



# Use of Multispecies Occupancy Models to Evaluate the Response of Bird Communities to Forest Degradation Associated with Logging

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**Abstract:** Forest degradation is arguably the greatest threat to biodiversity, ecosystem services, and rural livelihoods. Therefore, increasing understanding of how organisms respond to degradation is essential for management and conservation planning. We were motivated by the need for rapid and practical analytical tools to assess the influence of management and degradation on biodiversity and system state in areas subject to rapid environmental change. We compared bird community composition and size in managed (ejido, i.e., communally owned lands) and unmanaged (national park) forests in the Sierra Tarahumara region, Mexico, using multispecies occupancy models and data from a 2-year breeding bird survey. Unmanaged sites had on average higher species occupancy and richness than managed sites. Most species were present in low numbers as indicated by lower values of detection and occupancy associated with logging-induced degradation. Less than 10% of species had occupancy probabilities  $>0.5$ , and degradation had no positive effects on occupancy. The estimated metacommunity size of 125 exceeded previous estimates for the region, and sites with mature trees and uneven-aged forest stand characteristics contained the highest species richness. Higher estimation uncertainty and decreases in richness and occupancy for all species, including habitat generalists, were associated with degraded young, even-aged stands. Our findings show that multispecies occupancy methods provide tractable measures of biodiversity and system state and valuable decision support for landholders and managers. These techniques can be used to rapidly address gaps in biodiversity information, threats to biodiversity, and vulnerabilities of species of interest on a landscape level, even in degraded or fast-changing environments. Moreover, such tools may be particularly relevant in the assessment of species richness and distribution in a wide array of habitats.

**Keywords:** Chihuahua, community analysis, Cumbres de Majalca National Park, forest management, occupancy models, Sierra Tarahumara, species richness estimation

Uso de Modelos de Ocupación para Múltiples Especies para Evaluar la Respuesta de las Comunidades de Aves a la Degradación de Bosques Asociada con la Tala

**Resumen:** Se puede decir que la degradación de bosques es la mayor amenaza para la biodiversidad, los servicios ecosistémicos y las comunidades rurales. Por esto, incrementar el entendimiento de cómo los organismos responden a la degradación es esencial para el manejo y la planeación de la conservación. Esta necesidad de herramientas analíticas rápidas y prácticas nos motivó a estudiar la influencia del manejo y la degradación sobre la biodiversidad y el estado del sistema en áreas sujetas al cambio ambiental rápido. Comparamos la composición y tamaño de una comunidad de aves en bosques manejados (ejidos, esto es: terrenos comunales) y no manejados (parque nacionales) en la región de la Sierra Tarahumara, México, usando modelos de ocupación para múltiples especies y datos de un sondeo de 2 años de aves en reproducción. Los sitios sin manejo tuvieron en promedio una mayor ocupación de especies y una mayor riqueza que los

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*sitios manejados. La mayoría de las especies estuvieron presentes en números bajos, indicados por valores más bajos de detección y ocupación asociados con la degradación inducida por la tala. Menos del 10% de las especies tuvo probabilidades de ocupación >0.5, y la degradación no tuvo efectos positivos sobre la ocupación. El tamaño estimado de la metacomunidad de 125 excedió estimaciones previas para la región, y los sitios con árboles maduros y características de bosques con edades irregulares tuvieron la riqueza más alta de especies. La incertidumbre más alta en la estimación y las disminuciones en la riqueza y la ocupación para todas las especies, incluyendo a los generalistas de hábitat, estuvieron asociadas con bosques jóvenes degradados de edades regulares. Nuestros resultados muestran que los métodos de ocupación para múltiples especies proporcionan medidas manejables de la biodiversidad y el estado del sistema y un apoyo valioso en la toma de decisiones para los dueños y manejadores de tierras. Estas técnicas pueden usarse para resolver rápidamente vacíos en la información de la biodiversidad, amenazas a la biodiversidad y vulnerabilidades de las especies de interés en un nivel paisajístico, incluso en ambientes degradados o de cambio rápido. Además, dichas herramientas pueden ser particularmente relevantes en la evaluación de la distribución y riqueza de especies en una variedad amplia de hábitats.*

**Palabras Clave:** Análisis de comunidad, Chihuahua, estimación de riqueza de especies, manejo de bosques, modelos de ocupación, ocurrencia, Parque Nacional Cumbres de Majalca, Sierra Tarahumara

## Introduction

Forest degradation is an important management concern and arguably the greatest threat to global biodiversity, ecosystem services, and rural livelihoods (Brooks et al. 2006; Diaz et al. 2006). Yet managing and protecting forests remains a difficult task, especially in biologically rich developing regions where the implementation of forest policies is hampered by limited regulatory and institutional capacity (FAO 2011). In addition, robust scientific assessments, which are essential for the validation and formulation of comprehensive long-term strategies, are often lacking (Brooks et al. 2006; Nel et al. 2007).

These issues are exemplified in Mexico, a megadiverse developing country with a somewhat limited regulatory and management framework. Between 1970 and 2005, the lack of effective land management policies contributed to extensive deforestation, often at a rate of >5000 km<sup>2</sup>/year (Cairns et al. 2000). Widespread degradation of forests resulted in extirpations and range reductions for numerous vertebrate species (Fuller et al. 2007). Paradoxically, during this period the number and size of protected areas increased 10-fold (20,000–205,000 km<sup>2</sup>) whereas the representation of species in them declined dramatically. Such an outcome can be partly attributed to the lack of sufficient knowledge regarding the status of biodiversity, which in turn resulted in poorly designed land management strategies (Cartron et al. 2005; Fuller et al. 2007). Considering that degradation is expected to worsen due to increasing human pressure and climate change, increasing understanding and predictive capacity regarding the response of biological communities to disturbance has never been more important (Cook et al. 2010).

At the outset of designing a conservation or management plan for a resource or ecological system, developing accurate measures to assess and monitor its state is an essential first step. In the case of forests, remote sensing

techniques are among the most common approaches to monitoring long-term, large-scale effects of forestry and other activities (Boyd & Danson 2005). However, common remote sensing methods can underestimate degradation by as much as 50% (Asner et al. 2005). Therefore, to better understand the structure and functional processes of an ecological system and how these components might be affected by degradation or management, it becomes necessary to determine alternative state variables that provide inference about organism-environment interactions (Yoccoz et al. 2001).

Species richness (number of species in an area) is the most widely used measure of biodiversity (Dorazio et al. 2006, 2011) and is considered a system state variable, which when paired with environmental covariates, can provide vital information about the variability of a system (Yoccoz et al. 2001). The relationships between state and environmental covariates can be used to derive objective functions to identify the status and trend of ecological systems and to provide decision support for managers (Nichols & Williams 2006). Species richness can be estimated from detection data with multispecies occupancy (or community) models (Dorazio & Royle 2005; Dorazio et al. 2006) while accounting for imperfect detection of species (MacKenzie et al. 2002; Tyre et al. 2003). In nature, observing all individuals of a population is typically impossible; therefore, occupancy-model-based estimates serve a fundamental purpose in ecology (Royle & Dorazio 2008). Community models offer advantages over traditional species richness estimators that do not account for detection heterogeneity. Traditional approaches tend to be biased toward the more common and abundant taxa, making them of limited use for science and conservation (Dorazio et al. 2011). As an extension of occupancy models, community models incorporate species-specific detection probabilities explicitly and therefore improve the ability to make inferences about rare and abundant species (Royle & Dorazio 2008). The ability to

make robust inferences about endangered and rare taxa is particularly useful for conservation purposes because such inferences are usually the focus of management interventions and protected area design (Fleishman et al. 2000).

We studied the effects of timber harvesting on forest breeding birds using community models in the Sierra Tarahumara region (STR), Mexico. The STR is a conservation priority for birds (U.S. NABCI Committee 2000) and part of the greater Madrean pine-oak forest region, a threatened biodiversity hotspot in North America (Brooks et al. 2006). In Mexico, the majority of forest resources and biodiversity are located outside protected areas on communal lands owned by user groups made up of indigenous and rural communities (i.e., *ejidos*). *Ejidos* are a legal form of communal land tenure in which members collectively own and manage a territory and its resources. Because communal lands as a whole contain such a vast amount of natural resources, effective landscape-based conservation is unattainable without the inclusion of *ejido* lands and the enhancement of community-based forestry practices that explicitly incorporate local livelihoods (CONANP 2012). Often, technical and organizational capacity, in addition to the social structures of indigenous people and cultural linkages to the land, assure that forestry and other traditional uses remain in balance with forest regeneration rates. However, there are cases, in which the rate of extraction exceeds regeneration, that conflict with conservation goals. This is a recurring theme in the STR (Perez-Cirera & Lovett 2006) and many regions of Mexico (Cartron et al. 2005). Although political and social processes such as regulation and awareness are necessary to modify forest use patterns, the consequences of forest degradation must be solved by informed planning and management.

We focused on forest breeding birds because the large number of species and range of specialization makes them a tractable measure of biodiversity and environmental change (Ceballos & Márquez 2000; Manley et al. 2006). Our objectives were to determine the impact of forest degradation associated with logging on bird species occupancy and to quantify the magnitude of the effects of logging intensity on avian species richness.

## Methods

### Study Region

The STR covers roughly 70,000 km<sup>2</sup> or about 15% of Mexico's forest biomass. The region is sparsely populated with isolated settlements. Roughly 90% of all land is owned by *ejidos*, <1% is publicly owned as national parks (NP), and the rest is private. Forestry-derived income and small-scale pastoralism and agriculture are the main

sources of income (Guerrero et al. 2000). Our study area consisted of 9 sampling units in 1228 km<sup>2</sup>: 7 in *ejidos* and 2 in NP lands (Cumbres de Majalca) in Bocoyna, Carichi, and Chihuahua municipalities. The topography is undulating valleys and rugged slopes; elevations range from 2100 to 2400 m. Forests are dominated by ponderosa pine (*Pinus ponderosa*) and oak (*Quercus* spp.) trees. In NP forests, degradation is caused by illegal livestock grazing and firewood harvesting, whereas in *ejidos* it is mainly caused by logging (Fig. 1). Earlier studies found that the current forestry model has resulted in widespread decline of forest productivity (Weaver 2000) and estimated that only 0.6% of the original forest remains unlogged (Lammertink et al. 1996). This model applies clearcutting to promote short-term regeneration from seed trees followed by removal of residual trees after establishment of even-aged regeneration.

### Survey Design and Data Collection

A random sampling design was not feasible due to logistical limitations on the ground (i.e., manpower, road conditions). Instead, we used a form of systematic sampling (Poon & Margules 2004) to select the spatial and temporal replicate samples needed to meet the assumptions of occupancy models. Sampling locations (i.e., sites) were identified based on vegetation, land tenure, terrain, presence of secondary and tertiary roads, and the absence of human settlements within a 1-km radius. Ground-truthing and field protocol testing resulted in 32 sites distributed among 7 *ejidos* and 2 NP that could be reliably accessed within a short time frame. The 7 *ejidos*, where 23 of the sampling sites were located, varied in surface area (20–550 km<sup>2</sup>), user group size (30–512 members), time since last logging (0–15 years [ $n = 12$ ] and >15 years [ $n = 11$ ]), and time since the last fire (0–15 years [ $n = 9$ ] and >15 years [ $n = 14$ ]). Fire and logging occurred within the past 50 years in one NP sampling unit at 4 different sites. The recommended minimum distance of 250 m between bird monitoring sites for spatial independence (Ralph et al. 1995) was exceeded in all cases.

All data were collected by E.C.R. during a 2-year breeding bird survey conducted at the beginning of the local reproductive season (5–28 May 2008 and 15 May to 4 June 2009). Ten-minute point counts, starting 30 min before sunrise and ending 5 h later, were used to sample sites 3–5 times each year. All birds were recorded as detected or undetected based on visual and auditory identification within a 75-m radius (Ralph et al. 1995). To maximize demographic closure (MacKenzie et al. 2002), we timed sampling with the beginning of the local breeding season when the behavior and distribution of birds were more constant. Habitat characteristics were documented on separate visits, at which point canopy cover, basal area, and height of all trees (>1.5 m) were measured in a main plot of 400 m<sup>2</sup> (20 × 20 m). In a nested subplot of





*Figure 1. Images from the study sites in the Sierra Tarabumara region, Mexico (clockwise from left): mature forest in Cumbres de Majalca National Park, restoration of degraded communal forest by ejido members, mosaic of agriculture and forest successional stages, and young forest after logging. Photos by E.C.R.*

100 m<sup>2</sup> (20 × 5), we estimated shrub cover (<1.5 m) (Manley et al. 2006). With the point count location as the starting point, we chose a random cardinal direction to establish the first 20-m side of the main plot, which was also used as the long side of the 20 × 5 subplot, and delineated the perimeter by walking in a clockwise direction.

### Modeling Overview

To be able to make inferences about the bird community, we adapted a multispecies occupancy model described by Dorazio and Royle (2005). This model estimated species richness and other community parameters based on species-specific occurrence indicators. We implemented it in the BUGS language using WinBUGS (Spiegelhalter et al. 2003), parameter-expanded data augmentation (PX-DA) (Royle et al. 2007; Royle & Dorazio 2008, 2012), and BUGS code originally written by Kéry and Royle (2009). One of the main advantages of this framework is that observation (detection) and state processes (occupancy) are modeled

separately. An observation model provides a map of the probabilistic true state of occurrence of each species in the community. Detection probability is estimated as a parameter of the observation process. In turn, the process model describes the process of interest (in this case, occupancy) and its variation among sites and species (Royle & Dorazio 2008). The model's joint posterior distribution could be expressed simply as

$$[z, \psi, \mu, \alpha, v | x] \propto \left( \prod_{i=1}^N \prod_{j=1}^J [x | z, p] [z | \psi] \right) [\psi | \mu, \alpha] [\mu] [\alpha] [v], \quad (1)$$

where occupancy  $z(i, j)$  is a binary process in which  $z(i, j) = 1$  if species  $i = 1, 2, \dots, N$  occurs at site  $j = 1, 2, \dots, J$  during a 10-min point count, and  $z(i, j) = 0$  if species  $i$  does not occur. Also,  $z$  is a (partially) latent variable because  $z = 1$  can be observed as a 0 when the species is undetected. The model for species occurrence is defined as  $z(i, j) \sim \text{Bernoulli}(\psi_{i,j})$ , where  $\psi_{i,j}$  is the probability that species  $i$  occurs at site  $j$ . The probabilistic description of the mechanisms that produce

the observed data is defined in the observation model as  $x_k(i, j) \sim \text{Bernoulli}(z(i, j) \times p(i, j, k))$  and is conditional on  $z(i, j)$  and the detection probability parameter  $p(i, j, k)$  for species  $i$  at site  $j$  for survey  $k$ . Thus, if  $z(i, j) = 0$ , then all resulting observations are fixed zeros. In this particular situation, we were interested in describing site-specific effects on species-specific occurrence probability  $\psi(i, j)$  as linear functions of covariates tree density per hectare (density) and quadratic mean diameter (dbhq) and in estimating detection probabilities  $p(i, j, k)$  for all species. We used logit transformations for both models and expressed occupancy as

$$\text{logit}(\psi(i, j)) = \mu_i + \alpha_{1j} \times \text{dbhq}_j + \alpha_{2j} \times \text{density}_j + \alpha_{3j} \times \text{dbhq}_j \times \text{density}_j \quad (2)$$

with species- and site-specific effects given by  $\mu_i$  and  $\alpha_j$ , respectively. Detection was described as

$$\text{logit}(p(i, j, k)) = v_i, \quad (3)$$

where  $v$  is assumed to be normally distributed effects for  $i$  species at site  $j$  on survey  $k$ . We thought the following covariates might influence occupancy: canopy cover, forest age, tree height, density, and dbhq. We chose density and dbhq because these variables described well the forest structure differences between sites and because these covariates are widely used by foresters to calculate harvest quotas and forest inventories (Long & Shaw 2005). We did not include seasonal effects on occupancy because we assumed there would be at best minor changes in the occurrence states during the short 2-year sampling period. We also assumed that detection remained constant throughout the duration of the study because several trial model runs fitted with environmental and seasonal effects on detection failed to converge. We also fitted the model to data from each year separately and obtained qualitatively the same results for species richness.

### Bayesian Analysis with PX-DA

Recent publications have provided excellent treatments of PX-DA techniques (e.g., Kéry & Schaub 2012; Royle et al. 2014). We used PX-DA to fit our model in a Bayesian inference mode (Royle et al. 2007; Royle & Dorazio 2008, 2012). That is, we added to our data all-zero observations for a large, say  $K$ , number of hypothetical species that were potentially present and expanded our model by another hierarchical layer represented by an indicator ( $w_i$ ) for whether or not each species was part of the sampled community. Thus, rather than analyzing the observed data from  $n$  species, we analyzed the augmented data set with  $M = n + K$  species, where  $K$  was chosen such that the target parameter community size ( $N$ ), was certainly smaller than  $M$ . The choice of  $K$  is a simple matter of trial and error. We defined  $K$ , ran the model, and if the posterior for  $N$  was truncated by  $M$ , we repeated the analysis with a larger  $K$  (Kéry & Schaub 2012). Though PX-DA can

be considered a computational trick to simplify Markov chain Monte Carlo (MCMC)-based analysis of models with unknown quantities, it is also equivalent to imposing a discrete uniform prior on  $N$ , the total number of species present in the community [i.e.,  $N \sim DU(0, M)$ ]. Estimation of  $N$  is achieved by introducing the latent indicator variable  $w_i$  for  $i = 1, 2, \dots, n, n + 1, n + 2, n + \dots, N, N + 1, N + 2, \dots, M$ , with  $w_i \sim \text{Bernoulli}(\Omega)$ . Thus, in a sense, the Bernoulli parameter  $\Omega$  takes the place of  $N$  in the original model and the model's ecological process for species occurrence is modified to  $z(i, j) \sim \text{Bernoulli}(w_i \times \psi(i, j))$ . Therefore, only a species that is part of the sampled community (and for which  $w_i = 1$ ) can occur at a site. Unknown species richness  $N$  was estimated as the sum of all species-specific latent occurrence states such that

$$N_k = \sum_{i=1}^M z_{i,k}. \quad (4)$$

### Model Implementation and Evaluation

We fitted our model with diffuse priors (Kéry & Royle 2009), assuming  $N(0, 0.1)$  and  $DU(0, 5)$  for the means and SD of all  $\alpha$  hyperdistributions, respectively, with MCMC methods implemented in software packages R and WinBUGS. Three chains were run from random starting values for 30,000 iterations with a thinning rate of 1 in 10 and a 5000 burn-in. To improve convergence, we standardized all covariates to mean zero and an SD of one. We assessed convergence using the Brooks–Gelman–Rubin statistic (assuming convergence when Rhat value  $< 1.1$ ) and inspected the trace plots visually. To assess model fit, we compared the original data with a simulated data set and calculated a Bayesian  $p$  value to quantify the discrepancy (posterior predictive check, Gelman & Hill 2007). Because goodness of fit cannot be assessed directly for a binary response model like ours, we aggregated the data (Royle et al. 2014) by adding the number of times each species was detected at a site. Comparing the observed number of detections with the expected number of detections under the model allowed us to compute a chi-square discrepancy measure, which, summed over all species, represented our test criterion. Because the replicate data fit the model perfectly (after all, they were simulated under the same model with the same parameter values estimated from our data), they provided the reference distribution of the test statistic under the null hypothesis of a model that fits.

We based our inference on a single model which appeared to us biologically plausible and relevant and avoided model selection for several reasons. Arguably, model selection is most helpful in situations with high uncertainty about which models to use, when these models provide strikingly different results, and when seeking to find the best predictors for a specific outcome (Link

& Barker 2010). Instead of relying on model-selection statistics such as Akaike information criteria to guide our choice of model to use for inference, which are not available for complex hierarchical models such as ours, we specified the model's structure based on our objectives for model-derived inference and on well-established biological mechanisms that generated the observed data. Operationally, this type of model cannot be fitted using the frequentist methods for which model-selection procedures can be easily implemented (Johnson & Omland 2004). There are Bayesian model-selection procedures such as the deviance information criterion (Spiegelhalter et al. 2003), but they appear inadequate for hierarchical mixture models such as ours (M.K., unpublished data).

## Results

Our posterior predictive check showed that the data simulated from the occupancy model Eq. 2 resembled the original data. The Bayesian  $p$  value (0.52), which represented the proportion of times when the discrepancy measures for the simulated data exceeded the discrepancies for the observed data, also indicated adequate model fit.

Seventy-three bird species were recorded during 2008–2009. The posterior distributions revealed that the average probability of occupancy for the metacommunity

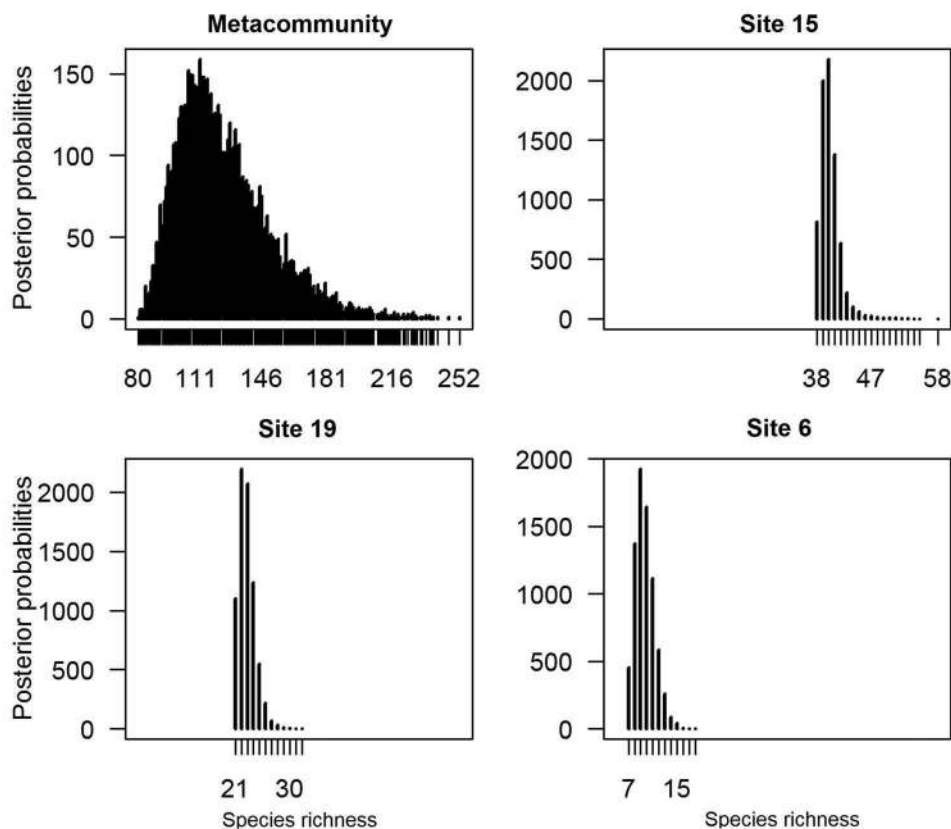
**Table 1.** Community-level posterior summary statistics under the community model for the 2008–2009 forest breeding bird survey data in the Sierra Tarahumara region, Mexico.

Parameters	Mean	SD	95% CI <sup>a</sup>
$p$ : detection probability	0.26	0.1	0.13–0.46
$\psi$ : occurrence probability	0.13	0.2	0.0004–0.82
$\mu\alpha_1$ : effect of density	-1.07	0.39	-1.88 to -0.28
$\mu\alpha_2$ : effect of qdbh	3.16	1.55	0.16–6.19
$\mu\alpha_3$ : effect of density-qdbh interaction	4.14	1.85	0.23–7.82
Ntotal: metacommunity species richness	125.8	25.12	90.0–186.0

<sup>a</sup>Lower and upper bounds of a 95% Bayesian credible interval.

was 0.13 (95% Bayesian credible interval [CI] 0.0004, 0.82), and detection probability was 0.26 (CI 0.13, 0.46) (Table 1). Model estimates indicated that increasing dbhq would increase occurrence (3.16; CI 0.16, 6.2), whereas increasing density would have the opposite effect (-1.07; CI -1.9, -0.28). The interaction term (4.14; CI 0.24, 7.8) indicated that the effect of density would decline with greater dbhq values.

The metacommunity was estimated to contain 125 species (CI 90, 190); thus, we estimated that in our surveys about 53 species were never detected. The posterior distribution of  $N$  indicated that the probability of metacommunity size being equal to the observed 73 was virtually zero (Fig. 2). We also found that the posterior



**Figure 2.** Posterior means of forest bird species richness under the community model for the metacommunity (125.82). Site 15 is in Cumbres de Majalca National Park (40.17, >50 years since last logging), site 19 is an ejido (22.9, >15 years since last logging), and site 6 is an ejido (9.7, <15 years since last logging, fire) in the Sierra Tarahumara region, Mexico.



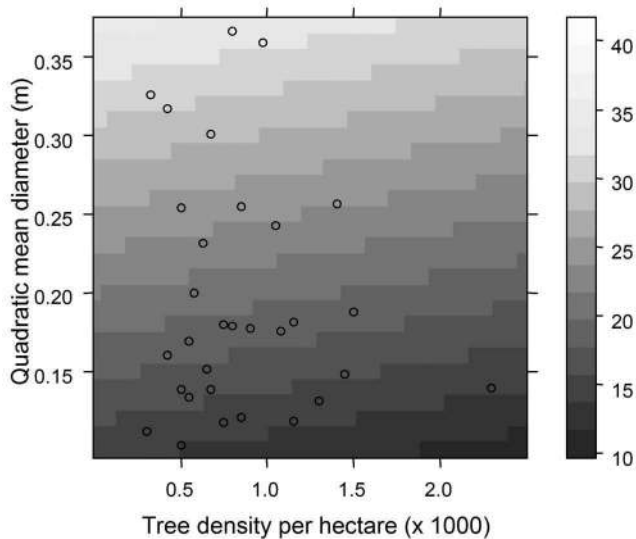


Figure 3. Posterior means of forest bird species richness as a function of tree density and average tree diameter in the Sierra Tarahumara Region, Mexico. Gray scale from dark to light indicates increasing number of species, and circles represent sampling sites.

distribution of  $N$  did not touch the upper bound of 252, indicating that the data augmentation of 200 additional, hypothetical species was sufficient to impose a vague rather than an informative prior on community size  $N$ . The highest occupancy and richness estimates were in sites within NP lands (e.g., site 15; Fig. 2) and ejidos not subject to recent logging (Fig. 2). Higher estimates of site-specific species richness were strongly associated with greater dbhq values and lower density (Fig. 3). Estimated species richness and uncertainty measures (SD, undetected species) were inversely related. For example, site 15 (NP, >50 years since last logging) had the highest richness (40.2; CI 38, 44) and a very low number of undetected species (2.1, 5% of the total; Table 2). This site had a stocking density of 970 trees/ha and a dbhq of 0.36 m. In contrast, site 6 (ejido, <15 years since last logging) had the lowest richness (9.7; CI 7, 13), a density of 1150 trees/ha, and an average dbhq of 0.12 m.

Species-specific occupancy and covariate coefficient estimates are presented in Supporting Information. Habitat changes had a significant effect on occupancy estimates for most species, including widespread (generalists) and restricted (rare) species. Only 7 species had occupancy >0.5 and 53 had estimates <0.25. All 73 species responded negatively to density and 50% showed significant occurrence heterogeneity as indicated by CI values. This included all of the high occupancy species except for the Mexican Jay (*Abelocoma ultramarina*) and Northern Flicker (*Colaptes auratus*). Although covariate effect dbhq was associated with occupancy increases for all species, the Tree Swallow

Table 2. Site characteristics and community model summary statistics for the 2008–2009 forest breeding bird survey data in the Sierra Tarahumara region, Mexico.

Site	Land use <sup>a</sup>	Recent changes <sup>b</sup>	Mean	Median	SD	95% CI <sup>c</sup>
1	NP	F	19.11	19	1.41	17–22
2	NP	F	21.87	22	1.36	20–25
3	NP	F	21.84	22	1.96	19–26
4	NP	F	16.35	16	1.79	13–20
5	For	F and L	17.03	17	1.93	14–21
6	For	F and L	9.68	9	1.61	7–13
7	For	F and L	9.97	10	2.1	6–14
8	For	L	15.17	15	1.73	12–19
9	For	L	16.27	16	1.78	13–20
10	For	L	20.82	21	1.87	18–25
11	For	F and L	14.81	15	1.43	13–18
12	For	F and L	13.76	14	1.92	11–18
13	For	F and L	12.24	12	1.71	9–16
14	NP	/	37.64	37	1.27	36–40
15	NP	/	40.17	40	1.71	38–44
16	NP	/	28.47	28	1.71	26–32
17	NP	/	30.09	30	2.21	27–35
18	NP	/	30.31	30	1.88	27–34
19	For	/	22.89	23	1.41	21–26
20	For	/	23.97	24	1.51	22–27
21	For	/	19.67	19	1.33	18–23
22	For	/	15.62	15	1.85	13–20
23	For	/	24.12	24	1.89	21–28
24	For	/	18.68	19	2.24	15–24
25	For	/	20.1	20	1.71	17–24
26	For	/	21.62	21	2.08	18–26
27	For	/	24.04	24	2.49	20–30
28	For	/	17.2	17	1.48	15–20
29	For	/	17.06	17	1.52	15–20
30	For	F	17.99	18	1.69	15–22
31	For	F	15.99	16	1.66	13–20
32	For	F	12.46	12	1.85	9–16

<sup>a</sup>Abbreviations: NP, national park; For, forestry.

<sup>b</sup>Detailed logging and fire history information was unavailable, but we were able to determine if a site had been subject to fire (F) or logging (L) within the past 15–30 years prior to data collecting from visual inspections and interviews with local people. No change is indicated by a slash (/).

<sup>c</sup>Lower and upper bounds of a 95% Bayesian credible interval.

(*Tachycineta bicolor*), a second-cavity nester, showed the most significant association. All but 6 species had significant positive associations with the interaction term density  $\times$  dbhq, including the Mexican Jay and 2 large tree and snag-dependant species: Acorn Woodpecker (*Melanerpes formicivorus*) and Brown Creeper (*Certhia americana*). Species-specific occupancy estimates for selected species and study sites showed that Northern Flicker and Mexican Jay were among the most widespread, whereas the Brown Creeper and rare Common Black-Hawk (*Buteogallus anthracinus*) occurred sporadically (Fig. 4). Occurrence for all species decreased in logged sites, whereas estimation uncertainty increased. Sites 6 and 19, despite comparable timber volume estimates, differed significantly in habitat characteristics and species richness estimates (9.7 vs. 22.9 species).

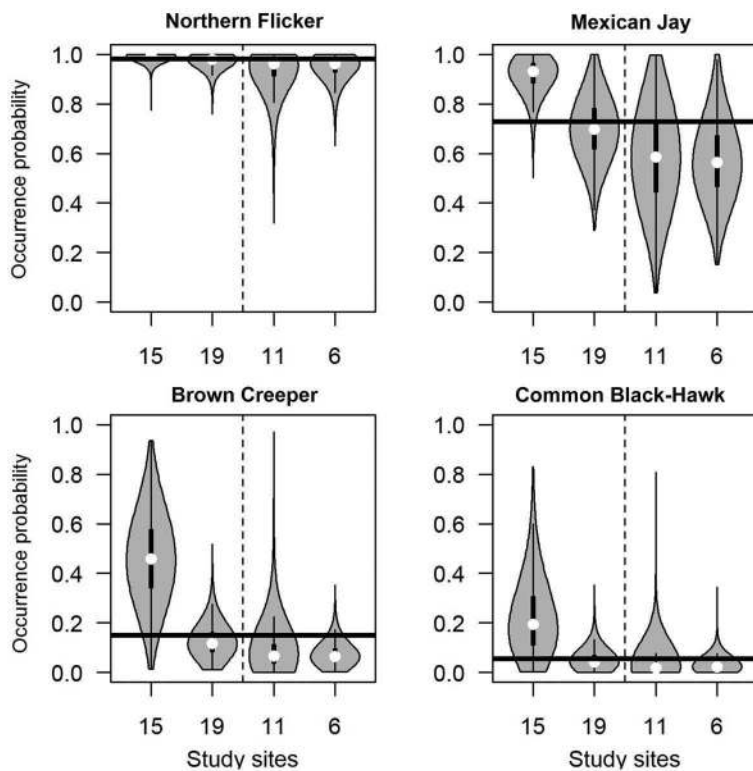


Figure 4. Occurrence probabilities with covariate effects for 2 widespread (top) and rare (bottom) species in 4 sites with different forest structures and management regimes in the Sierra Tarabumara region, Mexico (middle white dot, posterior median; black rectangle, quartiles; whiskers, last data points within the median  $\pm 1.5$  times the interquartile range; solid horizontal line, mean species occurrence probability; dashed vertical line, site-specific richness greater [left] or less [right] than 20 species).

## Discussion

### Estimates of Species Occupancy and Richness

We found that occupancy-based community summaries can be used to derive reliable conclusions about the status of avian communities and system state in intact and degraded sites. Such models could be applied to other species of both animals and plants to evaluate current status of community structure and function. We documented a diverse number of species, with the highest numbers in mature forest stands in Cumbres de Majalca NP, where forest structures have not been altered substantially by logging or other uses. In these sites, species richness estimates ranged from 28 to 40 species. In contrast, the lowest estimates were found in ejido sites that had been subject to recent logging; they contained on average a quarter of the species found in NP sites and about a half the number of species found in less degraded ejido sites that had not been recently logged. The estimated metacommunity size of 125 species greatly exceeded a previous (but methodologically flawed) count of 44 (Miller & Chambers 2007), was larger than an earlier estimate of 93 (Marshall 1957), and was well within the range that could occur in the greater Madrean pine-oak woodland region (Audubon 1997).

The relationships between occupancy, richness, and forest covariates showed clear patterns associated with forest change and indicated the effects of logging degradation could be predicted in terms of species occurrence

and richness. Overall, logging modified occupancy for all bird species in the STR and the majority were rare in terms of low local abundance as indicated by the lack of correlation between detection and occurrence ( $r^2 = -0.032$ ). Occupancy and covariate effects coefficients also provided a good measure of habitat specialization, which allows us to comment on the relative functional importance of species in the community. Occupancy  $>0.5$  corresponded to species that could use different types of areas (habitat generalists). Our findings also showed that these species were affected negatively by degradation but not as much as nongeneralist species. Moreover, the observed relationship between occupancy and community structure and function extends to many groups of species other than birds (Dorazio et al. 2011).

Research concerning the value of species richness as an indicator of biodiversity and system state has not been entirely consistent. It is argued that species richness may be unsuitable for such purposes given that the number of species in an area can remain stable in the face of environmental and species composition changes (Brown et al. 2001). Although the short duration of our study does not allow us to comment on long-term dynamics, our model results show a clear influence of covariates on occupancy and richness estimates linked to forest changes. In addition, uncertainty estimates (SD, CI) revealed patterns consistent with the effects of degradation on species distributions. As the model posteriors showed, estimation uncertainty increased



with greater forest degradation, whereas occupancy decreased and became more erratic relative to less degraded sites.

To make inferences only about those species that were detected (our 73 species), we could have fitted a community model without data augmentation (Russell et al. 2009). However, we were interested in obtaining an estimate of species richness and did not want to use only the observed number of species to characterize the avian biodiversity of a site or the entire metacommunity. As our results and those of others cited here show, the observed total number of species can be a highly biased measure of biological richness due to imperfect detection and patchy occurrences.

### Policy and Management Implications

Our findings have implications for policy, management, and conservation of avian species and more general biodiversity in the STR, the greater Madrean region, and beyond. Our findings are consistent with those of Weaver (2000), who found that forestry under the current model in this region has resulted in widespread degradation and loss of forest productivity. We believe increasing overall diversity could be achieved through management; however, measures that reduce harvest quotas would conflict with local livelihoods and would need to be reconciled by policy.

Overall, we found that avian diversity, and likely biodiversity in general, was greater in sites that retained moderately disturbed uneven-aged stand characteristics, often containing mature trees and structures such as snags and large woody debris that are not available in even-aged managed forests. Mature stands provide unique habitats for species; thus, we urge decision makers to protect all such habitats located in Cumbres de Majalca NP and adjacent areas and recommend that all remaining mature stands in the study region be excluded from future indiscriminate timber harvesting. Beyond parks, maximization of biodiversity could be achieved by restoring degraded habitats and not harvesting trees  $\geq 0.4$  m in diameter. In the middle to long term, we consider it necessary to transition from clearcutting and even-aged management, to selective logging and uneven-aged management. Simultaneously, a broader ecosystem perspective should be adopted, based on biological productivity and ecological functionality, to restore forest balance and maximize biodiversity (Abella et al. 2006). To offset economic trade-offs from reduced timber production, compensation mechanisms for local communities may be required to avoid social conflicts that could result in further degradation (i.e., deforestation spillover). As an example, compensation to landholders as part of payments for environmental services could be based on projected species occupancy and richness increases, which would provide an incentive to maintain and increase species diversity.

Using Eq. 2 and the model coefficients presented here, managers could predict how occupancy for single or multiple species would change after specific management interventions and incorporate this information into forest management plans.

The analytical techniques we used are widely applicable for landscape-based biodiversity monitoring and modeling and provide a tractable decision-support tool in situations where resource use and biodiversity conservation goals conflict. In many developing regions, there is a growing interest in conservation of biodiversity outside protected areas and communal lands (Porter-Bolland et al. 2012). Although this trend is encouraging, comprehensive biodiversity surveys and management frameworks often are lacking and would benefit from analytical frameworks like the one we used. For example, in the STR numerous areas have been set aside as ecological reserves on private and communal lands; however, most of these exclusions were designated on lands that have limited value for biodiversity or connectivity to other ecologically important areas (E.C.R., unpublished data). The addition of species occupancy models could relieve the potential shortcomings of traditional species assessment techniques by providing a valuable tool for rapid measurements of biodiversity and identify anthropogenic impacts or vulnerability to degradation, poor management, or environmental change. The flexible analytical framework of these models can easily accommodate additional samples, covariates, and model extensions to integrate other sources of data that may be readily available and inexpensive, such as bird checklists and other opportunistic observations (Kéry et al. 2010). Application of these analyses at a local level could provide direct feedback to landowners and communities, reinforcing current practices or encouraging changes in pace or intensity of harvest activities. On a broader landscape level, multispecies occupancy estimates could help identify important areas for conservation and generate projections of biodiversity patterns, which are useful to regional managers and decision makers. Moreover, these methods can be applied to a diversity of ecosystems or habitats and would be extremely useful for rapidly assessing diversity and distribution of a broad array of animal and plant species, especially in regions of high biodiversity and rapid change, including rare and endangered biota.

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## Supporting Information

A table with model coefficients for all species (Appendix S1) is available on-line. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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