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Patterns of forest use and endemism in resident bird communities of north-central Michoacán, Mexico

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Abstract

We compared breeding avian communities among 11 habitat types in north-central Michoacán, Mexico, to determine patterns of forest use by endemic and nonendemic resident species. Point counts of birds and vegetation measurements were conducted at 124 sampling localities from May through July, in 1994 and 1995. Six native forest types sampled were pine, pine–oak, oak–pine, oak, fir, and cloud forests; three habitat types were plantations of *Eucalyptus*, pine, and mixed species; and the remaining two habitats were shrublands and pastures. Pastures had lower bird-species richness and abundance than pine, oak–pine, and mixed-species plantations. Pine forests had greater bird abundance and species richness than oak forests and shrublands. Species richness and abundance of endemics were greatest in fir forests, followed by cloud forests. Bird abundance and richness significantly increased with greater tree-layer complexity, although sites with intermediate tree complexity also supported high abundances. When detrended correspondence-analysis scores were plotted for each site, bird species composition did not differ substantially among the four native oak-and-pine forest types, but cloud and fir forests, *Eucalyptus* plantations, and mixed-species plantations formed relatively distinct groups. Plantations supported a mixture of species found in native forests, shrublands, and pastures. Pastures and shrublands shared many species in common, varied greatly among sites in bird-species composition, and contained more species specific to these habitats than did forest types. © 1998 Elsevier Science B.V.

Keywords: Cloud forests; *Eucalyptus* plantations; Pastures; Species richness; Correspondence analysis

Resumen. Se compararon las comunidades de aves entre 11 tipos de vegetación en el centro-norte del estado de Michoacán, México. Se realizaron puntos de conteo de aves y mediciones de la vegetación en 124

sitios desde mayo a julio de 1994 y 1995. Los tipos de vegetación muestreados fueron bosque de pino, de pino-encino, de encino-pino, de encino, de oyamel y mesófilo de montaña, plantaciones de eucalipto, de pino y mixtas, matorral subtropical y pastizal. El pastizal tuvo menor riqueza y abundancia de especies que el bosque de pino, encino-pino y las plantaciones mixtas. Además, el bosque de pino tuvo mayor abundancia de individuos y riqueza de especies que el

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bosque de encino, pastizal y matorral subtropical. La abundancia y riqueza de especies endémicas fue mayor en el bosque de oyamel, seguido por el bosque mesófilo de montaña. La abundancia y riqueza de aves se incrementó significativamente en relación directa a la complejidad de la estructura de la vegetación, aunque sitios con complejidad intermedia también tuvieron abundancias elevadas. Cuando los puntos de análisis de correspondencia fueron graficados para cada sitio, la composición de especies no difirió sustancialmente entre cuatro tipos de bosque de encino y de pino, los cuales se agruparon. Pero el bosque de oyamel y el mesófilo de montaña, las plantaciones de eucalipto y mixtas formaron grupos relativamente distintos. Las plantaciones presentaron una mezcla de especies encontradas en los demás tipos de vegetación. El pastizal y el matorral subtropical compartieron muchas especies en común, la composición de especies tuvo una alta variación entre sitios, y se encontraron más especies únicas que en los tipos de vegetación forestal.

Palabras clave: Mesófilo de montaña; Plantaciones de eucalipto; Pastizal; Riqueza de especies; Análisis de correspondencia.

1. Introduction

Recently, a great deal of attention has been focused on migratory birds owing to reported population declines of some species (for a review see Martin and Finch (1995)). As a result, much new information in Mexico has been generated on habitat use by Nearctic-breeding migrants and resident species during the non-breeding season (Petit et al., 1995). Most available information on breeding birds, however, consists of presence and absence records from bird collection expeditions or from species lists for an area. In one important work, Escalante et al. (1993) compared species diversity of resident landbirds among biotic provinces and habitat types of Mexico. But few studies have quantified relative abundances and distributions of resident birds among breeding habitats within specific regions or states (Villaseñor and Villaseñor, 1994a; Garcia et al., 1995), and consequently, basic data on avian diversity are lacking for many critical geographical areas in Mexico.

The mountainous regions of Mexico are centers of high endemism and diversity for plants and animals (Toledo and Ordóñez, 1993). The Sierra Madre Oriental, Sierra Madre Occidental, and Transvolcanic Belt, for example, contain high bird species diversity and large numbers of endemic species (Escalante et al., 1993). The Middle Sierra Madre Occidental and the Transvolcanic Belt rank first and second, respectively, in numbers of endemic bird species among biotic provinces in Mexico. The mountainous areas of Mexico are covered mainly by subhumid temperate forests of pines, oaks, and mixed tree species (Toledo and Ordóñez, 1993). Humid temperate forests are located in the mid-elevation parts of mountain chains (600–2500 m) and are characterized by cloud forests. Among Mexico's habitats, pine-oak forests rank third greatest in total number of bird species (218 species) and second highest in total number of endemic species (43). Cloud forests are also high in number of endemic species (30) and total species richness (182).

Subhumid temperate forests of Mexico have been exposed to intense human use. About 37% of pine-oak forests have been modified by agricultural practices (Toledo and Ordóñez, 1993). Cloud forests, which are under intense pressure from livestock grazing, are one of the most threatened habitat types in Mexico (Flores-Villela and Gerez, 1988; Toledo and Ordóñez, 1993). Habitat destruction is considered to be the greatest threat to avian diversity in Mexico (Soulé, 1986). Deforestation is one of the most common forms of habitat loss in Mexico; only 28% of native forest cover remains (World Resources Institute, 1992). Forests are frequently cleared for agriculture, to create pastures for cattle grazing, or for lumber or firewood. Regular abandonment of cleared areas results in the establishment of successional seres, of which shrublands and grasslands are early stages (Rzedowski, 1978). Often, pastures are maintained as early seral stages by humans for continued use by cattle. Wildfires maintain the successional shrubland stage. As a result, deforestation creates a shift in the structure and composition of the vegetation. Deforested areas in Mexico are sometimes, but not frequently, reforested with plantations. Some plantations are monocultures; others are composed of several tree species, including both exotic and native tree species. Plantations are reported to have lower bird species richness than

other habitat types (Villaseñor and Villaseñor, 1994a; Pérez, 1995).

In this paper, we compared richness and bird abundance of all species and endemic species detected from May through July of 1994 and 1995 in 11 habitat types in north-central Michoacán, Mexico. Our objective was to determine which native, introduced, and altered habitats had highest conservation values based on breeding bird responses, at both the species and community levels. We identified which sampled habitats were most valuable to the greatest numbers of endemic species and specialists, by comparing observed numbers in each habitat to those expected. To understand overall species and community responses to habitat variation, we compared variation in bird species richness and abundance to gradients of vegetational structures among pastures, shrublands, plantations, and native forests. We interpreted similarities and differences in bird species composition among pastures, shrublands, plantations, and native forests based on degree of disturbance by forest management.

2. Methods

2.1. Study area

Michoacán is located in the west-central part of Mexico and is characterized by two physiographic provinces including the Transvolcanic Belt and Sierra Madre del Sur provinces (INEGI, 1985), although Correa (1979) recognizes three additional provinces, including Pacific Coastal Plains, Balsas River Basin, and Lerma River Basin. Michoacán contains the sixth largest area of subhumid temperate forest in Mexico, with ca. 1 550 000 hectares, although tropical dry forests are also an important component of vegetation with ca. 860 000 hectares (SARH, 1991). Michoacán ranks fifth in vertebrate diversity among Mexican states and is rich in endemic species (Flores-Villela and Gerez, 1988). A total of 492 bird species have been recorded in Michoacán (48.9% of all species recorded in Mexico), and this number includes 116 species endemic to Mesoamerica (Villaseñor and Villaseñor, 1994b).

Habitats and birds were sampled in the north-central part of Michoacán, primarily in the Transvolcanic

Belt, within an area encompassing ca. 18 500 km². Elevation of sampled sites ranged from 1300 to 3030 m. This area is primarily covered by subhumid temperate forests which are classified as pine–oak, oak–pine, oak, pine, and fir forests based on patterns of tree species dominance (INEGI, 1985). Fir forests and cloud forests are uncommon in Michoacán. Common pine species included *Pinus leiophylla*, *P. montezumae*, *P. lawsoni*, and *P. pseudostrobus*. The most common oak species included *Quercus rugosa*, *Q. candicans*, *Q. obtusata*, and *Q. laurina*. Fir forests were dominated by *Abies religiosa* and pines, while cloud forest species included *Symplocos prionophylla*, *Meliosma dentata*, *Fraxinus uhdei*, and *Bocconia arborea*. In the extreme northern part of the study area, shrublands and grassland pastures occur as natural vegetation types, but elsewhere these two habitats extend into formerly forested areas as a result of deforestation (Rzedowski, 1978). Shrubland vegetation was characterized by *Euphorbia calyculata*, *Bursera cuneata*, *Calliandra grandiflora*, and *Opuntia tomentosa*. Pastures were dominated by *Andropogon saccharoides*, *Bouteloua repens*, *Digitaria ciliaris*, and *Panicum hallii*. For more information on plant-species characteristics of each habitat type, see Rzedowski (1978) and Garcia et al. (1995).

Plantations occurred throughout the study area. Tree species planted vary depending on the plantation's purpose but usually include *Eucalyptus camaldulensis*, *Cupressus lindleyi*, and native and exotic *Pinus* species (native species include *P. michoacana*, *P. pseudostrobus*, *P. montezumae*, and *P. leiophylla*; exotic species include *P. greggii*, *P. halepensis*, *P. brutia*, and *P. pinaster*) (Mas et al., 1992). Some plantations are monocultures of *E. camaldulensis* or *Pinus* species, while other plantations contain several of the species listed above.

Data were collected from May through July in 1994 and 1995. In 1994, 63 sites were sampled, and 61 sites were sampled in 1995, resulting in 124 sites distributed among 11 habitat types. Each site was sampled once. Sites were located using an INEGI Uso del Suelo y Vegetación map (1:250 000; 1984). Sampling intensity was stratified among habitats based on cover proportions on the INEGI map, although scarce habitats, such as cloud forests, were sampled to a greater extent in order to obtain adequate sample sizes. Each habitat was assigned a two-letter acronym for use in

subsequent tables and figures. Habitats were classified following the INEGI map (1984) classification, except for plantations. Plantations were classified by the dominant genera found in the plantation. The classification of native forest types reflects the differences in tree species dominance.

2.2. Vegetation sampling

Vegetation was sampled at each of the five bird-count stations at each site. We used methods outlined in Ralph et al. (1993). For each habitat type, a plot radius was established by walking from the center of the plot until no new plant species were added. The plot center was the location of the bird-count station. All measurements were taken within the circular plot. The vegetation was divided into three layers: the tree layer included plants taller than 5 m; the shrub layer included those between 50 cm and 5 m; and the herbaceous layer included any plant <50 cm. The amount of cover of each layer was estimated using the Braun–Blanquet Cover Abundance Scale (Mueller-Dombois and Ellenberg, 1974). The scale is: 5, 75–100% cover; 4, 50–75% cover; 3, 25–50% cover; 2, 5–25% cover; and 1, 0–5% cover. For each layer, the number of plant genera and number of sublayers were recorded. The range in canopy height was estimated by measuring the height of the lowest canopy in the lower bound of the tree layer and the height of the highest canopy of the upper bound of the tree layer. The range in diameter at breast height (DBH) of trees was estimated by measuring the DBH of the thinnest and thickest trees.

2.3. Bird sampling

Birds were sampled using point counts (Hutto et al., 1986). Five count stations spaced 200 m apart were established at each sample site. At each count station, the numbers of individuals of each species detected by sight and sound were recorded during a 10 min count period. Birds detected at >100 m were recorded but not used in analyses to reduce the possibility of counting the same individual twice in consecutive points. Birds detected when not conducting counts were also recorded and used to calculate total species richness. Counts were conducted between 0700 and 1100 in the morning.

2.4. Data analyses

Vegetation characteristics were summarized for each site by averaging data, except for ordinal variables, across the five count stations. For ordinal variables, we assigned each site one value by identifying the dominant value across the five count stations, or randomly picking a value in cases of ties. We tested for differences in each of the vegetation variables among habitats using analysis of variance (ANOVA) or Welch's test, and contingency tables for ordinal variables. The number of tree genera was log-transformed to approximate normality; transformations of other variables did not improve the distributions. Several variables demonstrated heterogenous variance across habitats, including the range in DBH, range in canopy height, number of tree sublayers, number of herbaceous sublayers, and number of tree genera. For these variables, Welch's test was used instead of ANOVA, while multiple comparisons were conducted using Dunnett's T3 procedure (Dunnett, 1980; Milliken and Johnson, 1984). Multiple comparisons of variables with homogenous variance were carried out using Tukey's honestly significant difference (HSD) procedure ($p \leq 0.05$). Variation in ordinal variables was assessed by selecting post-hoc multiple comparisons of habitat types. The reported significance level was adjusted for each paired comparison by multiplying the significance level by the number of comparisons (Westfall and Young, 1993). We grouped habitats when there were no differences among them based on the multiple comparison tests. A principal components analysis (PCA) on the correlation matrix of vegetation variables was used to summarize variation in vegetation structure and to further explore differences among habitats by plotting habitats in PCA space.

The basic sample unit for calculating bird abundance and species richness was a site; therefore, relative abundance and richness for each site was estimated by averaging numbers of birds or species across the five count stations at a site. Site means were then averaged by habitat, and ANOVA was used to test for differences in richness and abundance of all species and endemic species among habitats. Variances were homogenous and, therefore, we applied Tukey's HSD procedure ($p \leq 0.05$) for multiple comparison tests of bird data. To measure the evenness of a species

distribution among the 11 habitats, we calculated Levins (1968) niche breadth index ($B = 1 / \sum p_i^2$) for each species based on its abundance within each habitat. A species equally abundant across all 11 habitats would demonstrate the broadest breadth ($B=11.0$), while a species restricted to one habitat would have the smallest breadth ($B=1.0$). Each detected species was classified as a true endemic, 'quasi-endemic', or non-endemic. True endemic species were defined as those restricted to Mexico, while quasi-endemics were species whose distribution narrowly overlapped adjacent countries (Escalante et al., 1993). Distributions were based on the A.O.U. checklist (American Ornithologists' Union, 1983, 1985). The Appendix A lists abundance/habitat, habitat breadth, and endemism classification of each detected species.

We tested the null hypothesis that the distribution of habitat generalist and specialist species among habitats was proportional to the total number of species in each habitat, using a Chi-square analysis. Results verified which, if any, habitats contained more or fewer generalists or specialists than expected, based on the total number of species found in that habitat. We defined generalists as those species whose breadth value ≥ 4.0 and specialists as species whose breadth value $= 1.0$. Species with breadth ≥ 4.0 were listed as generalists in each habitat where they occurred. To determine if vegetation structural gradients influenced bird communities, we calculated Pearson product-moment correlation coefficients between species richness or abundance and PCA axes. These relationships were visually displayed by plotting mean richness/site and abundance/site by habitat gradient. Detrended correspondence analysis (DCA) was conducted using log-transformed relative abundances of each species at every site. We restricted the DCA analysis to species detected at a minimum of five sites in order to reduce the potentially spurious influence of rare species on the results (ter Braak, 1995). The program CANOCO was used to run the DCA (ter Braak, 1987). DCA produces a series of uncorrelated axes that maximize site dispersion along each axis and computes axes values for sites and species (ter Braak, 1995). Distances between individual sites and habitat groups along DCA axes indicate site and habitat similarities in bird species composition. Similarities among sites (with habitat types differentiated by distinct symbols)

were visually displayed by plotting them on DCA axes. In addition, we graphed the 20 most abundant species in DCA space to visually compare their locations to the plot of sites and habitats in the same space.

3. Results

3.1. Vegetation variation

Proportion of cover values of tree, shrub, and herbaceous layers differed among habitats ($df=50$ and $p<0.001$ for each layer and test; $\chi^2=178.4$, 138.4, and 104.0, respectively). All plantations (*Eucalyptus*, mixed-species, and pine) were similar in the proportion of high values of tree cover to all native forests (pine-oak, oak-pine, pine, oak, cloud, and fir forests) ($\chi^2=10.4$; $df=4$; and $p=0.18$). Neither did shrublands and pastures differ in the proportion of tree cover ($\chi^2=6.5$; $df=3$; and $p=0.45$). High shrub cover values were proportionately lower in plantations than in all native forests ($\chi^2=36.2$; $df=5$; $p<0.001$) and shrublands ($\chi^2=23.9$; $df=5$; and $p<0.001$) but were similar between native forests and shrublands ($\chi^2=4.6$; $df=5$; and $p>0.50$). The proportion of herbaceous cover values did not differ among all native forests and all plantations ($\chi^2=3.3$; $df=4$; and $p>0.50$), among shrublands and pastures ($\chi^2=6.5$; $df=2$; and $p=0.20$), or among shrublands and all plantations ($\chi^2=4.9$; $df=4$; and $p>0.50$). All native forests had a greater proportion of low herbaceous cover values than shrublands ($\chi^2=13.9$; $df=4$; and $p=0.035$).

Results of ANOVA and the Welch tests showed that all but one of the vegetation variables differed among habitats (Table 1). Pine plantations usually could not be distinguished from other habitats due to low sample size (Tables 1 and 2). Cloud and fir forests demonstrated highest values for tree-layer variables when compared to other native forests, although not all comparisons were significant. There was little variation in shrub-layer variables, except for a significantly greater number of shrub sublayers and shrub genera in shrublands than plantations and pastures. The number of herbaceous genera was greater in shrublands than in mixed species plantations, *Eucalyptus* plantations, and pine-oak forests, but overall there were few differences.

Table 1

Mean values of vegetation variables among 11 habitat types and results of ANOVA and the Welch tests comparing habitats (df=10 123 for all tests). Habitats not significantly different have the same superscript. Standard deviations are in parentheses.

Variable ^a	Habitat type ^b											F	p
	PI	PO	OP	OA	CL	FI	EP	MP	PP	SH	PA		
DBHRANGE	42.1 ^{ab} (11.9)	39.0 ^{ab} (12.3)	34.1 ^{ab} (8.2)	27.0 ^b (16.4)	59.3 ^{ab} (16.7)	60.3 ^a (17.4)	25.4 ^{bc} (11.3)	32.1 ^{ab} (6.3)	15.5 ^{abc} (7.8)	4.3 ^c (6.7)	0.4 ^c (1.5)	64.9	<0.001
HGTRANGE	24.3 ^a (6.1)	15.2 ^b (6.1)	15.1 ^b (5.3)	10.7 ^b (5.8)	24.2 ^{ab} (6.5)	27.3 ^a (3.6)	13.9 ^b (3.0)	18.9 ^{ab} (4.7)	15.2 ^{abc} (12.2)	1.3 ^c (1.8)	0.1 ^c (0.3)	89.0	<0.001
TREESUB	2.5 ^{abc} (0.5)	2.4 ^b (0.4)	2.4 ^{abc} (0.5)	1.8 ^c (0.6)	2.9 ^{abc} (0.2)	2.8 ^a (0.6)	2.2 ^{bc} (0.3)	2.3 ^{bc} (0.2)	1.7 ^{abcd} (1.0)	0.3 ^d (0.5)	0.0 ^d (0.1)	289.9	<0.001
SHRUBSUB	1.7 ^{ab} (0.5)	1.7 ^{ab} (0.5)	1.7 ^{ab} (0.4)	1.8 ^{ab} (0.4)	1.7 ^{ab} (0.5)	1.6 ^{ab} (0.4)	1.5 ^{abc} (0.3)	1.3 ^{bc} (0.7)	0.8 ^{bc} (0.3)	2.2 ^a (0.6)	0.7 ^c (0.5)	8.1	<0.001
HERBSUB	1.1 ^a (0.2)	1.2 ^a (0.4)	1.1 ^a (0.3)	1.2 ^a (0.4)	1.2 ^a (0.3)	1.0 ^a (0.0)	1.0 ^a (0.0)	1.2 ^a (0.3)	0.9 ^a (0.1)	1.2 ^a (0.4)	1.3 ^a (0.3)	1.1	0.398
TREENUM	0.9 ^c (0.2)	1.3 ^b (0.2)	1.3 ^b (0.1)	1.1 ^{bc} (0.4)	1.9 ^a (0.1)	1.1 ^{bc} (0.4)	0.8 ^{cd} (0.2)	1.0 ^{bc} (0.2)	0.7 ^{abcde} (0.0)	0.3 ^{de} (0.5)	0.1 ^e (0.1)	179.6	<0.001
SHRUBNUM	4.8 ^{abcd} (1.8)	5.1 ^{abc} (1.1)	4.5 ^{abcd} (0.9)	5.3 ^{ab} (1.8)	6.1 ^a (0.7)	4.7 ^{abcd} (1.6)	3.1 ^{cde} (0.9)	2.8 ^{de} (1.7)	2.1 ^{bcde} (1.3)	6.0 ^a (1.5)	1.5 ^e (1.3)	13.1	<0.001
HERBNUM	6.8 ^{abc} (1.1)	6.8 ^{bc} (2.0)	7.1 ^{abc} (1.6)	7.6 ^{ab} (2.1)	7.7 ^{abc} (1.2)	7.9 ^{ab} (1.0)	5.6 ^{bc} (0.9)	4.4 ^c (0.5)	7.0 ^{abc} (1.4)	8.7 ^a (1.9)	8.2 ^{ab} (2.3)	3.8	<0.001

^a DBHRANGE, range in DBH; HGTRANGE, range in canopy height; TREESUB, number of tree sublayers; SHRUBSUB, number of shrub sublayers; HERBSUB, number of herbaceous sublayers; TREENUM, number of tree genera; SHRUBNUM, number of shrub genera; HERBNUM, number of herbaceous genera.

^b PI, pine; PO, pine-oak; OP, oak-pine; OA, oak; CL, cloud; FI, fir; EP, *Eucalyptus* plantation; MP, mixed species plantation; PP, pine plantation; SH, shrubland; PA, pasture.

Table 2

Distribution of sites among 11 habitat types and two letter acronym for each habitat. The total numbers of species and of all endemic species (true endemics and quasi-endemics) detected in each habitat through all means of detection.

Habitat type	No. of sites	No. of species	No. of endemic species
Pine forest (PI)	13	52	11
Pine–oak forest (PO)	20	65	13
Oak–pine forest (OP)	13	65	12
Oak forest (OA)	20	77	13
Cloud forest (CL)	6	30	8
Fir forest (FI)	7	37	11
<i>Eucalyptus</i> plantation (EP)	6	21	2
Mixed-species plantation (MP)	5	24	3
Pine plantation (PP)	2	16	2
Shrubland (SH)	17	49	6
Pasture (PA)	15	52	4
Total	124	130	25

3.2. Principal components analysis

The PCA resulted in three axes representing 76% of the variation in the data (Table 3). Principal component (PC) axes were interpreted by examining the

weights of factor loadings for variables in each axis. We interpreted increasing values of PC I as representative of increasing tree-layer complexity and increasing values of PC II as indicative of increasing shrub-layer complexity. The third PC axis weighted the

Table 3

Principal component (PC) analysis based on a correlation matrix among 11 vegetation variables and factor loadings for each variable among the three important PC axes

Vegetation variable ^a	PC I	PC II	PC III
TREECOV	0.40	−0.17	0.03
SHRUBCOV	0.29	0.48	0.31
HERBCOV	−0.27	0.05	0.31
HGTRANGE	0.38	−0.22	0.11
DBHRANGE	0.41	−0.15	0.12
TREESUB	0.42	−0.13	−0.03
SHRUBSUB	0.14	0.54	−0.20
HERBSUB	−0.04	0.22	−0.57
TREENUM	0.37	0.00	−0.00
SHRUBNUM	0.21	0.53	0.20
HERBNUM	−0.11	0.15	0.67
Eigenvalue	4.88	2.14	1.39
Percent of variation explained	44.3	19.5	12.7
Cumulative variation explained	44.3	63.8	76.4

^aTREECOV, tree cover; SHRUBCOV, shrub cover; HERBCOV, herbaceous cover; all other variables are defined in Table 1.

number of herbaceous genera and number of herbaceous sublayers the highest, and with opposite signs, indicating that an increase in the number of herbaceous plants was offset by a decrease in the number of herbaceous sublayers. This relationship is uninformative due to the lack of variation in the number of herbaceous sublayers across habitats (Table 1).

The plot of sites in PC space visually demonstrated differences among habitats in vegetation structure (Fig. 1). Pastures clearly had lower complexity in the shrub and tree layers than in all other habitats. All plantation types displayed lower shrub-layer and slightly less tree-layer complexities than native forests. The native forests overlapped considerably, although all of the cloud forest sites tended to cluster at higher values of PC I. Oak forests demonstrated the greatest variation among forests in both PC I and PC II, and several sites showed high values of shrub-layer complexity. PC III did not result in increased separation of habitats, nor did it provide additional information, indicating little variation among habitats in the herbaceous layer.

3.3. Bird abundance and species richness

We detected a total of 136 bird species through all means of detection; of these, 14 species were true endemics and 11 were quasi-endemics. During point

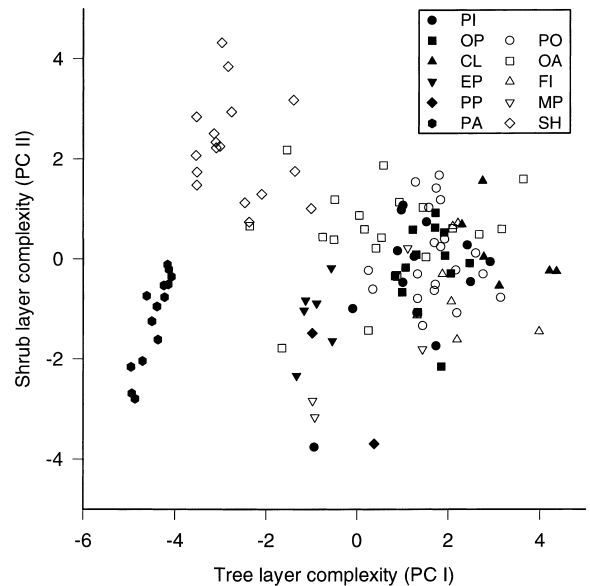


Fig. 1. Distribution of sites among the two most important principal component (PC) axes summarizing vegetation structure. Increasing values along each axis represent increasing complexity. The amount of scatter among sites of the same habitat indicates variability in vegetation structure, while separation among habitat types indicates differences in vegetation structure. Habitat codes are defined in Table 2.

counts, 130 species were detected, including 13 true endemics and 11 quasi-endemics. Oak forests con-

tained the most species, pine plantations the fewest (Table 2). Pine-oak and oak forests supported the most endemic species, and *Eucalyptus* and pine plantations contained the fewest (Table 2). Overall species richness was not uniform among habitats ($F=6.24$; $df=10, 123$; and $p<0.001$). Shrublands and pastures supported fewer species than most other habitat types, while native forests and plantations, on average, demonstrated similar species richness (Fig. 2(B)). Although bird abundance and species richness in pine plantations appeared lower (Fig. 2(A) and (B)) than

other habitats, they were statistically similar to numbers in native forests, possibly because our sample size of sites in pine plantations ($n=2$) was low.

Point-count effort was split between 1994 and 1995 to achieve a total of 124 sampling sites. Consequently, variation in bird abundance within and among species between years may explain some of the variation in total bird abundance. Nevertheless, counts among sites and years were averaged to obtain intra-habitat estimates of total abundance; therefore, any variation in abundance within habitats owing to year-to-year differences was uniformly treated across habitats which improved the validity of our inter-habitat comparisons of abundance. Relative total bird abundance differed among habitats ($F=4.55$; $df=10, 123$; and $p<0.001$), but multiple comparison tests revealed that many habitats had similar bird abundances (Fig. 2A). *Eucalyptus* plantations and mixed species plantations supported, on average, as many birds as all native forest types.

Endemic species (true endemics and quasi-endemics combined) differed in total bird abundance ($F=8.86$; $df=10, 123$; $p<0.001$) and species richness ($F=9.81$; $df=10, 123$; and $p<0.001$) across habitats. Fir forests clearly supported more individuals (Fig. 3(A)) and more species (Fig. 3(B)) and Appendix A) of endemic status than all other habitat types. Endemic (E) and quasi-endemic (Q) species observed most frequently in fir forests included pine flycatcher (E) (*Empidonax affinis*; E), pileated flycatcher (*Xenotricus mexicanus*; E), Mexican chickadee (*Parus sclateri*; Q), gray wren (*Campylorhynchus megalopterus*; E), red warbler (*Ergaticus ruber*; E) and Mexican junco (*Junco phaeonotus*, Q). Pastures had significantly fewer endemic species than five other habitats. No true endemic or quasi-endemic species reached peak abundance in pastures, whereas violet-crowned hummingbird (*Amazilia violiceps*, Q), blue mockingbird (*Melanotis caerulescens*, E), and rusty-crowned sparrow (*Melospiza kieneri*, E) were most frequently detected in shrublands. Abundances of true endemics varied across habitats and was greater in fir forests than all other habitats ($F=13.39$; $df=10, 123$; and $p<0.001$) (Fig. 4(A)). Cloud forests supported higher abundances of true endemics (e.g. russet thrush, *Catharus occidentalis*; white-striped creeper, *Lepidocolaptes leucogaster*; striped finch, *Atlapetes virenticeps*) than seven habitat types (Fig. 4(A)), a pattern

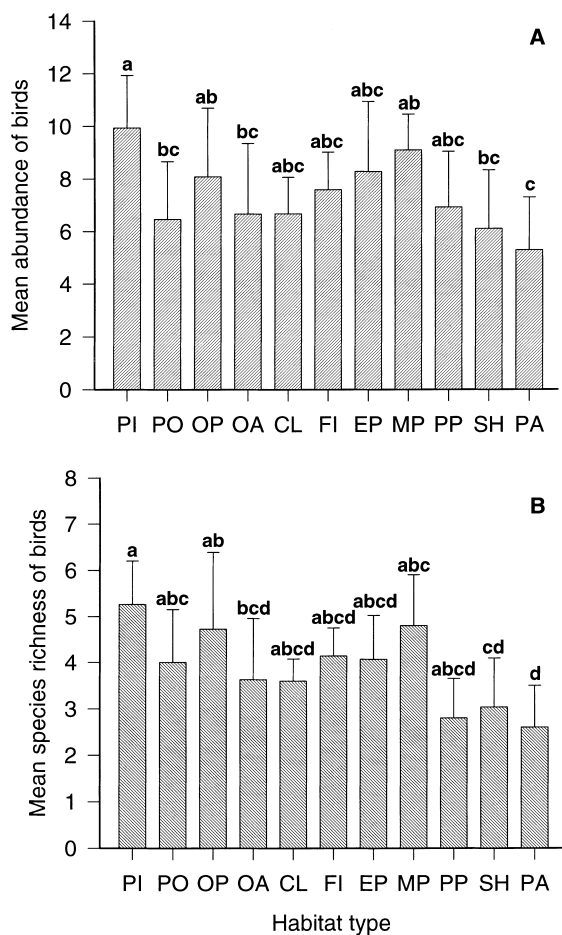


Fig. 2. Result of multiple comparisons evaluating differences in (A) bird abundance (mean number of birds/station/site) and (B) species richness (mean number of species/station/site) across 11 habitat types. Habitats with the same letter are not significantly different ($p>0.05$). Bars represent standard deviation. Habitat codes are defined in Table 2.

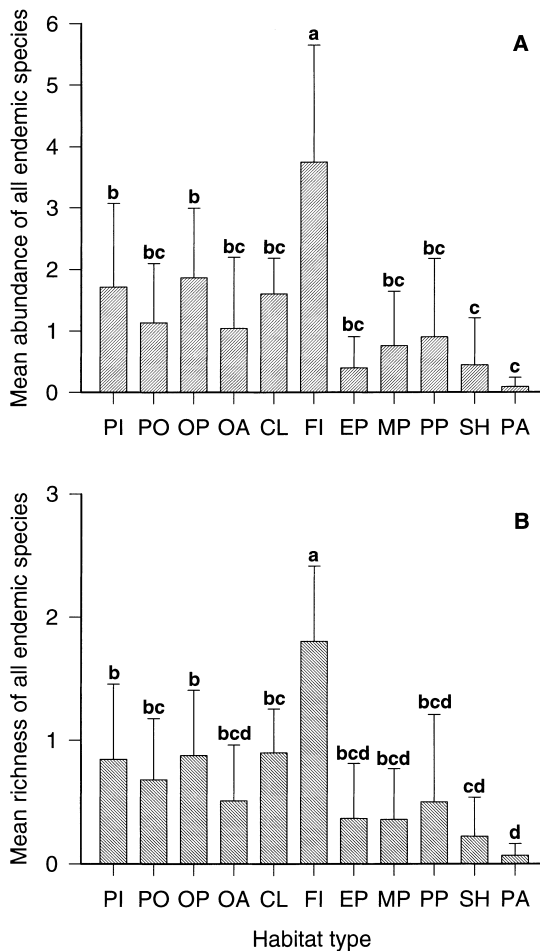


Fig. 3. Differences in (A) abundance and (B) species richness of all endemic bird species (quasi-endemics and true endemics) across 11 habitat types. Habitats with the same letter are not significantly different ($p>0.05$). Bars represent standard deviation. Habitat codes are defined in Table 2.

not evident when quasi-endemics were included (Fig. 3A). Species richness of true endemics differed across habitats ($F=10.40$; $df=10$ 123; and $p<0.001$), but multiple comparisons showed that native forests, with the exception of cloud and fir forests, had few differences among each other or from shrublands and pastures (Fig. 4(B)).

Thirty-nine species were classified as specialists and 24 species as generalists based on habitat breadth (see Appendix A). The number of generalist species among habitats was not significantly different from the number expected based on total species numbers in

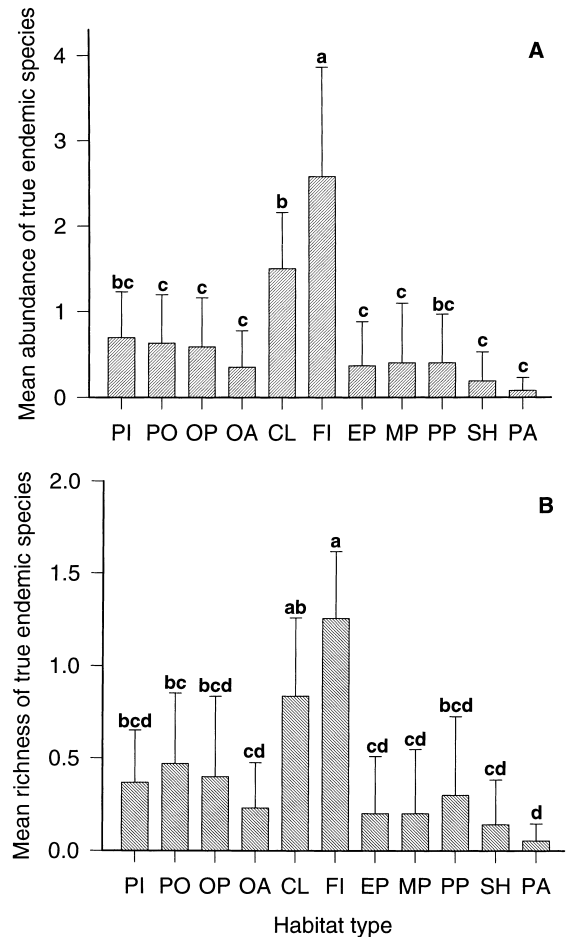


Fig. 4. Differences in (A) abundance and (B) species richness of true endemic bird species across 11 habitat types. Habitats with the same letter are not significantly different ($p>0.05$). Bars represent standard deviation. Habitat codes are defined in Table 1.

each habitat ($\chi^2=15.1$; $df=10$; and $p=0.13$). The greatest numbers of generalists were detected in pine, pine-oak, oak-pine, and oak forests, but the number of generalists was proportional to the total number of species in these habitats (Table 4). Pastures contained fewer generalists than expected, based on the habitat's high negative residual. The null hypothesis, stating that numbers of specialists in each habitat were proportional to total species numbers in each habitat, was rejected ($\chi^2=26.1$; $df=10$; and $p=0.004$). The largest positive residuals were found in pastures and shrublands (Table 4), suggesting that a greater number of

Table 4

The number of generalists and specialists species found in each habitat. The number expected based on total numbers of species found in each habitat and residuals from chi-square analysis

Habitat type	Generalists number			Specialists number		
	observed	expected	residual	observed	expected	residual
Pine	22	18.7	3.35	5	4.2	0.84
Pine-oak	24	23.3	0.69	5	5.2	−0.19
Oak-pine	22	23.3	−1.31	4	5.2	−1.19
Oak	23	27.6	−4.61	4	6.2	−2.15
Cloud	17	10.8	6.24	0	2.4	−2.40
Fir	16	13.3	2.73	1	3.0	−1.96
<i>Eucalyptus</i> plantation	9	7.6	1.47	1	1.7	−0.68
Mixed-spp plantation	10	8.6	1.39	1	1.9	−0.92
Pine plantation	10	5.7	4.26	0	1.3	−1.28
Shrubland	12	17.6	−5.57	6	3.9	2.08
Pasture	10	18.7	−8.65	13	4.2	8.74

specialists were found in these habitats than expected. Plantations, cloud forests, and fir forests supported fewer specialists than other habitats.

3.4. Relationships between PC axes and bird communities

Correlations and plots of bird species richness and abundance with PC axes (Fig. 5(A) and (B)) demonstrated significant positive linear relationships between species richness and PC I (tree-layer complexity) ($r=0.42$; $p<0.001$), and between bird abundance and tree-layer complexity ($r=0.28$; $p=0.002$). Neither species richness nor abundance had linear or non-linear relationships with PC II (shrub-layer complexity) or PC III. Although points are widely scattered in Fig. 5(B), it can be seen that species richness was never high at low values of tree-layer complexity, and sites with high tree-layer complexity yielded the highest species richness. The site with the greatest species richness was an oak–pine forest habitat (7.4 species/station). Nine out of ten of the richest sites were pine, oak–pine, or oak forest habitats, while one site was a mixed species plantation. Bird abundance also increased with tree-layer complexity (Fig. 5(A)), but the scatter of points was less revealing. A *Eucalyptus* plantation site contained the greatest number of birds (12.8 birds/station), while eight of the 10 sites with the highest abundances were pine, oak–pine, and oak forests.

3.5. Bird species composition

Seventy-four bird species were observed in at least five sites and included in the detrended correspondence analysis (DCA). Only the first two DCA axes provided information for differentiating habitats in DCA space. DCA axes I and II explained 8.8 and 5.5% of the variation in species composition, respectively, while the eigenvalues were 0.694 and 0.439, respectively. The amount of variation in species composition explained by the two DCA axes was small, and a large amount of scatter in species composition among sites was revealed (Fig. 6). The plot of DCA I and DCA II showed large variation in species composition among sites of the same and different habitats, but distinct patterns did emerge (Fig. 6). Habitats tended to group with similar habitats along DCA I. Pine, pine–oak, oak–pine, and oak forests were assigned the same symbol in the DCA plot because of considerable overlap among these forest sites (Fig. 6). These four forest types demonstrated considerable variation along DCA I, but the majority of sites grouped in a cluster distinct from pastures, shrublands, plantations, and cloud and fir forests. Cloud and fir forests, with the exception of two sites, revealed the highest values and furthest separation from all other habitat types on DCA I. *Eucalyptus* and mixed species plantations showed relatively low variation along DCA I and DCA II, forming a discrete cluster that excluded most native forest sites. *Eucalyptus* planta-

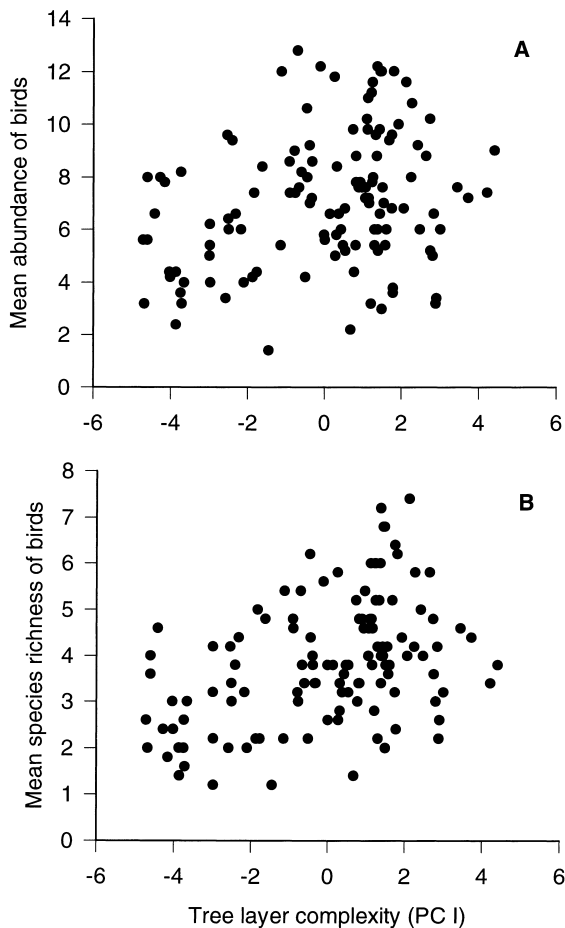


Fig. 5. Variation in (A) bird abundance and (B) species richness across tree-layer complexity (PC I). Note that low bird abundance and richness occur through all values of tree-layer complexity.

tion sites also showed more overlap with shrublands than with other native habitats. Shrubland and pasture sites overlapped and showed wide variation on DCA II with habitat separation at DCA II extremes, but displayed lower variation and distinct separation from native forests on DCA I. Clearly, there was an increase in the scatter of sites with decrease of DCA I as non-forest sites replaced forest sites, possibly signifying an overall decrease in similarity of bird species composition in pastures and shrublands compared to forests.

The 20 most abundant bird species were plotted using DCA I and DCA II values (Fig. 7). The location of each species indicates at which sites and habitats it

was potentially most abundant (overlay Figs. 6 and 7). Species characteristic of shrublands and pastures had extreme values along DCA II, while forest species tended to cluster. A few of the common species shared among different forest types were gray silky-flycatcher (*Ptilogonys cinereus*), Coues' flycatcher (*Contopus pertinax*), black-headed grosbeak (*Pheucticus melanocephalus*), and orange-billed thrush (*Catharus aurantiirostris*). Red warbler and white-striped creeper were found more commonly in cloud and fir forests than in other forest types, and Bewick's wren (*Thryomanes bewickii*), vermilion flycatcher (*Pyrocephalus rubinus*), Cassin's kingbird (*Tyrannus vociferans*), rufous-crowned sparrow (*Aimophila ruficeps*), and house finch (*Carpodacus mexicanus*) were most common in plantations. Fig. 6 demonstrated that more than half the shrubland sites were found in the upper half of DCA II, while more than half the pasture sites were found in the lower half, such that DCA II distinguished bird species found predominantly in shrublands (e.g. yellow-breasted chat, *Icteria virens*) from those found in pastures (e.g. barn swallow, *Hirundo rustica*) (Fig. 7). The large overlap in species composition in shrubland and pasture sites (Fig. 6) is attributable to sharing of several species by both habitats. For example, brown towhee (*Pipilo fuscus*) and rusty sparrow (*Aimophila rufescens*) were most abundant in shrublands, but they were also common in pastures, a pattern repeated by less common species also (Appendix A).

4. Discussion

4.1. Vegetation structure and bird communities

In this study, bird species richness was positively correlated with tree-layer complexity, similarly to that reported by many others (see, e.g. MacArthur and MacArthur, 1961; Karr and Roth, 1971; Roth, 1976; but not Power, 1971; Lovejoy, 1972; Pearson, 1975). A more challenging pattern to explain is the presence of a constraint on species richness at low values of tree-layer complexity. Constraint spaces may characterize many relationships between species and ecological variables that affect them (Brown and Maurer, 1987, 1989). High species richness only occurred at sites with high tree-layer complexity, although sites

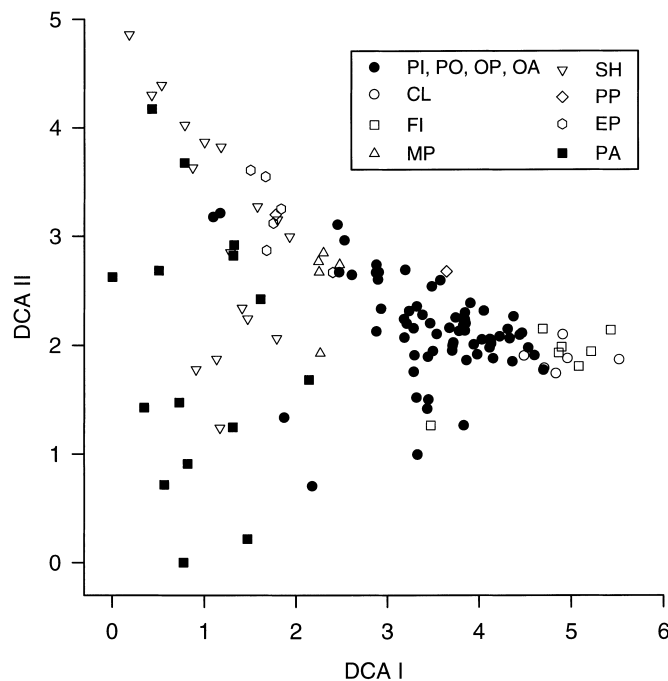


Fig. 6. Site scores among the two important axes of detrended correspondence analysis (DCA) demonstrating variation in species composition among habitats. The amount of separation between habitats indicates similarity in bird species composition. Habitat codes are defined in Table 1.

with high tree-layer complexity also demonstrated low species richness. These findings support the idea that structurally more complex habitats can support higher bird diversity than less complex habitats, but diversity in complex habitats is more variable by site. Sites with the highest tree-layer complexity did not support the highest bird species richness in our study. Similarly, Karr and Roth (1971) found a sigmoid relationship between percent cover and Bird Species Diversity (BSD); BSD increased most at intermediate levels of percent cover and stopped increasing at highest cover values. Karr and Roth speculated that extremely dense vegetation may restrict bird movement, resulting in decreased BSD. The vegetation was very dense in the cloud forests we sampled, possibly resulting in decreased bird species richness. A more intuitive explanation for the cutoff we observed in species richness, however, is that it was limited by other site factors not measured in this study (e.g. habitat area, habitat isolation, competition, predation).

Our results suggest that tree species presence and composition are significant factors influencing habitat

selection by bird species. The plot of PCA scores showed that forest sites were structurally similar to each other for the variables we measured, with the exception of cloud forests and *Eucalyptus* plantations. Despite this, bird-species compositions in plantations, cloud forests, and fir forests were relatively distinct from each other and from pine and oak forests in DCA space. Finding unique species composition in structurally similar habitats suggests that bird species use plant taxa to distinguish among habitats, an observation noted by other workers also (Karr, 1971; Rice et al., 1984; Rotenberry, 1985). Several workers have demonstrated associations between individual bird species and individual plant species (Smith, 1977; Holmes and Robinson, 1981; Maurer and Whitmore, 1981; Rice et al., 1983). The INEGI classification of forest types was based on the proportion of dominant tree species. Therefore, cloud forests, fir forests and *Eucalyptus* plantations were unique in the tree genera that dominated their sites; pine–oak forests contained a greater proportion of pine trees than oak trees; oak–pine forests had the opposite proportion;

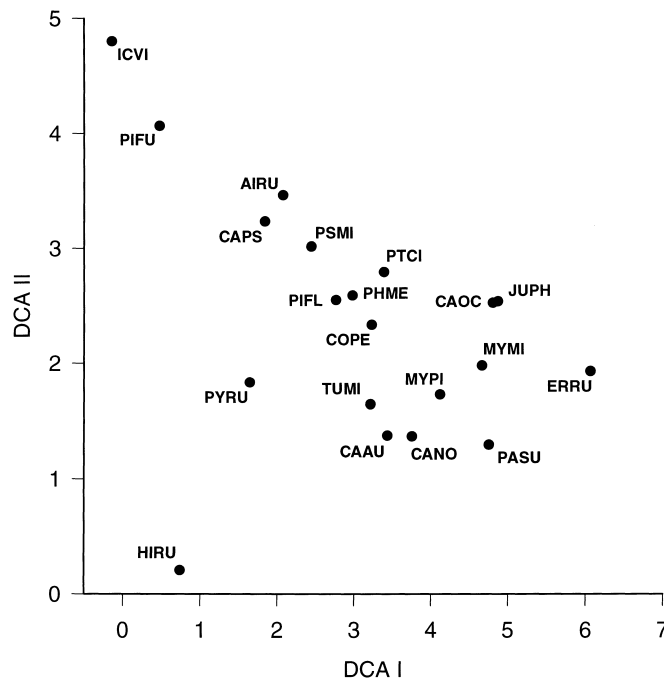


Fig. 7. Species scores of the 20 most abundant bird species from DCA. Location of species in DCA space indicates at which sites and habitat(s) each is potentially the most abundant by determining what sites are nearest to each species in Fig. 6. (AIRU, *Aimophila ruficeps*; CAAU, *Catharus aurantiirostris*; CANO, *Carduelis notata*; CAOC, *Catharus occidentalis*; CAPS, *Carduelis psaltria*; COPE, *Contopus pertinax*; ERRU, *Ergaticus ruber*; HIRU, *Hirundo rustica*; ICVI, *Icteria virens*; JUPH, *Junco phaeonotus*; MYMI, *Myioborus miniatus*; MYPI, *Myioborus pictus*; PASU, *Parus superciliosus*; PHME, *Pheucticus melanocephalus*; PIFL, *Piranga flava*; PIFU, *Pipilo fuscus*; PSMI, *Psaltiriparus minimus*; PTCI, *Ptilonotus cinereus*; PYRU, *Pyrocephalus rubinus*; and TUMI, *Turdus migratorius*).

and oak and pine forests shared dominant tree species with pine–oak and oak–pine forests. The sharing of dominant tree genera among the four oak and pine types helps to explain why so many bird species were shared among these sites. Quantification of tree density by tree species may help to distinguish bird–habitat relationships further.

4.2. Influence of management

Winter studies of migrants and resident birds in Mexico have suggested that migratory species as a group used disturbed habitats more often than undisturbed habitats, while resident species showed the opposite trend (e.g. Hutto, 1989; Lynch, 1989; Greenberg, 1992; Hutto, 1992). In a comprehensive review of habitat use by wintering migrants, Petit et al. (1995) found that disturbed sites supported 14% more

migrant species than undisturbed sites. Hutto (1992) found that species richness of residents was significantly lower in cloud forests than in tropical deciduous forests and pine–oak–fir forests. Hutto's cloud forest sites had coffee plantations in the understories, and, therefore, their lower species richness is consistent with a disturbance effect.

Disturbance in this study could be defined in various ways because of the habitat types sampled. The impact and intensity of disturbance was based on overall impressions from field notes taken at every site. For the purposes of this discussion, deforestation was identified as the principal disturbance, because most shrublands and pastures and all plantations were products of deforestation. Among native forests, oak forests appeared to be the most heavily disturbed type. At several sites, agriculture heavily fragmented forests resulting in clumps of oak trees surrounded

by agriculture. Cloud and fir forests appeared to demonstrate the least disturbance among all forest types. Six of the seven fir forests sampled were located in protected areas. While none of the cloud forests were found in protected areas, they were exposed to little disturbance owing to their remote locations.

When habitats were reclassified in this light, the distribution of habitats formed a disturbance gradient that shadowed PC axis I, the tree layer complexity gradient (Fig. 1). The least disturbed habitat types, cloud and fir forests, showed greatest tree-layer complexity, while the most disturbed habitats, oak forests, plantations, shrublands, and pastures, were less structurally complex. Because bird species richness was positively correlated with tree-layer complexity (Fig. 5(B)), it seems obvious that continued conversion of forested habitats to shrublands, pastures, and plantations will lower species richness of resident breeding birds at these sites and perhaps regionally. An exception to the general trend of decreasing richness with increasing disturbance was the mixed species plantation which demonstrated high bird species richness (Fig. 2(B)). Mixed species plantations generally contained at least one native *Pinus* species and demonstrated values of tree layer measures similar to native forests (Table 1). Other studies have also found decreases in bird species richness as a result of deforestation (Loyn, 1980; Driscoll, 1984; Johns, 1989; Thiollay, 1992), however, some studies found increased richness in lightly cut forests (Chadwick et al., 1986; Thompson et al., 1992; Welsh and Healy, 1993). According to Lent and Capen (1995), habitat changes caused by large-scale disturbances can lead to ecological dominance by a few early-successional species and decreased richness, whereas forest specialists and early-successional species can coexist at a higher level of species richness after small-scale disturbances. The intermediate disturbance hypothesis predicts increased diversity at medium levels of disturbance (Petraitis et al., 1989). In our study, forest clearing that yielded pastures and shrublands was a major disturbance, resulting in decreased bird species richness, whereas forest clearing that was followed by reforestation to plantations produced a moderately high species richness and a mix of early and late seral species associated with an intermediate disturbance effect.

The relationship between axis I and bird abundance demonstrated that high and low abundances occurred over a wide range of axis I values. Interpreting axis I as a disturbance gradient suggests that high bird abundance did occur at moderately disturbed sites. This was reinforced by the high average abundances in *Eucalyptus* plantations and mixed species plantations (Fig. 2(A)). This is consistent with the finding of many studies that populations of some bird species numerically respond in a positive way to the formation of new habitats created by disturbance (e.g. Chadwick et al., 1986; Thompson et al., 1992). Strong positive numerical responses to plantations by such generalists as *Thryomanes bewickii*; *Turdus migratorius*; *Pyrocephalus rubinus*; *Aimophila ruficeps*; *Carduelis psaltria* may then swamp out negative responses to disturbance by less common species. To evaluate the influences of disturbance on individual bird species within forest types, we recommend manipulative watershed experiments that monitor bird population responses to treatments such as thinning, clearing, planting, and grazing.

In contrast to the Hutto (1992) winter study in western Mexico, the cloud forests we sampled did not demonstrate significantly lower species richness than other habitat types. While Hutto's habitat classifications were broader than ours, a general comparison between our study and his is warranted owing to the scarcity of comparable studies. Hutto (1992) found that cloud forests contained significantly more migratory species and significantly fewer resident species than tropical deciduous forests, thorn forests, and pine-oak-fir forests. Hutto's study emphasized winter migrants in cloud forests disturbed by coffee cultivation while our study focused on breeding residents in undisturbed cloud forests. These differences in sampling season and coffee presence/absence may explain why species richness of avian residents was relatively high in cloud forests of our study but not in those sampled by Hutto. Also, our small number of cloud forest sites ($n=6$) may have masked some statistical differences in species richness among habitats. More research comparing bird species use of cloud forests and other habitats among seasons are needed to adequately evaluate the year-round significance of these habitats. We have reservations about using winter data alone to identify the conservation value of Mexico's habitats for birds.

4.3. Bird species composition

A striking feature of the DCA of species composition among habitats was the increased scatter of sites along DCA II as the value of axis I decreased. Shrublands and pastures demonstrated the largest scatter along DCA II, while cloud and fir forests had the smallest scatter. The large scatter of pasture and shrubland sites along DCA II represented high variability in species composition among sites. This was, in part, explained by disproportionately higher concentrations of specialists, species unique to pastures and shrublands, compared to other habitats. In contrast, cloud and fir forests harbored zero and one specialist species, respectively, and supported disproportionately more species having broad habitat breadths. Specialist species were generally rarer than generalists in our study (unpublished data) and were thus present at fewer sites resulting in large variation among sites most of which were shrublands and pastures. Generalists were shared among sites leading to decreased variation among sites as illustrated in cloud and fir forests. Our definitions of specialist and generalist are based on habitat breadth only and are not intended to convey information about finer specializations in foraging, nesting, or morphology.

In our study, native forests were divided into six habitat types while grasslands and shrublands were more coarsely classified, based on INEGI map classifications. This probably contributed to finding a greater number of unique species in shrublands and grasslands than in native forests. The finer division of native forests was warranted in our study because of the considerable interest by government agencies, conservationists, and researchers in quantifying the contributions of native habitats to avian richness and biological diversity, and identifying the possible factors that negatively or positively affect local and regional diversity of native forests such as deforestation, introduction of exotic trees, and agricultural crops. Furthermore, many native forests in Michoacán are managed for timber, fuelwood, recreation, and agroforestry crops (Leñero et al., 1990). We caution against using our results to conclude that forests are less important to specialists than non-forested habitats. Rather, when establishing conservation priorities, we recommend using our Appendix A to distinguish

specialists within forested ecosystems from pasture and shrubland bird species.

In our study, deforestation influenced species composition, leading to a different set of species inhabiting early second growth habitats such as pastures and shrublands. Although disturbance can substantially alter species composition (Johns, 1989; Thiollay, 1992), the intensity of the effect varies (Chadwick et al., 1986; Breininger and Schmalzer, 1990; Yahner, 1993; Lent and Capen, 1995). Whether deforestation or fragmentation results in large or small effects depends on the frequency, size, arrangement, and boundary distinctness of habitat patches (Wiens, 1976; Schemske and Brokaw, 1981; Lent and Capen, 1995). In our study area, most deforestation occurred at a large scale, resulting in large, well-defined habitat patches of shrubland and pasture. As a result, deforestation substantially altered site composition of bird species, creating avifauna unique to the altered sites and increased variability of species composition among sites.

4.4. Endemic species and conservation

Mexico is classified as a megadiversity country because it contributes in a critical way to global diversity, ranking third in biological diversity by country (Mittermeier, 1988). A total of 769 bird species are reported to breed in Mexico, and an additional 257 species occur as migrants or accidentals (Escalante et al., 1993). The Transvolcanic Belt is an important contributor to avian diversity and endemism within Mexico. We detected 82% of the 165 species reportedly found in the province. As expected, our sample totals of species numbers were lower than overall totals summarized from the literature by Escalante et al. (1993). We detected less than one-third of the species reported to occur in pine–oak forests, 44% in pine forests, 57% in oak forests, and only 16% in cloud forests. Our study results do not directly compare to Escalante et al. (1993) because our sampling area, sampling period (summer only) and number of sampling years (2 years only) were more restricted. Escalante et al. (1993) referenced Friedmann et al. (1950) and Miller et al. (1957) primarily, both of which relied heavily on work done in the early part of the century when some forest types and associated bird species may have been more common. When we

computed species accumulation curves, we found that new species were still detected at moderate rates in all forest types except pine and pine–oak forests (unpublished data). Thus, we probably failed to detect a relatively small percentage of the species inhabiting each forest type. Some forest types such as pine, oak–pine, cloud, and fir were rarer than other types in our study area, and sample sizes were limited by their availability.

Endemic species are important contributors to biological diversity because their restricted distributions make them globally rare and particularly vulnerable to population declines or extinction (Terborgh and Winter, 1983; Diamond, 1986). Species with small ranges are also less abundant at a local scale than large-range species (Brown, 1995) and, thus, populations of endemic species may be more susceptible to local factors such as human disturbance, predation, and competition. In this study, we detected 25 endemic species (true endemics and quasi-endemics). Escalante et al. (1993) reported that 37 endemic species are found in the Transvolcanic Belt. In Mexico as a whole, 43 endemics occur in pine–oak forests, 23 in cloud forests, 15 in oak forests, and 12 in pine forests. Based on our totals by habitat, we detected substantially fewer endemic species in pine–oak and cloud forests in our study area than reported by Escalante et al. (1993) for all of Mexico; however, this was expected owing to our limited study area and sample. In addition, the sampling method we used, point counts, tends to underestimate the abundance and presence of rare or secretive species and, therefore, endemic species may have been undersampled (Karr, 1981; Hutto et al., 1986).

The most abundant endemic species in our study was *Ptilononys cinereus* (quasi-endemic), which was common in oak and oak–pine forests (see Appendix A), followed by *Junco phaeonotus* (quasi-endemic) and *Ergaticus ruber* (true endemic), which were most abundant in fir forests. In our study area, fir forests provided habitats for more endemic species than all other vegetation types. Cloud forests were also important to endemic species. The importance of fir and cloud forests to endemic species makes their habitat contribution critical to sustaining regional, biological diversity. The relative rarity of these forest type in Michoacán, and in Mexico (Rzedowski, 1993), further highlights the need to conserve them locally.

A conservation strategy for a region or country should attempt to conserve habitats or geographic regions of high biotic diversity and endemism (Soulé, 1986). We would add that rare and endangered habitats and species should factor into a conservation strategy since they are likely to be lost first, causing a reduction in biotic diversity (Scott et al., 1993). The economic and logistical difficulties inherent in implementing a conservation program for a large region are magnified in Mexico owing to high rates of human population growth, a struggling economy, rapid environmental changes, shortages of inventory and monitoring data, and lack of an infrastructure to facilitate a coordinated conservation program (Ramos, 1988). Assessment of regional biodiversity using geographical information systems has begun in Mexico, although a limiting factor is availability of local species distributions (Bosch and Sanchez-Cordero, 1993; Bojórquez-Tapia et al., 1995). Our results provide constructive information applicable to local forest management efforts because we identified habitats important for conserving endemic species and overall avian diversity during the breeding season in Michoacán and documented probable factors causing variation in numbers of birds and species (some factors can be managed to produce a desired future). We also clarified habitat availability and rarity (based on our stratified sampling design) which can be compared to patterns of avian diversity for the purpose of identifying high-priority forest types for conservation; and documented positive, negative, and mixed responses of bird species to deforestation, as indexed by the relationships between native and second growth habitats, and bird species composition and habitat breadth.

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Appendix A

Bird species abundance in north-central Michoacán (Table 5)

Table 5

The abundances (# birds/station/site) of all bird species detected during counts among 11 habitat types in north-central Michoacán. Abundances were calculated by averaging all sites of the same habitat ^a. Refer to Table 2 for habitat names

Species	Habitat type											breadth	status ^b
	PI	PO	OP	OA	CL	FI	EP	MP	PP	SH	PA		
<i>Casmerodius albus</i>	—	—	—	—	—	—	—	—	—	—	0.23	1.00	N
<i>Bubulcus ibis</i>	—	—	—	—	—	—	—	—	—	—	0.01	1.00	N
<i>Cathartes aura</i>	—	—	0.02	0.02	—	—	0.03	0.28	—	0.06	0.11	2.78	N
<i>Chondrohierax uncinatus</i>	—	—	—	—	—	—	—	—	—	—	0.01	1.00	N
<i>Accipiter cooperii</i>	—	—	—	0.01	—	—	—	—	—	—	—	1.00	N
<i>Accipiter striatus</i>	—	—	—	0.01	—	—	—	—	—	—	—	1.00	N
<i>Buteo jamaicensis</i>	—	0.03	0.02	0.03	—	—	—	—	—	—	0.01	3.55	N
<i>Zenaidura macroura</i>	0.02	—	0.05	0.01	—	—	—	—	—	0.06	0.04	3.86	N
<i>Columbina inca</i>	—	—	0.03	0.02	—	—	—	—	—	—	0.04	2.80	N
<i>Leptotila verreauxi</i>	0.02	—	—	—	—	—	—	—	—	—	—	1.00	N
<i>Chordeiles acutipennis</i>	—	0.01	—	—	—	—	—	—	—	—	—	1.00	N
<i>Crotophaga sulcirostris</i>	—	—	—	—	—	—	—	—	—	0.04	—	1.00	N
<i>Colibri thalassinus</i>	—	—	0.17	—	—	—	—	—	—	—	—	1.00	N
<i>Cyananthus latirostris</i>	—	—	0.02	0.02	—	0.03	—	0.36	—	—	—	1.37	Q
<i>Hylocharis leucotis</i>	0.06	0.12	0.15	—	0.27	0.03	0.07	—	—	—	—	4.11	N
<i>Amazilia beryllina</i>	—	—	0.05	0.15	—	0.11	—	0.52	—	—	—	2.24	N
<i>Amazilia violiceps</i>	—	—	—	—	—	—	—	—	—	0.24	—	1.00	Q
<i>Lampornis clemenciae</i>	—	—	—	0.03	—	0.03	—	—	—	0.01	—	2.67	Q
<i>Eugenes fulgens</i>	—	—	0.02	0.01	—	—	—	—	—	—	—	1.92	N
<i>Trogon elegans</i>	0.28	0.09	0.17	0.08	—	—	—	—	—	—	—	3.17	N
<i>Trogon mexicanus</i>	0.03	0.05	—	—	0.70	—	—	—	—	—	—	1.24	N
<i>Colaptes auratus</i>	0.20	0.05	0.08	0.02	—	0.03	—	0.04	—	—	—	3.76	N
<i>Melanerpes formicivorus</i>	0.06	0.22	0.14	0.07	0.03	0.06	—	—	—	—	—	4.18	N
<i>Melanerpes aurifrons</i>	—	—	—	0.04	—	—	0.23	0.12	—	0.06	0.01	2.92	N
<i>Picoides villosus</i>	0.14	—	0.02	0.01	—	—	—	—	0.10	—	—	2.36	N
<i>Picoides scalaris</i>	0.02	—	0.03	0.06	—	—	—	—	—	0.08	—	3.15	N
<i>Picoides stricklandi</i>	0.02	—	—	—	—	—	—	—	—	—	—	1.00	Q
<i>Lepidocolaptes leucogaster</i>	0.12	0.17	0.26	0.02	0.30	0.29	—	—	—	—	—	4.73	E
<i>Pachyrhamphus aglaiae</i>	—	0.04	0.03	0.07	—	—	—	—	—	0.01	—	3.07	N
<i>Pyrocephalus rubinus</i>	—	0.02	0.06	0.10	—	0.09	0.77	0.28	—	0.06	0.20	3.38	N
<i>Tyrannus melancholicus</i>	—	—	—	—	0.03	—	—	—	—	—	—	1.00	Q
<i>Tyrannus crassirostris</i>	—	—	—	—	—	—	—	—	—	—	0.01	1.00	N
<i>Tyrannus vociferans</i>	0.05	—	—	0.08	—	—	0.83	0.40	—	0.01	0.17	2.67	N
<i>Myiodynastes luteiventris</i>	—	—	0.05	—	—	0.03	—	—	—	—	0.01	2.48	N
<i>Myiozetetes similis</i>	—	—	—	0.01	—	—	—	—	—	—	—	1.00	N
<i>Pitangus sulphuratus</i>	—	—	—	—	—	—	—	—	—	0.06	—	1.00	N
<i>Myiarchus cinerascens</i>	—	0.02	—	—	—	—	—	—	—	0.04	0.03	2.85	N
<i>Myiarchus tuberculifer</i>	—	0.10	—	0.04	—	—	—	—	—	0.04	—	2.39	N
<i>Myiarchus tyrannulus</i>	—	0.01	—	—	—	—	—	—	—	—	—	1.00	N
<i>Contopus pertinax</i>	0.72	0.41	0.46	0.38	0.13	—	0.17	0.56	—	0.04	0.03	5.95	N
<i>Mitrephanes phaeocercus</i>	0.06	0.08	0.03	0.02	0.13	—	—	—	—	—	—	3.62	N
<i>Empidonax affinis</i>	—	0.01	—	0.01	—	0.09	—	—	—	—	0.01	1.83	E
<i>Empidonax albicularis</i>	—	—	—	—	—	—	—	—	—	0.02	0.01	1.86	N
<i>Empidonax difficilis</i>	0.18	0.06	0.06	0.02	0.13	—	—	—	—	—	—	3.54	N
<i>Eremophila alpestris</i>	—	—	—	—	—	—	—	—	—	—	0.01	1.00	N

Table 5 (Continued)

Species	Habitat type											breadth	status ^b
	PI	PO	OP	OA	CL	FI	EP	MP	PP	SH	PA		
<i>Xenotriccus mexicanus</i>	—	0.04	—	0.01	—	0.06	—	—	—	—	—	2.31	E
<i>Tachycineta thalassina</i>	—	—	—	—	—	—	—	0.48	—	—	—	1.00	N
<i>Stelgidopteryx serripennis</i>	—	0.10	—	—	—	—	—	—	—	0.08	0.23	2.45	N
<i>Hirundo rustica</i>	—	0.02	—	0.16	—	0.17	—	0.20	—	0.59	1.19	2.93	N
<i>Corvus corax</i>	0.08	0.15	0.25	0.12	0.03	0.17	0.07	—	—	—	0.03	5.71	N
<i>Aphelocoma ultramarina</i>	0.22	0.06	0.11	0.08	—	—	—	—	—	—	—	3.33	Q
<i>Cyanocitta stelleri</i>	—	—	—	0.02	—	0.09	—	—	—	—	—	1.44	N
<i>Parus sclateri</i>	0.14	0.14	0.11	0.09	0.07	0.43	—	—	—	—	—	3.83	Q
<i>Parus wollweberi</i>	0.03	—	0.02	0.14	—	—	—	—	—	—	—	1.67	N
<i>Psaltiriparus minimus</i>	0.37	0.17	0.14	0.37	—	0.03	0.53	—	1.30	0.41	—	4.47	N
<i>Sitta carolinensis</i>	0.15	0.05	—	0.01	—	—	—	—	—	—	—	1.74	N
<i>Sitta pygmae</i>	0.25	—	—	—	—	—	—	—	—	—	—	1.00	N
<i>Certhia americana</i>	0.09	0.03	0.02	0.01	0.10	0.29	—	—	—	—	—	2.81	N
<i>Campylorhynchus megalopterus</i>	—	—	0.03	—	0.10	0.11	—	—	—	—	—	2.50	E
<i>Campylorhynchus brunneicapillus</i>	—	—	—	—	—	—	—	—	—	0.06	—	1.00	N
<i>Campylorhynchus gularis</i>	0.14	0.03	—	0.20	—	0.09	0.37	0.28	—	0.06	0.05	5.13	E
<i>Thryomanes bewickii</i>	—	—	0.03	0.02	—	—	0.93	0.40	—	0.16	0.03	2.34	N
<i>Troglodytes aedon</i>	0.32	0.07	—	0.02	0.07	0.03	—	—	—	—	—	2.25	N
<i>Henicorhina leucophrys</i>	—	0.01	—	—	—	—	—	—	—	—	—	1.00	N
<i>Toxostoma curvirostre</i>	—	—	—	0.02	—	—	—	—	—	0.07	0.07	2.52	N
<i>Melanotis caerulescens</i>	—	—	0.03	0.02	—	—	—	—	—	0.05	0.01	3.30	E
<i>Mimus polyglottos</i>	—	0.03	0.03	0.01	—	—	—	—	—	—	—	2.57	N
<i>Turdus migratorius</i>	0.42	0.19	0.29	0.15	0.03	—	—	0.68	—	—	0.01	4.03	N
<i>Turdus rufopalliat</i>	—	—	0.08	—	—	—	—	—	—	—	—	1.00	E
<i>Turdus assimilis</i>	0.08	0.04	0.06	0.03	0.07	—	—	—	0.10	—	—	5.28	N
<i>Myadestes occidentalis</i>	0.14	0.14	0.15	0.12	0.13	0.03	—	—	—	—	—	5.35	N
<i>Catharus occidentalis</i>	0.25	0.20	0.06	0.08	0.73	0.20	—	0.12	0.40	—	—	4.83	E
<i>Catharus frantzii</i>	—	0.03	—	0.02	—	—	—	—	—	—	—	1.92	N
<i>Catharus aurantirostris</i>	0.22	0.27	0.18	0.30	0.27	0.09	0.07	0.20	—	0.01	—	6.99	N
<i>Sialia mexicana</i>	—	—	—	—	—	—	—	—	—	—	0.03	1.00	N
<i>Sialia sialis</i>	0.22	0.03	0.08	0.02	—	0.06	—	0.20	—	—	0.04	4.15	N
<i>Poliopitila caerulea</i>	—	—	0.03	—	—	—	—	—	—	—	0.01	1.73	N
<i>Regulus satrapa</i>	—	—	—	—	—	0.26	—	—	—	—	—	1.00	N
<i>Ptilogonys cinereus</i>	0.11	0.17	0.60	0.46	0.03	—	—	—	—	—	—	3.12	Q
<i>Lanius ludovicianus</i>	—	0.01	0.02	0.02	—	—	—	—	—	0.05	0.17	2.14	N
<i>Vireolanius melitophrys</i>	0.02	—	—	—	—	—	—	—	—	—	—	1.00	Q
<i>Vireo huttoni</i>	0.05	0.08	0.03	0.05	0.03	—	—	—	—	0.02	—	5.10	N
<i>Vireo solitarius</i>	—	—	—	0.07	—	0.06	—	—	—	—	—	1.98	N
<i>Vireo gilvus</i>	—	—	0.08	—	0.03	0.06	—	—	—	—	—	2.72	N
<i>Diglossa baritula</i>	—	0.04	—	—	—	—	—	—	—	—	—	1.00	N
<i>Parus superciliosus</i>	0.08	0.25	0.38	0.21	0.43	0.26	—	—	—	—	—	5.05	N
<i>Peucedramus taeniatus</i>	0.26	0.04	0.02	0.01	—	—	—	—	0.30	—	—	2.45	N
<i>Dendroica graciae</i>	0.06	0.10	0.05	0.04	—	—	0.32	0.10	—	—	—	3.43	N
<i>Geothlypis poliocephala</i>	—	—	—	—	—	—	—	—	—	0.09	—	1.00	N
<i>Icteria virens</i>	—	—	—	0.02	—	—	—	—	—	0.72	0.11	1.35	N
<i>Myioborus pictus</i>	0.22	0.42	0.68	0.20	0.63	0.29	—	—	0.20	0.01	—	5.62	N
<i>Myioborus miniatus</i>	0.94	0.59	0.34	0.21	0.67	0.51	—	—	0.50	—	—	6.02	N
<i>Ergaticus ruber</i>	0.17	0.12	—	0.01	0.30	1.74	—	—	—	—	—	1.73	E
<i>Basileuterus belli</i>	0.08	0.01	0.02	—	—	0.80	0.74	—	—	—	—	2.26	N
<i>Basileuterus rufifrons</i>	—	0.08	0.03	0.09	0.03	—	—	—	—	0.06	—	4.29	N
<i>Passer domesticus</i>	—	—	—	—	—	—	0.17	—	—	0.01	—	1.14	N
<i>Molothrus aeneus</i>	—	0.04	0.02	—	—	—	—	—	—	0.04	0.05	3.50	N
<i>Molothrus ater</i>	—	—	—	—	—	—	—	—	—	—	0.04	1.00	N

Table 5 (Continued)

Species	Habitat type											breadth	status ^b
	PI	PO	OP	OA	CL	FI	EP	MP	PP	SH	PA		
<i>Icterus spurius</i>	—	—	—	—	—	—	—	—	—	—	0.01	1.00	N
<i>Icterus wagleri</i>	—	—	—	—	—	—	—	—	—	—	0.07	1.00	N
<i>Icterus parisorum</i>	—	—	—	—	—	—	—	—	—	—	0.01	1.00	N
<i>Icterus pustulatus</i>	—	—	0.03	—	—	—	—	—	—	0.16	0.03	1.71	N
<i>Agelaius phoeniceus</i>	—	—	—	—	—	—	—	—	—	—	0.03	1.00	N
<i>Sturnella magna</i>	—	—	—	0.02	—	—	0.10	—	—	0.01	0.67	1.40	N
<i>Euphonia elegantissima</i>	—	0.04	0.11	0.08	—	—	—	0.12	—	—	—	3.56	N
<i>Piranga flava</i>	0.32	0.11	0.12	0.08	0.03	0.09	0.13	0.16	0.30	0.20	0.09	8.20	N
<i>Piranga bidentata</i>	—	—	—	0.02	—	—	—	—	—	—	—	1.00	N
<i>Piranga erythrocephala</i>	—	0.02	—	—	—	—	—	—	—	—	—	1.00	E
<i>Cardinalis cardinalis</i>	—	—	—	—	—	—	—	—	—	0.01	—	1.00	N
<i>Pheucticus melanocephalus</i>	0.11	0.08	0.45	0.21	—	—	—	0.08	0.20	0.07	0.01	4.66	N
<i>Guiraca caerulea</i>	—	—	—	0.07	—	—	0.07	—	0.30	0.18	0.15	3.80	N
<i>Passerina versicolor</i>	—	—	—	0.01	—	—	—	—	—	0.04	—	1.52	N
<i>Volatinia jacarina</i>	—	0.01	0.03	—	—	—	—	—	—	0.02	—	2.31	N
<i>Atlapetes pileatus</i>	0.02	0.02	0.12	—	0.03	—	—	—	—	—	—	2.18	E
<i>Atlapetes virenticeps</i>	—	0.02	—	—	0.03	—	—	—	—	—	—	1.88	E
<i>Pipilo erythrophthalmus</i>	0.20	0.08	0.17	0.14	0.03	0.09	—	—	—	0.01	0.01	5.20	N
<i>Pipilo fuscus</i>	—	0.02	0.05	0.15	—	—	0.20	0.04	—	0.51	0.41	3.83	N
<i>Melospiza kieneri</i>	—	—	—	—	—	—	—	—	—	0.08	—	1.00	E
<i>Aimophila ruficauda</i>	0.03	0.03	—	0.02	—	—	—	—	—	—	0.03	3.90	N
<i>Aimophila ruficeps</i>	0.18	0.09	0.02	0.08	—	—	1.43	1.68	1.80	0.01	0.08	3.54	N
<i>Aimophila rufescens</i>	0.02	—	—	0.14	—	—	0.10	—	0.10	0.41	0.16	3.66	N
<i>Aimophila botterii</i>	—	—	—	—	—	—	—	—	—	—	0.11	1.00	N
<i>Spizella atrogularis</i>	—	—	—	0.02	—	—	—	—	—	0.12	—	1.33	N
<i>Junco phaeonotus</i>	0.52	0.13	0.37	0.01	—	0.69	—	—	0.50	—	—	4.29	Q
<i>Coccothraustes abeillei</i>	—	—	0.08	—	—	—	—	—	—	—	—	1.00	Q
<i>Carpodacus mexicanus</i>	—	0.04	—	0.06	—	—	0.17	0.24	0.50	0.12	0.08	4.02	N
<i>Carduelis pinus</i>	—	0.06	—	—	—	—	—	—	—	—	—	1.00	N
<i>Carduelis notata</i>	0.89	0.10	0.12	—	0.03	—	—	—	—	0.02	—	1.66	N
<i>Carduelis psaltria</i>	0.31	0.21	0.15	0.54	—	—	1.43	1.16	0.20	0.54	0.08	5.10	N
<i>Loxia curvirostra</i>	0.20	—	—	—	—	—	—	—	—	—	—	1.00	N

^a The scientific names of all species are based on the A.O.U. Check-list (American Ornithologists' Union, 1983, 1985).

^b E=true endemic; N=non-endemic; Q=quasi-endemic.

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