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RESEARCH ARTICLE

Directional effects of biotic homogenization of bird communities in Mexican seasonal forests

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ABSTRACT

Biotic homogenization—the erosion of biological differences between ecosystems owing to human perturbation—is a trait of the global biodiversity crisis that can affect tropical dry forest biodiversity. We tested whether biotic homogenization was occurring in resident forest bird communities in west-central Mexico. We conducted point-count surveys to assess biotic dissimilarity between resident bird communities in tropical deciduous and oak forests in the upper Balsas River basin across 3 levels of anthropogenic perturbation: primary forest, second-growth forest, and human settlements. We detected a reduction in species richness and taxonomic dissimilarity with increasing anthropogenic effects, due to a directional pattern in which lowland species expanded their elevational distributions up into oak forests. These results point to a need to change agricultural strategies to mitigate impacts on natural vegetation cover and biodiversity.

Keywords: anthropogenic perturbation, beta diversity, biodiversity, tropical dry forest, oak forest

Efectos direccionales de la homogeneización biótica en las comunidades de aves en bosques estacionales de México

RESUMEN

La homogeneización biótica – la erosión de diferencias biológicas entre ecosistemas debido a la perturbación humana – es un rasgo de la crisis global de biodiversidad, que puede afectar seriamente la biodiversidad de los bosques tropicales secos. En este trabajo evaluamos si la homogeneización biótica está afectando a las comunidades de aves residentes en la región centro-occidente de México. Realizamos puntos de conteo de aves para evaluar la disimilitud biológica entre las comunidades de aves residentes del bosque tropical caducifolio y el bosque de encino en la Cuenca Alta del río Balsas, considerando tres niveles diferentes de perturbación: bosque primario, crecimiento secundario y asentamientos humanos. Registramos la reducción tanto de la riqueza de especies como de la disimilitud taxonómica en función del incremento de las actividades antropogénicas, debido a un patrón direccional en el que las aves tropicales expanden su distribución altitudinal hacia los bosques de encino. Nuestros resultados presentan evidencia de que las actividades humanas promueven la homogeneización biótica, mediante un cambio direccional en las comunidades de aves. Estos resultados señalan la necesidad de cambiar las estrategias agrícolas para mitigar el impacto sobre la cobertura vegetal y la biodiversidad.

Palabras clave: perturbación antropogénica, biodiversidad, bosque tropical caducifolio, bosque de encino, diversidad beta

INTRODUCTION

Human activities are modifying natural systems around the planet, leading to the replacement and modification of original vegetation types with anthropogenic systems that meet human needs (e.g., food, housing, economic activity). Because many human requirements are similar among

sites, these modifications appear to increase similarity among disturbed areas (Kareiva et al. 2007, Corlett 2014), inducing selective removal of endemics, as well as habitat and food specialist species, while promoting the success of broadly distributed, generalist species (McKinney and Lockwood 1999, McKinney 2006). Several studies focused on bird communities in anthropogenic habitats have

shown that this environmental filtering favors generalist species' ecological success (i.e. resource attainment, survival, and reproductive output; Wilson 1987, Salgado-Negret and Paz 2015). Conversely, filtering affects specialist birds by reducing their specific habitats and food resources, which may in turn decrease survival, reproductive output, and ultimately population size, potentially driving them to local extinction (Crocini et al. 2008, Newbold et al. 2013, Paz Silva et al. 2016). Human-mediated transport also increases connectivity among formerly separated ecosystems, promoting biotic invasions (Hulme 2009, Baiser et al. 2012).

Biotic homogenization, a reduction in differences among the biotas of contrasting natural systems, has been described as a general consequence of human activities (McKinney and Lockwood 1999, Olden and Rooney 2006). Numerous studies of biotic homogenization have examined temperate forest bird communities in North America and Europe. These studies have identified spatial scales that define extinction and invasion processes in homogenization of biotas. At local scales, dissimilarity is reduced owing to the interplay of extinction and invasion processes, whereas regional biodiversity pools maintain higher turnover rates and dissimilarity values, despite local invasions and extinctions (Blair 2001, La Sorte and Boecklen 2005, Clergeau et al. 2006, Olden et al. 2006, Sorace and Gustin 2008). Recent studies have advanced our understanding of ecological changes in biological communities resulting from urbanization and agricultural activities (La Sorte and Boecklen 2005, Davey et al. 2012), and also of the effects of these phenomena on changes in latitudinal and seasonal species richness and the distribution of birds (Filloy et al. 2015, Leveau et al. 2015). In Neotropical wet forests, biotic homogenization occurs in disturbed environments at local scales; however, at landscape scales, high species turnover drives differentiation processes (Solar et al. 2015, Morante-Filho et al. 2016). In contrast, in seasonal forests, intensification of human perturbation drives biotic homogenization at landscape scales (Karp et al. 2012).

The major consequence of biotic homogenization, in the context of the current biodiversity crisis, is loss of biodiversity uniqueness (unshared elements that define the identity of biotas) owing to erosion of biological differences (beta diversity) among ecosystems (Olden et al. 2004, McGill et al. 2015), although species richness in regional pools (gamma diversity) seems to be increasing due to human-induced biotic interchange (Sax and Gaines 2003, McGill et al. 2015). Due to its global influence (Baiser et al. 2012), the study of homogenization is a priority on the biodiversity conservation agenda (Socolar et al. 2016). A long-term goal is to achieve strategies for reducing the effects of biotic homogenization on biodiversity and ecosystem functionality (Olden et al. 2005,

Şekercioğlu 2006, McGill et al. 2015), especially in ecosystems holding high numbers of species and endemics (Olden 2006, Rooney et al. 2007).

Neotropical seasonal forests are among the most vulnerable in the world, because of human modification for use in agriculture and livestock grazing (Sánchez-Azofeifa and Portillo-Quintero 2011). According to recent evaluations, $\geq 60\%$ of the original extent of Neotropical dry forest has already been transformed into anthropogenic habitats (Sánchez-Azofeifa and Portillo-Quintero 2011). Furthermore, the biodiversity of Neotropical dry forests is characterized by high species turnover and endemism (Stotz et al. 1996), making it vulnerable to effects of biotic homogenization. Despite their rich biodiversity and vulnerability, biotic homogenization in Neotropical seasonal forests remains poorly studied (but see Karp et al. 2012). In west-central Mexico, Neotropical forest areas have a complex topography that creates high species turnover between ecosystems (Balvanera et al. 2002, Ceballos et al. 2010), with many endemic species (Koleff et al. 2008, Ceballos et al. 2010). Anthropogenic activities reduce bird species richness and increase the abundance of generalist birds in Neotropical seasonal forests, but the effects on beta diversity have not been explored (MacGregor-Fors and Schondube 2011, 2012, Maya-Elizarrarás and Schondube 2015).

We examined biotic homogenization in resident bird communities across a perturbation gradient in the Balsas River basin of west-central Mexico. In this region, almost 26% of the bird community is endemic to Mexico (Navarro-Sigüenza et al. 2014), leading to its designation as a global priority endemic area (Stattersfield et al. 1998, Birdlife International 2017). We conducted bird surveys in tropical deciduous forest and oak forest, 2 well-preserved, endemism-rich, and ecologically contrasting seasonal forest types at different elevations. We evaluated biotic homogenization as the loss of biotic difference between the 2 forest types at 3 levels of human perturbation: primary forest, secondary forest, and human settlements.

METHODS

Study Area

We worked in a 225 km² area in the upper Balsas River basin (18°03'–17°54'N, 98°49'–98°59'W) in northeastern Guerrero, Mexico. The area presents an elevational gradient from 650 to 1,950 m. The climate is warm and semiarid with a summer rainy season ('Aw' according to the Köppen climate classification) and mean annual precipitation of 780 mm (Meza and López García 1997). Dominant vegetation types are tropical deciduous forest (650–1,200 m) and oak forest (1,400–1,950 m; Rzedowski 2006), with a transition zone around 1,300 m (Figure 1).

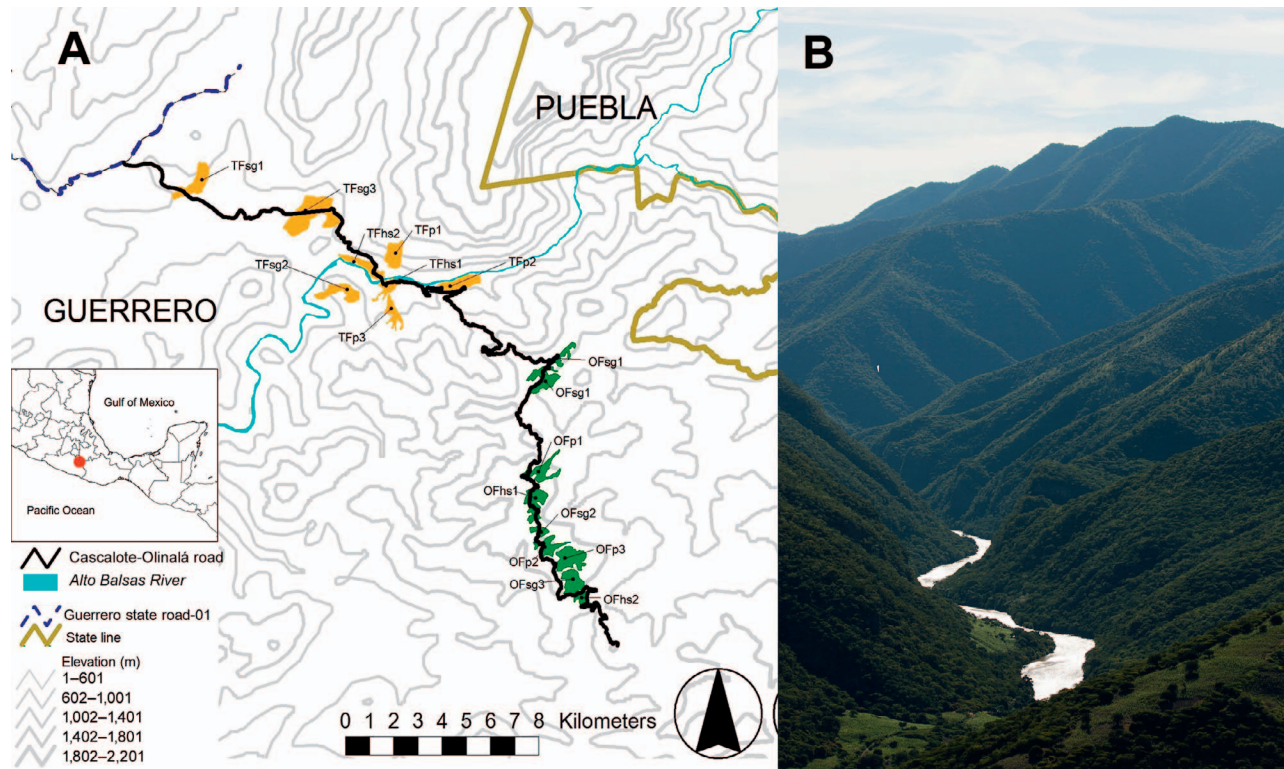


FIGURE 1. (A) Tropical dry forest and oak forest study sites in northeastern Guerrero, Mexico. Colored areas indicate the approximate locations of habitat patches surveyed at different perturbation levels in tropical deciduous (TF, orange areas) and oak forests (OF, dark green areas). p = primary forest; sg = secondary growth; and hs = human settlement. Gray lines indicate elevation. (B) Photograph illustrating the topography of the region (Photo credit: L.D.V.-R.).

Local human communities affect both forest types by clearing natural vegetation for subsistence agriculture, livestock grazing, firewood, and timber for building material. These activities define 3 levels of anthropogenic perturbation: (1) Primary forest, in which the original forest structure is practically unaltered. Human activity is limited to occasional human and livestock movements. Tropical deciduous primary forests are located at elevations between 726 and 994 m. Primary oak forests are found between 1,742 and 1,930 m. (2) Second-growth forest, in which the forest has been transformed by human activities within the last ~20 yr. Some vegetation has regrown, although cattle grazing frequently continues. Tropical deciduous secondary forests are located between 735 and 887 m. Oak secondary forests occur between 1,578 and 1,780 m. Our habitat characterization of primary and second-growth forests showed that primary forest had smaller vegetation clearances and more vertical strata than second-growth forest (Appendix Table 1). (3) Human settlements, in which most trees of the original forest have been replaced by houses, streets, dirt roads, orchards, and paddocks for cattle and poultry. Human settlements that have replaced tropical deciduous forest are located between 640 and 735 m. In former oak

forest, human settlements are located between 1,600 and 1,800 m.

Bird Counts

We performed surveys of bird communities along the perturbation gradient described above (Figure 1). For both tropical deciduous forest and oak forest, we selected 3 primary forest sites (a total of 175 ha in tropical deciduous forest, 196 ha in oak forest), 3 second-growth sites (355 ha and 211 ha), and 2 human settlements (97 ha and 109 ha). The size of individual habitat patches varied from 31 to 199 ha (mean = 71.5 ± 40.5 ha). The distance between adjacent stands of the same forest type was always >300 m, and between tropical deciduous and oak forest stands was 8–21 km.

We used 50-m fixed-radius point counts to record all species and the number of individuals of all species seen or heard during a 10-min sampling period. Observations were conducted during the first 4 hr after sunrise, avoiding rain. To ensure the independence of point counts in each survey event, points were located ≥ 200 m apart whenever possible, as recommended by Ralph et al. (1996). Our survey considered 100 point count stations, at which we performed a total of 342 point counts distributed across 4

sampling events between February and September, 2014, so that seasonal changes in habitat use by permanent resident birds (Navarro-Sigüenza et al. 2014; see full species list in Appendix Table 2) were taken into account (Vega-Rivera et al. 2010). In each survey event, we conducted between 6 and 9 point counts in each of the 3 primary and second-growth forest patches, and between 4 and 7 point counts in each of the 2 human settlements.

We based our analyses only on permanent resident species, excluding winter residents, summer residents, transients, and vagrants (Komar 2002). Residency status was assigned based on the seasonal occurrence of each species across the study area from surveys completed in 2009–2014 (L. Vázquez-Reyes personal observation) and on the existing literature (Howell and Webb 1995, Navarro-Sigüenza et al. 2014, Berlanga et al. 2015).

Data Analyses

Loss of species richness. We calculated an incidence-based coverage estimator (ICE) in EstimateS (Colwell 2013) to assess the effectiveness of our surveys for estimating species richness. This indicator separates frequent and infrequent species, and assumes heterogeneity in the detection probabilities of these groups. The estimated coefficient of variation for infrequent species characterizes the degree of heterogeneity among species incidence probabilities. These data are used to estimate the number of undetected species and the completeness of the survey (Lee and Chao 1994).

To assess whether human activities affected species richness, we performed a sample-based rarefaction analysis in EstimateS to calculate the expected species richness if all samples were reduced to a standard number of individuals (i.e. cut-off point). Thus, we compared species richness between communities with different sample sizes through the interpolation of expected species richness (Colwell and Coddington 1994, Gotelli and Colwell 2001). The rarefaction analysis was conducted with the maximum abundance recorded for each species in the surveys to avoid the bias caused by using the sum of individual bird abundances in each count event of the surveys.

We used 3 separate comparisons to evaluate whether perturbation had differential effects on subsets of the species pool: the first included all species considered in the survey (cut-off point of 308 individuals); the second included only widely distributed species (cut-off point of 205 individuals); and the third included only species endemic to Mexico (cut-off point of 40 individuals). If the 84% confidence intervals for species richness at the different levels of human perturbation were nonoverlapping, we considered values to be significantly different. Mathematical simulations showed that these confidence intervals represented adequate levels of $\alpha = 0.05$ (Payton et al. 2003, MacGregor-Fors and Payton 2013).

Biotic homogenization assessment. To test whether biotic homogenization occurred as a function of human perturbation intensity, we assessed taxonomic dissimilarity between tropical deciduous forest and oak forest patches at the same perturbation level with incidence-based dissimilarity indices (Olden and Rooney 2006). First, we explored the general association of all habitat patches with a classification analysis by constructing a dendrogram based on the Sørensen dissimilarity index (Sørensen 1948) using a complete linkage method. This analysis was done using the betapart package (Baselga and Orme 2012) in R 3.2 (R Development Core Team 2008).

To evaluate whether taxonomic differences between tropical deciduous forest and oak forest were eroded across the perturbation gradient, we compared biotic dissimilarity associated with nested dissimilarity and species turnover between communities using incidence data (Baselga 2010). The nestedness component reflects dissimilarity owing to changes in species richness when one community is a subset of other, whereas the turnover component is associated with species replacement between communities, regardless of species richness in each (Baselga 2010).

The nestedness component of dissimilarity was assessed using the nested resultant Sørensen index, β_{nestSor} (Baselga 2012), while the turnover component was assessed with the turnover resultant Sørensen index, β_{turnSor} (Baselga 2012). We evaluated differences between dissimilarity components by comparing β_{nestSor} and β_{turnSor} values for primary forest, second-growth forest, and human settlements for both tropical deciduous forest and oak forest to evaluate whether temporal variability affected the dissimilarity pattern. For these comparisons, we applied a Kruskal-Wallis test and post hoc Mann-Whitney paired comparisons at $\alpha = 0.05$, using the PAST software package (Hammer et al. 2001). When 84% confidence intervals were nonoverlapping, we assumed significant differences (Payton et al. 2003, MacGregor-Fors and Payton 2013).

RESULTS

We recorded 81 resident bird species, in 65 genera, 29 families, and 13 orders; 58 were found in tropical deciduous forest and 61 in oak forest. According to the ICE estimator, we recorded $\sim 93\%$ of predicted total richness, which suggests nearly complete sampling of bird communities. Twenty-four species (29%) were endemic or near-endemic to Mexico, 18 of which occurred in each forest type (Appendix Table 2).

Species richness compared using rarefaction revealed significant loss of bird species richness with increasing intensification of human activities. This pattern was consistent across the entire bird community, widely

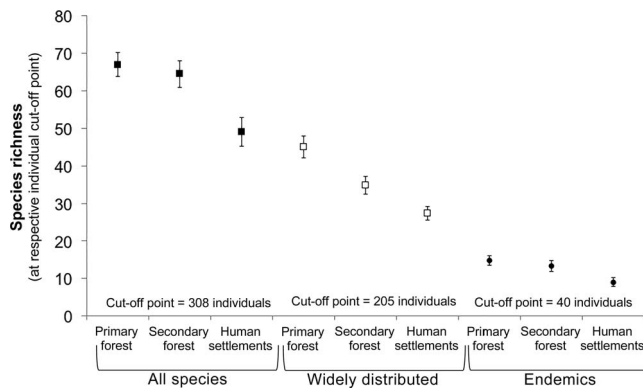


FIGURE 2. Bird species richness comparisons at 3 levels of perturbation (primary forest, secondary forest, and human settlement) in seasonal forests within the Balsas River basin, west-central Mexico. We used 3 separate comparisons to evaluate whether perturbation had differential effects on subsets of the species pool, each of them with a particular cut-off point for their rarefaction interpolation: the whole bird community (all species; cut-off point: 308 individuals); widely distributed species only (cut-off point: 205 individuals); and endemic species only (cut-off point: 40 individuals). Error bars show 84% confidence intervals for each subsample.

distributed species, and endemic species (Figure 2). For the whole community, secondary forest held 96% of the species richness of primary forest, whereas human settlements held only 73%. For widely distributed species, these proportions were 89% and 62%, and for endemic species, the proportions were 90% and 61% (Figure 2).

Biotic Homogenization Assessment

The cluster analysis based on all birds recorded in the 3 habitats indicated 2 general clusters, each with at least 1 subdivision (Figure 3). The first cluster was composed of a group that included all human settlements (in both forest types), and a group corresponding to tropical deciduous forest, which in turn separated into a cluster corresponding to second-growth tropical deciduous forest and a cluster corresponding to primary tropical deciduous forest. The other general cluster included all remaining oak forest patches, both primary and secondary (Figure 3).

Assessing the biotic homogenization hypothesis, we found low values for the nestedness component of dissimilarity (β_{nestSor}), and we did not find significant differences for β_{nestSor} values in any comparison (Figure 4), either for habitat patches ($H_{2,21} = 0.69$, $P = 0.70$) or for count events ($H_{2,15} = 3.5$, $P = 0.17$). However, we found a statistically significant decrease of the dissimilarity turnover component (β_{turnSor}) along the human perturbation gradient. This pattern was consistent when bird data were separated by habitat ($H_{2,21} = 12.48$, $P = 0.002$, Figure 4A) and by count event ($H_{2,15} = 8.95$, $P = 0.011$, Figure 4B). Turnover was highest in bird communities in primary

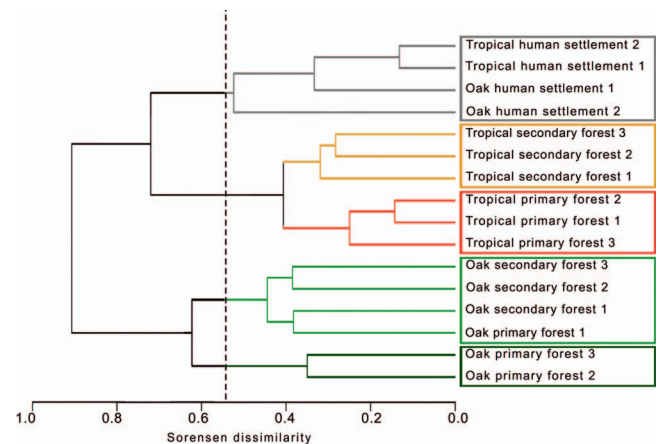


FIGURE 3. Classification analysis of habitat patches along the human perturbation gradient in seasonal forest in the Balsas River basin, west-central Mexico. The Sørensen dissimilarity matrix and complete linkage method were used. Colors and boxes in the graph indicate the clustering arrangement of each habitat patch within the analysis. From top to bottom: Human settlements (gray clusters); tropical secondary (yellow cluster) and primary forests (red cluster); and both secondary and primary oak forests (green clusters). Vertical dashed line shows the average value of the dissimilarity matrix. Analysis was based on occurrence data of all resident bird species recorded in each habitat patch.

forests, and lowest in human settlements. Mean β_{turnSor} among habitat patches (84% confidence interval) was 0.66 (0.76–0.96) for primary forests, 0.49 (0.29–0.69) for second-growth, and 0.32 (0.27–0.37) for human settlements (Figure 4A). β_{turnSor} for count events was 0.66 (0.59–0.71) for primary forest, 0.54 (0.44–0.64) for second-growth, and 0.38 (0.30–0.46) for human settlements (Figure 4B).

DISCUSSION

Our results show that anthropogenic perturbation can lead to biotic homogenization of bird communities in Neotropical dry forests. Specifically, our results show that human activities can promote the loss of taxonomic differences between tropical deciduous forest and oak forest through a directional shift in bird communities, reflected in the occurrence of tropical deciduous forest birds in disturbed oak forest areas, and the presence of exotic human-commensal species in human settlements within both forest types.

Loss of Forest Specialists

The loss of bird diversity as a function of intensification of human activities as found in our study has been previously documented in other tropical deciduous forest and oak forest systems, driven by agricultural activities (MacGregor-Fors and Schondube 2011), cattle grazing (Maya-Elizarrarás and Schondube 2015), and land-use changes

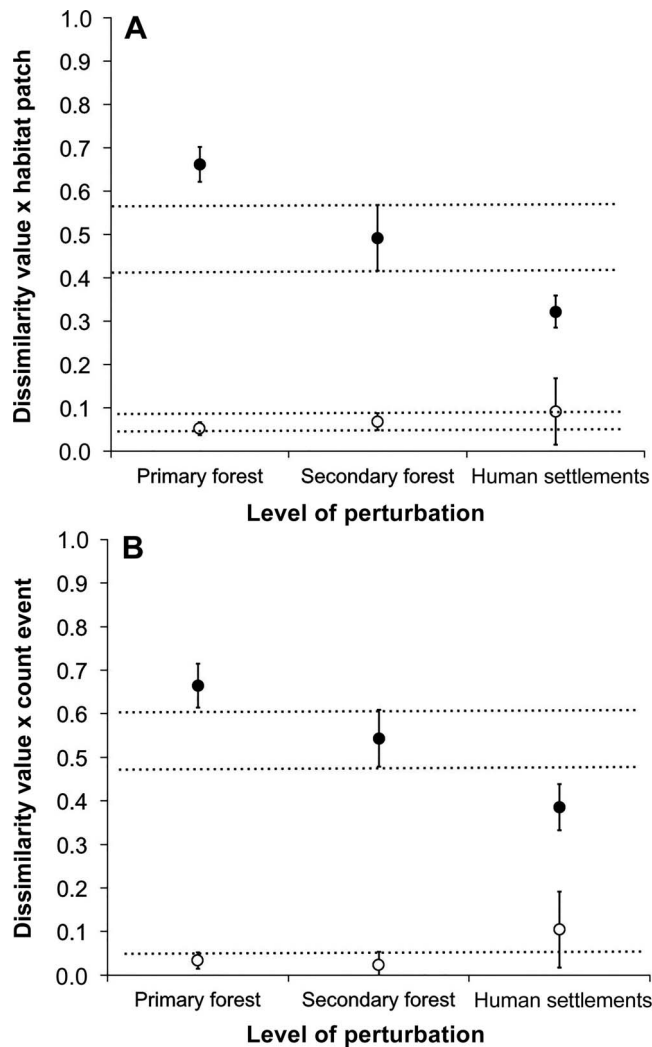


FIGURE 4. Mean values of taxonomic dissimilarity along the perturbation gradient (primary forest, secondary forest, and human settlements) in the Balsas River basin, west-central Mexico. We considered values for: (A) habitat patches and (B) count periods. Open circles indicate the nestedness component of dissimilarity, which reflects dissimilarity owing to changes in species richness when one community is a subset of the other. Filled circles indicate the turnover component, which is associated with species replacement between communities, regardless of species richness in each. Error bars and horizontal dotted lines show 84% confidence values, equivalent to significant differences at $\alpha = 0.05$.

associated with human settlements (Ramírez-Albores 2007, MacGregor-Fors and Schondube 2012). Anthropogenic landscape transformation can promote an environmental filtering effect that reduces the availability of resources and changes ecological conditions. This filtering decreases the ecological success of bird species that have traits associated with the specialized use of natural environments (e.g., large body mass, low fecundity, limited ecological plasticity), eventually leading to local extirpation

(Crocini et al. 2008, Newbold et al. 2013, Paz Silva et al. 2016). In this way, habitat perturbation can drive a selective process of erosion of bird diversity in highly disturbed environments (McKinney and Lockwood 2001).

In our study, forest specialists were concentrated in primary habitats, occasionally occurred in second-growth habitats, and were never found in human settlements. In tropical deciduous forest, these specialist species included the West Mexican Chachalaca (*Ortalis poliocephala*) and Military Macaw (*Ara militaris*), both large-bodied bird species that feed on fruits in the canopy (Gurrola 2002, Contreras-González et al. 2009). Other relevant species included the Balsas Screech-Owl (*Megascops seductus*), Elegant Trogon (*Trogon elegans*), and Pale-billed Woodpecker (*Campephilus guatemalensis*), which are dependent on large trees in mature forest for nesting and foraging (Monterrubio-Rico and Escalante-Pliego 2006). In oak forest, a bird species dependent on large trees for nesting is the Mountain Trogon (*Trogon mexicanus*; Monterrubio-Rico and Escalante-Pliego 2006), and a species dependent on forest trees for foraging is the White-striped Woodcreeper (*Lepidocolaptes leucogaster*). Other bird species associated with this habitat were the Woodhouse's Scrub-Jay (*Aphelocoma woodhouseii*), Gray Silky-Flycatcher (*Ptiliogonys cinereus*), and Painted Redstart (*Myioborus pictus*; Ramírez-Bastida et al. 2015).

Anthropogenic influences can act on bird species through different mechanisms. Extinction risk owing to habitat loss is higher for habitat specialists. Extinction risk for large-bodied birds is often better explained by direct human persecution (Owens and Bennett 2000, Kattan et al. 2016). The West Mexican Chachalaca, Pale-billed Woodpecker, and Military Macaw are large-bodied birds that suffer direct human pressure (L. Vázquez-Reyes personal observation), and their exclusion from human-disturbed habitat can be related directly to human hunting.

Loss of Endemic vs. Widely Distributed Species

Proportional losses of endemic species and widely distributed species were similar in human settlements (39% compared with 38%; Figure 2). Nine of 39 (23%) species in human settlements were endemics. Eight bird species were recorded at all levels of perturbation in both forest types (full species list in Appendix Table 2), including 2 species endemic to the Balsas River basin, the Dusky Hummingbird (*Cyananthus sordidus*) and Black-chested Sparrow (*Peucaea humeralis*), as well as the Russet-crowned Motmot (*Momotus mexicanus*), a Mexican near-endemic associated with tropical deciduous forest (Gordon and Ornelas 2000, Berlanga et al. 2015). The fact that restricted-range species did not show a greater rate of loss differs from the typical expectation of increasing vulnerability with decreasing range (McKinney and Lockwood 1999).

Habitat Shapes Avian Community Composition

Communities in primary and second-growth oak patches were grouped separately from all other habitats. This result was driven by species found only in oak forests in the study region, including the Acorn Woodpecker (*Melanerpes formicivorus*), Woodhouse's Scrub-Jay, Bridled Titmouse (*Baeolophus wollweberi*), Painted Redstart, and Hepatic Tanager (*Piranga flava*; Ramírez-Bastida et al. 2015). Tropical deciduous forest patches were clustered through shared species with tropical affinity, such as the Balsas Screech-Owl, Golden-cheeked Woodpecker (*Melanerpes chrysogenys*), Pale-billed Woodpecker, Orange-fronted Parakeet (*Eupsittula canicularis*), and Military Macaw (Vega-Rivera et al. 2010).

However, human settlements within oak forest were clustered with other human settlements and tropical deciduous forest, rather than with other oak habitat patches. This pattern is evidence of the reduction in taxonomic differences in bird communities in the face of human perturbation (Figure 4). Six species occurred only in human settlements but in both forest types (full species list in Appendix Table 2), including 2 invasive species, the Rock Pigeon (*Columba livia*) and House Sparrow (*Passer domesticus*), increasing the number of species shared among human settlements and contributing to the homogenization of bird communities (Lockwood et al. 2000). As well as exotic species, native bird species capable of using anthropogenic habitats in both forest types, including the range-restricted Dusky Hummingbird, Russet-crowned Motmot, and Black-chested Sparrow, further reduced biotic differences between environments under anthropogenic pressure (Davey et al. 2012).

Erosion of Beta Diversity Defines Biotic Homogenization

The major consequence of biotic homogenization is the loss of biodiversity between ecosystems (Olden et al. 2004, McGill et al. 2015), and our results confirm this pattern for both taxonomic dissimilarity and beta diversity. In dissimilarity comparisons between tropical deciduous forest and oak forest at the same perturbation level, the nested component showed that differences in species richness were not significant (Figure 4). It may be that species loss affected species richness in the 2 habitats similarly, such that species were lost at similar rates with perturbation in both forest types (Baselga 2012). Several studies have documented reduced taxonomic differences between biotas in response to agricultural management (Luck and Smallbone 2011, Karp et al. 2012), land-cover change, and urbanization (Blair 2001, La Sorte and Boecklen 2005, Clergeau et al. 2006, Olden et al. 2006, Sorace and Gustin 2008). Our results, which showed a reduction in species turnover associated with perturbation intensification in tropical seasonal forests, are consistent

with those of studies in other Neotropical seasonal forests, where intensification of agriculture reduced bird species turnover at local and landscape scales (Karp et al. 2012). However, in birds of the Atlantic forest of Brazil, homogenization processes showed a different path (Villegas Vallejos et al. 2016). In this case, loss of dissimilarity was due to the loss of the nested component of dissimilarity, instead of species turnover, because of the floristic and ecological differences between compared environments. Recent studies at the continental scale in North America have also found homogenization in urban birds due to species turnover loss (Murthy et al. 2016). Results are different in tropical wet forests, where turnover has been found to increase between ecosystems (Solar et al. 2015, Morante-Filho et al. 2016). Hence, environmental filters may act in different ways (Morante-Filho et al. 2016), emphasizing the need for further investigation in other Neotropical forests (Socolar et al. 2016).

Expansion of Tropical and Exotic Birds as Homogenization Drivers

Biotic homogenization is relevant to modern conservation planning, so it is necessary to identify and understand the patterns and processes behind this phenomenon (Rooney et al. 2007). Our results provide information toward understanding the taxonomic homogenization process. Reduction of taxonomic dissimilarity between tropical deciduous and oak forests was driven by: (1) directional expansion of species representative of tropical deciduous forest into oak forest areas; and (2) invasion of nonnative, human-commensal species that occurred exclusively within human settlements.

Some birds of tropical deciduous forest (e.g., Dusky Hummingbird, Russet-Crowned Motmot) were able to exploit the whole perturbation gradient, expanding their upper elevational ranges by >1,200 m into the highlands, where human settlements in former oak forest were located. This pattern is consistent with previous studies that have shown that some bird species can expand their ranges in the face of land use change, especially when they are locally abundant and express ecologically plastic traits (La Sorte and Boecklen 2005, Tabarelli et al. 2012).

Changes in avian community composition seem to have a directional pattern. While some tropical deciduous forest birds were consistently recorded in the disturbed patches of oak forest, no distinctive oak forest species were found in tropical deciduous forest (Ramírez-Bastida et al. 2015). This may indicate a pattern behind the process of biotic homogenization, in which tropical deciduous forest birds expand their altitudinal distributions up to 1,200 altitudinal meters. This upward, but not downward, altitudinal shift in geographic range may be explained by increasing temperatures (Şekercioğlu et al. 2012). Recent studies based on coarse-scale distributional data of Mexican

endemic birds suggest that changes in their geographical distribution over the past century have been driven by temperature increases due to climate change (Peterson et al. 2015). As additional supporting evidence, studies of land-cover change have shown that temperature in the region has increased by 0.6°C during the last 50 yr, probably as a result of deforestation for cattle grazing (Cruz Hernández et al. 2007). The occurrence of invasive Eurasian species (Rock Pigeon, House Sparrow) in all human settlements but not in any forest patch is evidence that human transportation contributes to break down biogeographical barriers, a principal driver in the homogenization process (Hulme 2009, Winter et al. 2010, Baiser et al. 2012).

Implications for Use and Management of Dry Forests

Our results demonstrate that agriculture, cattle grazing, and human settlement have eroded the biodiversity of the Alto Balsas region, a process that has probably been repeated in other tropical deciduous forests and oak forests (e.g., Ramírez-Albores 2007). At present, primary tropical dry forest covers only 34% of its original area; primary oak forests and related temperate forests retain only 64% of their original extent (Sánchez Colón et al. 2009). Annual rates of deforestation for tropical and temperate forests represent losses of 0.76% and 0.25% of coverage, respectively (Mas et al. 2004). Even so, it is unrealistic to expect that these activities can be stopped, as they are fundamental for human subsistence in the region (Good-Eshelman and Barrientos-López 2004).

Because habitat loss is a general pattern across Latin America (Wright 2005), homogenization threatens biotic distinctiveness across the whole region. Biotic homogenization may affect ecological and evolutionary processes beyond the loss of species (Olden 2006, Şekercioğlu 2006, Şekercioğlu et al. 2012, Morelli et al. 2016). To confront these threats, it is necessary to consider mitigation strategies (Olden 2006, Rooney et al. 2007). One possible strategy is to maintain scattered native trees and shrubs throughout cultivated plots, as was practiced in traditional agriculture in west-central Mexico. This management practice maintains species richness similar to that of native primary forests (Vallejo et al. 2014). Leaving scattered native trees also improves connectivity among forest patches, favoring the maintenance of functional ecosystem integrity (Manning et al. 2006). Such a strategy, instead of total clearance of original vegetation, should be considered to preserve the biodiversity of forest ecosystems in the Balsas River basin, and other areas in Latin America.

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APPENDIX TABLE 1. Habitat characterization (mean \pm SE) showed that physical structure was different between primary and second-growth forests in the Balsas River basin, west-central Mexico.

	Tropical deciduous forest		Oak forest	
	Primary forest	Secondary forest	Primary forest	Secondary forest
Number of vegetation gaps	1.83 \pm 1.47	6.00 \pm 3.00	3.60 \pm 2.19	5.66 \pm 1.52
Average length of gaps (m) ^a	1.64 \pm 1.24	4.83 \pm 0.64	3.08 \pm 2.33	7.57 \pm 1.60
Number of vertical strata ^{a,b}	20.66 \pm 2.87	11.66 \pm 2.51	20.20 \pm 4.60	13.66 \pm 1.15

^a Kruskal-Wallis tests showed significant differences at $\alpha < 0.05$.

^b Measured using 0.5-m intervals.

APPENDIX TABLE 2. Resident bird species detected during point count surveys in the seasonal tropical forest of the Alto Balsas River basin, Mexico. Scientific names follow the AOU Checklist of North and Middle American Birds (<http://checklist.aou.org/>). Mexican endemic species sensu Berlanga et al. (2015) are indicated with superscripts as follows: 1 = Alto Balsas River basin; 2 = Mexican western slope; 3 = Central and western Mexico; 4 = Almost all of Mexico; 5 = Near-endemic (distribution out of Mexican territory <35,000 km²); 6 = Semiendemic (species whose whole population occurs exclusively in Mexico during seasonal migration). * = Exotic and invasive bird species, found only within human settlements. Habitat type abbreviations are: OF = oak forest; TF = tropical forest; p = preserved forest; sg = secondary forest; and hs = human settlement.

Taxon and habitat patch	Tropical deciduous forest										Oak forest					
	TFp1	TFp2	TFp3	TFsg1	TFsg2	TFsg3	TFhs1	TFhs2	OFp1	OFp2	OFp3	OFsg1	OFsg2	OFsg3	OFhs1	OFhs2
GALLIFORMES																
Cracidae																
<i>Ortalis poliocephala</i> ²	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Odontophoridae																
<i>Philortyx fasciatus</i> ¹					X	X	X	X								
COLUMBIFORMES																
<i>Columba livia</i> [*]							X	X	X	X	X	X	X	X	X	X
<i>Columbina inca</i>				X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Columbina passerina</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Leptotila verreauxi</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Zenaida macroura</i>				X	X	X	X	X	X	X	X	X	X	X	X	X
CUCULIFORMES																
Cuculidae																
<i>Playa cayana</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Morococcyx erythropygus</i>	X		X	X	X	X	X	X								
<i>Geococcyx velox</i>					X	X	X	X								
<i>Crotophaga sulcirostris</i>							X	X								
CAPRIMULGIFORMES																
Caprimulgidae																
<i>Antrastomus ridgwayi</i>									X							
APODIFORMES																
Trochilidae																
<i>Chlorostilbon auriceps</i> ²	X															
<i>Cyananthus sordidus</i> ¹	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Amazilia beryllina</i>									X	X	X	X	X	X	X	X
<i>Amazilia violiceps</i> ⁶	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Hylocharis leucotis</i>									X	X	X	X	X	X	X	X
CATHARTIFORMES																
Cathartidae																
<i>Cathartes aura</i>									X							
STRIGIFORMES																
Strigidae																
<i>Megascops seductus</i> ¹			X						X							
<i>Glauccidium gnoma</i>									X							
<i>Glauccidium palmarum</i> ²	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Glauccidium brasilianum</i>		X	X													
TROGONIFORMES																
Trogonidae																
<i>Trogon elegans</i>	X	X	X													

APPENDIX TABLE 2. Continued.

Taxon and habitat patch	Tropical deciduous forest										Oak forest					
	TFp1	TFp2	TFp3	TFsg1	TFsg2	TFsg3	TFhs1	TFhs2	OFp1	OFp2	OFp3	OFsg1	OFsg2	OFsg3	OFhs1	OFhs2
<i>Trogon mexicanus</i>											X					
CORACIIFORMES																
Momotidae																
<i>Momotus mexicanus</i> ⁵	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
PICIFORMES																
Picidae																
<i>Melanerpes formicivorus</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Melanerpes chrysogenys</i> ²																
<i>Melanerpes hypopolius</i> ¹																
<i>Picoides scalaris</i>			X													
<i>Campephilus guatemalensis</i>			X													
FALCONIFORMES																
Falconidae																
<i>Caracara cheriway</i>																
PSITTACIFORMES																
Psittacidae																
<i>Eupsittula canicularis</i>	X	X	X				X	X								
<i>Ara militaris</i>	X	X	X													
PASSERIFORMES																
Furnariidae																
<i>Lepidocolaptes leucogaster</i> ³																
Tyrannidae																
<i>Camptostoma imberbe</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Myiopagis viridicata</i>																
<i>Xenotriccus mexicanus</i> ¹			X						X	X	X	X	X	X	X	X
<i>Contopus pertinax</i>									X	X	X	X	X	X	X	X
<i>Pyrocephalus rubinus</i>									X	X	X	X	X	X	X	X
<i>Myiarchus tuberculifer</i>							X		X	X	X	X	X	X	X	X
<i>Myiarchus nuttingi</i>	X	X	X	X	X	X			X	X	X	X	X	X	X	X
<i>Myiarchus tyrannulus</i>	X	X	X	X	X	X			X	X	X	X	X	X	X	X
<i>Pitangus sulphuratus</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Tyrannus melancholicus</i>	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
<i>Tyrannus crassirostris</i> ⁶	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Vireonidae																
<i>Vireo hypochryseus</i> ²									X	X	X	X	X	X	X	X
Corvidae																
<i>Calocitta formosa</i>	X	X	X	X	X	X			X	X	X	X	X	X	X	X
<i>Aphelocoma woodhousei</i>									X	X	X	X	X	X	X	X
Hirundinidae																
<i>Steigodopteryx serripennis</i>							X	X						X		
Paridae																
<i>Baeolophus wollweberi</i>									X	X	X	X	X	X	X	X
Troglodytidae																
<i>Catherpes mexicanus</i>									X	X	X	X	X	X	X	X

APPENDIX TABLE 2. Continued.

Taxon and habitat patch	Tropical deciduous forest										Oak forest									
	TFp1	TFp2	TFp3	TFsg1	TFsg2	TFsg3	TFhs1	TFhs2	OFp1	OFp2	OFp3	OFsg1	OFsg2	OFsg3	OFhs1	OFhs2				
<i>Campylorhynchus jocosus</i> ¹	X	X	X					X	X						X					
<i>Phegopedius felix</i> ²		X	X					X	X						X					
<i>Thryophilus pleurostrictus</i>	X	X	X	X	X	X	X	X	X						X	X				
Polioptilidae																				
<i>Polioptila albiloris</i>	X	X	X	X	X	X	X	X	X					X	X					
Turdidae																				
<i>Turdus rufopalliatus</i> ²			X		X		X	X												
Mimidae																				
<i>Melanotis caerulescens</i> ³			X					X	X											
Ptiligonatidae																				
<i>Ptiliogonys cinereus</i> ⁵									X	X				X						
Passeridae																				
<i>Passer domesticus</i> *							X	X						X						
Fringillidae																				
<i>Euphonia elegantissima</i>							X	X	X					X		X				
<i>Haemorhous mexicanus</i>							X	X	X					X		X				
<i>Spinus psaltria</i>				X	X	X	X	X	X					X		X				
Panulidae																				
<i>Geothlypis poliocephala</i>																				
<i>Basileuterus rufifrons</i> ⁵					X				X	X				X						
<i>Myioborus pictus</i>																				
Thraupidae																				
<i>Volatinia jacarina</i>					X		X	X												
<i>Sporophila torqueola</i>					X	X	X	X												
Embenizidae																				
<i>Aimophila rufescens</i>						X		X												
<i>Aimophila ruficeps</i>						X		X												
<i>Melospiza kieneri</i> ²						X		X												
<i>Peucaea ruficauda</i>	X	X	X	X	X	X	X	X						X	X					
<i>Peucaea humeralis</i> ¹	X	X	X	X	X	X	X	X						X	X					
Cardinalidae																				
<i>Piranga flava</i>		X	X					X	X					X						
<i>Pheucticus chrysopheplus</i> ⁵	X	X	X					X	X					X						
<i>Pheucticus melanocephalus</i>																				
<i>Passerina caerulea</i>		X	X	X	X	X	X	X						X						
<i>Passerina leclancherii</i> ²	X	X	X	X	X	X	X	X						X						
<i>Passerina versicolor</i>		X	X	X	X	X	X	X												
Icteridae																				
<i>Molothrus aeneus</i>	X	X	X	X	X	X	X	X						X	X	X				
<i>Icterus wagleri</i>	X	X	X	X	X	X	X	X						X	X	X				
<i>Icterus pustulatus</i>	X	X	X	X	X	X	X	X						X	X	X				