

RESEARCH ARTICLE

ECOLOGY

Twentieth century turnover of Mexican endemic avifaunas: Landscape change versus climate drivers

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Numerous climate change effects on biodiversity have been anticipated and documented, including extinctions, range shifts, phenological shifts, and breakdown of interactions in ecological communities, yet the relative balance of different climate drivers and their relationships to other agents of global change (for example, land use and land-use change) remains relatively poorly understood. This study integrated historical and current biodiversity data on distributions of 115 Mexican endemic bird species to document areas of concentrated gains and losses of species in local communities, and then related those changes to climate and land-use drivers. Of all drivers examined, at this relatively coarse spatial resolution, only temperature change had significant impacts on avifaunal turnover; neither precipitation change nor human impact on landscapes had detectable effects. This study, conducted across species' geographic distributions, and covering all of Mexico, thanks to two large-scale biodiversity data sets, could discern relative importance of specific climatic drivers of biodiversity change.

INTRODUCTION

Although the reality of climate change and its implications for Earth's natural systems is appreciated (1), detailed information on biodiversity dynamics, particularly in the face of changing landscapes and climates, has remained somewhat opaque. Observational studies have documented changes that associate temporally with climate change (2). Multitudes of correlational studies have assessed climate effects on species' distributional potential, the best of which consider multiple drivers and multiple sources of uncertainty (3–6), but a more broadly integrative approach is critically needed (7–9), both for conservation and for policy questions.

Previous studies assessing gains and losses of species across broad landscapes have generally focused on individual species' trends and patterns manifested across many such species [for example, Living Planet Index, (10)], but this approach depends on sampling and distribution of studies, and thus is superconcentrated in the “developed” world (11). Other such analyses have used proxies, developing correlational niche models based on associations with original vegetation distributions, but transferring results to land-use classifications (12); however, such approaches are highly assumption-laden and have not seen broad adoption. Much preferable would be a data-driven approach, in which actual changes can be observed and documented from real-world data.

This study aimed to develop a detailed picture of range dynamics of Mexican endemic bird species over the past half-century. We took advantage of the confluence of two large-scale data streams: first, a detailed compilation of historical museum specimens of Mexican birds, and second, a growing storehouse of modern observational data on Mexican birds. We documented original distributions of species via ecological niche models based on the historical data in the context

of historical climate data, and compared with recent records across 72 well-sampled 1° squares across the country. We then related avifaunal change to aspects of landscape modification and human presence, and to actual, observed climate change over the same period, to assess likely drivers of these changes.

RESULTS

The two data sets characterizing Mexican bird distributions provided dense coverage across much of the country (Fig. 1), including 331,800 historical (1920–1950) and 892,512 recent (post-2000) overall occurrence records of Mexican birds, permitting detailed mapping of distributional areas in each time period. Interpolating distributions from the historical data via ecological niche models based on historical climate data yielded detailed distributional maps for each species. Recent occurrence data were distributed less evenly across the country, concentrating along routes of access and around tourist destinations (Fig. 1), but 72 1° pixels across the country (Fig. 2) had both sufficient sample size (≥ 300 records) and acceptable inventory completeness ($C \geq 0.8$); these well-documented current avifaunas formed the basis for our before-and-after comparisons.

Comparing historical and recent avifaunas revealed that the relatively few gains of species were focused in the central-northern Chihuahuan Desert, and in northwestern Baja California along the California border (Fig. 3). Losses of species concentrated in the northwest (Sonora, Sinaloa), southern Chihuahuan Desert (Durango, Jalisco, Guanajuato, Querétaro), and in the southeast in Chiapas (Fig. 3); we note that the northernmost foci of losses reflect high proportional losses of the very few Mexican endemic species found there. Overall turnover basically amounted to the union of the gains and losses, without any new patterns emerging.

Relating drivers of anthropogenic landscape modification [maximum and average human influence index (HII)] and climate (precipitation change, temperature change) to these three avifaunal responses, multiple regression analyses detected three significant outliers for species losses and four for gains (Fig. 1). Of the four independent variables in the multivariate regression analyses, only temperature

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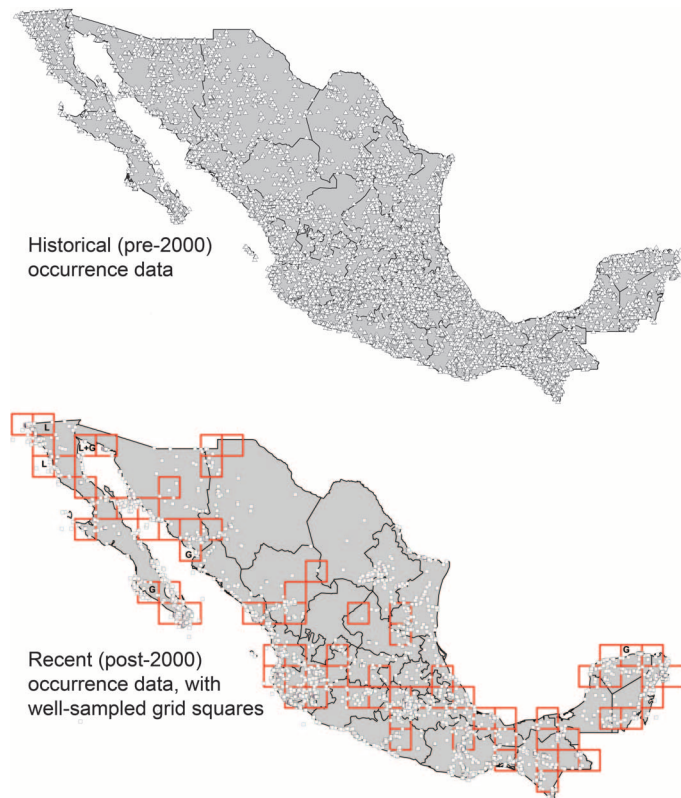


Fig. 1. Historical and recent occurrence data for Mexican birds. Maps illustrate the density of occurrence data available as sampling underlying the records of endemic species used in this study. For recent data, well-sampled 1° pixels are shown as red boxes. “G” and “L” indicate pixels that appeared as significant outliers in the final regression analysis, for gains and losses, respectively.

showed significant effects, which were manifested in both response variables (F test, $P < 0.005$, in both cases). Precipitation and HII showed no significant effects in any of the regression models.

DISCUSSION

This study explores an approach that is only now becoming feasible to implement: data-driven studies of biotic dynamics. That is, with biodiversity informatics emerging as a discipline (13–15), some regions and taxa are represented with sufficiently dense information that such before-and-after comparisons become possible. In this case, we have explored avifaunal change across Mexico, where the efforts of Mexico’s national biodiversity commission (CONABIO) have assembled large-scale biodiversity resources (16); another world region where such a temporal sequence of rich biodiversity data might be assembled would be Australia (17), but the list of possibilities is not long, which represents a significant limitation of these approaches.

Another limitation of this study is that of the historical range summaries used. That is, our historical data set is quite rich, but holds all of the usual sampling biases characteristic of biodiversity data, such as concentration along roads and in accessible areas services (18). For that reason, we developed ecological niche models as a climate-based interpolation of these data to represent species’ distributional patterns in the early to middle 20th century. Although richness estimates from

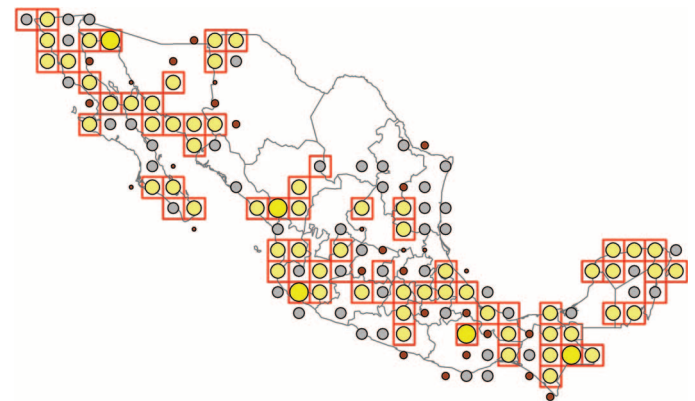


Fig. 2. Summary of recent occurrence data of Mexican endemic bird species derived from aVerAves observational data sets. Data are summarized in terms of inventory completeness (C), which is expressed as the size of the circle; 1° pixels meeting the criteria for “well characterized” (that is, ≥ 300 records, $C > 0.8$) are outlined as red squares.

“stacking” exercises based on such suites of ecological niche models have been criticized for tendency to overestimate species richness (19), we note that we have not created aggregate statistics (for example, richness) and rather are seeking species-by-species correspondence; that gains and losses of species in such comparisons would have artifactual associations with environmental parameters is unlikely. The observational data we used to summarize current distributions of species carry distinct spatial biases, but our focus on well-sampled grid squares avoids much of this complication.

Gains and losses of endemic bird species across Mexico have rather markedly nonrandom distributions, with numbers of losses greatly outnumbering gains, likely owing to the subset of species on which we concentrated (species endemic to Mexico). Previous such studies have tended to be global in nature, conducted at very coarse scales (20), and model projections comparing multiple drivers often point to additive effects (21). Single-species analyses of multiple drivers (for example, land use, fire frequency, and climate) have identified climate change as a prime driver (22); other studies have analyzed numerous species (9) but have looked only at climate change drivers and assumed temperature to be the causal factor (23). There is little analysis of the relative roles of changes in temperature and precipitation, but one global analysis pointed to a greater role of precipitation (24), whereas another found additive effects of climate, land-use change, and pathogens (25), both in terms of determining faunal change. Our results comparing effects of changes in temperature, precipitation, and human impacts on landscapes (note that land-use change was not assessed) focused attention rather absolutely on temperature change.

MATERIALS AND METHODS

Experimental design

This study connected four data streams: (i) historical information regarding bird species’ distributions based on historical specimen information synthesized as ecological niche models, (ii) recent distributional information obtained from aVerAves (<http://ebird.org/content/averaves>), (iii) information on human impacts on Mexican landscapes, and (iv) information on observed degrees of climate change across the country.

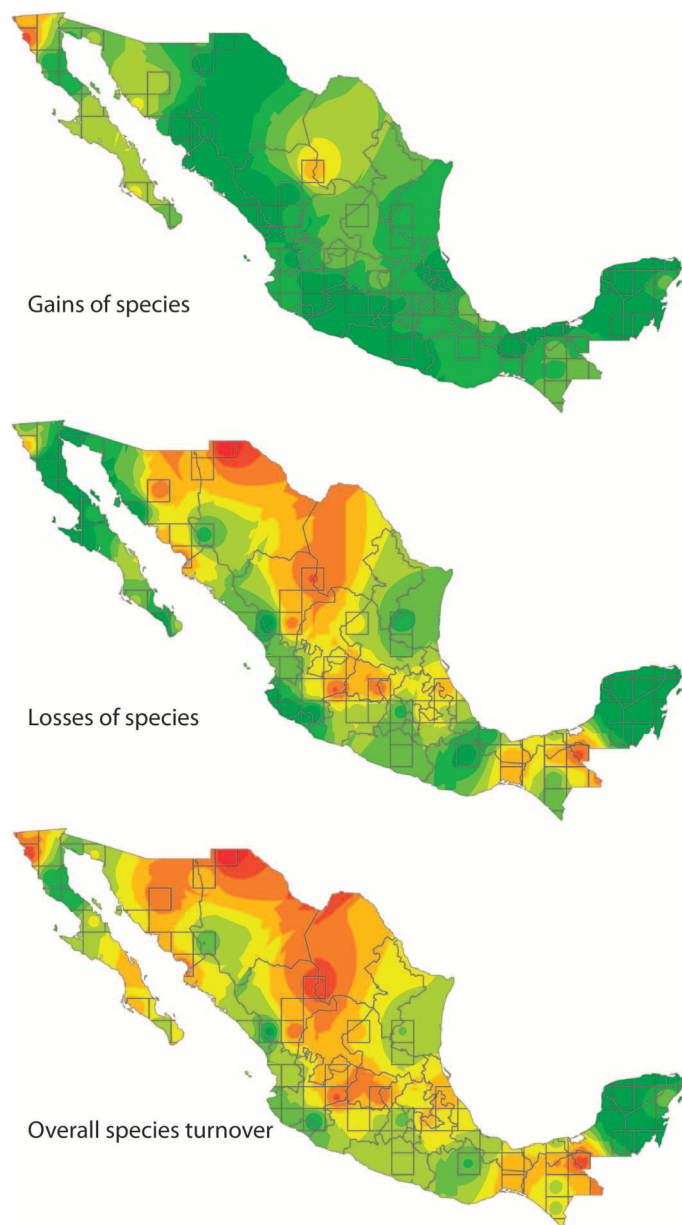


Fig. 3. Summary and interpolation of gain, loss, and overall turnover of Mexican endemic bird species. These patterns were measured within well-sampled pixels (shown as squares) and interpolated across the entire country. Green indicates low values, grading to red (high values).

Assembling these diverse data streams into a single, coherent framework required considerable effort aimed at data integration, but permitted multivariate statistical tests comparing the relative effects of human landscape modification and aspects of climate change on Mexican endemic avifaunas.

Characterizing “original” avifaunas

We summarized distributions of 115 endemic species of birds across Mexico (26) via two large-scale databases that we assembled and quality-controlled in the course of previous projects. That is, we used point-occurrence data for the birds of Mexico that were assembled as part of

the *Atlas of Distributions of Birds of Mexico* project (27), which represents 331,800 specimen records of birds from 1814 to 1999, with a modal peak in 1920 to 1950. Although this data set carries many gaps and spatial biases, which we have documented in previous publications (28), it represents as complete a summary of the country’s avifauna as can be assembled from historical specimen data.

To generalize these occurrence data and fill gaps in spatial coverage, also in a previous project (29), we used ecological niche modeling to process raw occurrence data into raster (grid-based) maps of geographic ranges for each species. Complete methodological information is available in the original project publications (29), but in brief, these maps were developed on the basis of mid-20th century climatologies (30), and niches were estimated using a genetic algorithm (31). We quality-controlled each map individually via comparison with published range maps (32), checking every record that strayed from expectations. These maps thus represent a mid-20th century set of occurrence data interpreted and interpolated in terms of mid-20th century climate conditions; to summarize these data at 1° spatial resolution, we created a point shapefile with points at the center of each coarse grid cell, and extracted values of the species’ distribution grids to these points.

Characterizing current avifaunas

We obtained a complete extract of occurrence data from aVerAves (<http://ebird.org/content/averaves>) as of July 2012. The initial data set consisted of 892,512 records, which reduced to 698,459 unique combinations of year, month, day, scientific name, latitude, and longitude. Of these records, 634,252 records came from the year 2000 and after, which reduced to 542,189 records after removing nonstandard species names (26). Further reducing to 1° pixels, this data set distilled to 38,324 records unique in terms of year, month, day, scientific name, and 1° pixel, of which 18,465 records pertained to the 115 Mexican endemic species [sensu (26)]. This data set thus represents a summary of recent occurrence data for birds across Mexico—although it has clearly grown since our analyses, and will continue to grow, it provides a dense coverage of modern occurrence information for the country.

We summarized records in 259 1° pixels that covered the country, and filtered those pixels to retain only those with at least 300 occurrence records. We further filtered the pixels according to their inventory completeness, as follows—we calculated observed (S_{obs}) and expected (S_{exp}) numbers of species in each 1° pixel via the Chao2 indicator (33), which is calculated as $S_{exp} = S_{obs} + a^2/2b$, where a represents the number of species observed on only a single day in the pixel, and b represents the number of species observed on only 2 days in the pixel. We then calculated inventory completeness as $C = S_{obs}/S_{exp}$. We retained only those pixels presenting $C > 0.8$ as well-inventoried pixels; these pixels are thus of comparable completeness in their avifaunal characterization. See Sousa-Baena *et al.* (34) for additional detail on these calculations.

Summary and integration of data from two periods

We omitted extinct species (*Oceanodroma macrodactyla*, *Quiscalus palustris*, *Campephilus imperialis*, and *Zenaida graysoni*) represented only in the historical data, as well as a few island-restricted taxa [*Mimodes graysoni*, *Puffinus auricularis*, *Synthliboramphus hypoleucus*, *Synthliboramphus craveri*, “*Thryomanes*” (= *Troglodytes*) *sissonii*, and *Troglodytes tanneri*] that would not be well represented or well sampled in the modern data sets. We included two nonoverlapping seasonal distributional areas (each endemic or quasiendemic to Mexico) for *Vermivora crissalis*

separately in all calculations. Finally, we fixed instances of noncompatibility in the taxonomy of the two data sets, mostly related to changed generic allocations (for example, *Aimophila* species now in *Peucaea* and *Amphispiza*, *Buarremon* in *Arremon*).

We summarized historical and recent views of Mexican endemic species' distributions and occurrences as a 2×2 matrix for each 1° pixel: a = historically present and recently recorded, b = historically absent but recently recorded, c = historically present but not recorded recently, and d = neither present historically nor recorded recently. From these numbers, for each pixel, we calculated percent gain of species as $G = 100b/(a + b)$, percent loss of species $L = 100c/(a + c)$, and overall percent turnover as $T = 100(b + c)/(a + b + c)$. For the purpose of visualization, we interpolated these indices across the country via inverse distance weighting based on the four nearest neighbor pixels.

Analysis of landscape drivers

We related G , L , and T to two suites of variables that may cause avifaunal change. In particular, we explored the HII, version 2 (<http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-influence-index-geographic>; 35), which provides an index of human impacts on global landscapes based on nine data layers summarizing human population pressure (population density), human land use and infrastructure (built-up areas, nighttime lights, land use/land cover), and human access (coastlines, roads, railroads, navigable rivers); we note that this index does not include dimensions of land-use change. The spatial resolution of the HII was 0.008333° , such that 14,400 HII pixels filled each 1° pixel. We used average and maximum values of HII within each 1° pixel to characterize HII within each coarser pixel.

We also explored observed patterns of climate change between 1910–1949 and 1980–2009, developed from ~800 and ~4000 weather stations across Mexico for the first and second time periods, respectively. Raw station data were interpolated and synthesized into country-wide raster coverages for each period by ANUSPLIN, version 4.35 (36). We summarized differences between the two time periods in terms of average temperature and total annual precipitation. We linked the climatic data to the avifaunal data by plotting 21,000 random points across the country, extracted values from the climate grids to the points, and averaged values for all points within each of the coarse-resolution (1°) pixels under analysis.

Finally, to summarize and assess overall influences on avifaunal change across Mexico, we assessed four independent variables (temperature difference, precipitation difference, and average and maximum HII) in relation to three dependent variables (G , L , and T). We used multiple regression analyses performed independently on G , L , and T , as functions of the independent variables. We detected significant outliers as those records for which standardized residuals were $>|2|$.

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