

Abundance and habitat relationships of breeding birds in the Sky Islands and adjacent Sierra Madre Occidental of northwest Mexico

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ABSTRACT. The Sierra Madre Occidental and neighboring Madrean Sky Islands span a large and biologically diverse region of northwest Mexico and portions of the southwestern United States. Little is known about the abundance and habitat use of breeding birds in this region of Mexico, but such information is important for guiding conservation and management. We assessed densities and habitat relationships of breeding birds across Sky Island mountain ranges in Mexico and adjacent portions of the Sierra Madre from 2009 to 2012. We estimated densities at multiple spatial scales, assessed variation in densities among all major montane vegetation communities, and identified and estimated the effects of important habitat attributes on local densities. Regional density estimates of 65% of 72 focal species varied significantly among eight montane vegetation communities that ranged from oak savannah and woodland at low elevations to pine and mixed-conifer forest at high elevations. Greater proportions of species occurred at peak densities or were relatively restricted to mixed-conifer forest and montane riparian vegetation likely because of higher levels of structural or floristic diversity in those communities, but those species were typically rare or uncommon in the Sky Islands. Fewer species had peak densities in oak and pine-oak woodland, and species associated with those communities were often more abundant across the region. Habitat models often included the effects of broadleaf deciduous vegetation cover (30% of species), which, together with tree density and fire severity, had positive effects on densities and suggest ways for managers to augment and conserve populations. Such patterns combined with greater threats to high-elevation conifer forest and riparian areas underscore their value for conservation. Significant populations of many breeding bird species, including some that are of concern or were not known to occur regionally or in mountain ranges we surveyed, highlight the importance of conservation efforts in this area of Mexico.

RESUMEN. Abundancia y relaciones de hábitat de aves reproductivas en las Islas del Cielo y la contigua Sierra Madre Occidental del noroeste de México

La Sierra Madre Occidental y las vecinas Islas del Cielo Madreñas abarcan una extensa y biológicamente diversa región del noroeste de México y porciones del sudoeste de Estados Unidos. Poco se sabe sobre la abundancia y el uso de hábitat de las aves que crían en esta región de México, pero dicha información es importante para guiar la conservación y el manejo de la zona. Evaluamos densidades y relaciones de hábitat de aves reproductoras a lo largo de las cadenas montañosas de las Islas del Cielo en México y puntos adyacentes de la Sierra Madre desde el 2009 al 2012. Estimamos densidad a múltiples escalas, analizamos la variación en la densidad entre las principales comunidades vegetales montañosas, e identificamos y estimamos los efectos de importantes atributos de hábitat en las densidades locales. Estimaciones de densidad regional de 65% de 72 especies focales variaron significativamente entre ocho comunidades de vegetación montana que van desde sabana con robles y bosques a baja elevaciones hasta bosque de pino y bosque de coníferas mixto a altas elevaciones. Mayores proporciones de especies ocurrieron en densidades pico o se encontraron relativamente restringidas a bosque mixto de coníferas y a vegetación montana riparia, seguramente debido a los altos niveles de estructura o de diversidad florística en esas comunidades, pero dichas especies fueron típicamente raras o poco comunes en las Islas del Cielo. Pocas especies tuvieron su densidad pico en bosques de roble y pino-roble, y las especies asociadas con estas comunidades fueron muchas veces muy abundantes a lo largo de la región. Los modelos de hábitat muchas veces incluyeron el efecto de la cobertura vegetal decidua de hoja ancha (30% de las especies), que junto con la densidad de árboles y la severidad de los incendios, tuvo un efecto positivo en las densidades y sugieren formas a los encargados de planes de manejo para aumentar y conservar poblaciones. Dichos patrones combinados con las mayores amenazas en bosques de coníferas de altura y áreas riparias recalcan su valor para la conservación. Poblaciones significativas de varias especies de aves reproductivas, incluyendo algunas que son de interés o no eran conocidas sus ocurrencias regionales o en las cadenas montañosas que hemos sondeado, resaltan la importancia de los esfuerzos de conservación en esta área de México.

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Madrean oak, pine-oak, and montane conifer forest and woodland cover much of the Sierra Madre Occidental (SMO) of northwest Mexico and neighboring Madrean Sky Islands. The Madrean Sky Islands are an extensive series of disjunct highlands dominated by those vegetation communities and surrounded by lowlands of grassland, foothills thornscrub, and desert scrub between the SMO in Mexico and Rocky Mountains in the southwestern United States (Gehlbach 1981, Warshall 1995). The SMO and Sky Islands are global conservation priorities because they support high levels of biodiversity and endemism, and span portions of a broad transition zone between the Nearctic and Neotropical faunal realms (Halffter 1987, Felger and Wilson 1995, Mittermeier et al. 2004). Pine-oak woodland, for example, supports high floristic diversity, and the SMO supports the largest area of temperate vegetation in Mexico, most of which is pine-oak woodland (Rzedowski 1978, González-Elizondo et al. 2012). With regard to landbirds in Mexico, pine-oak woodlands support an estimated 218 breeding species, which is the highest richness known among temperate vegetation communities and exceeded only in lowland tropical forests (Escalante-Pliego et al. 1993, Navarro-Sigüenza et al. 2014).

Marshall (1957) studied the distribution, abundance, and habitat relationships of breeding birds in pine-oak woodland and adjacent riparian vegetation in the early 1950s in six Sky Islands in the United States, nine in Mexico, and five areas in the adjacent SMO. Although his findings were remarkably insightful and helped establish the ecological and biogeographical significance of the region (Warshall 1995), they were largely qualitative and focused at moderate elevations. Since then, studies of breeding birds in the Madrean Sky Islands have focused almost entirely on the United States (e.g., Balda 1969, Corman and Wise-Gervais 2005, Kirkpatrick et al. 2006), and those in Mexico remain either largely qualitative (Flesch and Hahn 2005, Flesch 2008) or of limited spatial and taxonomic scope (Landres and MacMahon 1983). Similarly, studies in the

neighboring northern SMO have focused on a few species of concern such as Thick-billed Parrots (*Rhynchopsitta pachyrhyncha*), Spotted Owls (*Strix occidentalis lucida*), and Eared Quetzals (*Euptilotis neoxenus*; Lanning and Shifflett 1983, Young et al. 1998, Monterrubio-Rico and Enkerlin-Hoeflich 2004, González-Rojas et al. 2008), with gaps of knowledge increasing to the south in more humid regions of the SMO (Stager 1954, Medina-Macías et al. 2010, Flesch et al. 2015). Thus, although we know pine-oak woodland supports a rich community of breeding birds in this region of Mexico, and understand habitat use by some species in the region based largely on work in the United States (Stromberg 1990, Hall and Mannan 1999, Conway and Kirkpatrick 2007, Kirkpatrick and Conway 2010, Ganey et al. 2015), the abundance and habitat relationships of breeding birds have not been assessed quantitatively at large scales or across a full range of montane vegetation communities and breeding species in Mexico. Moreover, although contemporary information is available in the United States (e.g., Corman and Wise-Gervais 2005), breeding bird communities in many Sky Islands in Mexico have not been described and available information remains largely historical (Marshall 1957, Russell and Monson 1998, Flesch 2008). Filling those information gaps is important for better understanding the status and habitat needs of birds and for confronting threats to wildlife that are focused in the United States-Mexico borderlands and at high elevations where climate change could have pervasive effects (Flesch et al. 2010, Rehfeldt et al. 2012, Monterrubio-Rico et al. 2015).

Our objectives were to assess the abundance and habitat relationships of breeding bird species across the Madrean Sky Islands in Mexico and portions of the adjacent SMO. To do so, we estimated densities at multiple spatial scales and described variation in densities among all major montane vegetation communities in the region. Additionally, we identified and estimated the effects of important habitat attributes on local densities, and

compared our inferences on bird–habitat relationships with those from past studies. More broadly, our objectives were to establish quantitative baselines for monitoring bird communities in the future and provide information useful for management and conservation of this significant, but little known, region of Mexico.

METHODS

Study area. The SMO is the largest mountain range in Mexico and dominated by broad highland plateaus incised by deep canyons, over 70% of which is covered by montane vegetation (González-Elizondo et al. 2012). The adjacent Madrean Sky Islands are steep mountain ranges separated from the SMO by semi-arid lowland vegetation (Warsshall 1995). Those valleys create the only gap in the vast highland cordillera that forms the backbone of western North America between Alaska and southern Mexico. We focused on Sky Islands in Mexico that were north and west of the SMO, west to the Sierra el Humo, and south to the sierras Aconchi, Oposura, and Bacadéhuachi (Fig. S1). We also considered areas in the adjacent northern SMO that included ridgeline extensions of the SMO (Cebadilla and Huachinera) and areas on the plateaus to the south and east (El Poleo and Sierra Cinco Millas).

Eight major montane vegetation communities dominate the region (Figs. S1–S8). Oak savannah occurs at low elevations (1180–2045 m; mean = 1487 m) near the margins of lowland vegetation communities and consists of scattered patches of oak woodland embedded in grasslands and occasionally desert scrub or thornscrub. Oak woodland typically occurs at low elevations (1155–2410 m; mean = 1740 m) and is dominated by various species of evergreen oaks. Oak-pine woodland occurs at moderate elevations (1445–2375 m; mean = 1975 m) where oaks and pines are co-dominant. Pine-oak woodland occurs at moderate to high elevations (1530–2520 m; mean = 2075 m) where taller pines often dominate a mid-story of oaks. Those woodland communities often support juniper (*Juniperous* spp.) in arid areas and madrone (*Arbutus* spp.) in mesic areas. Mountain scrub occurs at a broad range of elevations (1185–2600 m; mean = 1800 m)

and is dominated by shrubby oaks, manzanita (*Arctostaphylos* spp.), and mountain mahogany (*Cercocarpus* spp.). Pine forest occurs at high elevations (1780–2750 m; mean = 2320 m) and is dominated largely by Arizona pine (*P. arizonica*) and at higher elevations by southwestern white pine (*P. strobiformis*). Mixed-conifer forest occurs at the highest elevations (1845–2730 m; mean = 2360 m) and is dominated by those same pines, Douglas fir (*Pseudotsuga menziesii*), and rarely white fir (*Abies concolor*). Montane riparian vegetation occurs at nearly all elevations (1170–2415 m; mean = 1685 m) and is dominated by linear stands of broadleaf deciduous trees such as Arizona sycamore (*Platanus wrightii*), bigtooth maple (*Acer grandidentatum*), Arizona alder (*Alnus oblongifolia*), and Arizona walnut (*Juglans major*) mixed with oaks and pines, and locally by Arizona cypress (*Cupressus arizonica*). Land uses other than grazing are rare in the Sky Islands. Logging largely ceased in the mid-1900s, but continues in the SMO.

Design. We surveyed nearly all Sky Islands of sufficient elevation to support pines, with few exceptions (Buenos Aires, Jucaral, and Pinito-Sombrerillo), and most Sky Islands that supported oaks, but no pines. Our basic sampling units were transects along which we systematically placed survey stations at 200–300-m intervals or, occasionally, closer on steep slopes. We placed most transects non-randomly in representative areas in each major vegetation community because initial attempts at random placement stratified by vegetation community were difficult due to rugged terrain, access constraints, and lack of accurate vegetation maps. To assess communities available for sampling, we scouted ranges, evaluated satellite imagery, and interviewed local residents. Because bird communities in larger ranges required more effort to describe, we allocated effort in proportion to the size of ranges and number of vegetation communities they supported. We placed transects on slopes, ridges, and flats in uplands, and near drainage channels in riparian areas in mountain ranges rather than on surrounding outwash plains. Portions of some transects occasionally followed old logging roads and trails.

Bird surveys. We surveyed birds from early May to mid-July 2009–2012. To survey

birds, we conducted point counts at stations for 8 min during the period from 30 min before to 3.5 h after sunrise on calm, rain-free mornings. For each detection, we used rangefinders to measure the minimum horizontal distance from stations to the actual or estimated initial location of individuals or center of each pair or flock, and noted the number of individuals, sex (if known), and detection type (visual, calling, singing, or other auditory detection such as wing or drumming sounds). We recorded wind speed, cloud cover, and noise levels at the first and last stations along transects. To maximize coverage across the region, we surveyed most (96%) stations once. To assess breeding status, we recorded observations of breeding behavior during, but mainly after, point counts, and used breeding bird atlas techniques to classify breeding status as possible, probable, confirmed, or non-breeding (NAOAC 1990).

Environmental measurements. We described vegetation structure and composition, land use and disturbance, and other environmental features at survey stations and averaged measurements for each transect. At the largest scale, we estimated the ground coverage of each major vegetation community within 100 m of stations. To describe land use and disturbance, we classified intensity of grazing and woodcutting, and severity of recent wildfire on a scale from zero (none) to three (high) based on degree of vegetation disturbance (see Table S1). We used rangefinders to estimate distances to the nearest cliff face (>2-m tall) and surface water, and 30-m digital elevation models to estimate distances to nearest drainages.

To describe vegetation, we used keyhole prisms to estimate basal area of live woody trees at breast height. To measure vegetation cover and physiognomy, we used point-intercept methods (Elzinga et al. 1998) at points spaced every 6 m along four 48-m lines placed at 90° intervals from a random bearing, and at center points of stations in six horizontal strata (0–1, 1–3, 3–6, 6–12, 12–20, and >20 m) above ground. For each ‘hit’, we classified dominant vegetation in seven categories: (1) conifer, (2) evergreen oak, (3) other broadleaf evergreen (e.g., madrone, *Arbutus* spp.), (4) broadleaf deciduous, (5) succulent, (6) dead woody vegetation, and

(7) grass/forb. To describe species composition, we estimated the proportion of total volume comprised by each dominant tree species in the tall- and short-tree layers. To estimate density of canopy trees (tallest vegetation strata) and snags (>20-cm diameter at breast height), we used point-quarter methods (Cottam and Curtis 1956). We classified degree of snag decay in five categories from one (recently dead; all bark, some foliage) to five (rotting trunk >2-m tall). All measurements focused within 50 m of survey stations unless noted otherwise, and all proportions were estimated to the nearest 10% when values were between 20–80% or to the nearest 5% otherwise.

Analyses. We used distance-sampling methods (Buckland et al. 2001) and the *mrds* library in R (Laake et al. 2012, R Development Core Team 2013) to estimate density (number of individuals, pairs, or groups/ha) of each species at four spatial scales (station, transect, mountain range, and region). Distance analyses use frequency histograms of distance data to model a detection function, which adjusts estimates for variation in detection probability. Here, we focus on 72 species that represent nearly half the breeding bird community in the region by considering species encountered ≥ 30 times; inferences on rarer species are reported elsewhere (Flesch 2014). In all cases, distance data were suitable for fitting detection functions.

To estimate densities, we first fit a detection function to data for each species. For species with ≥ 50 encounters, we also fit detection functions with covariates. As covariates, we considered time-of-day (minutes after sunrise), time-of-year (Julian day), noise level (mean wind and noise scores), detection type (e.g., visual, aural-calling, or aural-singing), sex (male, female, both, or unknown), and vegetation (community and percent tall- and short-tree cover). Because more complex models of detection functions require sufficient numbers of encounters, we based the maximum number of covariates included in models on sample sizes. For species with 50–139 encounters, we fit up to two covariates, and for those with 140–399 or ≥ 400 encounters, we fit up to three or four covariates, respectively. We considered all possible additive combinations of covariates and used Akaike information criterion adjusted for

small sample sizes (AIC_c) to rank models. To select final models, we evaluated shapes of detection functions, precision of parameter estimates, and goodness-of-fit tests for highly ranked models, and selected the best overall model (Thomas et al. 2010). We considered uniform, half-normal (HN), and hazard-rate (HR) detection functions for models without covariates, and HN and HR functions for models with covariates. When fitting HN and HR functions, we considered models with 0–2 cosine or simple polynomial adjustment terms and, for uniform functions, 0–2 hermite polynomial terms. Before analyses, we inspected histograms of distance data and established bin sizes that smoothed data, right truncated 0–5% of encounters, and excluded observations of species in ranges where there was no evidence of breeding.

We used two approaches to describe habitat relationships. First, we assessed variation in densities of each species among vegetation communities. We classified stations based on the community with greatest coverage within 100 m in eight categories, including oak savannah, oak woodland (including oak-juniper and oak-pinyon woodland), mountain scrub, oak-pine woodland, pine-oak woodland, pine forest, mixed-conifer forest, and montane riparian vegetation. Because riparian vegetation often occurred in narrow linear stands where we often placed stations, we classified it as dominant when coverage was $\geq 20\%$. To assess variation in densities among communities, we fit community type as a nominal factor in a linear mixed-effect model for each species where station-specific estimates of density were the response variable. Because variation in elevation, aspect, and soils drive changes in vegetation communities in complex ways, and because some communities spanned nearly all elevations (Whittaker and Niering 1965), we also assessed variation in densities across continuous elevation gradients by fitting models with linear and quadratic elevation terms. To adjust for correlations in observations from the same transects and transects from the same mountain ranges, we fit nested random intercepts for transect and range, which AIC_c for models with different random effects confirmed was optimal.

As a second approach, we modeled the effects of environmental factors on variation in local densities among transects along which

each species was present and possibly breeding. We considered estimates at the transect scale because they varied more broadly and continuously than those at stations and were more precise. We log transformed density estimates, developed a linear mixed-effect model for each species, and fit mountain range as a random intercept. We focused on species detected along ≥ 50 transects because low spatial variation in densities of rarer species provided limited inferences. Because the number of potential explanatory factors was high and data to develop candidate models a priori were limited, we used stepwise procedures with mixed variable selection and the stepAIC function in the MASS library in R (Venables and Ripley 2002) to select explanatory factors. We used Bayesian information criterion (BIC) to guide variable selection because it penalizes model complexity more than AIC and reduces chances of overfitting. All models were fit with the nlme library in R (Pinheiro et al. 2012).

To develop models, we considered a group of 18 potential explanatory factors that we generated by eliminating one factor from correlated ($r \geq 0.60$) pairs of factors that we assumed was less descriptive (e.g., tree dominance vs. tree basal area and vegetation physiognomy vs. species composition; Table S1). To describe vegetation cover, we used principal components analysis on point-intercept data from all strata, which reduced six correlated variables into two uncorrelated components that explained 61% of variation in cover. A component representing increasing tall-tree cover and decreasing shrub cover (PC1; eigenvalue = 2.34) was positively correlated with cover > 6 m above ground ($r = 0.60$ – 0.84) and negatively correlated with cover ≤ 3 m above ground ($r = -0.52$ – -0.60). A second component representing increasing short-tree cover (PC2; 1.32) was highly correlated with vegetation cover 3–6 m above ground ($r = 0.93$), but not in other strata ($r = -0.31$ – 0.38). To describe vegetation physiognomy, we computed the proportion of point intercept ‘hits’ in five categories: conifer, evergreen oak, broadleaf evergreen, broadleaf deciduous, and grass/forb. Because categories sometimes summed to one, we removed a category with the least explanatory power before modeling. Because the effect of snags could depend on levels of decay, we

considered interactions between snag density (or dominance) and decay class. Because few stations (18%) showed signs of recent logging, we excluded it from models, but considered fire (40%) and grazing (43%) that occurred more frequently. Estimates are presented as means \pm SE.

RESULTS

Effort. We conducted 1851 point counts at 1562 stations along 210 transects located between 1155 and 2750 m in elevation in 26 Sky Islands ($N = 181$ transects) and six areas in the SMO (Table S2; Fig. S1). Transects totaled 288.9 km in length, averaging 1369 ± 22 m long (range = 614–2335 m) and including 7.3 ± 0.1 stations spaced 215 ± 2 m apart. Overall, we observed 165 species that were possibly (6% of species), probably (49%), or confirmed (45%) breeding. Effort was largely proportional to the regional coverage of each major vegetation community. Accordingly, most stations were dominated by either oak woodland (41.9%) or pine-oak woodland (19.1%), with fewer dominated by pine forest (8.1%), oak-pine woodland (8.1%), mountain scrub (5.4%), and mixed-conifer forest (2.2%). Effort in montane riparian vegetation (9.5%) was relatively higher, and that in oak savannah (5.7%) was relatively lower than their regional coverage. Effort among vegetation communities also varied markedly among mountain ranges (Table S2).

Abundance. Detection functions based on HR functions fit best for most species (69%), followed by HN (28%) and uniform (3%) functions. Of 56 species for which we considered detection functions with covariates, 91% included ≥ 1 covariate. Detection type was the most important covariate in explaining detection probabilities and present in 80% of models with covariates. Temporal covariates were also important and present in 49% of those models, and time-of-year was more important (84%) than time-of-day (28%). Sex (18%), noise (10%), and vegetation (6%) were less important.

At a regional scale, density estimates varied markedly among species and were generally higher for species that occur at lower elevations (Tables 1 and S3). Among songbirds, Rufous-crowned Sparrows (scientific names in

Tables 1 and S3) and Bewick's Wrens were most abundant (0.74–0.80/ha). Densities of species that use more structurally complex oak woodlands such as Hutton's Vireos, Bridled Titmice, and Hepatic Tanagers (0.28–0.42/ha) were moderately high, whereas those of species that use communities dominated by conifers such as Steller's Jays, Grace's Warblers, and Yellow-eyed Juncos (0.11–0.22/ha) were often lower (Tables 1 and S3). Densities of species that occur in riparian areas such as Sulphur-bellied Flycatchers, Thick-billed Kingbirds, and Summer Tanagers (0.015–0.029/ha), that are restricted to high-elevation coniferous forest such as Thick-billed Parrots, Mountain Trogons, and Townsend's Solitaires (0.0063–0.011/ha), and larger species such as Wild Turkeys, Red-tailed Hawks, and Greater Roadrunners (0.0038–0.0062/ha) were typically lowest.

At the scale of individual mountain ranges, densities varied both within and among species (Table S4), and variation in densities of most species was higher within than among ranges (Table S5). In general, densities of species associated with oaks were higher in the Sky Islands, whereas densities of species associated with conifers were often higher in the SMO. Moreover, species associated with oaks were often distributed widely whereas those associated with high-elevation coniferous forest often occurred in few mountain ranges.

Bird-habitat relationships. Densities of most species varied among vegetation communities, indicating important habitat associations. Evidence of such variation was convincing ($P \leq 0.05$) for 65% of species, suggestive ($P = 0.051$ – 0.10) for 6%, but weak ($P \geq 0.13$) for 29% of species (Tables 1 and S3). Among species where evidence was convincing ($N = 47$), densities of 30% ($N = 14$) peaked in mixed-conifer forest (Fig. 1). They included Thick-billed Parrots, Mountain Trogons, and seven other species with densities that averaged >2 -times greater in mixed-conifer forest than elsewhere, as well as Broad-tailed Hummingbirds, Greater Pewees, and three other species that occurred at similar densities in either pine forest or pine-oak woodland (Fig. 1). Densities of 26% ($N = 12$) of species peaked in montane riparian areas (Fig. 2), including Acorn Woodpeckers, Sulphur-bellied Flycatchers,

Table 1. Regional variation in densities of common breeding bird species in the Sky Islands and adjacent Sierra Madre de northwest Mexico, 2009–2012. Regional density estimates \hat{D} ; no./ha., standard errors (SE), and coefficients of variation (CV) are based on distance-sampling methods along 210 transects; relative abundance (RA) equals encounters N divided by total counts. Elevation effects are slope parameters (Est.) for linear or quadratic terms from linear mixed-effects models with island and transect fit as nested random intercepts. Where linear terms fit best, trend notes direction of effects and the % change in density with each 100-m increase in elevation. Where quadratic terms fit best, densities were highest at moderate elevations Ω . Type notes vegetation community in which densities peaked. Estimates for less common species are in Table S3.

Species	Scientific name	Abundance				Elevation			Vegetation community			
		N	\hat{D}	$SD_{\hat{D}}$	$CV_{\hat{D}}$	RA	Est.	SE	Trend ^a	Type ^b	F	P
Band-tailed Pigeon	<i>Patagioenas fasciata</i>	109	0.035	0.007	0.21	0.069	0.45	0.12	+	PF	3.0	0.002
White-winged Dove	<i>Zenaidura macroura</i>	291	0.080	0.01	0.12	0.18	-0.99	0.17	-	OS	1.4	0.20
Mourning Dove	<i>Zenaidura macroura</i>	114	0.053	0.012	0.23	0.072	-0.58	0.14	-	MS	1.3	0.23
Broad-billed Hummingbird	<i>Cyananthus latirostris</i>	79	0.98	0.26	0.26	0.050	-2.31	0.58	-	OS	1.2	0.32
Broad-tailed Hummingbird	<i>Selasphorus platycercus</i>	74	0.40	0.11	0.28	0.047	1.30	0.51	+	MCF	3.0	0.003
Elegant Trogon	<i>Trogon elegans</i>	406	0.061	0.007	0.11	0.26	-1.06	0.16	-	MR	1.2	0.30
Acorn Woodpecker	<i>Melanerpes formicivorus</i>	337	0.10	0.01	0.11	0.21	-1.41	0.23	-	MR	5.2	<0.001
Arizona Woodpecker	<i>Picoides arizonae</i>	312	0.12	0.02	0.13	0.20	-0.27	0.062	Ω	OW	1.6	0.13
Northern Flicker	<i>Colaptes auratus</i>	156	0.033	0.005	0.16	0.099	0.55	0.11	+	MCF	6.8	<0.001
Greater Pewee	<i>Contopus pertinax</i>	221	0.035	0.005	0.15	0.14	0.80	0.13	+	MCF	5.3	<0.001
Western Wood-Pewee	<i>Contopus sordidulus</i>	289	0.21	0.03	0.15	0.18	-1.81	0.42	-	MR	2.2	0.026
Dusky-capped Flycatcher	<i>Myiarchus tuberculifer</i>	1010	0.27	0.02	0.06	0.64	-2.20	0.35	-	MR	8.0	<0.001
Ash-throated Flycatcher	<i>Myiarchus cinerascens</i>	380	0.15	0.02	0.12	0.24	-1.41	0.23	-	MR	5.2	<0.001
Brown-crested Flycatcher	<i>Myiarchus tyrannulus</i>	138	0.065	0.014	0.22	0.087	-1.71	0.21	-	MR	2.5	0.011
Cassin's Kingbird	<i>Tyrannus vociferans</i>	136	0.035	0.007	0.20	0.086	-0.62	0.15	-	MR	2.1	0.033
Plumbeous Vireo	<i>Vireo plumbeus</i>	200	0.094	0.011	0.11	0.13	1.27	0.27	+	PF	5.0	<0.001
Hutton's Vireo	<i>Vireo huttoni</i>	400	0.28	0.03	0.12	0.25	-0.29	0.11	Ω	MR	1.8	0.072
Steller's Jay	<i>Cyanocitta stelleri</i>	380	0.14	0.03	0.19	0.24	2.36	0.26	+	MCF	9.6	<0.001
Mexican Jay	<i>Apelocoma wollweberi</i>	542	0.099	0.007	0.07	0.34	-0.29	0.044	Ω	OW	4.9	<0.001
Mexican Chickadee	<i>Parus sclateri</i>	104	0.19	0.04	0.20	0.066	1.86	0.30	+	MCF	7.1	<0.001
Bridled Titmouse	<i>Baeolophus wollweberi</i>	449	0.42	0.04	0.09	0.28	-3.51	0.46	-	MR	7.8	<0.001
Bush-tit	<i>Psaltriparus minimus</i>	168	0.24	0.03	0.12	0.11	0.16	0.38	na	MS	2.3	0.021
White-breasted Nuthatch	<i>Sitta carolinensis</i>	371	0.15	0.02	0.11	0.23	0.54	0.23	+	MCF	1.2	0.31
Brown Creeper	<i>Certhia americana</i>	245	0.29	0.03	0.10	0.15	2.92	0.53	+	MCF	4.3	<0.001
Canyon Wren	<i>Catherpes mexicanus</i>	275	0.083	0.021	0.25	0.17	-0.79	0.20	-	MR	0.9	0.56
Bewick's Wren	<i>Thryomanes bewickii</i>	1268	0.74	0.04	0.05	0.80	-3.34	0.59	-	MS	7.4	<0.001

(Continued)

Table 1. Continued

Species	Scientific name	Abundance					Elevation			Vegetation community		
		N	\hat{D}	$SD_{\hat{D}}$	$CV_{\hat{D}}$	RA	Est.	SE	Trend ^a	Type ^b	F	P
House Wren	<i>Troglodytes aedon</i>	139	0.17	0.04	0.20	0.088	1.91	0.34	+	MCF	10.1	<0.001
Blue-gray Gnatcatcher	<i>Poliophtila caerulea</i>	198	0.21	0.03	0.13	0.13	-0.43	0.099	∅	OPW	2.8	0.005
American Robin	<i>Turdus migratorius</i>	363	0.18	0.02	0.11	0.23	2.36	0.36	+	PF	8.8	<0.001
Northern Mockingbird	<i>Mimus polyglottos</i>	103	0.050	0.015	0.30	0.065	-0.19	0.11	-**	MS	2.9	0.004
Olive Warbler	<i>Peucedramus taeniatus</i>	109	0.064	0.014	0.21	0.069	1.18	0.15	+	MCF	12.9	<0.001
Grace's Warbler	<i>Setophaga graciae</i>	214	0.11	0.02	0.16	0.14	1.47	0.28	+	PF	11.4	<0.001
Black-throated Gray Warbler	<i>Setophaga nigrescens</i>	111	0.11	0.03	0.24	0.070	-0.24	0.29	na	POW	2.1	0.038
Red-faced Warbler	<i>Cardellina rubrifrons</i>	121	0.25	0.08	0.30	0.077	2.01	0.41	+	MCF	8.6	<0.001
Painted Redstart	<i>Myioborus pictus</i>	697	0.43	0.04	0.08	0.44	-1.16	0.16	∅	MR	3.5	<0.001
Spotted Towhee	<i>Pipilo maculatus</i>	878	0.28	0.02	0.08	0.56	4.08	0.47	+	MS	3.4	<0.001
Rufous-crowned Sparrow	<i>Aimophila ruficeps</i>	694	0.80	0.15	0.18	0.44	-3.31	0.53	-	OS	16.3	<0.001
Yellow-eyed Junco	<i>Junco phaeonotus</i>	287	0.22	0.03	0.13	0.18	4.93	0.39	+	PF	31.3	<0.001
Hepatic Tanager	<i>Piranga flava</i>	674	0.36	0.03	0.07	0.43	-0.45	0.13	∅	OPW	1.8	0.081
Black-headed Grosbeak	<i>Pheucticus melanocephalus</i>	818	0.41	0.04	0.09	0.52	-1.53	0.49	-	MR	0.9	0.52
Brown-headed Cowbird	<i>Molothrus ater</i>	112	0.085	0.013	0.15	0.071	-1.38	0.21	-	MS	2.2	0.025
Scott's Oriole	<i>Icterus parisorum</i>	280	0.065	0.01	0.15	0.18	-0.49	0.14	-	MS	3.5	<0.001

^aNo notation indicates $P \leq 0.05$, ** $P = 0.051-0.10$, na = $P > 0.10$.

^bCommunity types are: OS, oak savannah; OW, oak woodland; MS, mountain scrub; OPW, oak-pine woodland; POW, pine-oak woodland; PF, pine forest; MCF, mixed-conifer forest; MR, montane riparian.

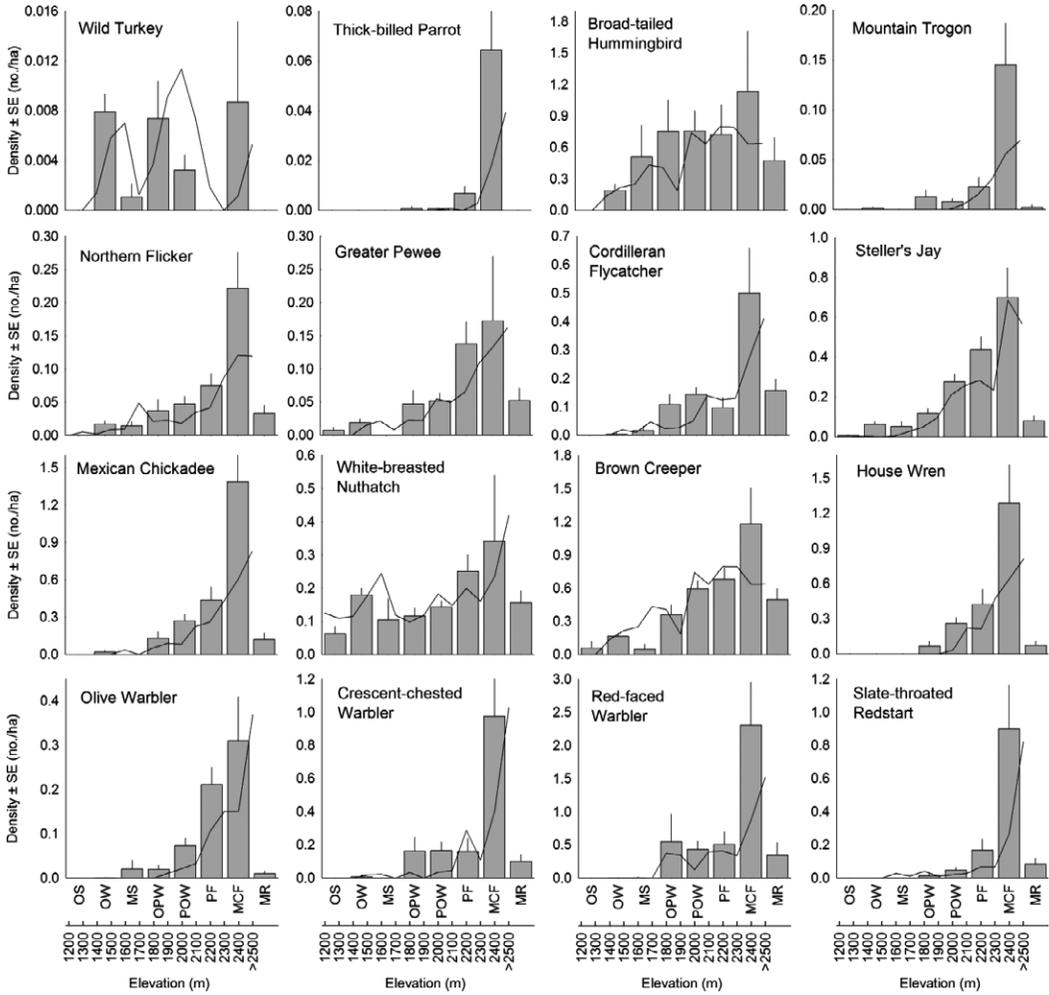


Fig. 1. Variation in densities (number/ha) of species of breeding birds associated with mixed-conifer forest in the Madrea Sky Islands and adjacent Sierra Madre de northwest Mexico, 2009–2012. Bars illustrate mean densities (\pm SE) in each of eight montane vegetation communities whereas lines connect average densities at 100-m intervals; values >2500 m include points between 2450 and 2750 m. Vegetation communities are oak savannah (OS), oak woodland (OW), mountain scrub (MS), oak-pine woodland (OPW), pine-oak woodland (POW), pine forest (PF), mixed-conifer forest (MCF), and montane riparian vegetation (MR), and are listed in order of their mean elevation except montane riparian areas that spanned nearly the entire elevation gradient. Values along the y-axes vary among species.

and four other species with densities that averaged >2 -times greater in riparian areas than elsewhere (Fig. 2), and Dusky-capped Flycatchers, Painted Redstarts, and four other species that occurred at similar densities in upland communities of oaks and pines. Densities of 15% ($N=7$) of species, such as Hairy Woodpeckers, Grace's Warblers, and Yellow-eyed Juncos, peaked in pine forest, but were often similar in pine-oak woodland

or mixed-conifer forest (Fig. 3). Densities of 13% ($N=6$) of species such as Bewick's Wrens and Spotted Towhees peaked in mountain scrub, but were often similar in communities dominated by oaks with the exception of Spotted Towhees (Fig. 4). Densities of Buff-breasted Flycatchers and Black-throated Gray Warblers peaked in pine-oak woodland, whereas only densities of Mexican Jays peaked in oak woodland (Fig. 5).

Densities of Rufous-crowned Sparrows and species with affinities to lowland vegetation peaked in oak savannah (Fig. S9).

Some general habitat associations were also apparent for species that exhibited little variation in densities among communities. Densities of Elegant Trogons, for example, were highest in riparian vegetation, similar in all communities dominated by oaks, but lower in pine forest. Densities of Arizona Woodpeckers followed a similar pattern, but were lower in mountain scrub, mixed-conifer forest, and riparian vegetation. Densities of Black-headed Grosbeaks were similar in all upland communities, but higher in riparian vegetation.

Densities of 88% ($N = 63$ of 72) of species varied with elevation (Tables 1 and S3), with densities of more species decreasing (33) than increasing (23) with elevation, and densities of seven species peaking at moderate elevations. Variation in densities across elevation often corresponded with patterns among

vegetation communities (Fig. 1), but was more complex for species associated with communities that span broad elevation ranges. Densities of most species associated with montane riparian areas, for example, decreased with elevation, a few peaked at moderate elevations, but none increased (Fig. 1b). Similarly, densities of most species associated with mountain scrub decreased with elevation, but densities of Spotted Towhees increased.

Models that identified and estimated the effects of important environmental factors on local densities varied widely (Table 2). Conifer cover (11 of 30 species), a principal component representing increasing tall-tree cover and decreasing shrub cover (nine species), and broadleaf deciduous cover (seven species), were present in the greatest number of models. Moreover, broadleaf deciduous cover, fire severity, and tree density had universally positive effects on densities. After considering other important

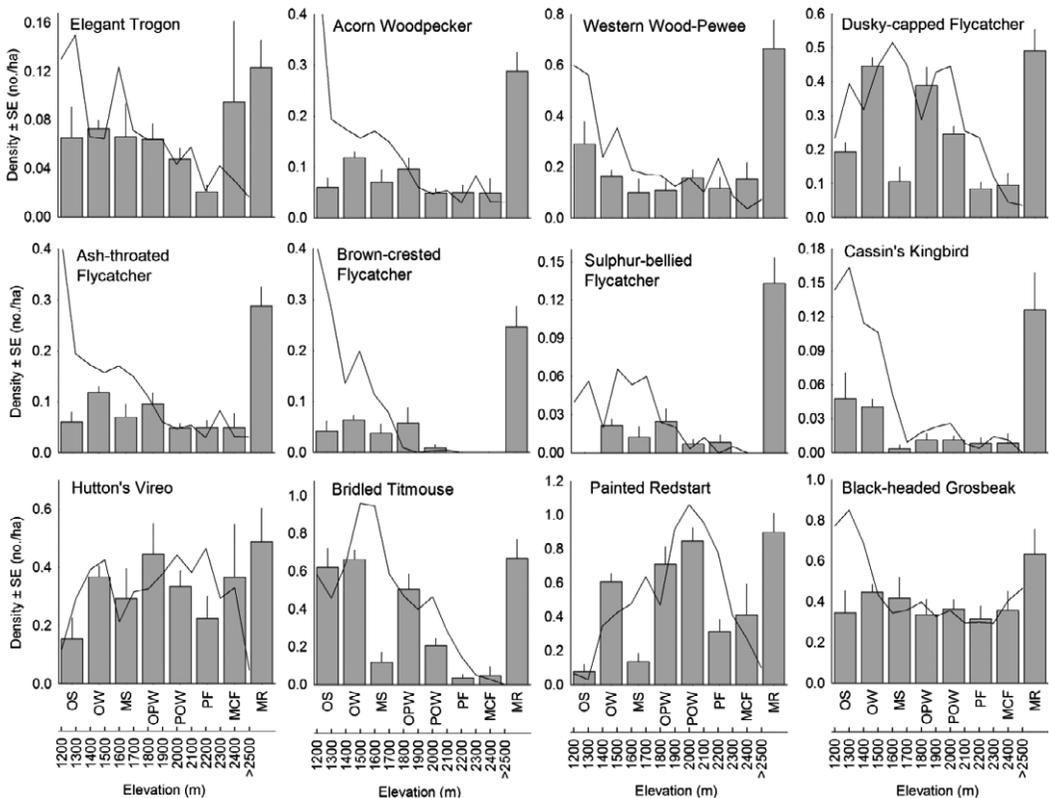


Fig. 2. Variation in densities (number/ha) of species of breeding birds associated with montane riparian vegetation in the Madrean Sky Islands and adjacent Sierra Madre of northwest Mexico, 2009–2012.

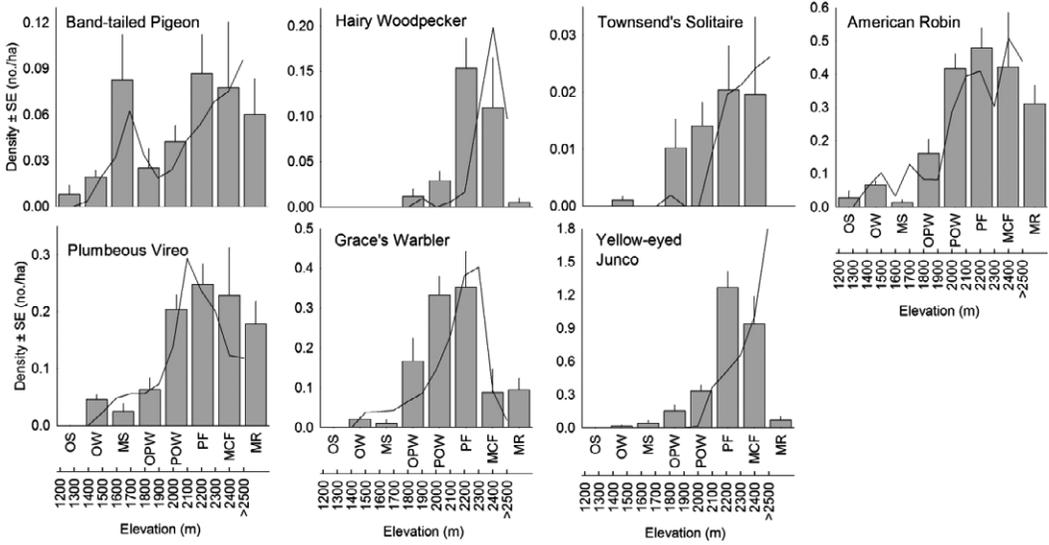


Fig. 3. Variation in densities (number/ha) of species of breeding birds associated with pine forest in the Madrean Sky Islands and adjacent Sierra Madre of northwest Mexico, 2009–2012.

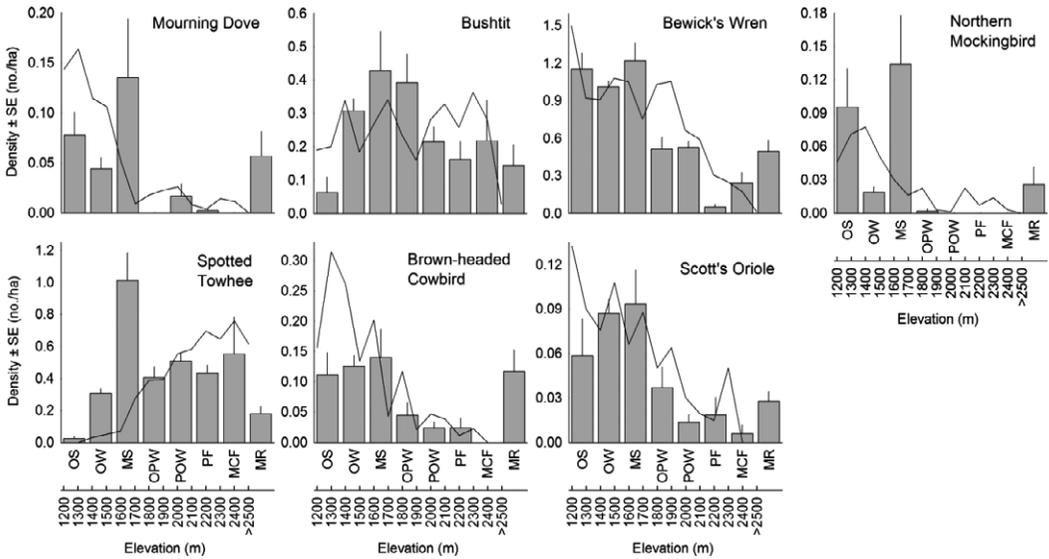


Fig. 4. Variation in densities (number/ha) of species of breeding birds associated with mountain scrub in the Madrean Sky Islands and adjacent Sierra Madre of northwest Mexico, 2009–2012.

factors, densities of American Robins, Grace's Warblers, Spotted Towhees, and Yellow-eyed Juncos increased with fire severity ($P \leq 0.026$). Densities of several species, such as Band-tailed Pigeons, Grace's Warblers, and Hepatic Tanagers, increased with density or dominance of canopy trees.

Densities of 67% ($N = 20$ of 30) of species varied with attributes of vegetation physiognomy (Table 2). Densities of Elegant Trogons, Acorn Woodpeckers, and Scott's Orioles decreased, whereas those of Greater Pewees, Steller's Jays, Grace's Warblers, and Yellow-eyed Juncos increased with conifer

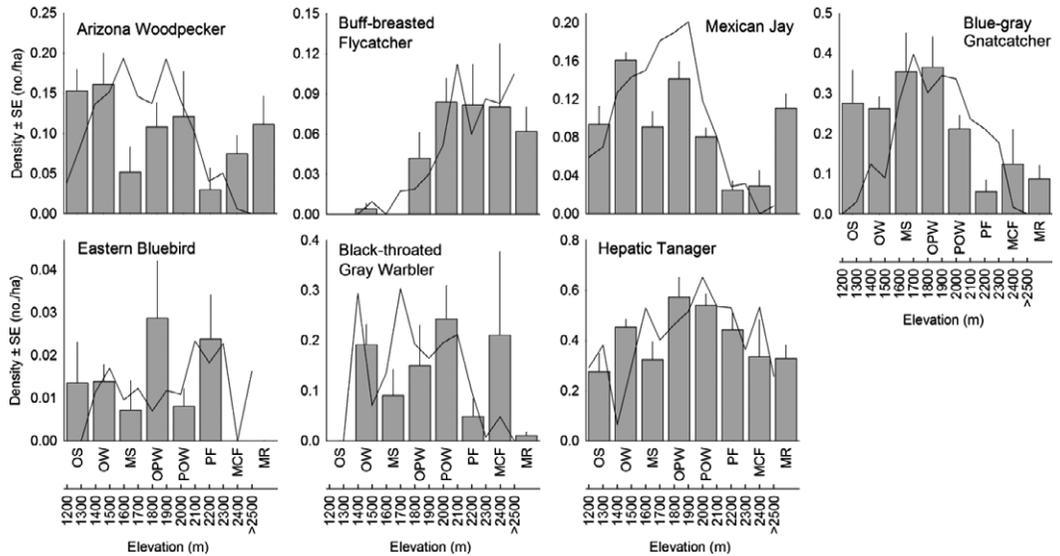


Fig. 5. Variation in densities (number/ha) of species of breeding birds associated with pine-oak, oak-pine, or oak woodland in the Madrean Sky Islands and adjacent Sierra Madre of northwest Mexico, 2009–2012.

cover. Densities of Dusky-capped Flycatchers, Bridled Titmice, and Painted Redstarts increased with cover of evergreen oaks. Densities of Hepatic Tanagers increased with cover of both conifers and oaks, but oaks had a greater effect.

Vegetation cover and the vertical position of that cover had important effects on densities of 37% of the species. A principal component representing increasing tall-tree and decreasing shrub cover (PC1) had positive effects on densities of Painted Redstarts, Plumbeous Vireos, and Brown Creepers. In contrast, increasing values of PC1 had negative effects on densities of Blue-gray Gnatcatchers, Spotted Towhees, and four other species, suggesting the importance of shrubs. A principal component representing increasing short-tree cover (PC2) had positive effects on densities of Hutton's Vireos and Mexican Jays, but negative effects on densities of Bewick's Wrens and Rufous-crowned Sparrows. Densities of Yellow-eyed Juncos decreased with PC1 and PC2, suggesting the importance of shrubs and an open mid-story and canopy.

Proximity of some habitat features also explained local densities. Densities of cavity-nesting Acorn Woodpeckers and White-breasted Nuthatches, for example, increased

with snag dominance, whereas densities of Elegant Trogons and Bridled Titmice increased as snags became more decayed. Densities of Northern Flickers, Dusky-capped Flycatchers, and Bridled Titmice increased, whereas densities of Blue-gray Gnatcatchers and Scott's Orioles decreased with increasing proximity of drainages, suggesting associations with upland or riparian areas. Densities of American Robins increased markedly with proximity to surface water.

DISCUSSION

We assessed densities and habitat relationships of breeding birds in montane vegetation communities across the Madrean Sky Islands and portions of the SMO in northwest Mexico. Those efforts elucidated the status of nearly half the bird species that likely breed in the region, identified habitat associations and important resources that drive variation in abundance, and established quantitative baselines for monitoring.

Abundance. At regional scales, we found that densities of species associated with vegetation communities at lower elevations were typically higher due to greater landscape coverage of those communities and our design, which sampled communities in approximate

Table 2. Factors that explained local variation in densities (In number/ha) of breeding bird species in the Sky Islands and adjacent Sierra Madre of northwest Mexico, 2009–2012. Estimates are percent change in density with each 1-unit change in explanatory factors from linear mixed-effects models with mountain range fit as a random effect. Stepwise selection based on Bayesian information criterion (BIC) was used to select fixed effects. Sample sizes are number of mountain ranges and transects occupied by each species. Units and definitions of variables are in Table S1 and estimates of random effects are in Table S5.

Variable transformation	Est.	SE	<i>t</i>	<i>P</i>
Species (sample size)				
Band-tailed Pigeon (21;55)				
Tree dominance	0.0014	0.0005	2.7	0.012
Elegant Trogon (25;98)*				
Snag decay class	0.028	0.015	1.9	0.069
Conifer cover	−0.11	0.061	1.7	0.087
Acorn Woodpecker (27;105)				
Conifer cover	−0.26	0.083	3.1	0.003
Tree species richness	0.018	0.0079	2.2	0.028
Arizona Woodpecker (27;126)				
Snag dominance	0.0094	0.0034	2.8	0.007
Northern Flicker (22;65)*				
Distance to drainage ln	−0.028	0.013	2.1	0.040
Fire severity	0.032	0.020	1.6	0.11
Tree density ln	0.031	0.014	2.3	0.028
Greater Pewee (20;65)				
Conifer cover	0.22	0.077	2.8	0.007
Western Wood-Pewee (22;78)				
Broadleaf deciduous cover	0.70	0.24	3.0	0.005
Dusky-capped Flycatcher (29;181)				
Distance to drainage ln	−0.055	0.018	3.0	0.003
Broadleaf deciduous cover	0.36	0.14	2.5	0.015
Oak cover	0.40	0.085	4.7	<0.001
Tree density ln	0.058	0.020	2.9	0.005
Ash-throated Flycatcher (27;105)				
Conifer cover	−0.26	0.083	3.1	0.003
Tree species richness	0.018	0.0079	2.2	0.029
Plumbeous Vireo (19;68)				
PC1: tall tree vs. shrub cover	0.066	0.017	4.0	<0.001
Hutton's Vireo (29;150)				
Broadleaf deciduous cover	0.36	0.18	2.1	0.047
PC2: short-tree cover	0.042	0.023	1.8	0.072
Steller's Jay (22;93)				
Conifer cover	0.43	0.12	3.7	<0.001
Broadleaf deciduous cover	0.45	0.20	2.2	0.029
Mexican Jay (29;151)				
PC1: tall tree vs. shrub cover	−0.023	0.0052	4.4	<0.001
PC2: short-tree cover	0.024	0.0078	3.1	0.002
Bridled Titmouse (28;146)				
Distance to drainage ln	−0.081	0.024	3.4	0.001
Grass-forb cover	0.94	0.21	4.5	<0.001
Oak cover	0.47	0.14	3.4	<0.001
Snag decay class	0.12	0.041	2.9	0.005
Bushtit (28;91)*				
Conifer cover	0.24	0.12	2.0	0.056
Broadleaf evergreen cover	0.56	0.30	1.9	0.067
White-breasted Nuthatch (25;123)				
PC2: short-tree cover	−0.054	0.018	3.0	0.004

(Continued)

Table 2. Continued

Variable transformation	Est.	SE	t	P
Species (sample size)				
Snag dominance	0.013	0.0042	3.1	0.003
Brown Creeper (22;75)				
PC1: tall tree vs. shrub cover	0.11	0.029	3.7	<0.001
Canyon Wren (26;97)				
Cliff dominance ln	0.12	0.039	3.1	0.0026
Broadleaf deciduous cover	0.47	0.16	3.0	0.004
Tree density ln	0.057	0.024	2.4	0.021
Bewick's Wren (30;161)				
Broadleaf evergreen cover	1.08	0.45	2.4	0.017
PC1: tall tree vs. shrub cover	-0.066	0.025	2.6	0.011
PC2: short-tree cover	-0.067	0.029	2.3	0.023
Blue-gray Gnatcatcher (23;90)*				
PC1: tall tree vs. shrub cover	-0.045	0.020	2.3	0.026
Distance to drainage ln	0.047	0.027	1.7	0.088
American Robin (22;91)				
Distance to water	0.073	0.017	4.3	<0.001
Fire severity	0.14	0.045	3.0	0.004
Grace's Warbler (17;64)				
Cliff dominance ln	0.22	0.057	3.9	<0.001
Fire severity	0.16	0.049	3.3	0.002
Conifer cover	0.31	0.14	2.2	0.032
Tree density ln	0.069	0.030	2.3	0.025
Painted Redstart (25;143)				
PC1: tall tree vs. shrub cover	0.14	0.021	6.6	<0.001
Oak cover	0.58	0.15	3.8	<0.001
Spotted Towhee (27;134)				
Grass-forb cover	-0.65	0.27	2.4	0.016
Fire severity	0.14	0.054	2.5	0.013
Grazing intensity ln	-0.37	0.084	4.4	<0.001
PC1: tall tree vs. shrub cover	-0.096	0.021	4.5	<0.001
Rufous-crowned Sparrow (29;148)				
Conifer cover	-0.73	0.22	3.3	0.001
PC2: short-tree cover	-0.14	0.041	3.6	<0.001
Tree species richness	-0.059	0.023	2.5	0.013
Yellow-eyed Junco (17;52)				
Broadleaf deciduous cover	2.11	0.51	4.1	<0.001
Conifer cover	1.11	0.30	3.7	0.001
Fire severity	0.23	0.097	2.4	0.026
Grazing intensity ln	0.78	0.18	4.3	<0.001
PC1: tall tree vs. shrub cover	-0.12	0.048	2.6	0.016
PC2: short-tree cover	-0.22	0.058	3.7	<0.001
Hepatic Tanager (29;172)				
Conifer cover	0.32	0.130	2.6	0.012
Oak cover	0.53	0.13	4.0	<0.001
Tree density ln	0.062	0.025	2.5	0.013
Black-headed Grosbeak (32;172)*				
Broadleaf deciduous cover	0.40	0.21	1.9	0.058
Brown-headed Cowbird (22;58)				
Tree dominance	-0.0023	0.0008	3.0	0.006
Scott's Oriole (26;98)				
Conifer cover	-0.15	0.067	2.2	0.032
Distance to drainage ln	0.028	0.0093	3.0	0.004
Snag dominance	-0.0054	0.0023	2.4	0.021

*Models based on BIC included no fixed effects, so Akaike information criterion was used.

proportion to their coverage. Thus, Rufous-crowned Sparrows that occur in openings in woodlands on slopes, and Bewick's Wrens that occur in a variety of woodlands and shrublands were among the most abundant species. These results match those previously reported for some Sky Islands (Landres and MacMahon 1983, Powell et al. 2006), but contrast with those of Marshall (1957), likely because he focused on pine-oak woodland at moderate elevations. Although densities of some species of hummingbirds were also high, estimates were likely biased high due to their tendency to approach observers. Densities of species dependent on tall conifers and other resources restricted to high elevations were typically low in our study due to the rarity of those communities and possibly because some of those species such as Thick-billed Parrots and Mountain Trogons occur at the margins of their geographic ranges and likely ecological tolerances in the region. Although densities of species limited largely to riparian areas were also low, our estimates may be biased high because effort in riparian vegetation was greater than its actual coverage (Scott et al. 2009). Regardless, our results suggest that regional population sizes of species dependent on tall coniferous forest and riparian areas are low, especially in the more arid Sky Islands.

Although we considered nearly half the bird species that likely breed in the region, inferences on many species were lacking and suggest questions for future research. Those species include some rare songbirds and hummingbirds, most diurnal raptors, and nocturnal species. Although distributional data on all breeding species are available (Flesch 2014), future studies should focus on understanding the status and habitat needs of rare species, which tend to be of greater conservation concern. Regardless, we considered some species of concern such as Thick-billed Parrots and Townsend's Solitaires, which are listed as endangered or subject to special protection in Mexico, and other rare species that had not been reported in this region of Mexico until recently such as Mountain Trogons, Brown-backed Solitaires, Crescent-chested Warblers, and Slate-throated Redstarts (Flesch 2014). Moreover, we also surveyed areas where observations of birds had not been reported since the late 1800s (e.g., Sierra San

José, Cíbuta) or probably ever (e.g., Juri-quipa, Bacadéhuachi, Mariquita, and Pan Duro; Van Rossem 1945, Marshall 1957, Russell and Monson 1998). Because the regional coverage of each montane vegetation community we considered is unknown and difficult to quantify, and because effort was not allocated randomly, estimating regional population sizes is complex. Nonetheless, because we considered spatiotemporal variation in detection probabilities, our inferences facilitate comparisons among species and vegetation communities.

Bird-habitat relationships. Densities of most species in our study varied among eight montane vegetation communities, but more species occurred at peak densities or were relatively restricted to mixed-conifer forest and montane riparian vegetation. Such patterns are likely driven by high levels of structural diversity in those communities and the presence of tree species such as Douglas fir and sycamore that provide important sources of food and nest sites for many species of birds (Bock and Bock 1984, Hall and Mannan 1999, Powell and Steidl 2000, Monterrubio-Rico and Enkerlin-Hoeflich 2004). Mixed-conifer forests, for example, often have larger trees and denser canopies than adjacent pine forests, and montane riparian areas have greater cover of shrubs and herbaceous vegetation than adjacent uplands, which are important resources for birds (Whittaker and Niering 1975, Kirkpatrick and Conway 2010). Such results are similar to those reported by Marshall (1957: 65) and suggest that habitat breadths of species associated with those communities are narrow. By differentiating pine from mixed-conifer forest, however, our results highlight the importance of associations of tall pines and Douglas fir. Although densities of some species also peaked in pine forest, many of those species often occurred at similar densities in adjacent communities, suggesting broader habitat breadths.

Pine-oak woodland is the dominant montane vegetation community in the SMO and considered an important community for birds in Mexico because it supports high levels of species richness and endemism (Escalante-Pliego et al. 1993, González-Elizondo et al. 2012, Navarro-Sigüenza et al. 2014). Nonetheless, we found that few species

occurred at peak densities in pine-oak woodland, which contrasts with descriptions of 12 species once thought to be most abundant in pine-oak woodland in the region (Marshall 1957). Such differences are likely due to the quantitative techniques we used and past inclusion of nocturnal species such as Whiskered Screech-Owls (*Megascops trichopsis*) and Mexican Whip-poor-wills (*Caprimulgus arizonae*) that may or may not be more abundant in pine-oak woodland. More generally, because oaks and pines are dominant components of many other montane vegetation communities in the region, and because few species seem to depend on the combined life forms of oaks and pines (e.g., Painted Redstart; Marshall 1957), bird communities in pine-oak woodland are comprised of species with greater affinities for and thus likely abundances in neighboring communities at relatively lower and higher elevations. From an ecological perspective, this amalgamation of species from adjacent vegetation communities that support relatively higher dominances of oaks or pines is likely why pine-oak woodland supports higher species richness than other temperate vegetation communities in Mexico, but few species that occur at peak densities within it. Because pine-oak woodland in our study region covers relatively smaller, more isolated areas near its northern limit, such patterns should be evaluated further south where pine-oak woodlands are more extensive.

We found varying habitat relationships for most species once thought to be associated with pine-oak woodland such as Montezuma Quail, Acorn Woodpeckers, Greater Pewees, and Hutton Vireos (Marshall 1957). For example, Montezuma Quail were considered an indicator species of pine-oak woodland in Mexico (Leopold and McCabe 1957), but we found they were more abundant in oak savannah, oak woodland, and riparian vegetation probably because those communities provide key resources that drive habitat use such as dense grasses for cover and forbs for food (Stromberg 1990, 2000). Similarly, Acorn Woodpeckers were more abundant in riparian areas than in oak and especially pine-oak woodland, and densities decreased with conifer cover, suggesting that pines are of little importance. Although riparian areas where we observed Acorn Woodpeckers often supported

large oaks and pines, and were adjacent to oak or pine-oak woodland, the presence of large trees for granaries and a tendency to roost in tall trees with good visibility likely explain those patterns. In contrast, our results suggest that oaks are of little importance to Greater Pewees.

Our inferences about habitat relationships of species once thought associated with communities other than pine-oak woodland were similar to those of past studies to varying degrees. For example, Marshall (1957) considered Buff-breasted Flycatchers to be a species of montane riparian vegetation, but noted use of other communities, and Martin and Morrison (1999) found strong associations between occupancy and areas with low slope and open canopies of large pines, but we found densities were similar in all communities dominated by tall conifers and somewhat lower in riparian vegetation. Had we only considered riparian areas near uplands dominated by pines, however, our results may have better matched those of past studies. Marshall (1957) found Elegant Trogons to be most abundant in riparian vegetation and secondarily in pine-oak woodland, and Hall and Mannan (1999) noted associations with both riparian and upland vegetation communities. Although we also found that densities of Elegant Trogons peaked in riparian areas, our results also indicate the importance of oaks and broadleaf deciduous trees (vs. pines) that are often used when foraging (Marshall 1957). In the SMO, Thick-billed Parrots were considered a species of coniferous forest that nested mainly in pines (Marshall 1957, Lanning and Shiflett 1983), but we found that densities were much higher in mixed-conifer than in pine forest. Such patterns suggest the importance of large trees and Douglas fir that are now more frequently used for nesting, possibly due to logging of pines and the greater biomass and net primary productivity of forest communities at higher elevations (Whittaker and Niering 1975, Monterrubio-Rico and Enkerlin-Hoefflich 2004).

Snags are an important resource for cavity-nesting birds in montane forests of western North America (Hejl 1994, Monterrubio-Rico and Escalante-Pliego 2006). In pine-oak woodland and coniferous forest in Mexico, large percentages of resident avifaunas depend

on cavities in snags (Monterrubio-Rico and Escalante-Pliego 2006). We found that local densities of only four of 10 cavity-nesting focal species varied with indices of snag abundance or decay. Although those results indicate the importance of snags for some species, we likely would have detected similar associations for more species had we focused measurements only on large snags that tend to be used with greater frequency by birds (Mannan et al. 1980).

Wildfire is an important agent of disturbance in western North American forests, but there are few studies of fire effects on birds in Madrean communities (e.g., Horton and Mannan 1988, Ganey et al. 1996, Saab and Powell 2005). After adjusting for the effects of important habitat attributes, we found that densities of 17% of species varied with an index of fire severity and that fire effects were universally positive. Thus, the proportion of species affected by fire in our region conforms to that in the adjacent United States where occupancies of 17% of 65 species and relative abundances of 25% of 16 species varied with a similar index of fire severity, and where fire effects were positive for 73% of species (Kirkpatrick et al. 2006). Specifically, we found that densities of Grace's Warblers and Spotted Towhees increased with fire severity, as also noted by Kirkpatrick et al. (2006). Moreover, we found that densities of American Robins, Yellow-eyed Juncos, and possibly Northern Flickers responded positively to fire. Others have reported similar observations elsewhere in the west (Hejl 1994, Smucker et al. 2005, Dickson et al. 2009), but not in Madrean communities that are structurally and floristically different from communities to the north. In the case of Spotted Towhees, such patterns are likely driven by an abundance of epicormic oak sprouts that create a dense shrub layer soon after fire. For American Robins, Yellow-eyed Juncos, and perhaps Grace's Warblers, such patterns are likely due to preferences for more open forest conditions. In fact, Marshall (1963) attributed lower densities of American Robins, Yellow-eyed Juncos, and other species in Sky Islands in the United States to denser stand structure driven by fire suppression, and suggested that higher densities in Mexico were due to more open conditions maintained by frequent low-severity fire. Notably, such cross-border

differences in presence and extent of fire sign persist today. In vegetation types dominated by pines in eight Sky Islands in adjacent Arizona, for example, Kirkpatrick et al. (2006) observed evidence of wildfire at 27% of 1513 points, with 73% showing signs of low-severity fire. In a broader range of vegetation communities in Mexico, in contrast, we observed evidence of wildfire at 42% of points, with 84% showing signs of low-severity fire.

Implications. The Madrean Sky Islands and SMO are global conservation priorities threatened by logging, drought, and other stressors linked to climate change (Felger and Wilson 1995, Lammertink et al. 1996, Rehfeldt et al. 2012). Climate change is expected to cause up-elevation shifts in the distribution of montane taxa and widespread mortality of conifers, which may already be occurring in the region (Brusca et al. 2013, Flesch 2014, Monterrubio-Rico et al. 2015, McDowell et al. 2016). Nonetheless, comparisons of recent (Flesch 2008, 2014) and historical (Mearns 1907, Van Rossem 1945, Marshall 1957) data suggest that large areas of pine forest and pine-oak woodland are recovering in the Sky Islands of Mexico following cessation of commercial logging in the early and mid-1900s. As a likely result, distributions of many pine-dependent species such as Cordilleran Flycatchers, Plumbeous Vireos, and Grace's Warblers have expanded across the region, but species dependent on snags and mature coniferous forest such as Thick-billed Parrots, Violet-green Swallows (*Tachycineta thalassina*), and Pygmy Nuthatches (*Sitta pygmaea*) have yet to recover (Flesch 2014). Despite continued logging in the SMO, our results further indicate ongoing recovery of some pine-dependent bird populations in the Sky Islands as evidenced by higher abundances than suggested by past efforts (Van Rossem 1945, Marshall 1957). Given the time required for large snags and mature forest conditions to develop following logging (Hejl 1994), our results suggest that active forest restoration aimed at augmenting those resources and conditions will advance conservation.

Much larger proportions of species occurred at peak densities or were relatively restricted to mixed-conifer forest and montane riparian vegetation, and resources linked to those communities were often highly associated with variation in local densities. Given

the rarity of mixed-conifer forest and montane riparian vegetation in this region of Mexico (González-Elizondo et al. 2012, Scott et al. 2009) and greater threats posed by climate change at high elevations and in more mesic environments (Rehfeldt et al. 2012, Monterrubio-Rico et al. 2015), those communities and birds that depend on them are good targets for conservation efforts. However, because breeding bird species richness in mixed-conifer forest is much lower than in pine-oak woodland (Escalante-Pliego et al. 1993), where many species occurred at significant, but not peak densities, conservation efforts focused in pine-oak woodland are also important. More generally, managers endeavoring to augment and conserve populations should focus on specific environmental attributes that explained variation in local densities.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website.

Fig. S1. Study region and survey locations in Sky Islands and Sierra Madre Occidental.

Appendix S1. Figs. S2–S8. Illustrations of vegetation communities and study sites in the Sky Islands and adjacent Sierra Madre Occidental, Mexico.

Table S1. Definitions and units of variables in models of bird–habitat relationships.

Table S2. Survey effort, timing, and coverage among vegetation communities and study areas.

Table S3. Regional variation in densities of uncommon breeding species.

Table S5. Estimates of random effects from models that explained local variation in densities of breeding bird species.

Fig. S9. Variation in densities of species of breeding birds associated with oak savannah in the Madrean Sky Islands and Sierra Madre Occidental.

Table S4. Density estimates of each bird species in each mountain range.