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Taxonomic, Phylogenetic and Functional Diversity of Bird Assemblages in Urban Green Spaces: Null Model Analyses, Temporal Variation and Ecological Drivers

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Urban expansion is a pervasive driver of biodiversity loss. To understand the effects of urbanization on diversity, we investigated the response of bird taxonomic, phylogenetic, and functional diversity to urban green spaces' characteristics in thirty-one green spaces of Mexico City. Selected sites encompassed variation of environmental factors along a transformation gradient, from natural protected areas to landscaped parks. Bird observations were conducted during winter (non-breeding season), spring (dry breeding season), and summer (wet breeding season). We used multi-model inference to assess the relationship of green space area, shape, isolation, tree richness, habitat diversity, and vegetation cover with species richness, Faith's phylogenetic diversity, and functional richness. We calculated standardized effect sizes from null models to assess phylogenetic and functional structure. We registered 91 species belonging to 28 families across all sites and seasons. The number of detected species was largest in winter and decreased toward the dry breeding season, and then toward the wet breeding season. We found a moderate to strong positive relationship of species richness with phylogenetic diversity and functional richness. Overall, phylogenetic and functional structure of bird communities in green spaces was neither clustered nor over-dispersed. However, few cases of functional clustering, phylogenetic clustering, or both were observed, and they corresponded to natural protected areas. Results showed a predominant role of green space area in determining community diversity and phylogenetic structure while it did not influence functional structure. Contrary to our predictions, habitat diversity had a negative effect on species richness and phylogenetic diversity and this effect was detected only during the wet breeding season, whereas

isolation showed a positive relationship with phylogenetic and functional structure, during the wet breeding season and winter, respectively. This study emphasizes the use of complementary measures of diversity together with the comparison between observed and expected values to get a better insight into the mechanisms by which green spaces' characteristics affect bird diversity across the seasons.

INTRODUCTION

Habitat degradation and habitat loss resulting from human activity are among the dominant drivers of the current mass extinction of fauna, the so-called Anthropocene defaunation (Dirzo et al., 2014; Young et al., 2016). Considered a pervasive and long-lasting transformation, urban growth contributes to the loss of natural habitats (Liu et al., 2016) and leads to declines in local species richness and abundance (Newbold et al., 2015). Given the global expansion of urban areas (Seto et al., 2011), we require a better understanding of those factors that support biodiversity in these areas in order to reconcile urban development and biodiversity conservation.

Green spaces are a key element for biodiversity conservation in cities since they represent available habitat for a wide range of organisms (Cornelis and Hermy, 2004; MacGregor-Fors et al., 2016) and much of the research on diversity in urban green spaces has focused on birds (Magle et al., 2012; Beninde et al., 2015). Studies have mainly reported reductions in both the number of species and diversity indices together with compositional changes (Carvajal-Castro et al., 2019; Di Pietro et al., 2020 but see Benitez et al., 2021). Although species richness has been a widely-used measure of biodiversity to assess the effect of urbanization on bird communities (Rush et al., 2014; Canedoli et al., 2017; Matthies et al., 2017) the assumption of species being equivalent may not be ecologically precise (Chave, 2004). In addition, in recent years, the multidimensional nature of biodiversity (Naeem et al., 2016) has been acknowledged in urban bird research and studies have increasingly included measures of functional, genetic, and phylogenetic diversity (Filippi-Codaccioni et al., 2009; Delaney et al., 2010; Morelli et al., 2016; Schmidt et al., 2020).

Here, we use taxonomic, phylogenetic, and functional measures of diversity to get a more complete insight into the response of bird communities to urban habitats. Functional diversity can be defined as the diversity of functional traits of those species found in an assemblage (Mason and Mouillot, 2013). A functional trait is any phenotypic characteristic that can influence ecosystem processes or the species' response to the environmental conditions (Hooper et al., 2005). Phylogenetic diversity represents an alternative to quantify the biological attributes in an assemblage (Faith, 1992) and it differs from functional diversity in the fact that it comprises observed and unobserved characters (Faith, 2002). To do so, the diversity of features is estimated from the phylogenetic relationships among the species under the assumption that estimated amounts of divergence, measured as the branching pattern and branch lengths in a cladogram, can be used to derive feature diversity (Faith, 1994).

Besides its inherent value, functional and phylogenetic diversity hold conceptual relevance for community ecology since functional and phylogenetic clustering patterns can provide insights into community assembly mechanisms such as the environmental filtering of species from the regional species pool (Weiher, 2011). So far, there is evidence that suggests that urban areas may be acting as filters for some lineages and functional traits (Sol et al., 2017; Leveau, 2021). To test this, departure from randomness is assessed through the comparison of observed values against random expectations obtained from null models that take into account differences in species richness (Swenson, 2014; for an example see Weideman et al., 2020).

Previous works conducted in human-modified areas have shown that environmental effects on biological diversity can be dimension specific (Cisneros et al., 2015). As an example, bird species richness, functional richness and evolutionary distinctiveness responded to different attributes of Beijing's urban parks (Morelli et al., 2017). While species richness showed a positive relationship with water cover, functional richness decreased with shrub cover, and evolutionary distinctiveness increased with deciduous tree cover. Furthermore, bird diversity dimensions can vary among seasons in urban areas (Alexander et al., 2019; Ibáñez-Álamo et al., 2020). Therefore, to achieve an effective urban bird conservation, it is necessary to employ a multidimensional approach with a temporal perspective for its diversity assessment (Devictor et al., 2010).

A wide range of factors can influence bird diversity in urban green spaces (Yang et al., 2015; Morelli et al., 2018b; Liu et al., 2019). While there is strong support for the main role of some factors such as area, habitat diversity, and plant species richness, evidence is still inconclusive about the effects of others such as shape and isolation of green spaces (Nielsen et al., 2014; La Sorte et al., 2020). In this context, we aimed to examine the taxonomic, phylogenetic, and functional bird diversity and their relationship with green spaces' characteristics. Additionally, we explored the influence of these characteristics on phylogenetic and functional clustering.

Based on the abovementioned information and previous works (Ibáñez-Álamo et al., 2020), our first hypothesis concerning seasonal variation would be that studied bird diversity dimensions and their relationship with environmental factors would differ among seasons. We also expected to detect

a departure from randomness of phylogenetic and functional diversity observed values under the assumption that urbanization acts as an ecological filter. More specifically, we hypothesized that bird assemblages in the most heavily transformed sites would show a clustered phylogenetic and functional pattern considering that some lineages and traits could be favored by urban areas (Sol et al., 2014; Evans et al., 2018). A third hypothesis was that bird diversity, measured in any of its dimensions, would increase as green space area and habitat heterogeneity increased based on existing information (Matthies et al., 2017; Yang et al., 2020; Benitez et al., 2021).

MATERIALS AND METHODS

Study Site

We conducted this study in Mexico City which forms part of the Metropolitan Area of the Valley of Mexico. Mexico City has an approximate area of 1,499 km^2 and an estimated population of 9,209,944 inhabitants (INEGI (Instituto Nacional de Estadística y Geografía), 2021) and despite its high urbanization degree, near one third of its extent is covered by natural vegetation (471 km^2) (INEGI (Instituto Nacional de Estadística y Geografía), 2016). The climate of Mexico City varies geographically, being temperate toward the northeastern part of the city and cool toward the southwestern part. Hence, mean annual temperate ranges between 8 and 10°C in the southwestern region and can be over 16°C in the northeastern part (Hernández-Cerda et al., 2016). The average annual rainfall is 1,200 mm in the wettest areas and 600 mm in the driest areas. The dry season occurs from October to May and the rainy season from June to September (INEGI (Instituto Nacional de Estadística y Geografía), 2017).

We surveyed 31 green spaces distributed from near downtown to the southwestern urban fringe (**Figure 1**). Site selection was intended to encompass variation of environmental factors along a transformation gradient. As a result, surveyed green spaces included recreational parks, an arboretum, a university campus, and natural protected areas. At one extreme, in heavily modified green spaces, vegetation was dominated by the broadleaf trees *Fraxinus uhdei* ("ash," native species) and *Jacaranda mimosifolia* ("blue jacaranda," exotic species) and the coniferous tree *Cupressus lusitanica* ("cypress," native species). In these sites, artificial structures were abundant and natural ground covers were substituted by concrete to differing extents. At the other extreme, in the most natural sites, dominant plant species were conifers that belonged to the genus *Pinus* ("pine," native species) and *Abies* ("fir," native species) and artificial structures such as electric poles or wires were scarce or absent.

Bird Surveys

Birds were counted by a single observer (RND) in three different periods of 2018 which corresponded to: (1) the wintering season (from January 3rd to January 22nd), (2) the dry part of the breeding season (from May 1st to May 27th) and the rainy part of the breeding season (from August 1st to September 4th). Hereafter, we will refer to these periods as winter, dry breeding, and wet breeding seasons. The distinction between dry and wet seasons is relevant since fluctuations in food availability and

temperature can affect bird distribution across the studied green spaces (Zuckerberg et al., 2011; Sainz-Borgo, 2016). Data on bird richness and abundance were collected within four hours after sunrise and by using standardized 5-min point counts with a fixed radius of 25 m. Points were separated by at least 200 m to avoid double-counting of individual birds (Bibby et al., 1993). All points were visited twice each season, on different days in a random order. Point counts were used to obtain a reliable species' relative abundance estimate (Bibby et al., 1993) and for each point count and each species, the highest number of individuals recorded in any of the two visits was used as the abundance estimate. The number of points located in each green space ranged from one to nine based on green space size and accessibility. In total, we sampled 107 points distributed in thirty-one green spaces. We recorded all birds detected visually or acoustically, except those that were flying over.
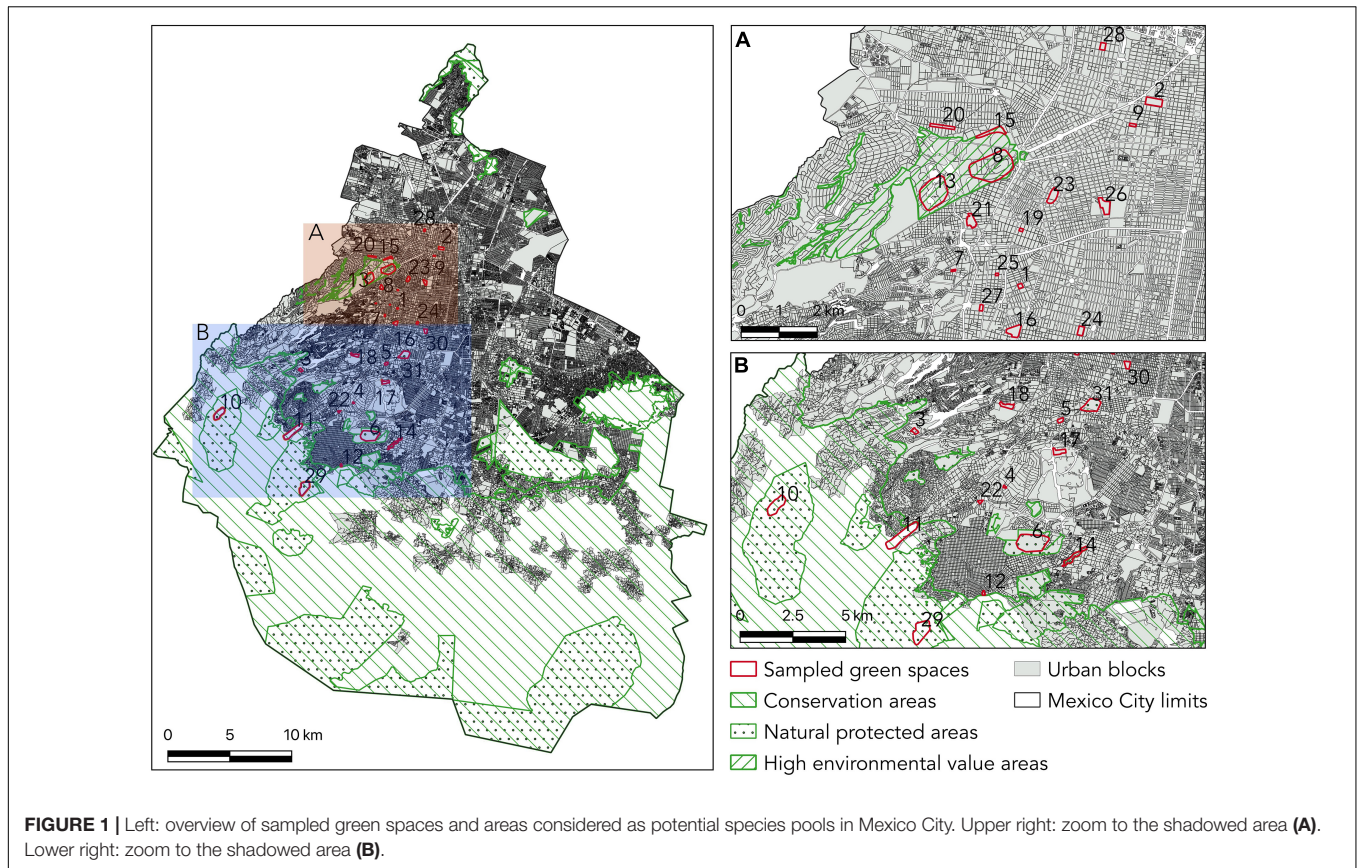
Predictor Variables

For each green space, we used eight predictor variables (**Table 1**). To determine the size of green spaces we delineated their perimeters with the aid of a Geographic Information System (QGIS) and high resolution images (Google Earth). Shape index was calculated with the following formula (Corey et al., 2012):

$$Index = \frac{perimeter}{2\sqrt{(\pi \times area)}}$$

Shape index ranges from 1 to ∞. A shape index of 1 corresponds to a circular patch, whereas an irregular patch has a shape index > 1. As the shape of the patch becomes more irregular, the shape index increases (Corey et al., 2012). To describe the distribution and amount of vegetation in each green space we used satellite imagery to derive a vegetation index. We computed the Normalized Vegetation Index (NDVI), an index that relies on the reflectance of red and near-infrared light (Huete et al., 1985). NDVI has been used for different purposes, including vegetation cover and vegetation density estimation (MacDonald et al., 2010; Odindi and Mhangara, 2012). In this work, NDVI was derived from Sentinel-2A multi-spectral images obtained from the European Space Agency. In order to reduce discrepancies, we used images whose acquisition date was as close as possible to the bird sampling seasons while maintaining a low cloud cover percentage. For winter, dry breeding, and wet breeding seasons the acquisition dates of images were January 7th, June 1st and July 26th 2018 respectively. NDVI was calculated from the Red and Near-infrared (NIR) bands which have a spatial resolution of 10 m using the following formula:

$$NDVI = \frac{NIR - RED}{NIR + RED}$$

NDVI is dimensionless and ranges from −1 to +1. Negative values indicate the absence of vegetation while positive values represent vegetated areas. NDVI values can be categorized into useful classes that separate different conditions of vegetation. Values above 0.2 are associated with vegetated areas and the larger the NDVI values the denser the vegetation (Fung and Siu, 2001; Hashim et al., 2019). We followed Odindi and Mhangara (2012) to group the NDVI values into five classes that describe

FIGURE 1 | Left: overview of sampled green spaces and areas considered as potential species pools in Mexico City. Upper right: zoom to the shadowed area **(A)**. Lower right: zoom to the shadowed area **(B)**.

different vegetation conditions: unvegetated (NDVI $\leq$ 0), very sparse vegetation (0 > NDVI < 0.2), sparse vegetation (0.2 $\geq$ NDVI < 0.4), dense vegetation (0.4 $\geq$ NDVI < 0.6), and very dense vegetation (0.6 $\geq$ NDVI $\leq$ 1).

For every studied season, two variables were derived from the corresponding NDVI data to describe vegetation cover of each green space. The first variable was the densely-vegetated fraction (DVF), estimated as a function of the number of pixels that represent dense and very dense vegetation. NDVI values above 0.5 can be considered as fully vegetated pixels (Sobrino et al., 2004), hence, DVF is a close approximation of the proportion of fully vegetated area in green spaces. Densely-vegetated fraction was computed as follows (Wong et al., 2019):

$$DVF =$$

$$\frac{\text{Count of dense vegetation pixels} + \text{Count of very dense vegetation pixels}}{\text{Total count of pixels in the green space}}$$

The second variable based on NDVI was the diversity of classes describing vegetation condition and this was used as a surrogate of habitat diversity (Habitat diversity). Simpson's diversity index was used to quantify the diversity of vegetation conditions (Nagendra, 2002). The index was calculated with the following formula:

$$Simpson's\ diversity\ index = 1 - \sum_{i=1}^{N} p_i^2$$

where p_i is the proportional abundance of the ith NDVI class.

Additionally, we calculated the DVF and Habitat diversity for 50-m width buffers surrounding each green space (**Figure 2**). These estimations (DFV$_{50}$ and Habitat diversity$_{50}$) did not include estimations within the green space, so the information of each buffer is spatially exclusive from that of the green space (the "doughnut" method according to Dunford and Freemark, 2005). We used 50-m width buffers because landscape variables extracted at this scale have been reported as significant drivers of bird communities (Meffert and Dziock, 2013) and because we consider that management interventions at these small scales

TABLE 1 | Predictors included in analyses to describe variation in response variables.

Code	Variable
Area	Area of the green space
DVF$_0$	Densely-vegetated fraction within the green space
Habitat diversity$_0$	Habitat diversity within the green space
Isolation	Euclidean distance to the closest species pool
Tree richness	Tree species richness within the green space
Shape	Shape index of the green space
DVF$_{50}$	Densely-vegetated fraction in a 50-m buffer around the green space without including DVF$_0$ estimations
Habitat diversity$_{50}$	Habitat diversity in a 50-m buffer around the green space without including Habitat diversity estimations within the green space

FIGURE 2 | Satellite image (Google Earth ©) showing three different green spaces and their corresponding 50-m width buffer. Green space numbers as in **Figure 1**.

are more likely to be accomplished in urban landscapes. We used the distance between each green space and its closest likely source of species as a proxy of isolation (Fernandez-Juricic, 2000). We assumed protected areas, environmental valuable areas, and areas designated for conservation to function as regional species pools (**Figure 1**). We measured the Euclidean distance from the centroid of each green space to the edge of the closest species pool as long as it was larger than 100 ha. The number of tree species was registered in each sampling point and these data were pooled for every green space.

Trait Data

We employed four traits to characterize all detected species: log-transformed body mass, main diet item, foraging strategy, and foraging stratum. Main diet items were the following: aquatic animals, fruit, generalist, invertebrates, nectar, seeds, and vertebrates. Foraging strategy categories were: aerial sallying, aerial screening, arboreal gleaning, bark gleaning, foraging generalist, and ground foraging. We considered the following foraging stratum categories: aerial, canopy, ground, mid height, understory, around water surface, below water surface. Foraging stratum is expressed as the estimated percentage use of each one of the all strata considered. The values of all the strata sum to 100. We selected these traits because their occurrence can be influenced by environmental conditions (Castaño-Villa et al., 2019). We built a species-trait matrix with information sourced from previous publications (Wilman et al., 2014; Tobias and Pigot, 2019).

Community Diversity Metrics

For each season, we quantified diversity in green spaces with three different metrics. Firstly, we obtained cumulative species lists for each sampling point based on the species detected on both visits. Then, for each green space, diversity metrics were calculated after the cumulative species lists of all the corresponding sampling points were pooled. We calculated taxonomic diversity as species richness. To quantify functional diversity we used functional richness, which measures the amount of trait space occupied by the species in the community (Villéger et al., 2008). For functional richness to be computed, the number of species recorded in

assemblages must be at least three. Phylogenetic diversity was quantified by means of the Faith's phylogenetic diversity which measures the total evolutionary history of the species in a community (Frishkoff et al., 2014). Faith's phylogenetic diversity is calculated as the sum of all branch lengths spanned by the tree connecting all the species in a community (Faith, 1992). For phylogenetic metric calculation, we used 1,000 dated phylogenies (Jetz et al., 2012): 500 phylogenies using the Hackett backbone and 500 phylogenies using the Erikson backbone following La Sorte et al. (2018). The use of sets of phylogenies can provide more robust comparative inferences than the use of a single consensus tree (Rubolini et al., 2015). Once the Faith's phylogenetic diversity was computed for every phylogeny, we averaged the values across the 1,000 phylogenies.

Data Analysis

Faith's phylogenetic diversity and functional richness tend to be positively correlated with species richness (Swenson, 2014; Voskamp et al., 2017) so we checked potential correlations by means of Spearman correlation. To remove the effects of species richness on both indexes, we generated 999 null assemblages. Null assemblages were obtained through the randomization of species names on the trait data matrix and on the phylogeny maintaining constant the number of species of each focal assemblage (Swenson, 2014). For each season, we used a phylogeny and a trait matrix that included the species recorded in the specific season. To compare observed Faith's phylogenetic diversity and functional richness values with expected values from null models we calculated standardized effect sizes (ses) and these were obtained using the following formula:

$$ses = \frac{Mean_{obs} - Mean_{rand}}{SD_{rand}}$$

where $Mean_{obs}$ is the observed diversity value, $Mean_{rand}$ is the mean value of the randomized assemblages, and SD_{rand} is the standard deviation of the randomized assemblages. Negative ses values indicate an observed value lower than the average value expected by chance, while positive values evidence an observed value higher than the average value expected by chance (Swenson, 2014).

In terms of community structure, negative ses values suggest phylogenetic or functional clustering, while positive ses values suggest phylogenetic or functional over-dispersion. In this way, ses values provide additional information to that obtained from non-standardized diversity measures. To test if observed values were either significantly lower or higher than the average value expected by chance, we assumed a normal distribution of observed and random values together. For a significance level = 0.05, observed values are considered not significantly different from random expectations if they range between -1.96 and 1.96 (Zar, 2014).

Previous to model fitting, we followed standard procedures in multiple regression analysis. We explored the distribution of the response variables to select the appropriate error structure. Models of species richness were fitted using a Poisson distribution, and models of functional richness, Faith's phylogenetic diversity, ses functional richness, and ses Faith's phylogenetic diversity employed a Gaussian distribution. Explanatory variables were standardized to mean = 0 and standard deviation = 1. We checked for potential multicollinearity between explanatory variables by means of Spearman correlation (r > 0.60) and we removed one variable of each strongly correlated pair of variables. Due to the presence of high significant correlations ($|r| > 0.60$, $P < 0.05$) of Tree richness, DVF_{50} and Habitat diversity$_{50}$ with other variables, these three variables were not included in further analysis. Multicollinearity was also tested by calculating variance inflation factors (VIF). Once highly correlated variables were deleted, VIF values of all explanatory variables were under 2.4.

To assess the relationships between the response variables and the explanatory variables (**Table 1**), we fitted generalized linear models (GLM) and used multimodel inference to find the most parsimonious and likely model (Burnham and Anderson, 2002). This approach ranks and weights candidate statistical models that function as biological hypotheses (Grueber et al., 2011). For each diversity metric × season combination (for example, functional richness – wet breeding season) we fitted all possible submodels following an all-subset approach. The full set of submodels equals 2^n, where n is the number of parameters.

Models were ranked based on Akaike information criterion modified for small sample size (AIC_c), where the model with the lowest AIC_c is considered the model with the best fit (Symonds and Moussalli, 2011). To quantify the relative performance of the models, we calculated the difference (Δ_i) between the best rated model and the rest. To quantify the relative support for each model, based on (Δ_i) we computed the Akaike weight (w_i) which measures the weight of evidence that supports model i as being the best model, given the data and the set of candidate models (Burnham and Anderson, 2002). Akaike weight can be interpreted as the probability that model i is indeed the best model (Symonds and Moussalli, 2011).

Then, we performed model selection including those models with a (Δ_i) value ≤ 2. To account for model uncertainty, we implemented model averaging with the selected set, using the two existing methods to perform model averaging (Symonds and Moussalli, 2011). Natural averaging, averages the estimator β_i just over the models where the predictor i appears. This method is recommended when there is strong support for a model ($w_i > 0.9$). The other method, zero averaging, averages β_i over the full set of models and is recommended when there is not strong support for any model ($w_i < 0.9$). In those models where the predictor i is absent, a value = 0 is used in the calculation of the average. This makes β_i shrink toward 0 for those predictors that appear in the less supported models (Burnham and Anderson, 2002; Grueber et al., 2011). All statistical analyses were performed in R version 3.5.2 (R Core Team, 2018). To obtain phylogenetic and functional diversity we employed functions found in the libraries "picante" (Kembel et al., 2010) and "FD" (Laliberté et al., 2014). The generation of candidate subset models, model ranking and model averaging were implemented with functions found in the library "MuMIn" (Bartón, 2020). GLM were fitted using core functions found in R.
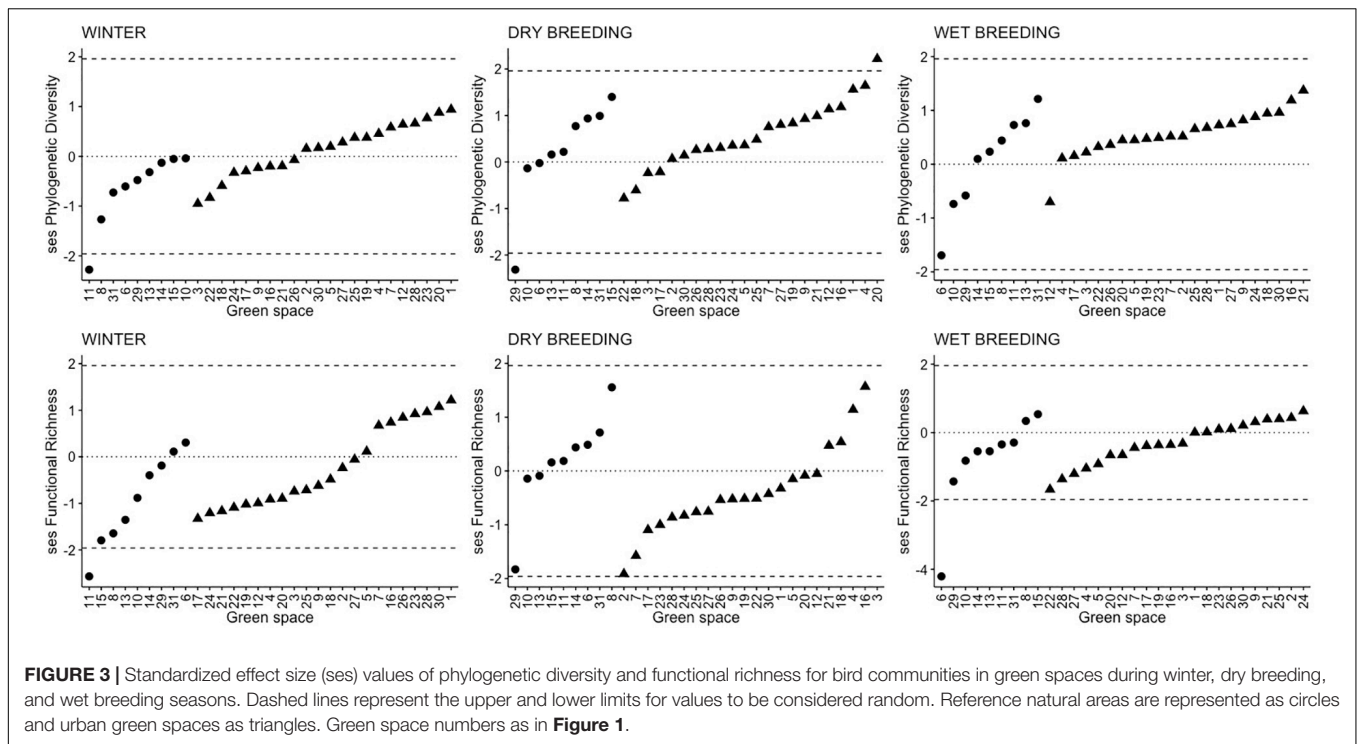
RESULTS

Diversity Patterns

A total of 91 species from 28 families were recorded across all sites and seasons with a mean (±standard error) of 10 (±0.6) species per site. The number of detected species decreased from winter (71 species) to the dry breeding season (63 species), and then to the wet breeding season (55 species). While thirty-seven species were recorded across seasons, some species were recorded in just one season (**Supplementary Material**). All the three diversity dimensions showed a similar trend across the year. On average, diversity values were higher for the winter season and decreased toward the early and the late breeding seasons (**Table 2**).

In general, phylogenetic and functional structure of bird communities in green spaces, assessed through standardized effect sizes, was neither clustered (ses ≤ -1.96) nor over-dispersed (ses ≥ 1.96) in any of the studied seasons (**Figure 3**). However, in four green spaces a non-random structure was observed. Noteworthy, functional and phylogenetic clustering were observed only in natural protected areas. In winter, a large natural protected area showed both phylogenetic and functional clustering. In the dry breeding season, phylogenetic clustering occurred in another large natural protected area while phylogenetic over-dispersion happened in a highly landscaped

TABLE 2 | Mean values ± standard deviation (minimum – maximum) of species richness, phylogenetic diversity, and functional richness of bird communities in green spaces in each of the studied seasons.

Diversity index	Winter	Dry breeding	Wet breeding
Species richness	12.5 ± 7.7 (3–41)	10.9 ± 5.0 (2–26)	8.5 ± 5.2 (3–27)
Faith's phylogenetic diversity	477.6 ± 191.5 (107.1–1008.6)	453.4 ± 144.2 (88.3–846.0)	386.3 ± 152.4 (117.6–772.6)
Functional richness	0.085 ± 0.045 (0.001–0.163)	0.010 ± 0.007 (0.00002–0.025)	0.075 ± 0.037 (0.006–0.145)

FIGURE 3 | Standardized effect size (ses) values of phylogenetic diversity and functional richness for bird communities in green spaces during winter, dry breeding, and wet breeding seasons. Dashed lines represent the upper and lower limits for values to be considered random. Reference natural areas are represented as circles and urban green spaces as triangles. Green space numbers as in **Figure 1**.

green space. In the wet breeding season, functional clustering was detected in a third natural protected area.

Across the studied seasons, species richness was significantly correlated with both phylogenetic diversity and functional richness (**Figure 4**). Correlation strength of species richness with phylogenetic diversity was high while it was moderate between species richness and functional richness. In contrast, ses phylogenetic diversity and ses functional richness were not significantly correlated with species richness. In the case of the species richness-functional richness relationship, species rich communities showed a pattern of functional redundancy based on their relative low functional richness.

Community Diversity and Structure Responses to Green Spaces' Characteristics

Model ranking showed that Area was the predominant predictor to describe the relationships between green spaces' characteristics and bird diversity, followed by Habitat diversity$_0$ (**Table 3**). However, Akaike weights indicated model uncertainty to some degree, with the weight of top-ranked models ranging from 0.14 to 0.46 with a mean = 0.27. Since models did not have a strong support ($w_i > 0.9$), zero-averaged coefficients are presented and discussed hereafter (**Table 4**).

Model averaging revealed that community diversity metrics and community structure were associated with different green spaces' characteristics. Model-averaged coefficients indicated that species richness, phylogenetic diversity, and functional richness increased with Area in all seasons, with a smaller effect in the dry breeding season (**Figure 5**). In contrast, Area showed a negative

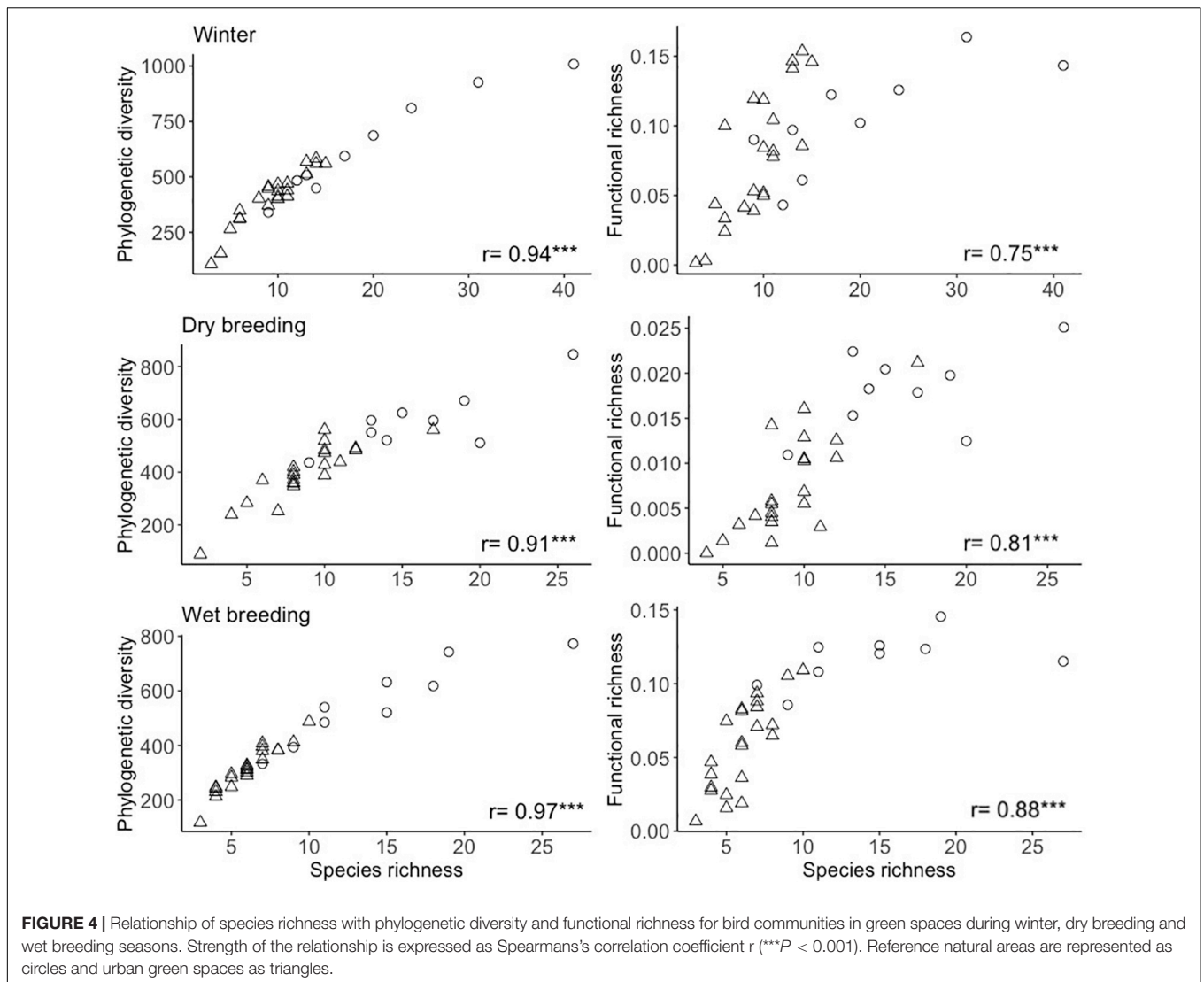relationship with ses phylogenetic diversity during winter and the dry breeding season.

Noteworthy, Habitat diversity$_0$ showed a negative relationship with species richness and phylogenetic diversity, and this effect was observed only for the wet breeding season. Finally, the analyses revealed a strong positive effect of isolation on ses phylogenetic diversity and ses functional richness during the wet breeding season and winter, respectively.

DISCUSSION

Diversity Patterns

Green spaces of Mexico City surveyed in this study harbored 34% of the land bird species reported in the state (Meléndez-Herrada et al., 2016) indicating that green spaces are important elements for diversity conservation in urban areas. Species richness, phylogenetic diversity, and functional richness differed among green spaces indicating that these sites possess different value for urban bird conservation. In accordance with hypothesis 1, bird diversity varied seasonally with the highest values of these indices observed during winter. Seasonal differences in urban bird assemblages can be explained by imperfect detection and seasonal use of alternative habitats (Murgui, 2010). In fact, detectability could have varied among seasons and habitats (Iknayan et al., 2014), but we used a 25-m point count to reduce detectability differences (Hutto et al., 1986). Though we assume these differences were not the main drivers of the detected seasonal variation, the results must be interpreted cautiously.

Both the presence of migratory species in urban green spaces during winter and the seasonal movements of birds are

FIGURE 4 | Relationship of species richness with phylogenetic diversity and functional richness for bird communities in green spaces during winter, dry breeding and wet breeding seasons. Strength of the relationship is expressed as Spearmans's correlation coefficient r (***P < 0.001). Reference natural areas are represented as circles and urban green spaces as triangles.

probably the main drivers of seasonal differences in bird diversity dimensions. A close inspection of species incidence across the seasons (**Supplementary Material**) reveals that during winter, additional species were present in surveyed green spaces and these species were functionally and phylogenetically distinctive. For example, American Krestel (*Falco sparverius*) and Plumbeous Vireo (*Vireo plumbeus*) were observed only during winter and they were, respectively, the only members belonging to order Falconiformes and family Vireonidae that were detected in this study. Hence, our study highlights the contribution of migratory species to bird diversity in urban settings and provides evidence about the importance of urban green spaces for migratory bird conservation (Dale, 2018).

Seasonal variation in diversity dimensions may also be produced by movement patterns of birds within Mexico City landscape throughout the year. These movements may arise from changes in local habitats, population parameters, or climatic conditions (Marone, 1992; Kawamura et al., 2019). In this regard, we registered variations of green spaces features related to habitat

characteristics such as the densely-vegetated fraction and habitat diversity. Observed differences in these variables might relate with differences in the availability of food, cover, and nesting resources, and in this way, may affect bird distribution and diversity (Holmes et al., 1996).

Our results showed a moderate to strong relationship of species richness with phylogenetic diversity and functional richness. Overall, based on these correlations, our results indicated that increases in species richness translated into increases in phylogenetic diversity and functional richness. However, our results suggest that some of the studied communities may have been phylogenetically or functionally redundant since for a given species richness value, different phylogenetic or functional diversity values were observed and some of the species rich assemblages showed relatively low phylogenetic or functional diversity values. This finding was more apparent for functional richness. Further work should examine how phylogenetic or functional diversity respond to species losses or gains associated with habitat transformation within

TABLE 3 | Top-ranked models proposed to explain diversity of birds in green spaces during winter, dry breeding, and wet breeding seasons.

Response variable	Model	k	LogLink	AICc	wi
Winter					
Species richness	Area	2	−93.52	191.5	0.19
Phylogenetic diversity	Area	3	−199.84	406.6	0.27
Phylogenetic structure	Area	3	−24.17	55.2	0.37
Functional richness	Area	3	55.07	−103.3	0.21
Functional structure	Isolation	3	−38.28	83.5	0.27
Dry breeding season					
Species richness	Area	2	−79.45	163.3	0.28
Phylogenetic diversity	Area	3	−190.75	388.4	0.30
Phylogenetic structure	Area + Shape Index	4	−34.23	78.0	0.21
Functional richness	Area	3	118.38	−229.8	0.37
Functional structure	DVF_0	3	−36.06	79.0	0.14
Wet breeding season					
Species richness	Area + Habitat diversity$_0$	3	−65.90	138.7	0.38
Phylogenetic diversity	Area + Habitat diversity$_0$	4	−176.97	363.5	0.46
Phylogenetic structure	Isolation + Habitat diversity$_0$	4	−22.88	55.3	0.20
Functional richness	Area + Habitat diversity$_0$	4	74.96	−140.4	0.28
Functional structure	Habitat diversity$_0$	3	−39.27	85.4	0.16

Models were fitted for species richness, Faith's phylogenetic diversity, functional richness, and the standardized effect sizes of Faith's phylogenetic diversity and functional richness. Model weight (w_i) indicates the level of support of model i, considering the entire set of candidate models. DVF_{50} and Habitat Diversity$_{50}$ were not included in multi-model inference due to their high correlation with other predictors. For more details about explanatory variables check **Table 1***.*

urban green spaces in order to get a more thorough insight of biodiversity conservation in these sites. For example, land use intensification associated with agriculture can lead to reductions of functional diversity more severe than would be expected based on species richness reductions (Flynn et al., 2009).

We highlight that the relationship of species richness with phylogenetic diversity and functional richness varied across the studied seasons and that it was stronger during the wet breeding season. We suggest that this could indicate a seasonal variation in the redundancy of species pools (*sensu* Aronson et al., 2016) from which communities in green spaces are assembled. In the study area, families such as Picidae (woodpeckers), Tyrannidae (flycatchers), Regulidae (kinglets), Turdidae (thrushes), Passerellidae (new world sparrows),

Parulidae (new world warblers), and Cardinalidae (tanagers) are part of the resident breeding assemblages, which during winter contain additional species of these families, either wintering or transient. An alternative and complementary explanation would be that for relatively small numbers of species, the addition of "unique" clades or traits is more likely. A saturation effect has been reported for phylogenetic and functional diversity of bird assemblages in farmlands (García-Navas and Thuiller, 2020). These authors found that the standardized effect size of both phylogenetic diversity and functional richness tended to decrease when species richness reached a threshold ($\approx$35 species). In this study, functional richness seemed to reach an asymptote above species richness $\approx$20. Regarding phylogenetic diversity, we did not find evidence of an asymptotic relationship with species richness.

Our results did not support our second hypothesis, which stated that studied bird assemblages would show phylogenetic or functional clustering as a result of urban environmental filtering. We found a predominantly random functional and phylogenetic structure of bird communities in green spaces of Mexico City. That is, there was no evidence to conclude that the environmental conditions of the most urbanized green spaces posed a filter to traits or clades. However, phylogenetic diversity and functional richness values lower than the expected ones were observed in three sites which resembled natural habitats and were located far from downtown and within natural forested areas of the city.

Based on this, we propose that species that prefer open habitats within cities might react to forests as local environmental filters, as has been suggested for forest-farmland and grassland-forest plantation systems (Jacoboski et al., 2019; García-Navas and Thuiller, 2020). Likewise, species that need large forest patches may be filtered out from small isolated green spaces. However, compensatory dynamics may be occurring (Supp and Ernest, 2014), by which losses of traits and lineages in small isolated green spaces are probably compensated by the introduction of exotic species, a mechanism not occurring in large and less landscaped green spaces. For example, in highly landscaped green spaces the exotic species House Sparrow (*Passer domesticus*) and Rock Pigeon (*Columba livia*), both favored by urbanization (Carbó-Ramírez and Zuria, 2011), were common and abundant. Moreover, in centrally located green spaces, species established in the city due to escapes from captivity such as Harris's Hawk (*Parabuteo unicinctus*) (Ortega-Álvarez and Calderón-Parra, 2014) or Green Jay (*Cyanocorax yncas*) could also be detected (for previous records of Green Jay in Mexico City see Charre et al., 2013). Further research should be conducted to determine if natural forested areas in Mexico City filter birds as has been reported for forest-agriculture systems (Sreekar et al., 2021).

Community Diversity and Structure Responses to Green Spaces' Characteristics

Area and habitat diversity within the green space were important habitat factors that influenced bird species richness, phylogenetic diversity, and functional richness of studied green spaces. Findings are consistent with previous reports about the positive

TABLE 4 | Zero-averaged estimates for predictors of species richness, Faith's phylogenetic diversity, functional richness, and the standardized effect sizes of Faith's phylogenetic diversity and functional richness.

Season	No. models $\Delta AIC_c \leq 2$	Area	DVF_0	Habitat diversity$_0$	Isolation	Shape
Species richness						
Winter	4	0.40 (0.05)***		−0.02 (0.04)	−0.02 (0.04)	
Dry breeding	2	0.34 (0.05)***	−0.02 (0.04)			
Wet breeding	1	0.40 (0.07)***		−0.14 (0.06)*		
Phylogenetic diversity						
Winter	3	110.29 (29.10)***		−10.00 (21.98)	−7.41 (19.63)	
Dry breeding	3	87.00 (22.06)***	−3.8 (12.95)			5.20 (14.07)
Wet breeding	1	107.24 (15.05)***		−49.09 (15.05)**		
ses Phylogenetic diversity						
Winter	1	−0.42 (0.09)***				
Dry breeding	2	−0.33 (0.14)*				0.14 (0.16)
Wet breeding	4	−0.02 (0.06)		0.06 (0.10)	0.30 (0.10)**	0.01 (0.05)
Functional richness						
Winter	3	0.02 (0.007)*			0.003 (0.006)	−0.002 (0.005)
Dry breeding	1	0.005 (0.0008)***				
Wet breeding	2	0.02 (0.004)***		−0.005 (0.005)		
ses Functional richness						
Winter	2				0.41 (0.15)*	−0.05 (0.12)
Dry breeding	6	0.08 (0.14)	0.01 (0.07)	0.01 (0.06)		0.08 (0.14)
Wet breeding	4	−0.06 (0.13)		0.17 (0.19)		

When the number of models in the subset $\Delta AIC_c \leq 2$ equaled 1, table displays coefficients of the top-ranked model. Models were fitted for winter, the dry breeding and the wet breeding seasons. Coefficients (standard error) are shown. *P < 0.05, **P < 0.01, ***P < 0.001.
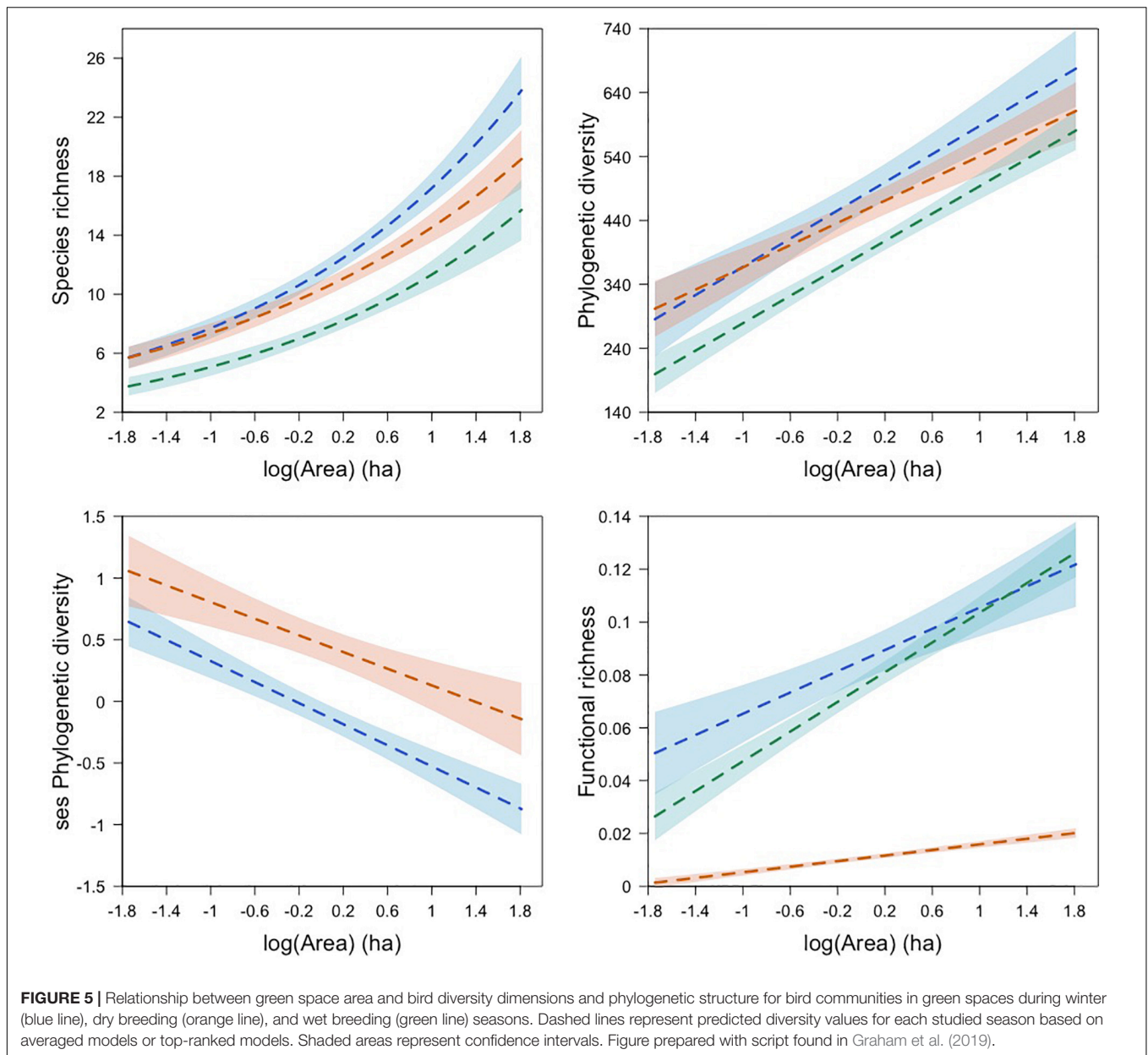
effect of area on different dimensions of bird diversity (Morelli et al., 2018a) and supported partially our third hypothesis, a positive relationship of area with the three diversity dimensions measured. However, our results did not support the prediction of a positive effect of habitat diversity on any of the diversity dimensions. Moreover, our findings showed that, during the wet breeding season, species richness and phylogenetic diversity decreased as habitat diversity increased. This was an unexpected result considering that habitat heterogeneity can affect positively species richness (Loss et al., 2009). And given the positive correlation of species richness with phylogenetic and functional diversity (Mouchet et al., 2010), we expected a positive relation of phylogenetic and functional diversity with habitat diversity.

In this regard, habitat diversity could have negative effects if it develops as a consequence of habitat fragmentation (Tews et al., 2004). The absence of urban avoiders in the more heterogeneous green spaces, which in this study are also the smallest and the more landscaped ones, could explain the observed relationship between bird diversity and habitat heterogeneity. In Mexico City, small green spaces close to downtown are at the same time the more heterogeneous, and despite they attract urban exploiters such as House Sparrow and Great-tailed Grackle (*Quiscalus mexicanus*), this does not compensate the loss of sensitive species.

In accordance with existing evidence (La Sorte et al., 2020), green space shape did not have a significant effect on species richness, phylogenetic diversity nor functional richness. Similarly, our results did not support a significant effect of isolation on bird diversity. In this regard, additional work is needed to understand the role of isolation in determining

bird diversity since existing evidence is still inconclusive (Charre et al., 2013; La Sorte et al., 2020). Of interest, was the large positive effect of isolation on ses phylogenetic diversity and ses functional richness, during the wet breeding season and winter, respectively. Two likely processes could explain this finding: more isolated green spaces were phylogenetically and functionally enriched to some degree due to the presence of exotic species while less isolated green spaces were phylogenetically and functionally impoverished due to clade and trait redundancy. This finding merits more research since isolation can influence other relevant community aspects such species composition (Peris and Montelongo, 2014; Leveau and Leveau, 2016). In addition, our study revealed a negative relationship of area with ses phylogenetic diversity during winter and the dry breeding season. This suggests that larger green spaces which have higher species richness, due to the species-area relationship, comprise phylogenetically close species and as green space area decreases, though some species are lost, the remaining species are phylogenetically distant.

Overall, our study provides little support for the hypothesis 1 with regard to the seasonal variation of the relationships between diversity and green spaces' characteristics. Results herein reported showed that the strength of the studied relationships varied across seasons but their direction did not. This is noteworthy considering that others have found that predictors can have contrasting effects among seasons (La Sorte et al., 2020). We propose that temporal changes in the strength of the diversity-environment relationships can be the result of mechanisms simultaneously operating

FIGURE 5 | Relationship between green space area and bird diversity dimensions and phylogenetic structure for bird communities in green spaces during winter (blue line), dry breeding (orange line), and wet breeding (green line) seasons. Dashed lines represent predicted diversity values for each studied season based on averaged models or top-ranked models. Shaded areas represent confidence intervals. Figure prepared with script found in Graham et al. (2019).

such as changes in anthropogenic food availability (Stofberg et al., 2019), the seasonal use of habitat (Marone et al., 1997), the species urban tolerance (Callaghan et al., 2021), and the anthropic related mortality (Bracey et al., 2016) among others.

CONCLUDING REMARKS

This study provides evidence about the value of green spaces for bird conservation in cities. The use of complementary measures of diversity together with the comparison between observed and expected values allowed a better understanding of the response of bird communities to urban green spaces. Our findings show that, green space area is the main factor

determining bird diversity. However, phylogenetic and functional structure did not respond to area but were affected by green space isolation. This information may be useful for future urban planning: in cases where it is not possible to enlarge green spaces, other characteristics such as their diversity of habitats or their interconnectedness to other green spaces or natural areas can be modified. Furthermore, future studies should consider both spatial and temporal variation of diversity patterns and of the influence of environmental factors.

DATA AVAILABILITY STATEMENT

The datasets presented in this article are not readily available because the raw data supporting the conclusions of this

article will be made available by the authors under request. Requests to access the datasets should be directed to RN-D, reminava@yahoo.com.mx.

AUTHOR CONTRIBUTIONS

RN-D: conception and design, data collection, data analysis and visualization, and manuscript writing. IZ and RP-L: supervision and writing – review and editing. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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