

# Patterns of Bird Diversity and Endemism Along an Elevational Gradient in the Southern Mexican Highlands

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Knowledge of bird species diversity along elevational gradients is key for understanding the distributional limits of species and, ultimately, for promoting measures that conserve biodiversity. In the present study, we evaluated changes in bird species richness, diversity, and endemism along an elevational gradient in the Sierra Madre del Sur in southern Mexico – a globally recognized biodiversity hotspot. Monthly bird surveys were carried out at localities with elevations of 1600, 1800, 2000, and 2200 m over the course of one year (2014–2015) covering an area of 2000 km<sup>2</sup> (10 circular plots with a radius of 25 m per elevation site). Diversity was calculated in terms of effective number of species or Hill numbers, while the composition of bird species along the elevational gradient was analyzed by non-metric multidimensional scaling, and endemic bird species turnover was assessed with faunal congruence curves. Overall, a total of 118 bird species belonging to 35 families were recorded along the elevational gradient. Although we found that bird richness and diversity increased with increasing elevation, we also observed significant turnover in bird composition and endemic species, which were likely linked to forest types and conditions, as well as proximity of sites to urban centers. Assessing biodiversity patterns across elevational gradients in a well-recognized biodiversity reservoir advances both understanding of ecological patterns and aids conservation efforts and management of biological resources.

**Key words:** Bird Richness, Conservation, Endemism, Spatial Heterogeneity, Species Turnover.

## BACKGROUND

Several biotic communities have been observed to have heterogeneous distributional patterns along elevational gradients (Gaston 2000; Koleff et al. 2008;

McCain and Grytnes 2010). Most commonly observed is that of decreasing species diversity with increasing elevation particularly for faunal groups like birds (Navarro 1992; Briones-Salas et al. 2005; McCain and Grytnes 2010; Medina-Macías et al. 2010). However,

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other elevational patterns for bird diversity and richness have been described as well. For example, McCain (2009) described a unimodal pattern with greater diversity at intermediate elevations, commonly referred to as the ‘mid-domain effect’ (Colwell and Lees 2000). McCain (2009) and McCain and Grytnes (2010) found high species diversity plateaus across lower elevations (~ 300 m) that tended to decrease monotonically with increasing elevation. In contrast, both a positive linear and exponential pattern, that is, increasing species richness with increasing elevation (*e.g.*, lichens and mammals; Grytnes et al. 2006; Bateman et al. 2010) and a U-shaped pattern in which species richness is greater at each end of the gradient, have also been observed in biotic communities (Ávila-Sánchez et al. 2018). In any case, these patterns of species diversity have been linked to a range of biotic factors, such as ecological interactions, and abiotic factors, such as climate, temperature, resource availability, ecotones, and even land management history (McCain 2009; McCain and Grytnes 2010; Kark 2013; Kim et al. 2018; Santillán et al. 2018).

Southern Mexico’s Sierra Madre del Sur (SMS) biogeographic province has a complex orography and geological history with notable diversification centers along its elevational gradients. These diversification centers arose during Pleistocene climatic fluctuations in this region (Luna-Vega et al. 2016) and from active intraspecific differentiation processes for distinct faunal groups like birds (Rocha-Méndez et al. 2019). For this reason, southwestern Mexico is a region with notable biological diversity, including high levels of endemism (García-Trejo and Navarro 2004; Ochoa-Ochoa and Flores-Villela 2006). For example, several bird species such as *Lophornis brachylophus*, *Eupherusa poliocerca*, *Cyanolyca mirabilis*, and *Arremon kuehnerii*, have a distribution restricted to the SMS (Banks 1990; Navarro-Sigüenza et al. 2013 2016). Similarly, the constant orogenic processes in SMS have resulted in functionally isolated tropical and temperate ecosystems with genetically differentiated populations arising from widely distributed bird species (*e.g.*, *Chlorospingus albifrons*, *Aulacorhynchus wagleri*, *Lampornis margaritae*; Navarro-Sigüenza and Peterson 2004; Sánchez-González et al. 2007; Cortés-Rodríguez et al. 2008; Puebla-Olivares et al. 2008). Even though the tropical montane regions of southern Mexico and particularly SMS have high biodiversity and high endemism levels, studies on changes in biotic composition along elevational gradients in different biological groups are still incipient (*e.g.*, Navarro 1992; Briones-Salas et al. 2005; Jaime-Escalante et al. 2016; Ávila-Sánchez et al. 2018). Therefore, expanding comprehensive distributional and biodiversity studies

stands to greatly advance our ecological understanding of SMS biological landscapes and the conservation strategies that support them.

In the present study, we analyzed bird species richness, diversity, and endemism along an elevational gradient ranging from 1600 to 2200 m in the SMS of the state of Guerrero in southern Mexico. The gradient was represented by four sites at an elevation of 1600, 1800, 2000, and 2200 m with different climate and vegetation types. Because higher elevations in this region are mainly dominated by forests of Nearctic affinity, such as oak, pine-oak, and pine forests, and the lowest elevation site was associated to tropical forests, which are generally known to have higher species diversity (Escalante et al. 1998; Espinosa-Organista et al. 2008), we hypothesized that bird richness and diversity would decrease with increasing elevation. On the other hand, we expected that endemism would show a U-shaped pattern to reflect the forest types at both ends of the gradient, which were tropical dryland forest and cloud forest, both of which are typically inhabited by several biological groups with high levels of endemism, including birds (Ceballos et al. 2010; Villaseñor 2010; Dirzo et al. 2011; Gual-Díaz and Rendón-Correa 2014). Because the lowest elevation site (1600 m) had fairly distinct ecological conditions (*e.g.*, climate, forest affinity), and even a different biogeographical affinity (presence of tropical forests) compared to the other sites, we also predicted that this elevation would be the most dissimilar from the others in terms of species composition. Finally, we expected the highest turnover of endemic bird species to occur at the highest elevation (2200 m), *i.e.*, in the cloud forest, an ecosystem known for its high levels of endemism throughout Mesoamerica (Gual-Díaz and Rendón-Correa 2014). Assessing biodiversity patterns along elevational gradients in the SMS advances understanding of ecological patterns and aids conservation efforts and management of biological resources in a region of southern Mexico that is historically considered one of the most important biodiversity reservoirs of the country (Luna-Vega et al. 2016).

## MATERIALS AND METHODS

### Study area and sampling sites

The study area was located within the biogeographical province of the Sierra Madre del Sur in the southern state of Guerrero, Mexico (17°30'0"N–99°26'40"W, 17°38'20"N–99°39'10"W; Fig. 1). Sampling sites were established along an elevational gradient from 1600–2200 m in four

localities: Chilpancingo (1600 m), Amojileca (1800 m), Xocomanatlan (2000 m), and Omiltemi (2200 m; Fig. 1). The 200 m separation in elevation between sites is appropriate for studying bird species turnover (Navarro 1992). The mean annual precipitation at the lowest site (Chilpancingo) ranged from 1000–1200 mm and at the highest site (Omiltemi; INEGI 2010) from 1500–1800 mm.

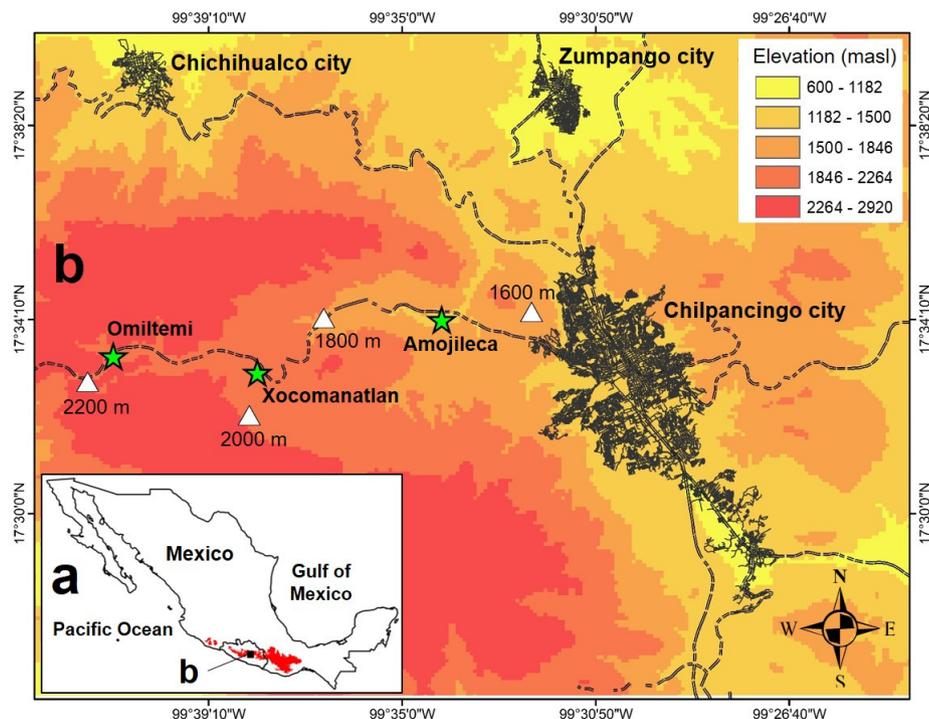
The lowest elevation site was located at 1600 m and approximately 1.2 km northwest of the city of Chilpancingo, which was also the largest urban area in the region (Fig. 1). Climate at the 1600 m locality was sub-humid and semi-warm and the vegetation was predominantly tropical dry forest with interspersed trees of *Juniperus flaccida*. The tree layer was mainly composed of *Bursera fagaroides*, *B. schlechtendalii*, *Pterocarpus acapulcensis*, and *J. flaccida*, and the shrub layer of *Tecoma stans*, *Dodonaea viscosa*, *Cordia* sp., *Rhus* sp., and *Mimosa* sp. Because of its proximity to the state capital, Chilpancingo, this site experienced the most anthropogenic influences such as small-urban settlements, livestock ranching, and timber extraction. Some dominant species and indicators of secondary vegetation, such as *Acacia farnesiana*, *Brahea dulcis*, and *Ipomoea murucoides* were also found as a consequence of anthropogenic disturbance in this site.

The site at 1800 m was located in an area adjacent to the small town of Amojileca (Fig. 1). Climate at

this locality was sub-humid, semi-warm, and the predominant vegetation type was oak forest composed of *Quercus magnoliifolia*, *Q. glaucoides*, *Q. castanea*, and *Q. conspersa*. Other less-common plant species such as *Pinus oocarpa*, *P. montezumae*, and *J. flaccida* were found. Common tropical dry forest species were found to a lesser extent, including *B. copalifera*, *B. fagaroides*, *P. acapulcensis*, *I. murucoides*, *B. dulcis*, *Agave cupreata*, *A. farnesiana*, and *Rhus* spp.

The site located at 2000 m was situated southeast of the small town of Xocomanatlan (Fig. 1). Climate at this locality was sub-humid and semi-warm temperate due to the higher altitude, and the vegetation type was dominated by pine-oak forest. Common plant species found in these forests include *Cupressus lusitanica*, *Pinus oocarpa*, *P. pseudostrobus*, *Q. elliptica*, *Q. castanea*, *Q. martinezii*, *Q. candicans*, *Arbutus xalapensis*, and *Clethra mexicana*.

The highest elevation site was located at 2200 m and situated southwest of the small town of Omiltemi (Fig. 1). Climate at this locality was sub-humid, temperate [C (w2) (w)]. This site represented an ecotone between pine-oak forest and cloud forest, the latter of which has the greatest coverage in the region. Within the pine-oak forest, the dominant species present included *P. pringlei*, *P. herrerae*, *Q. crassifolia*, and *A. xalapensis*, some of which exhibited evidence of selective logging (Almazán-Núñez et al. 2016). Representative cloud



**Fig. 1.** Geographic location of the (a) state of Guerrero in southern Mexico and (b) sampling sites (white triangles) within the Sierra Madre del Sur (red polygon). The nearest human settlements to each study site are shown as green stars.

forest plant species found at this site included *Q. uxoris*, *P. ayacahuite*, *Cornus disciflora*, *Fuchsia thymifolia*, *Rumfordia floribunda*, *Ternstroemia lineata*, *Miconia oligotricha*, *C. mexicana*, and *Carpinus caroliniana*.

### Bird surveys

Monthly bird observations were carried out over a one-year period from July 2014 to June 2015. Each month, a full-day survey was undertaken for each of the four sites resulting in 12 surveys per site and a total of 48 days of effective fieldwork. The bird species located in each site were recorded using a 25 m-radius point-count method (Hutto et al. 1986; Bibby et al. 2000). In each site, 10 sampling points were established with each separated by at least 200 m to ensure data independence, for a total of 40 point counts per survey. Observations were made during peak hours of bird activity in both the morning (07:00 to 10:30 h) and late afternoon (16:00 to 18:30 h). Binoculars (8 × 42 and 10 × 40) and field guides (Peterson and Chalif 1989; Howell and Webb 1995; Sibley 2000) were used to identify bird species.

All individuals that were seen or heard at the sampling points were counted. The visits at each point lasted 10 min, which is long enough to count most bird species, including rare species, yet short enough to minimize the probability of counting the same bird more than once (Reynolds et al. 1980). Because our focus was on bird species that heavily use local habitats, we excluded some highly aerial species such as swifts and raptor birds (Cathartidae) from the analyses (Hutto et al. 1986). Each recorded bird species was categorized according to its seasonality (Howell and Webb 1995) and endemism (Navarro-Sigüenza and Peterson 2004). Because the study area contains differentiated populations of widely distributed species, the taxonomic proposal of Navarro-Sigüenza and Peterson (2004) based on the phylogenetic/evolutionary species concept was used to identify birds in this study. Additionally, this taxonomic approach considers allopatrically differentiated populations as different species, thereby increasing the diversity and endemism in the region, which has important consequences for biological conservation (Rojas-Soto et al. 2010). We arranged bird observations systematically at the supraspecies level following the most updated guidelines of the American Ornithological Society (<http://www.americanornithology.org/>) and its most recent update (Chesser et al. 2020). To minimize observer variation, the bird observations were consistently performed by the same three observers (EAA-A, EV-S, and RCA-N).

### Data analyses

#### Bird species richness, diversity, and endemism

The sampling efficiency performed at each site was evaluated with an abundance-based coverage estimator (ACE) in EstimateS 9.1 (Colwell 2013). ACE is independent of the sampling effort and allows robust comparisons of species richness between samples using additional information on the proportional distribution of rare species (Chao and Lee 1992; Chao 2005). The average annual diversity of each site was estimated using effective number of species, or Hill numbers, where diversity is characterized at three levels: first-order diversity was calculated as species richness ( $q = 0$ ), second-order diversity is calculated based on all species in proportion to their relative abundance ( $q = 1$ ), and third-order diversity considers the effective number of dominant species in the community ( $q = 2$ ; Jost 2006). Additionally, first-order diversity ( $q0$ ) was also calculated specifically for the endemic bird species along the elevational gradient. All diversity values were compared using 84% confidence intervals (CI), as non-overlapping 84% CI robustly mimic  $P \leq 0.05$  statistical tests for symmetric and asymmetric confidence intervals (MacGregor-Fors and Payton 2013). In these cases, if the 84% CI for diversity values do not overlap, the differences among sites are interpreted to be significant. These analyses were carried out in the iNEXT software (Chao et al. 2016).

#### Structure of bird communities

We used species rank/abundance plots to compare the structure (dominance/evenness) of bird communities recorded at each elevation site over the entire year (Magurran 2004). This plot highlights differences in dominance/evenness among communities, where steep curves represent assemblages with high dominance and less pronounced curves indicate increasing uniformity (Magurran 2004; Moreno et al. 2018). In order to assess differences in dominance/evenness at elevational sites, and to test whether the proportion of dominant and rare species varied among sites, we compared the slopes of the rank/abundance plot regression lines using a covariance analysis (ANCOVA). Abundance data were  $\log$  transformed ( $\log_{10}$ ) as recommended by Magurran (2004).

#### Species turnover and bird endemism

Differences in species composition among sites were analyzed by a non-metric multidimensional scaling ordination (NMDS), using the Bray-Curtis

index based on the averaged abundance for the entire year surveyed (Faith et al. 1987; Clarke 1993). The NMDS uses a matrix of similarity between points and expresses the relative distance among sites based on species abundance (Minchin 1987). The Kruskal stress test, which gives values ranging from 0 (perfect fit) to 0.2 (poor fit), was calculated to evaluate the NMDS fit (de Leeuw and Mair 2009). Additionally, a one-way analysis of similarity (ANOSIM) to assess differences in species composition among sites was performed. ANOSIM is a nonparametric permutation test that uses similarity matrices or, in this case, the Bray-Curtis index (Clarke 1993). A similarity analysis (SIMPER) was also carried out to calculate the percentage contribution of each bird species to assemblage differentiation (*i.e.*, species that are characteristic of each site) along the elevational gradient (Clarke 1993). Finally, the turnover rate of endemic bird species along the elevational gradient was evaluated using faunal congruence curves (Terborgh 1971; Navarro 1992). This method allows detection of bird species turnover that may exist between sites and is also sensitive to abrupt changes in species turnover rate, which allows comparisons of proportions of species loss with respect to each site. All statistical analyses were performed using Past 2.17 (Hammer et al. 2001) and SPSS 20.0 (SPSS 2011) packages.

## RESULTS

### Bird richness, diversity, and endemism

A total of 118 bird species belonging to 35 families were recorded along the Mexican SMS elevational gradient studied here (Table S1). Bird richness ( $q0$ )

and diversity ( $q1$  and  $q2$ ) monotonically increased with increasing elevation so that the greatest diversity was found at 2200 m compared to the other three lower elevation sites (Fig. 2). The higher diversity found at the 2200-m site consisted of high numbers of resident and migratory bird species (54 and 17, respectively) as well as species exclusively found only at this elevation (25 species; Table S1). Based on the ACE estimator, 80%, 83%, 81%, and 82% of the expected species were recorded at 1600 m, 1800 m, 2000 m, and 2200 m, respectively. The number of endemic bird species was lower (mean = 9 species) at the 1600-m site compared to the rest of the sites (means > 11 species; Fig. 3).

### Structure of bird communities

Bird rank abundance significantly differed along the elevational gradient (ANCOVA:  $p < 0.01$ ; Table 1). *Tyrannus verticalis* was clearly dominant at 1600 m. *Myadestes occidentalis* and *Aphelocoma sumichrasti* were dominant species at 1800 m. *M. occidentalis* was slightly dominant at 2000 m. Dominance by a particular bird species was not observed at 2200 m (Fig. 4).

### Species turnover

Bird species composition varied significantly along the elevational gradient (ANOSIM global  $R = 0.71$ ,  $p < 0.001$ ; Fig. 5). The NMDS showed that the 1600-m site presented the most distinct species composition in comparison to the higher sites (2000 and 2200 m), and that these differences were significant (Fig. 5). *Myadestes occidentalis*, *Junco phaeonotus*, *Contopus pertinax*, and *Cyanocitta coronata*, which were more abundant at 1800 m, 2000 m, and 2200 m,

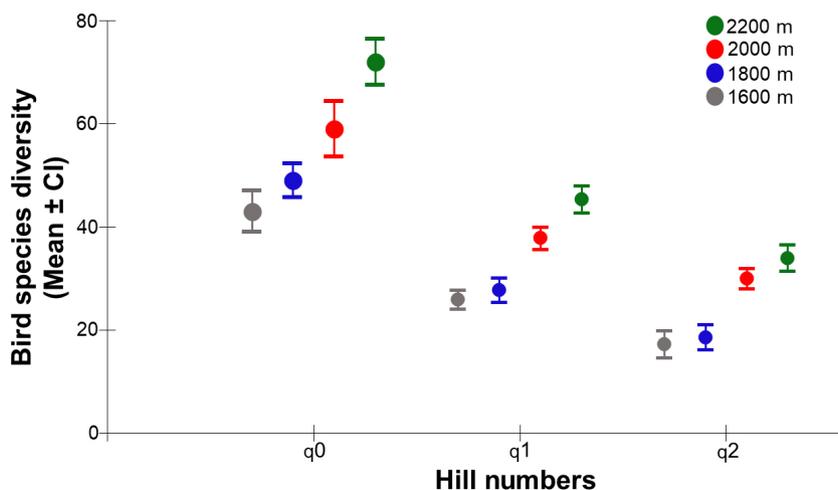


Fig. 2. Bird species richness ( $q0$ ) and diversity ( $q1$  and  $q2$ ) along an elevational gradient in the Sierra Madre del Sur in southern Mexico.

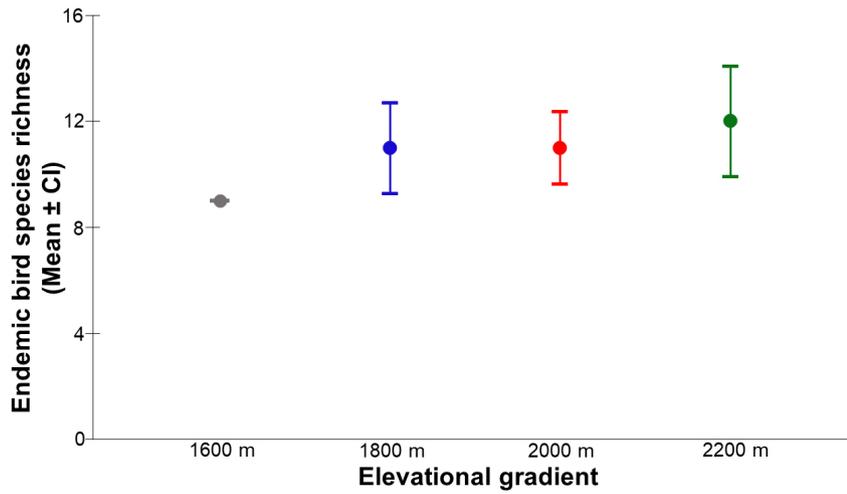


Fig. 3. Endemic bird species richness ( $q_0$ ) along an elevational gradient in the Sierra Madre del Sur in southern Mexico.

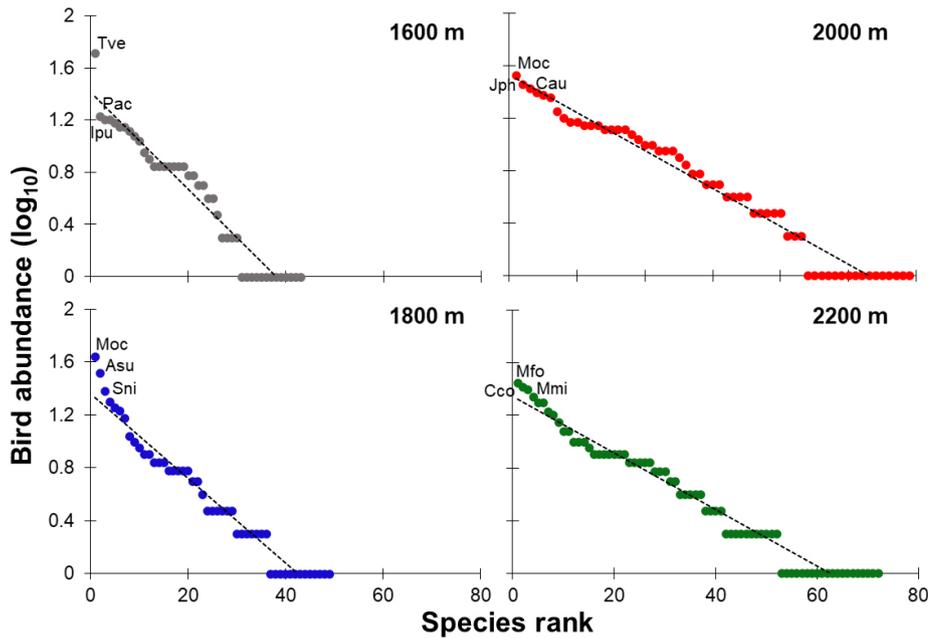


Fig. 4. Rank-abundance curves for bird species at each of the four elevation sites in the Sierra Madre del Sur in southern Mexico. Bird species code: *Aphelocoma sumichrasti* (Asu), *Catharus aurantiirostris* (Cau), *Cyanocitta coronata* (Cco), *Icterus pustulatus* (Ipu), *Junco phaeonotus* (Jph), *Melanerpes formicivorus* (Mfo), *Myadestes occidentalis* (Moc), *Myioborus miniatus* (Mmi), *Peucaea acuminata* (Pac), *Setophaga nigrescens* (Sni), *Tyrannus verticalis* (Tve).

Table 1. Covariance analysis (ANCOVA) for the rank-abundance curves along an elevational gradient in the Sierra Madre del Sur in southern Mexico. The  $F$  statistic (above the diagonal) and significance (below the diagonal) are indicated as  $p \leq 0.01$  (\*\*),  $p \leq 0.001$  (\*\*\*)

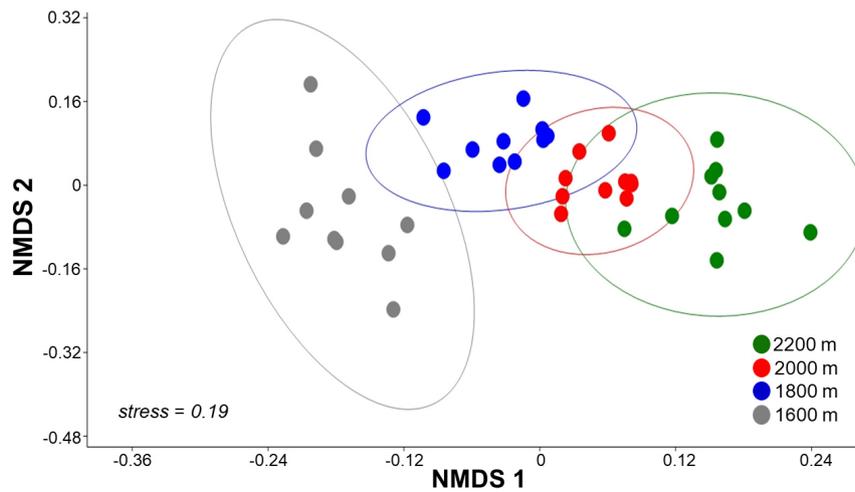
	1600 m	1800 m	2000 m	2200 m
1600 m		$F_{1,88} = 8.9$	$F_{1,98} = 32.1$	$F_{1,111} = 140$
1800 m	**		$F_{1,104} = 6.9$	$F_{1,117} = 98.5$
2000 m	***	**		$F_{1,127} = 80.2$
2200 m	***	***	***	

were the species that most influenced the dissimilarity of bird assemblages among sites (Table 2). Meanwhile, *Tyrannus verticalis* was the most abundant bird species at 1600 m (Table 2). Other species such as *Aphelocoma sumichrasti*, *Columbina passerina*, *Catharus aurantiirostris*, and *Amazilia beryllina* were present along the entire elevational gradient (Table 2). The faunal congruence curves showed that the 2200-m site had the highest rate of turnover of endemic bird species in relation to the rest of the sites which averaged a turnover rate of 76% (Fig. 6).

## DISCUSSION

### Bird richness, diversity, and endemism

Bird species richness and diversity increased with increasing elevation. Although contrary to our expectations of a monotonic decrease in species richness with increasing elevation, we offer the following explanations for the observed positive correlation between diversity and elevation. The presence of a transition zone, or ecotone, between cloud forest and pine-oak forest at 2200 m likely provides greater



**Fig. 5.** Differences in the abundance and composition of bird species per sampling point along an elevational gradient in the Sierra Madre del Sur in southern Mexico ordered by a non-metric multidimensional scaling based on the Bray-Curtis similarity index. Ellipses indicate 95% significance.

**Table 2.** Percentage contribution of bird species to assemblage differentiation along an elevational gradient in the Sierra Madre del Sur in southern Mexico according to a SIMPER analysis. Only bird species with a contribution greater than 2% are shown. Av. dissim = average dissimilarity

Bird species	Mean abundance (1600 m)	Mean abundance (1800 m)	Mean abundance (2000 m)	Mean abundance (2200 m)	Av. dissim.	% contribution	% cumulative
<i>Myadestes occidentalis</i>	-	4.4	3.4	2	4.03	4.69	4.69
<i>Aphelocoma sumichrasti</i>	1.4	3.3	1.5	0.1	3.17	3.70	8.39
<i>Tyrannus verticalis</i>	5.2	-	-	-	3.13	3.65	12.04
<i>Junco phaeonotus</i>	-	-	2.9	1.7	2.51	2.93	14.97
<i>Myioborus miniatus</i>	0.1	-	2.3	2.5	2.38	2.77	17.74
<i>Contopus pertinax</i>	-	2	2.5	0.6	2.35	2.74	20.47
<i>Columbina passerina</i>	0.2	2	2.5	0.6	2.34	2.73	23.20
<i>Catharus aurantiirostris</i>	0.6	1	2.7	1.4	2.12	2.47	25.67
<i>Columbina inca</i>	1.1	1.7	-	-	2.03	2.37	28.04
<i>Setophaga nigrescens</i>	0.2	2.4	1.3	-	2.03	2.36	30.40
<i>Cyanocitta coronata</i>	-	-	1	2.6	2.01	2.35	32.75
<i>Saucerottia beryllina</i>	0.7	0.6	2.4	0.1	1.92	2.23	34.98
<i>Melanerpes formicivorus</i>	-	-	0.3	2.8	1.81	2.11	37.09
<i>Archilochus alexandri</i>	-	0.1	1.4	2.2	1.77	2.07	39.16
<i>Basileuterus rufifrons</i>	0.9	1.8	0.3	0.2	1.76	2.05	41.21
<i>Regulus calendula</i>	1.5	0.6	1.5	0.1	1.73	2.01	43.22

ecological heterogeneity and resource availability that diversifies bird presence at that elevation (Terborgh 1985; Martínez-Morales 2007; Santiago-Pérez et al. 2009). This is in line with other studies that demonstrate how ecotones maintain high species diversity along environmental gradients by both housing a mixture of temperate and tropical plant communities that provide potential food resources for birds and also by forming an ecological barrier that limits species dispersal to other sites (Terborgh 1977 1985; Navarro 1992; Kark et al. 2007; Kark 2013). Another factor that can be contributing to higher bird species diversity in the upper portion of the elevational gradient is the presence of a greater number of species that exist exclusively in high elevation montane forests, such as *Dendrotyx macroura*, *Henicorhina leucophrys*, *Cardellina rubra*, and *Cyanolyca mirabilis* (Navarro and Escalante-Pliego 1993). Similarly, the presence of several resident bird species with Neotropical (e.g., *Lampornis clemenciae*, *Mitrephanes phaeocercus*, *Trogon collaris*) and Nearctic-affinity (e.g., *Loxia stricklandi*, *Peucedramus taeniatus*) explains higher diversity at the high elevation site. Finally, the high numbers of migratory bird species present at the higher elevation 2200 m site likely plays a role in the observed pattern as well. In general, Neotropical migratory birds arrive to the temperate forests of western Mexico during the autumn-winter migration or along their migration routes to South America, during which they use these forests as intermediate stopping points (Hutto 1992; Navarro and Escalante-Pliego 1993; Almazán-Núñez et al. 2009).

Upholding the pattern of increasing diversity with elevation, the second-highest richness and diversity levels were found at the 2000 m elevation site. The high bird diversity found at 2000 m is mainly related to the presence of pine-oak forest at this site, which has been

regularly observed to have higher bird diversity than other plant communities such as the lower-elevation oak forests at 1800 m (Navarro and Escalante-Pliego 1993; Escalante et al. 1998). For example, studies show that pine-oak forests provide greater resource abundance and a complex mosaic of microhabitats for several bird species (Almazán-Núñez et al. 2009 2018a), including *Icterus abeillei*, *Melospiza albicollis*, and *Trogon ambiguus*; all of which were observed in our pine-oak forest site at 2000 m. Pine-oak forests have also been shown to favor the presence of additional bird species, including woodpeckers (*Dryobates jardinii*, *Melanerpes formicivorus*), woodcreepers (*Lepidocolaptes affinis*, *L. leucogaster*) and warblers (*Cardellina rubrifrons*, *Setophaga occidentalis*), as these birds need pine or oak trees to make their nests and forage on the bryophytes associated to these species of tree trunks (Navarro and Escalante 1998; Sillett 1994; Almazán-Núñez et al. 2018a).

Habitat structure and environmental conditions, like temperature and precipitation associated with seasonal weather, have also been found to influence fluctuations in species richness and abundance along elevational gradients (Golawski and Mitrus 2018). For instance, our site at 1600 m was characterized by the presence and dominance of tropical dry forest, an ecosystem with marked dry and rainy seasons throughout the year (Dirzo et al. 2011). Tropical dry forest vegetation types lose foliage during the dry season, causing a decrease in resource availability for birds (e.g., less flowering and arthropod presence; Ceballos et al. 2010) and an increase in bird nest predation (Renton and Salinas-Melgoza 2004). The described climatic seasonality effects observed notably decreased our recorded bird richness at the lower elevation site. Moreover, we suspect that some

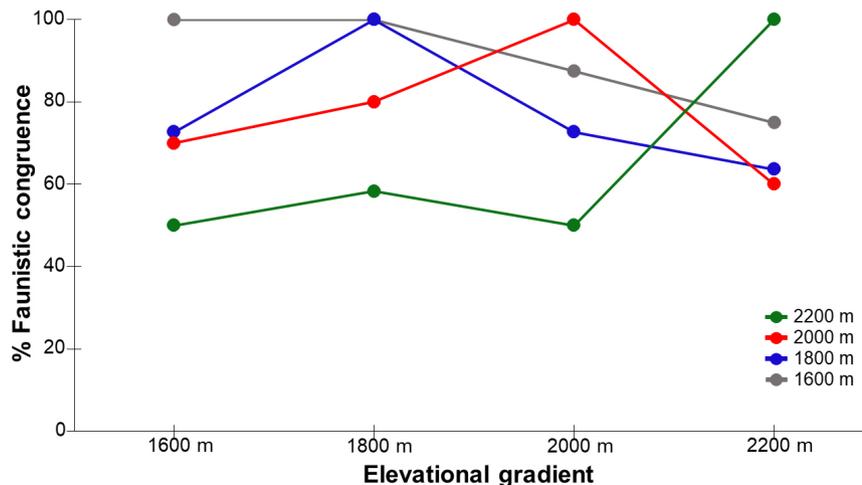


Fig. 6. Faunal congruence curves for endemic bird species along an elevational gradient in the Sierra Madre del Sur in southern Mexico.

of the bird species we recorded at the 1600-m site, such as some facultative insectivores, frugivores, and nectarivores (*e.g.*, *Cynanthus doubledayi*, *Icterus pustulatus*, *Piaya mexicana*) likely moved to higher elevations in the dry season to exploit more favorable food resources and nesting conditions that can enhance survival (Ornelas and Arizmendi 1995; Arizmendi 2001; Boyle 2008 2017). Future studies quantitatively assessing environmental conditions and variability would be valuable in this regard.

Anthropogenic modifications observed at the 1600-m site could have also influenced the resulting depressed bird species richness and diversity at lower elevations. Notable changes in vegetation structure were evident at this site, including, for example, the dominance of plant species that indicate disturbance or secondary succession (*e.g.*, *Acacia farnesiana*, *Brahea dulcis*, and *Ipomoea murucoides*; Pavón et al. 2006; Carranza 2007). These structural impacts are likely related to the proximity (within 1.2 km) of the city of Chilpancingo, one of the largest urban areas in the region. Urban sprawl has led to ongoing land-use change in this region especially along the periphery of the city including where our 1600-m site was located. A likely consequence is that most of the bird species distributed in this site are negatively affected (Sierra-Morales et al. 2016; Almazán-Núñez et al. 2018b). Although, the influence of human activity at this site could also promote an increase in the abundance of generalist bird species associated with disturbed areas such as *Tyrannus verticalis*, *Peucaea acuminata*, and *Icterus pustulatus* (Pizo 2007; Şekercioglu 2012; Alvarez-Alvarez et al. 2018).

In terms of endemic species, the 2200-m site contained the highest number of endemic bird species followed by the 1800-m and 2000-m sites. The high number of endemic bird species at 2200 m can be attributed to the presence of cloud forest at that elevation, an ecosystem with a naturally disjunct distribution throughout Mexico (Gual-Díaz and Rendón-Correa 2014). Therefore, *in situ* speciation of numerous bird populations, including *Arremon kuehnerii* and *Chlorospingus albifrons*, which we observed at our 2200 m site, have been documented in cloud forests (Sánchez-González et al. 2007; Navarro-Sigüenza et al. 2013). At the other end of the elevation gradient (1600 m), there were less endemic bird species observed which could be related to the aforementioned presence of agricultural crops, cattle ranching, and urban sprawl modifying the floristic composition of the tropical dry forest in a way that drastically reduces bird habitat and the presence of birds generally (Sierra-Morales et al. 2016; Almazán-Núñez et al. 2018b). That the 1600-m site had the lowest number of bird

endemism might also be linked to the fact that the tropical dry forest at our study site was located slightly above the characteristic upper elevation limit for this forest type (Rzedowski 1978). Tropical dry forests tend to develop in sub-humid warm climates below 1500 m along the southern Mexican Pacific slope (Trejo-Vázquez 1999; Dirzo et al. 2011). The higher elevation tropical dry forest in our study could have restrained the presence of other endemic birds that generally occur in this ecosystem, especially given characteristic climatic and physiognomic vegetative conditions of these southern Mexico forest types appeared to be missing (Bullock et al. 1995). For example, in our study area, several endemic bird species, such as *Colinus coyolcos*, *Habia affinis*, and *Haemorhous mexicanus* that have been recorded in other more structurally-conserved dry forests (and that are not mixed by scattered *Juniperus flaccida* trees as our site was), were absent at this site (Almazán-Núñez et al. 2015; Alvarez-Alvarez et al. 2018).

### Bird species turnover and conservation perspectives

The bird species composition at the 1600-m site differed the most in comparison to the other sites as was shown in the ordination analysis. This result confirms our prediction that the bird species composition at the lowest elevation site would differ from the others elevational sites. This result can be explained by the dominance of Nearctic-affinity plant communities, such as oak, pine-oak, and pine forests, in the sites located at 1800, 2000, and 2200 m; while the site at 1600 m was mostly dominated by tropical dry forest ecosystems of Neotropical affinity. This latter ecosystem, as mentioned previously, showed signs of disturbance, which increased the dominance of some generalist bird species, such as *Peucaea acuminata* and *Tyrannus verticalis*. As a consequence of the presence of dominant species, low evenness in rank-abundance was observed at this site. This finding is also related to the presence of other several granivore and omnivore bird species typical of disturbed habitats, including *Aimophila ruficeps*, *Columbina inca*, *P. acuminata*, and *Zenaida asiatica* (Pineda-Diez et al. 2012; Almazán-Núñez et al. 2015; Alvarez-Alvarez et al. 2018).

As we expected, the highest turnover rate of endemic bird species along the elevational gradient was found at the 2200-m site. This result is linked to geological, evolutionary, and ecological processes that gave rise to the disjunct distribution of Neotropical cloud forests across the southern Mexican highlands (Hernández-Baños et al. 1995). That is, the resulting distribution of isolated cloud forests act as 'island'

microcosms that affect bird species turnover due to distributional constraints (Sánchez-González et al. 2008). These distributional constraints have promoted speciation processes for several bird groups (e.g., *Arremon kuehnerii*, *Dendrocolaptes sheffleri*, *Lampornis margaritae*) within Mesoamerican humid montane cloud forests (Cortés-Rodríguez et al. 2008; Navarro-Sigüenza et al. 2013 2020). In fact, the presence of endemic bird species, such as *Cardellina rubra*, *Catharus occidentalis*, and *Chlorospingus albifrons* within our study's cloud forest at 2200 m, suggests that the distribution of bird species is heavily influenced by the ecological conditions along the elevational range. Similarly, the highest turnover rate of endemic bird species occurred at the highest 2200 m elevation site relates to the structural conditions of the cloud forest, which combines floristic elements of both tropical and temperate forests (Bruijnzeel et al. 2011). This intermixed forest structure results in a bird composition largely comprised of mixtures of both Neotropical and Nearctic birds (Hernández-Baños et al. 1995), which also contributed to the resulting high taxonomic diversity at the 2200-m site. Another important factor explaining the high endemism at higher elevations is the presence of an ecotone at 2200 m that could have contributed to the discontinuity in the elevational distribution of bird species we observed (Terborgh 1985; Navarro 1992; Kark 2013).

Interestingly, several bird species in the overall study area have high conservation value because of their degree of endemism and vulnerability in the face of accelerating land-use changes. For example, *Cyanolyca mirabilis*, *Dendrortyx macroura*, and *Geothlypis tolmiei* are considered threatened and/or endangered according to Mexican law (SEMARNAT 2010), and others such as *Aphelocoma sumichrasti*, *C. mirabilis*, and *Selasphorus rufus* are threatened and/or vulnerable according to the International Union for Conservation of Nature (IUCN 2019). *A. sumichrasti* and *C. mirabilis* are two species restricted to the montane forests of the Sierra Madre del Sur (Navarro and Escalante-Pliego 1993; Howell and Webb 1995; Navarro 1998). Given most of these bird species were exclusively observed in the 2200-m site that also retains traditional campesino resource management practices, this site can be considered to have the highest conservation value. Nevertheless, the biological importance of the remaining more impacted sites must also be highlighted as these areas still retain ecological structure and function in a way that provides critical habitat and resources for birds and other fauna that often move across elevations seasonally. In spite of urbanization, agriculture, cattle ranching, and forest fires that have affected local vegetation cover and reduced bird habitat availability, our results support effective

conservation strategies and biological resources management across the Sierra Madre del Sur in general – one of the most important biodiversity hotspots in Mexico (Luna-Vega et al. 2016).

## CONCLUSIONS

Our study demonstrates that bird species richness and diversity increase with increasing elevation within the Mexican Sierra Madre del Sur – a pattern that is likely linked to forest types, as well as proximity of sites to urban centers. Specifically, the highest elevation site (2200 m), which represents an ecotone between a cloud forest and pine-oak forest, had the highest bird species diversity, number of endemic, exclusive, and at-risk species, as well as the highest species turnover rate. On the opposite end of the elevational gradient, the lowest elevation site (1600 m), which was most impacted by urban sprawl, had the lowest values of diversity and endemism. Overall, our study not only captures changes in bird distribution and associated ecological influences along a subtropical elevational gradient, but advances ecological understanding of montane landscapes in a way that can inform conservation strategies across an important biodiversity hotspot in Mexico and Mesoamerica – the Sierra Madre del Sur.

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## Supplementary materials

**Table S1.** Bird species recorded along an elevational gradient in the central portion of Guerrero state within Sierra Madre del Sur in southern Mexico. Relative abundance values are presented. Seasonality (Sea): RP: permanent resident, MI: winter migratory. Endemism (End): E: endemic and CE: quasi-endemic to Mexico. (download)