variation in elevation and temperature/precipitation seasonality) may be significant indicators driving variation in different biodiversity patterns at regional scales (Golicher et al. 2012; Menéndez-Guerrero et al. 2019; Rodríguez et al. 2019). We found that progressive increases in temperature and a higher annual variation of precipitation might promote a reassortment of bird assemblages (with uneven richness patterns) across NSDF. Even considering a favorable dispersal scenario, both the individual taxa ranges and species richness patterns were modified significantly, including increased extinction risk and range shifts to higher elevations. These results are congruent with shifts expected for several biological groups, including mammals, birds, amphibians, and trees in dry biomes (Golicher et al. 2012; Prieto-Torres et al. 2016, 2020; Hidasi-Neto et al. 2019; Menéndez-Guerrero et al. 2019; Walsh et al. 2019; Medina et al. 2020). Therefore, climate warming must be considered a major threat to NSDF diversity, especially considering that climate-induced range contractions for species were equally significant for taxa considered threatened, data deficient, and least concern (Prieto-Torres et al. 2020).

Species' range shifts observed herein may also promote a generalized reduction of the alpha phylogenetic (i.e., loss of phylogenetic clades) and functional (ecological traits) diversities within the landscape across the taxonomic diversity. From this perspective, climate warming may lead to the potential conformation of novel biotic communities in the future (at least at local scales). However, the spatio-temporal variation obtained for the three diversity dimensions supports that these may differ substantially between species assemblages even with the same species richness values (Petchey and Gaston 2006). Likewise, the high proportion of grid-cells with increases in MPD and MFD values suggests that, for most sites, species persisting in future scenarios have similar phylogenetic and functional information to those locally extinct. Therefore, even after removing these phylogenetically or functionally redundant species within assemblages, alpha diversities tended to be high in the future. More studies are needed on these ideas.

Persisting functional diversity in future scenarios also explains why the acoustic space for assemblages were not affected even when dissimilarity among NSDF regions may increase in the future, i.e., new species that may join novel species assemblages may have similar functional (acoustic spaces) traits to those that may disappear from the same area (Sinsch et al. 2012; Bignotte-Giró et al. 2019). However, it is important to note that our dataset for birdsong frequencies and acoustic diversity may be limited due to a degree of pseudo-replication because not all birdsongs were recorded at the same time. Spatio-temporal factors such as weather conditions and local disturbances, such as maturation and aging of trees and anthropogenic noise, could impact our results on the acoustic space similarity in all NSDF regions (Bignotte-Giró et al. 2019; Burivalova et al. 2019). Therefore, the assumption that acoustic spaces among communities may not reflect true changes in beta functional diversity should be tested in future research, along with additional measures of soundscape beta diversity. Despite soundscape research is still at early stages, we know that environmental variables play an important role for many sound-dependent species (Farina 2018). Thus, its study has a large potential for conservation and natural resource management (see Burivalova et al. 2019).

Despite the decrease of average alpha diversities through time for these bird assemblages, we also observed that beta diversities in the future may increase the dissimilarity among sites and regions (see Menéndez-Guerrero et al. 2019; Medina et al. 2020; Prieto-Torres et al. 2020). Based on results for the habitat-dependent bird groups selected in this study, GCC is likely a biotic heterogenization driver influencing the three diversity values for the NSDF avifauna further highlighting the taxonomic uniqueness and conservation relevance of each NSDF region (Prieto-Torres et al. 2018, 2019a, 2019b, 2020). Other studies projecting future climate-induced changes in species' ranges have also identified lowlands as prone to high species losses, and with only few species gains (Hidasi-Neto et al. 2019; Menéndez-Guerrero et al. 2019; Medina et al. 2020). Overall, this pattern is explained mainly by local extinctions and/or reduction of most range sizes for most species, resulting in assemblages dominated by a greater proportion of specialists (Olden and Poff 2003; Hidasi-Neto et al. 2019).

Nevertheless, the northern NSDF avifauna shows a dominance pattern of small range sizes (Prieto-Torres et al. 2020); hence, it is important to highlight that this increase in local species extinction and subsequent biotic differentiation observed may promote in the medium- to long-term a biotic homogenization process. This was observed across 11% of NSDF sites, particularly in the Caribbean Islands (Tables 1 and 2). Therefore, species range contractions will increase the likelihood of complete extinction, both locally and regionally (Olden and Poff 2003). Likewise, the species turnover pattern in the avifauna under future climates will be led by invasion of widely distributed species likely adapted to the conditions in the regions (herein observed for ~11% of the studied species) in synergy with local extinction of narrowly distributed species (Zwiener et al. 2018; Hidasi-Neto et al. 2019).

From this perspective, GCC might be a driver of spatio-temporal not uniform biodiversity changes, implying both biotic homogenization and heterogenization in the Neotropical region (Menéndez-Guerrero et al. 2019). Therefore, different historical, environmental, and ecological processes may be structuring the NSDF bird assemblages. Thus, despite species sharing among different regions, there is differentiation with high endemism, supporting the unique composition of NSDF avifauna as a result of independent evolutionary histories (Prieto-Torres et al. 2019a, 2019b), as well as of ecological conditions (including complex biotic transition zones or ecotones) and the altitudinal gradient involved across the forests distribution (García-Trejo and Navarro-Sigüenza 2004; Ríos-Muñoz and Navarro-Sigüenza 2012).

Shifts in regional alpha and beta diversities, which may have significant consequences for ecosystem functioning (Lovejoy and Hannah 2019), indicate the importance of considering landscape-level variation in biodiversity responses to global change drivers. However, an important limitation in our study is that we considered only climate effects on the potential distributions of species. Because habitat fragmentation and degradation are considered to be the principal causes of current biodiversity declines across NSDF (Portillo-Quintero and Sánchez-Azofeifa 2010; Prieto-Torres et al. 2016), future research must be directed to combining both human and climate impacts on biodiversity. Previous studies in tropical plant community assemblies suggest that several species may not persist in human-modified landscapes in the absence of large forest fragments (Krishnadas et al. 2019). Synergistic effects of both GCC and habitat loss may intensify the extinction risk and range shifts for the avifauna, due to most focal species not generalists (Stotz et al. 1996). Therefore, incorporation of the human dimension will provide a better understanding about how habitat conversion may driver biotic homogenization changing ecological communities for this highly vulnerable avifauna (Vázquez-Reyes et al. 2017).

Considering that it is very difficult to predict how species will respond to GCC patterns and habitat changes, more studies assessing the adaptive potential of the species to respond to rapid environmental change (i.e., shifting bioclimatic niches to different elevations or the presence of novel climates) are needed as alternative hypotheses to species niche conservatism (Ortega et al. 2019; Peterson et al. 2018). As niche constraints (e.g., forest composition, structure) associated with birds respond to GCC, the use of only climate variables may be a limited approach to study species responses in comparison to measures of ecosystem dynamics, such as forest net primary productivity (Tingley et al. 2009; Walsh et al. 2019). In this sense, areas predicted to be climatically unsuitable but predicted to maintain habitat or resource persistence may still be suitable habitat for birds, especially for those ecologically-specialized groups. Therefore, accounting for ecosystem processes underlying vegetation dynamics is also important to understand the complex interactions between climate, habitat changes, edge effects, and anthropogenic influences in future species population dynamics (Krishnadas et al. 2019; Walsh et al. 2019).

4.1 Conservation implications

Here we show that NSDF future bird assemblages appear to be on the path to become increasingly heterogeneous. Although the projected increase in beta diversity for these lowland assemblages might appear to be as a “positive” outcome (based on a higher dissimilarity taxonomic), this outcome is largely driven by distributional range contraction and local extinction of generalist species, as well as to species’ tracking of GCC by moving upwards in elevation. These results are important because supports the idea that new and future efforts to maximize the performance of the current PA network have to be differently planned for specific regions, depending on how the species pool size and its composition are expected to change through time (Prieto-Torres et al. 2016). For instance, conservation is particularly urgent in the Caribbean Islands and the Yucatán Peninsula, where there is a low taxonomic diversity but the highest phylogenetic and functional diversities (Figs. 1 and 2). Failure to protect them would result in major losses of a unique avian diversity as sites are predicted to be homogeneous in the near future (see Tables 1 and 2 and Prieto-Torres et al. 2020). Unfortunately, these two regions lagged significantly behind the Aichi Target representativeness element (Prieto-Torres et al. 2018). Thus, information about spatio-temporal changes in biodiversity dimensions represent the background that should be integrated into guiding effective conservation decision-making for long-term protection (Carvalho et al. 2010). This last could represent a less costly strategy (in area and resources) than using a two-step process (i.e., representation of current ranges and afterwards addressing the consequences of GCC).

We hope that our study will trigger the interest of biologists and conservationists motivating them to delve more deeply into analysis of species diversity by incorporating both the functional and the phylogenetic dimensions of diversity for tropical forests. This integrative approach could inform new land-use planning and identification of priority areas complementing the current PAs network in NSDF, which could allow avoiding species lost or composition changes, clades, and species ecological traits in communities.

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