

# Population trends, extinction risk, and conservation guidelines for Ferruginous Pygmy-Owls in the Sonoran Desert.

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## ABSTRACT

Climatic flux together with anthropogenic changes in land use and land cover pose major threats to wildlife, but our understanding of their combined impacts is limited. In arid southwestern North America, ferruginous pygmy-owls (*Glaucidium brasilianum*) are of major conservation concern due to marked declines in abundance linked to changes in land use and land cover during the past century. We reassessed abundance trends of pygmy-owls in northern Mexico across 17 years (2000-2016), which included data gathered over four additional years since inferences were last reported. We also assessed spatiotemporal trends in territory occupancy ( $n = 151$  territories) across a much larger area that spanned 14 watershed regions in northern Mexico and adjacent Arizona over 16 years (2001-2016). Finally, we evaluated the influence of temperature, precipitation, land-use and land-cover change, spatial variation in local habitat quality, and interactions among these factors on occupancy dynamics. Large increases in abundance in 2015 and 2016 eliminated evidence of population declines that was described recently (e.g., Flesch 2014a) based on two modeling approaches. Moreover, there was little evidence of systematic temporal declines in territory occupancy across the broader bi-national study area, or for population units in Mexico and the adjacent U.S. Instead, occupancy dynamics varied at smaller spatial scales among watershed regions. We found that subpopulations in six regions declined or marginally declined across time, including two in the U.S. that declined to extinction; subpopulations in six other regions were stable; and those in two regions increased or marginally increased. Although variation in territory occupancy was associated with changes in temperature, precipitation, anthropogenic disturbance, and local differences in habitat quality, evidence for interactions among these factors was much greater than that for additive relationships. Territory occupancy declined with rising minimum air temperatures during winter at a much greater rate in disturbed landscapes compared to those with little to no anthropogenic disturbance. Moreover, occupancy increased with annual precipitation at increasingly positive rates as local territory quality increased. Such results suggest a complex set of processes simultaneously drove changes in territory occupancy, likely by influencing food abundance and the quantity, connectivity, and quality of habitat. Management focused on 1) protecting high-quality habitat, 2) enhancing and creating habitat (e.g., nest-cavity augmentation, riparian restoration), 3) reducing deleterious changes in land use and land cover, and 4) increasing landscape connectivity through both passive (e.g., landscape planning and restoration) and active (e.g., facilitated dispersal, translocations) techniques will enhance recovery prospects for pygmy-owls.

## INTRODUCTION

Climate and land-use change are having major impacts on global biodiversity often by altering the quantity, quality, and spatial arrangement of habitats (Warren et al. 2001, Parmesan 2006, Jetz et al. 2007). Although the impacts of climatic flux and land-use change on populations are often considered independently or additively, these stressors may have synergistic effects (Mantyka-Pringle et al. 2012, Oliver et al. 2015, Brodie 2016). For example, populations in areas where habitat has been lost, fragmented, or degraded by changes in land use and land cover, can be more vulnerable to the impacts of climatic flux than those in areas where habitat is less disturbed (Travis 2003, Opdam and Wascher 2004, Previtalli et al. 2010). If the combined

influence of these and other stressors are greater than their independent effects, current threat assessments and associated management strategies could be misguided and require more complex approaches (Brook et al. 2008, de Chazal and Rounsevell 2009). Moreover, if the influence of climate also interacts with spatial variation in habitat quality, such that high-quality habitats buffer the impacts of harsh weather or amplify the benefits of favorable weather on populations (e.g., Franklin et al. 2000, Flesch et al. 2015), identifying and protecting high-quality habitat may be critical for addressing threats posed by these stressors.

In arid and semi-arid environments, climate and land-use change could have especially severe impacts on populations. In these often resource-limited environments, small changes in precipitation and temperature can have large effects on population dynamics (Lima et al. 2002, Holmgren et al. 2006), and the velocity of climate change may be higher (Loarie et al. 2009). A recent review of >1300 studies, for example, found that the chances of a species being negatively impacted by habitat loss increased as mean maximum temperature increased (Mantyka-Pringle et al. 2012). In arid and semi-arid southwestern North America, evidence of climate change is pervasive, expected to intensify (Seager et al. 2007, Overpeck and Udall 2010, Cook et al. 2015, Pascale et al. 2017), and recent drought and extreme temperature events have been linked to declines in vital or population growth rates in a broad range of species (Barrows 2006, Zylstra et al. 2013, Flesch 2014a, Lovich et al. 2014, Cruz-McDonnell and Wolf 2015, Flesch et al. 2015, 2017). Nonetheless, the synergistic influence of climatic flux and land-use change on animal populations in arid systems has received little attention although existing studies suggest these stressors can interact (e.g., Previtali et al. 2010, Bennett et al. 2015). Addressing this question is critical for devising efficient conservation strategies across southwestern North America, and also timely given major increases in human population growth in the region (Brown et al. 2005).

Ferruginous pygmy-owls (*Glaucidium brasilianum*) are iconic predators in the Sonoran Desert that are threatened by climate and land-use change (USFWS 2011, Flesch 2014a, Flesch et al. 2015). In the late 1800s and early 1900s, pygmy-owls were described as locally common in mesic riparian vegetation in the Sonoran Desert of southern Arizona (Bendire 1888, Fisher 1893, Breninger 1898, Gilman 1909, Bent 1938), but also occurred in xeric riparian woodlands and adjacent desert scrub (Brandt 1951, Phillips et al. 1964). By the mid 1900s, vegetation clearing for agriculture, water diversion, and other land-use changes affecting wooded bottomlands drove widespread habitat loss and degradation, and associated declines in distribution and abundance (Johnson et al. 2003). As a result, the Arizona population of pygmy-owls was listed as endangered by the U.S. Fish and Wildlife Service (USFWS) in 1997, but then delisted for reasons unrelated to recovery in 2006 (USFWS 2011). Although populations of pygmy-owls in Arizona are thought to have continued to decline following listing, no quantitative estimates of population trends or factors that influence trends are available in the southwestern U.S.

In adjacent northern Sonora, Mexico, pygmy-owls are more common, occupy similar environments, and monitoring efforts that began in 2000 provide strong evidence that drought and extreme temperatures are driving marked declines in abundance (Flesch 2003, Flesch and Steidl 2006, Flesch 2014a). Between 2000 and 2011, abundance in four watershed regions in northern Sonora declined by an estimated 19-27%, with 75% of temporal variation in abundance explained by variation in precipitation and temperature (Flesch 2014a). Additionally, abundance was lower and varied more over time in areas with higher land-use intensity, but was higher and

less variable in areas that supported more potential nest cavities and riparian vegetation. Such patterns have alarming implications for population persistence and recovery, and thus data on the current status and threats to populations is critical for conservation and management.

Here, we update estimates of abundance trends reported recently for northern Sonora, Mexico (Flesch 2014a) with data gathered over four additional years (2013-2016). Second, we assess spatiotemporal trends in territory occupancy across a much larger bi-national region based on data from 11 watershed regions in northern Mexico, and three watershed regions in adjacent Arizona. Occupancy data from northern Sonora were gathered by A. D. Flesch of the University of Arizona since 2000, whereas data from southern Arizona were gathered by S. Richardson of USFWS and his collaborators since the mid 1990s, and are reported here for the first time. To assess environmental factors that explained spatiotemporal variation in territory occupancy, we developed research hypotheses focused on the potential influences of climatic variation, land-use change, spatial variation in local habitat quality, and interactions among these factors. Finally, we synthesized management and recovery guidelines for pygmy-owls based on data reported here and information from relevant literature.

## **OBJECTIVES**

Our Science Support Partnership proposal included the following objectives:

1. Estimate abundance and territory occupancy of pygmy-owls in northern Mexico in 2015 at sites that have been monitored continuously since 2000.
2. Integrate data on territory occupancy from southern Arizona with that from northern Mexico and assess spatiotemporal variation in occupancy dynamics.
3. Estimate trends in abundance and territory occupancy of pygmy-owls over a 16-year period.
4. Assess environmental factors that explain spatiotemporal variation in territory occupancy.
5. Conduct a time-series population viability analysis to estimate extinction risks for pygmy-owls over a 50-year forecast period based on past dynamics.
6. Summarize conservation, management, and recovery guidelines for pygmy-owls in a format useful for managers and policy makers.

We accomplished all of our objectives except for number five. We did not perform population viability analyses because field data from 2015 and 2016 indicated marked increases in abundance that effectively eliminated evidence of negative population growth across time. Given a lack of observed trends and low estimates of process variance reported here, quasi-extinction probability was low assuming a stable climate. However, the one year project extension we received in early 2016 combined with other support allowed us to gather field data in the U.S. and Mexico in 2016 to extend the time period of inferences.

## **METHODS**

*Study Area and System*—We considered populations of pygmy-owls in an approximately 20,000 km<sup>2</sup> region of northern Sonora within approximately 125 km of Arizona, and in a smaller portion

of adjacent Arizona (Figure 1). In Sonora, we considered 11 watershed regions between the upper Río San Miguel watershed near Cucurpe west to the upper Río Sonoyta watershed near Sonoyta. In Arizona, we considered three watershed regions including the southern Altar Valley (upper Arroyo Sasabe and Brawley watersheds), northern Altar Valley and adjacent southern Avra Valley (lower Brawley watershed), and areas in northwest Tucson and the outwash plain west of the Tortolita Mountains (lower Santa Cruz watershed). In these arid environments, pygmy-owls are generalist predators and non-migratory residents in woodlands associated with saguaro cacti (*Carnegiea gigantea*) that provide nest cavities. Our study region included both major vegetation communities occupied by pygmy-owls in the northern Sonoran Desert: the Arizona Upland subdivision of the Sonoran Desert and semi-desert grassland (Brown 1982). Arizona Uplands are dominated by woodlands and scrub of short leguminous trees such as mesquite (*Prosopis velutina*) and saguaros. Semi-desert grasslands are dominated by open mesquite woodlands and savannah, bunchgrasses, sub-shrubs, and saguaros are often uncommon. Riparian areas in both communities are dominated by mesquite woodlands. Annual precipitation in the region is bimodal and dominated by a summer monsoon in late June-Sept and winter storms that are most intense during the warm phase of the El Niño Southern Oscillation. Summers are hot with maximum temperatures  $>40^{\circ}\text{C}$  and winters are cool with minimum temperatures near  $0^{\circ}\text{C}$ . Throughout their range, pygmy-owls are diurnal and crepuscular generalists that in our region prey largely on lizards during the warm season. In the cool season when most lizards are seasonally dormant, pygmy-owls rely on other prey including small birds and mammals. In the Sonoran Desert, pygmy-owls establish breeding territories in January-March, and typically lay eggs in April and brood in May-June.

*Design and Survey Methods*—We estimated abundance in Sonora by repeatedly surveying the same transects across time. In spring 2000, we surveyed 71 transects that we selected at random in northern Sonora (see details in Flesch and Steidl 2006). After these initial surveys, we selected 18 transects in landscapes that were occupied by pygmy-owls at random and surveyed each transect in spring for 15 of the next 16 years (all years except 2012). All transects were within 75 km of the U.S.-Mexico border and placed along drainage channels. To survey transects, we placed 5-10 calling stations spaced 400 m apart along transects and broadcast recorded, territorial vocalizations of pygmy-owls to elicit responses from owls. This method combined with the arrangement of stations and timing of surveys yields nearly perfect detection probability of territorial males (Flesch and Steidl 2007a). To minimize the chances of double-counting individual owls that often move toward broadcasts, station spacing was increased to 550-600 m after initial detection of each male. For each owl detected, we recorded the time, distance and direction to the initial point of detection, and the sex based on vocalization type. To estimate the number of pygmy-owls along each transect, we used distance, timing, and direction of responses to differentiate among multiple individuals that did not respond simultaneously. As an index of abundance, we calculated the number of territorial males along each transect in each year. All transects were surveyed between April and early June from 1 hour before to 3 hours after sunrise. All 18 transects combined totaled 54 km in length (mean = 3.0 km, range = 2.3-3.9 km) and were located between 740 and 1,035 m elevation.

To assess territory occupancy, we delineated individual territory patches based on patterns of recurring space use by owls, which we estimated with repeated surveys and nest searches, and then surveyed each patch across time. To delineate territory patches in Sonora, we surveyed

transects near random and non-random points in spring of 2000-2002, and searched for nests along occupied transects until we located the nests of most individuals. From 2001 to 2011 and 2013 to 2016, we surveyed areas within 300 m of most nests (or occupied areas if nests were not found initially) found in prior years, and through 2010 searched for nests exhaustively at nearly all occupied sites. To delineate territories, we plotted nest coordinates across time, identified clusters of use in space, and placed 399-m radius circles (50 ha) around the average coordinates of each cluster, which is similar in area to a breeding territory (Flesch et al. 2015). This approach allowed easy identification of breeding territories because the spatial arrangement of potential nest cavities was clumped, owls used the same general areas over time, and owl abundance peaked in early years (Flesch 2014a) when presumably most habitat was occupied. Thus, the basic units of inference were individual territory patches that could each be occupied by single territorial individuals or breeding pairs. In Arizona, methods to delineate territories and assess occupancy across time were similar but often based on the results of surveys versus actual nest locations. Additionally, in Arizona most survey locations were not randomly selected and placed in areas based on the presence of habitat or at historical sites documented in the mid 1990s, and territories surveyed sporadically across time. Although, occupancy data for 11 territories in Arizona were available beginning in 1994-1999, we considered the same temporal frame as in Sonora (e.g., 2000-2016) so that effort was balanced across space and time.

*Occupancy Drivers*—We developed a set of research hypotheses to explain spatiotemporal variation in territory occupancy focused on four general themes: land-use and land-cover change, climatic flux, spatial variation in habitat quality, and interactions among these factors. Conversion of native vegetation to anthropogenic land uses can diminish the quantity, quality, and connectivity of habitats (Fischer and Lindenmayer 2007) in ways that reduce abundance and movement rates of potential colonists and increase predator abundance and edge effects thereby reducing occupancy rates. Thus, the *landscape disturbance hypothesis* predicts increasing cover of anthropogenic land use and land cover reduces territory occupancy. Temporal variation in local weather could influence owl occupancy directly through energetic and thermoregulatory constraints or indirectly by affecting prey or other resources in multiple ways. Low average daily minimum temperatures ( $T_{\min}$ ) during winter could cause direct mortality or reduce body condition of owls or prey. Conversely, high  $T_{\min}$  could reduce abundances of lizards by degrading low-temperature thermoregulatory refugia and increase costs of maintenance metabolism during periods of nocturnal and seasonal dormancy, thereby reducing abundance of important lizard prey (Zani 2008, Flesch et al. 2017). Thus, these *cold effects hypotheses*, predict decreasing or increasing  $T_{\min}$  during winter (November-March) reduces owl occupancy at lag times of  $\approx 0.5$ -1.5 years. High average daily maximum temperatures ( $T_{\max}$ ) during nesting (April-June) could reduce prey abundance or activity and degrade nestling condition or survival in ways that reduce reproductive output (Flesch et al. 2015) and hence territory occupancy one year later. Thus, the *temperature stress hypothesis* predicts that high  $T_{\max}$  during nesting (April-June) reduces owl occupancy the following year. In arid environments, precipitation ( $P$ ) can augment prey abundance directly and positively during the same year or indirectly by augmenting insect or plant resources important to prey and create lagged effects. Thus, the *prey enhancement hypothesis* predicts increasing  $P$  augments owl occupancy at lag times of  $\approx 0$ -2 years. Habitat selection theory posits that individuals select the highest quality habitat patches available so that the best patches are selected first and used more consistently over time (Fretwell and Lucas 1969, Sergio and Newton 2003). Thus, the *habitat quality hypothesis* predicts a positive

association between habitat quality and the probability a patch will be occupied. Finally, if populations in landscapes with higher levels of anthropogenic disturbance are more vulnerable to the impacts of climate flux (Travis 2003) or if the influence of climatic flux depends on spatial variation in habitat quality (Franklin et al. 2000), interactions between these factors explain variation in occupancy, with predictions varying depending on the functional form of these relationships.

*Environmental Measurements*—We estimated the aerial cover of landscape structures linked to anthropogenic land uses and land cover such as agriculture, vegetation clearings, housing and urban development, roadway corridors, and other man-made structures resulting from soil and vegetation disturbance. To estimate the location and size of these structures, we digitized their extent in Google Earth during each successive year that new structures appeared by evaluating all available imagery. We considered structures within 1 km of the center of each territory patch to quantify land-use and land-cover change both within estimated owl territories and adjacent landscapes. Because data were unavailable in some years, mainly in Mexico, we used field observations on the timing of disturbances to estimate transitions across time. To represent land use and land cover in a given year, we considered structures that appeared between May of the prior year through April of the current year to match the approximate phenology leading up to the breeding season.

To quantify climatic conditions we used data from eight weather stations located throughout the study region (Figure 1). To best represent climatic variation experienced by owls, we matched each territory with the most similar weather station based on proximity and elevation. In Arizona, we used data from three National Weather Service stations (Sasabe, Anvil Ranch, Tucson 17 km NW; <http://www.wrcc.dri.edu/summary/Climsmaz.html>) and one remote automated weather station (Sasabe; <http://www.raws.dri.edu/azF.html>). In Sonora, we used data from four weather stations maintained by Comisión Nacional de Auga in Mexico (Cucurpe, Magdalena de Kino, Altar, Sonoyta; G. Largada Vásquez, pers. comm.). Because the influence of  $P$  or  $T$  may depend on the season and lag time considered, we measured  $P$  during the recent ( $\approx 0.5$  year lag) and prior ( $\approx 1.5$  year lag) cool seasons (October-May), prior warm-season (June-September), and annually during two periods (October 2 years prior-September 1 year prior, and June 1 year prior-May of the current year) when assessing the *prey enhancement hypothesis*. We considered  $T_{\max}$  during incubation (April), brooding (May-June), and the overall nesting season (April-June) when evaluating the *temperature stress hypothesis*. Correlations between weather factors linked to different hypotheses were low ( $r = -0.29-0.35$ ).

Habitat quality represents variation in habitat-specific population growth rates ( $\lambda_h$ ) and thereby linked to spatiotemporal differences in reproduction and survival of individuals occupying a specific habitat. To measure habitat quality, we monitored annual reproductive output ( $R$ ; no. of young survived to within 1 week of fledging) of owls in occupied territories in Sonora between 2001 and 2010 during a separate study (see details in Flesch et al. 2015). Although  $R$  is just one component of  $\lambda_h$ , it provides a useful index of habitat quality because  $R$  was highly correlated with adult and juvenile survival in a subset of territories monitored intensively, and because in similar systems adult survival is high and nearly constant except at low  $\lambda_h$ , which is highly correlated with  $R$  (Franklin et al. 2000, Flesch et al. 2015). Thus, we estimated habitat quality by modeling the influence of habitat resources on  $R$  in each territory patch over time. This approach

yielded precise predictions of  $R$  that could be achieved by individuals in each patch based on the observed effects of various habitat resources, and inferences to territories that were rarely occupied. In this system,  $R$  increases with nest-site abundance and woodland aggregation within territories, and woody vegetation cover has increasingly positive effects as nest-site abundance increases. To estimate territory quality in adjacent Arizona, we applied this model to Arizona and based predictions on values of local habitat covariates. Although habitat quality is likely influenced by changes in land cover linked to anthropogenic disturbance, efforts focused on territory quality of patches in Arizona midway through the study based on estimates of woody vegetation derived from satellite imagery from 2007 (see details in Flesch et al. 2015).

## ANALYSES

*Trends in Abundance*—We used two approaches to estimate abundance trends in Sonora and assess spatial variation in abundance dynamics. To foster comparisons with past work, we used the same approach recently applied to these data that are briefly described here (see details in Flesch 2014a). First, we used multivariate state-space models (mSSM) to estimate population growth rates ( $\lambda$ ) and population structure across time and space. By explicitly estimating observation error and process noise, SSM are being increasingly used to model population dynamics despite high complexity and lower precision and power than more conventional approaches (Dennis et al. 2006, Wilson et al. 2011). Observation error includes measurement error (e.g., differences between truth and estimates at sampled locations) and sampling error (e.g., differences between sampled locations and the population). Process noise resulting from demographic and environmental stochasticity can produce short-term declines in populations that are actually stable over the long term (Dennis et al. 2006). We fit SSM with maximum likelihood (ML) methods and the expectation-maximization and Kalman filter algorithms in the MARSS library in R, and used parametric bootstraps to compute standard errors (SE; R Core Development Team 2016). To assess spatiotemporal variation in population growth rates and population structure, we considered three model structures: 1) time series for each transect as independent samples from one larger population with one growth rate and process error, 2) regional subpopulations with equal growth rates and equal or varying process errors with covariance, and 3) regional subpopulations with varying growth rates and equal or different process errors. Second, to enhance insights into the trajectory of populations, we compared inferences on trends and population structure from mSSM with those from a similar set of linear mixed-effects models (LMEM). Whereas SSM explicitly separate observation and process variance, both variances are confounded in LMEM of count data and all variance assumed to be observation error. To assess population structure, we specified additional models analogous to those for mSSM. To assess regional variation in intercepts, we fit a vector of random intercepts for regions and a vector of random intercepts for transects nested within regions. To assess regional variation in trends, we fit time by watershed region interactions as fixed effects. To assess spatial variation in observation error, we considered additional models that estimated observation variances for each region. To adjust for temporal autocorrelation, we considered first-order autoregressive [AR(1)] and various autoregressive-moving-average structures; AR(1) was supported in all cases and reported. We used restricted ML to assess models with different random effects, ML to estimate fixed effects, and fit models with the nlme library in R. To evaluate support among models in each set, we used Akaike information criterion adjusted for

small sample sizes ( $AIC_c$ ) and considered models within 2  $AIC_c$  points as competitive (Burnham and Anderson 2002). We used log transformed estimates of the number of territorial males along each transect as a response variable.

*Trends in Occupancy*—To assess spatiotemporal trends in territory occupancy across the broader study area, we fit generalized linear mixed-effects models (GLMM). These models fit occupancy data as a binary response variable (occupied or unoccupied) with a logit link function, and one or more of the following fixed effects depending on the focal question (see below): year, nation (U.S. or Mexico), watershed region, and time by nation or region interactions. To adjust for correlations in repeated measurements of the same territories across time and of territories embedded in the same landscapes and watershed regions, we considered three potential forms of the random effects: 1) random intercept for territory identity, 2) random intercepts for territory and landscape identities, and 3) random intercepts for territory, landscape, and region identities, and used model selection and  $AIC_c$  to determine optimal structures. We based landscape identities ( $n = 39$ ) on the proximity of territories in space, and assigned territories located within approximately 5 km to the same landscapes. To assess spatiotemporal trends in occupancy, we fit models representing three hypotheses regarding spatial patterns of change: 1) a simple trend model for all territories (e.g., year fit as a fixed effect) representing one broad population, 2) a model that considered variation in trends between nations (e.g., year, nation, and their interaction fit as fixed effects) to assess if dynamics varied nationally, and 3) a model that considered variation in trends among all 14 watershed regions (e.g., year, watershed region, and their interaction fit as fixed effects) to assess if dynamics varied regionally. We then used model selection procedures and  $AIC_c$  to compare models, and fit models with the lme4 library in R. To evaluate models and validate fit, we plotted scaled residuals against fitted values and assessed patterns in the mean and variance of those values and presence of outliers with large influence. Additionally, we plotted histograms of residuals and q-q plots to visually confirm normality, and confirmed estimates of random effects variances were greater than zero. When modeling occupancy, we assumed perfect detection probability based on evidence from experimental trials (Flesch and Steidl 2007a)

*Occupancy Drivers*—To assess factors that explained spatiotemporal variation in territory occupancy, we developed GLMM to represent our hypotheses and used model selection and  $AIC_c$  to evaluate support among models. In developing models, we first evaluated the influence of weather factors measured during the seasonal periods and lag times noted above. As a general strategy, we first compared models that included only a single related weather factor linked to each hypothesis during different lag times and seasonal periods. In assessing these preliminary models, we considered each factor on the untransformed and log transformed scales and used models with lowest  $AIC_c$  to represent hypotheses. Second, we considered models that included all possible combinations of hypotheses, after first confirming pair-wise correlations between factors linked to each hypothesis were low (see Appendix 1). Finally, we refined the top-ranked model by assessing the influence of including, excluding, or changing terms.

To fit models, we used the GLMM procedure described above and fit factors linked to each prediction as fixed effects. We fit transect and landscape as crossed random intercepts, which model selection and  $AIC_c$  confirmed was optimal. To assess relative effect magnitudes of factors linked to each hypothesis, we computed standardized (e.g., z-scored) regression coefficients for a

full model that included factors linked to all supported hypotheses. Because observed associations between occupancy and some factors could be driven by coincidentally co-occurring long-term trends (Grosbois et al. 2008), we further evaluated effect magnitudes with residual regressions of detrended variables. Comparisons based on detrended variables indicated similar relative effect magnitudes and thus are not reported.

## RESULTS

*Trends in Abundance*—We surveyed the 18 transects during 16 of 17 years between 2000 and 2016 ( $n = 123$  stations/year), and recorded an estimated total of 573 detections of territorial males across time. Despite high temporal variation in abundance, there was little evidence of systematic declines based on both modeling approaches (Table 1). The top-ranked SSM estimated declines in abundance of 0.6%/year (e.g.,  $\lambda = 0.994$ ) across the population, or 8.6% over all 17 years. A top-ranked LMEM estimated a decline of only 0.14%/year or 2.2% overall. Precision was low for SSM (SE = 3.2% for SSM; 0.54% for LMEM) with 95% confidence intervals that overlapped zero indicating no evidence of decline. Observed abundance was high initially (55 males in 2000), declined steadily to 2008 (21), increased in 2009-2011 (34-39), decreased somewhat in 2013 and 2014 (28-31), and then increased markedly during the final two years of study to near initial levels (49-51; Figure 2).

The top-ranked SSM indicated the presence of regional population structure with equal process variance that covaried among watershed regions ( $r = 0.80$ ) and one population growth rate among regions (Table 2). There was also some support ( $\Delta AIC_c = 1.60$ ) for a similar model that included different population growth rates among watershed regions, with populations increasing somewhat in the upper Río Altar watershed relative to declines in the middle Río Sasabe watershed and near Sasabe (Table 2). In contrast, there was little support ( $\Delta AIC_c = 2.95$ ) for a model parameterized with no regional population structure. In contrast, the top-ranked LMEM indicated regional variation in observation error but not intercepts. An estimate of process variance (0.020) from the top-ranked SSM was much lower than observation error (0.083; Table 2). An estimate of observation error from the top-ranked LMEM (0.072) was lower than the sum of both variances from SSM.

*Trends in Occupancy*—In Sonora, we conducted 1,346 occupancy surveys at 112 territory patches in years following the initial discovery of each patch. Aside from year 2012 when no data were gathered, effort was greatest in 2009 when 108 territory patches were surveyed and lowest in 2001 when only 31 patches were surveyed due to identification of few territories during initial efforts in 2000. Over time, we surveyed an average of  $89.7 \pm 5.7$  ( $\pm$  SE) patches per year. Annual territory occupancy averaged 59.7% among years and ranged from  $80.1 \pm 7.1\%$  in 2001 ( $\pm$  binomial SE) to  $45.4 \pm 4.8\%$  in 2009 (Figure 3).

In Arizona, we performed a total of 288 occupancy surveys at 39 territory patches in years following the initial discovery of each territory. Effort was greatest in 2014 when 37 territory patches were surveyed and lowest in 2008 when only 4 patches were surveyed. Over time, an average of  $18.0 \pm 2.9$  patches was surveyed each year. Annual territory occupancy averaged 39.8% among years and ranged from  $71.4 \pm 17.1\%$  in 2011 to  $11.1 \pm 6.1\%$  in 2003 (Figure 3). In

Sonora effort generally increased across time during the first several years of study as more patches were discovered, and then leveled off. In Arizona, however, survey effort was sporadic across time. Number of territory patches within watershed regions averaged  $10.6 \pm 1.4$  and ranged from 4 to 19 (Appendix B).

The top-ranked model of occupancy dynamics indicated strong evidence that temporal trends varied among watershed regions (Table 3). Despite the large number of parameters required to model regional variation in trends ( $K = 30$ ), there was no support for models parameterized for varying trends between nations or for one trend across the entire bi-national region ( $\Delta AIC_c \geq 63.11$ ). With regard to the last scenario, the odds of a territory being occupied declined by an estimated average of  $1.8 \pm 1.3\%$  per year across time across the entire region, but was not statistically significant ( $Z = 1.41$ ,  $P = 0.16$ ). Instead, trends varied markedly across space. Compared to the population in the upper Río Plomo watershed, which was relatively large (16 territories) and stable across time, occupancy declined in northwest Tucson and in the upper Brawley, lower Altar, and upper San Miguel watershed regions, with populations in the first two of those regions, both of which are in Arizona, declining to extinction (Table 4, Figure 1). In northwest Tucson, for example, the odds of a territory being occupied declined by an average of  $39.3 \pm 18.5\%$  per year across time ( $Z = 2.90$ ,  $P = 0.004$ ) with declines of somewhat lower magnitude elsewhere. There was also suggestive evidence of declines in the lower and upper Sasabe watersheds in Sonora (Table 4). Although occupancy increased across time in the lower Brawley watershed in Arizona, there was little evidence (e.g.,  $P \leq 0.098$ ) of positive trends in occupancy elsewhere. There was no evidence of temporal trends in occupancy in six other watershed regions (Table 4).

*Occupancy Drivers*—We found evidence for the combined influence of processes linked to the landscape disturbance, cold effects, prey enhancement, and habitat quality hypotheses, but no evidence for the temperature-stress hypothesis (Table 5). On average, occupancy probabilities decreased with increasing landscape disturbance and  $T_{\min}$  during the recent winter, but increased with increasing annual  $P$  during the prior 12 months (June 1 year prior-May of current year) and with increasing territory quality ( $Z \geq 2.11$ ,  $P \leq 0.033$ ; Table 6). Landscape disturbance and annual  $P$  had greater relative effects on occupancy than  $T_{\min}$  or habitat quality, for which effect sizes averaged 25% lower (Table 6). Despite those general patterns, evidence for the interactive effects of landscape disturbance and  $T_{\min}$ , and of annual  $P$  and habitat quality were much greater than that for additive effects ( $\Delta AIC_c = 10.07$ ; Table 5). For example, occupancy probabilities of territories imbedded in more distributed landscapes declined at a much greater rate with increasing winter  $T_{\min}$  than those in landscapes with little to no disturbance (Figure 4). Additionally, occupancy probabilities of high-quality territories increased with increasing annual  $P$  at greater rates than those of moderate and especially low quality (Figure 4). After adjusting for the influence of  $P$  and  $T_{\min}$ , there was no evidence of associations between occupancy and variation in  $T_{\max}$  ( $Z \leq 0.90$ ,  $P \geq 0.37$ ).

Estimates of landscape disturbance varied widely across space and time, and regions with the greatest increases in disturbance were sometimes those where owl occupancy declined the most. Among watershed regions, average cover of landscape disturbance among territories ranged from as low as  $<1.0\%$  in the lower and upper Brawley regions to as high as  $29.1\%$  in northwest Tucson, where disturbance was  $>300\%$  higher than the regional average (Appendix B). Notably,

there was also variation in disturbance levels in northwest Tucson, with little to no disturbance in and around the four northernmost territories and much higher levels to the south. In Sonora, disturbance levels were greatest in the Magdalena-Coyotillo (16.3%) and lower Sasabe (14.2%) regions, and lower elsewhere. Increases in landscape disturbance across time occurred at greater rates in regions where disturbance was highest on average. In northwest Tucson for example, disturbance cover increased by an average of  $0.7 \pm 0.1\%$  per year across time from an average of  $20.8 \pm 5.5\%$  in 2001 to  $43.9 \pm 6.1\%$  in 2016. In the lower Brawley region, however, there was no increase in disturbance cover across time.

## DISCUSSION

Despite marked declines in abundance of ferruginous pygmy-owls in northwestern Mexico reported in recent years (Flesch and Steidl 2006, Flesch 2014a), we found no evidence of systematic declines between 2000 and 2016. Similarly, there was little evidence of systematic declines in territory occupancy across an overlapping but much larger area of northern Sonora, Mexico and portions of adjacent Arizona between 2001 and 2016. Instead, spatial variation in population dynamics was more complex with the direction and magnitude of trends widely across space among various watershed regions. Despite these somewhat more auspicious patterns, had abundance and occupancy not increased markedly in Sonora 2015 and 2016, we would almost certainly have found significant declines in both parameters across time based on recent analyses (Flesch 2014b). Moreover, in Arizona, populations in two of three watershed regions we considered declined to extinction, whereas occupancy increased across time in a third region. Further, despite the relative stability of population units in several regions in Sonora, there was little evidence occupancy increased in any region. Such results indicate the importance of consistently monitoring populations of conservation concern across time and space so that short-term changes in populations can be distinguished from systematic declines over the long term. Despite the absence of systematic declines across the broad region considered here, large interactive effects of climatic flux and land-use change combined with anticipated environmental change suggest declines could develop in the future.

Populations are often structured spatially into varying subpopulation units, and these patterns often depend, in part, on levels of inter-population connectivity and spatial similarity in important environmental factors (Hanski and Gaggiotti 2004). Because the degree of connectivity and synchrony among population units influences their dynamics and viability at multiple scales, effective management often necessitates understanding population structure and identifying population units that are robust, independent, and can buffer declines at broader scales (Ranta et al. 1995, Heino et al. 1997, Ward et al. 2010). We found relatively strong support for population structure based on the results of both multivariate state-space models (mSSM) and more conventional mixed-effects models of time-series abundance data. When no process noise was assumed, observation error varied regionally suggesting some level of population structure. When observation error and process noise were partitioned, process noise did not vary regionally but year-to-year deviations in population growth were correlated among regions indicating somewhat synchronous dynamics across space, and there was also some evidence population growth rates varied regionally. Whereas mSSM are useful for evaluating population structure (Ward et al. 2010), determining what drives observed structure is more

complex. Synchronized dynamics can be driven by dispersal, climate forcing, and spatial similarity in important habitat attributes (Ranta et al. 1995). In this system, patterns we discuss below suggest synchronized dynamics are driven by climatic forcing with regional differences in land-use change and habitat quality likely having the opposite influence. Regardless, moderate levels of synchrony have important implications for population viability because highly synchronized populations face greater extinction risks (Heino et al. 1997).

State-space models estimated relatively low amounts of process noise (0.017-0.020) that were precise, within the range reported for other vertebrates, similar to estimates for other non-passerine birds, and higher than for many large mammals (Sabo et al. 2004, Holmes et al. 2007). Due to marked increases in abundance since inferences were last reported and data from four additional years, estimates of process noise and especially precision increased from those reported previously, which will help inform forecasts of extinction risk (Holmes et al. 2007, Flesch 2014a). In contrast, estimates of observation error (0.083-0.088) were higher, similar to that reported recently and also precise, similar to or lower than that for other non-passerine birds, and higher than those for long-lived mammals (Lindley 2003, Staples et al. 2004, Ward et al. 2010, Flesch 2014a).

Inferences from models of territory occupancy dynamics suggested patterns similar to those for abundance, but were broader in scope given a much larger sampling frame that spanned 14 watershed regions across the U.S. and Mexico. Similar to results for abundance, there was little evidence that occupancy declined systematically across time within the broader study area. Instead, changes in occupancy varied regionally with the number of declining ( $n = 4$ ) or marginally declining (2) subpopulations equal to those that were stable (6), and greatly exceeding the number that increased (1) or marginally (1) increased. Such results combined with marked differences in dynamics between subpopulation in neighboring regions, suggest moderate to high levels of population structure. For example, two of the three subpopulations we considered in Arizona experienced varying dynamics, with two decreasing to extinction while a third that was located in an intervening region increased markedly across time. In the southernmost region in Arizona (upper Brawley), such dynamics may have been driven by low habitat quality and quantity due to a scarcity of nesting substrates at these relatively high elevations, and by reductions in landscape connectivity with larger populations in Mexico linked to development along the U.S.-Mexico border. In northwest Tucson, in contrast, such changes were likely driven by major increases in landscape disturbance linked to urban development. For pygmy owls, landscape disturbance can disrupt dispersal movements in ways that reduce colonization success, functional connectivity, and local rates of patch occupancy (Flesch et al. 2010, Flesch 2017). Thus, despite relatively high regional abundance and increasing occupancy in a neighboring region (lower Brawley), which could provide an important source population, landscape degradation in and around northwest Tucson likely reduced dispersal movements into this region at a time when immigrants were needed to offset the impacts of drought and other stressors. Additionally, immediately before the northwest Tucson population declined to extinction, the Arizona Game and Fish Department removed the lone remaining known owl in this area (an adult male) in 2006 and placed it in captivity as part of a pilot captive breeding program. Despite apparent extirpation of pygmy-owls in two watershed regions in Arizona, occupancy dynamics did not vary between the U.S. and Mexico, suggesting differences in management and other factors between nations had little influence on population dynamics.

*Environmental Drivers*—We considered multiple research hypotheses to explain spatiotemporal variation in territory occupancy that focused on the influence of climatic flux, land-use change, and natural spatial variation in habitat quality. Although we found important associations between occupancy dynamics and each of these factors, evidence for interactions among them was much greater than that for additive relationships, suggesting a complex set of processes simultaneously influenced occupancy. Occupancy of territories imbedded in more disturbed landscapes, for example, declined at greater rates with increasing minimum air temperatures ( $T_{\min}$ ) during winter than those in less distributed landscapes. Additionally, although occupancy increased with quantities of annual precipitation ( $P$ ) on average,  $P$  had increasingly positive effects as territory quality increased. Understanding processes that drove these interactions can be aided by first evaluating the likely biological drivers of the main effects.

In arid environments, the positive bottom-up effects of  $P$  on vertebrate populations have been observed nearly worldwide (Lima et al. 2002, Holmgren et al. 2006). In these systems,  $P$  drives rapid increases in plant biomass, seed production, and insect abundance, creating resource pulses that directly bolster food availability for small consumers, which augments reproductive output and subsequently abundances at lag times of  $\approx 0.5$ -1.5 years depending on the species' life history (Beatley 1969, Anderson 1994, Jaksic 2001, Lima et al. 2002, 2008). Predator populations such as pygmy-owls, often respond indirectly to these resources pulses at somewhat longer lag times of two or more years (Jaksic et al. 1992, Dennis and Otten 2000, Letnic et al. 2005, Flesch 2014a). Accordingly, we found that occupancy rates increased with increasing  $P$  during the prior  $\approx 0$ -12 months but less so with  $P$  at shorter ( $\approx 0.0$ -0.5 years) or longer ( $\approx 1.5$ -0.5 years) lag times. Such associations correspond to the period during which  $P$  is also positively associated with reproductive output of pygmy-owls (Flesch et al. 2015), but contrasts with the somewhat longer lag time that most strongly influenced abundance (Flesch 2014a). Thus, pygmy-owls likely select and remain present on territories where rainfall is sufficient to promote higher abundances of prey because these choices augment performance.

Why then were the positive effects of increasing  $P$  on occupancy greater in territories of higher quality? Van Horne et al. (1997) suggested that when weather influences food supply, interactions between vegetation and weather can augment demographic performance. If these patterns are predictable, then they should reinforce selection of high-quality vegetation resources. Similarly, Franklin et al. (2000) found that high-quality habitat buffered the effects of harsh weather on survival of spotted owls (*Strix occidentalis*), and Flesch et al. (2015) found that territories with greater vegetation cover magnified the benefits of increasing  $P$  on reproductive output of pygmy-owls. Because in this system,  $P$  augments prey abundance, which is likely already greater in high-quality territories, owls that occupy these territories attain multiplicative benefits when conditions are favorable (Flesch et al. 2015, 2017). Understanding the extent to which habitat resources can mediate the influence of both harsh and favorable weather on populations has important implications for management in a changing climate.

In the Sonoran Desert, diurnal lizards are the primary prey of pygmy-owls during the warm season. As ectotherms, metabolic activity in lizards rises exponentially with temperature so that warmer air temperatures during periods of seasonal inactivity can consume energy important for growth, reproduction, and other life-history processes (Adolph and Porter 1993). If dormant or

inactive lizards experience unusually warm conditions sufficient to degrade low-temperature thermal refugia and trigger costly metabolic activities, it may necessitate increased activity and risk to replace lost energy, reduce body condition, and vital and population growth rates (Zani 2008, Zani et al. 2012, Clarke and Zani 2012, Brischoux et al. 2016). In the Sonoran Desert, strong negative associations between abundances of five common species of lizards that are consumed by pygmy-owls and increasing minimum air temperatures ( $T_{\min}$ ) at short lag times over a 25-year period, strongly suggest these processes influence lizard abundance (Flesch et al. 2017). Thus, we hypothesized warming  $T_{\min}$  would influence prey availability and hence occupancy of pygmy-owls, and as predicted, observed a strong negative association between owl occupancy and warming  $T_{\min}$ . Although additional study is needed to better understand how  $T_{\min}$  influences owl and prey populations, we believe observed associations are attributable to the influence of  $T_{\min}$  on lizard populations either directly by affecting metabolic processes or indirectly by affecting food or cover for prey. Other mechanisms, however, could also explain observed patterns including the influence of warmer winters on vegetation cover, which when low can augment predation risk. Regardless of the mechanisms, patterns we observed have grave implications for pygmy-owls and other wildlife because rising  $T_{\min}$  is among the most pervasive trends linked to regional and global climate change, especially in cooler months (Easterling et al. 1997, Weiss and Overpeck, 2005) that correspond to the timing of observed associations.

Occupancy rates declined markedly as territories and the landscapes surrounding them became increasingly dominated by anthropogenic land uses and disturbance. Such patterns are not surprising given well-known impacts of land-use and land-cover change on the quantity, quality, and connectivity of habitats, which simultaneously influence both abundance and movement of potential colonists, reduce colonization rates, and promote edge effects and other stressors that augment extinction risk (Hanski and Gaggiotti 2004, Fischer and Lindenmayer 2007, Lindenmayer and Fischer 2013). Due likely to a combination of these stressors, a population of pygmy-owls in the region that experienced the greatest increases in anthropogenic disturbance in the study area declined to extinction, and this region was at the northern end of the study. Such patterns mirror past population declines that occurred across a much larger region of southern Arizona over the last century (Johnson et al. 2003, USFWS 2011) during which the northern edge of the range of pygmy-owls contracted south by approximately 200 km.

Why then were the negative effects of increasing  $T_{\min}$  greater in areas with higher levels of anthropogenic disturbance? One possible explanation is that if warming  $T_{\min}$  degrades food availability by reducing abundance of ectothermic prey, such effects are greater in areas where the quantity of habitat and thus abundance of prey are lower, or where recolonization rates of vacant territories are increasingly limited by reductions in landscape connectivity. Another possible explanation is that if warming  $T_{\min}$  degrades vegetation cover in ways that promote predation risk, such effects are greater in more disturbed landscapes where both non-native (e.g., domestic cats) and native meso-predators are likely more abundant. Additionally, increasing urbanization can augment temperatures through heat-island effects that may not have been reflected in weather data we considered given stations were located some distance from owl territories. Although lizard prey can be common in suburban settings, it likely takes time for prey populations to recover following rapid changes in land cover such as those observed in the region. Regardless of the mechanisms, the fact that climatic flux had greater negative impacts on populations in areas with greater land-use change suggests the combined influence of these

stressors are greater than their independent effects, which has major implications for conservation and management (Opdam and Wascher 2004, Brook et al. 2008, Mantyka-Pringle et al. 2012).

Studies of the influence of climate flux on wildlife typically focus on expected negative impacts of rising maximum air temperatures ( $T_{\max}$ ), whereas threats posed by rising  $T_{\min}$  such as those described here are rarely considered (Huey et al. 2009, Sinervo et al. 2010, Flesch et al. 2017). By limiting activity to avoid lethally high environmental temperatures, rising  $T_{\max}$  linked to climate change is expected to drive pervasive declines in populations of diurnal lizards and other ectotherms (Huey et al. 2009, Sinervo et al. 2010). Despite these anticipated impacts, recent findings over 25 years in the Sonoran Desert indicate associations between lizard abundances and  $T_{\max}$  vary widely among species and are often weak or positive, suggesting the influence of climate warming on prey may be more complex than previously envisioned (Sinervo et al. 2010, Flesch et al. 2017). For pygmy-owls, however, both abundance (Flesch 2014a) and reproductive output (Flesch 2015) declined with increasing nesting-season  $T_{\max}$  at lag times of 1 and 0 years, respectively, but we found no associations between occupancy and  $T_{\max}$ . These patterns suggest increasing  $T_{\max}$  influences owls directly through thermoregulatory processes versus indirectly by affecting food supply. Heat stress can directly influence behavior and physiology of desert birds (Wolf 2000), and its potential influence on small owls is plausible given generally lower thermal tolerances than other desert species (Ligon 1969). Direct effects are also suggested by the facts that use of hotter west-facing nest cavities by pygmy-owls declines from relatively cool to hot regions of the Sonoran Desert, and nest success is higher in cavities with cooler microclimates (Flesch and Steidl 2010). More study is needed to understand the influence of  $T_{\max}$  and other factors on populations of pygmy-owl.

## CONSERVATION IMPLICATIONS

Information on the patterns and drivers of population dynamics of pygmy-owls in the Sonoran Desert is important for guiding management. While our results indicate a lack of systematic declines across the broader population, subpopulations in several regions declined, including some to extinction, and very few increased. Moreover, patterns of occupancy dynamics were complex across space with subpopulations in neighboring regions often exhibiting varying dynamics. Whereas changes in land use, land cover, and spatiotemporal variation in weather explained some of these patterns, and could drive declines in the future, differences in dynamics among neighboring subpopulations suggest some opportunities for management. Together with data reported here, recent information from the literature combined with recommendations from a draft recovery plan (USFWS 2003) suggest a number of management strategies for conserving, managing, and recovering populations of pygmy-owls. Below, we summarize some of these strategies to help guide management and conservation.

For populations that occupy networks of habitat patches in complex landscapes, uninhibited natural movement of individuals among patches can be essential for population persistence (Hanski and Gaggiotti 2004). Pygmy-owls in our region occupy such contexts and habitat comprises relatively small amounts of landscapes and is fragmented naturally and anthropogenically, which makes the influence of landscape connectivity especially significant in

driving distribution (Flesch 2017). Moreover, movement behavior and colonization success of dispersing pygmy-owls are negatively influenced by increasing landscape disturbance (Flesch et al. 2010), with landscape structures such as large agriculture fields and roadways depressing local occupancy and movement rates (Flesch and Steidl 2007b, Flesch et al. 2010, Flesch 2017). Here, we found that occupancy decreased with increasing cover of anthropogenic disturbance due likely to its role in degrading habitat quality, reducing habitat area, and limiting dispersal and colonization success. We also found that populations in northwest Tucson declined to extinction, and that this decline was associated with landscape degradation in interaction with climatic flux. Despite 10 years that have passed since extirpation of this population, to our knowledge, pygmy-owls have not re-colonized the region. Importantly, this region includes areas that remain largely undisturbed (e.g., west and north of the Tortolita Mountains) and areas that continue to support patches of habitat of at least moderate quality imbedded in disturbed landscapes (e.g., east of Interstate 10 and around the base of Santa Catalina Mountains). Despite presence of this habitat, ongoing development and urbanization continue to reduce habitat patch size and connectivity. Such patterns together with the existence of a relatively large and increasing population within dispersal range to the southwest and the overall significance of connectivity (Flesch 2017), suggest low dispersal rates into this region contributed to extinction and is precluding re-colonization.

To recover populations of pygmy-owls in Arizona, a recovery team convened by USFWS recommended facilitated dispersal of juveniles and translocation of adult pygmy-owls from neighboring populations (including those in northern Mexico) as potential recovery strategies. Although not yet tested, these techniques could be useful in Arizona because they address issues linked to degradation of landscape connectivity and dispersal limitation (USFWS 2003). In contrast, captive propagation was also recommended but considered feasible only after all other techniques to maintain or improve populations had failed or were expected to fail (USFWS 2003, pg. 123). Whereas management to enhance landscape connectivity should aid recovery, targeted efforts focused on facilitated dispersal and translocations could rapidly accomplish this objective before the results of more passive techniques are realized. Thus, active management to move individuals from regions where they are relatively common and populations are increasing or stable, into regions where landscape connectivity has been degraded and populations are small, dominated by unpaired males, or locally extinct, could reestablish populations and foster recovery. Information we provide here on the status and trends of population units in various watershed regions in the U.S. and Mexico can help identify source populations for such efforts.

By definition, high-quality habitats augment reproduction or survival in ways that enhance population growth rates and thus population persistence. Hence, efforts to identify and protect areas of high-quality habitat, enhance degraded or poor habitat, and create new high-quality habitat can be important tools for conservation and recovery. Nonetheless, understanding specific environmental attributes that promote habitat quality can be difficult due to major challenges in measuring local vital rates. Recent studies of pygmy-owls that have spanned more than a decade have made major strides in identifying factors that drive habitat quality. For example, abundance of pygmy-owls is higher and varies less over time in areas with more nest cavities, greater structural complexity and quantity of riparian vegetation, and lower land-use intensity (Flesch 2014a). Moreover, higher abundance of potential nest substrates, greater quantities of woody vegetation cover, and larger, less fragmented woodlands enhance

reproductive output of pygmy-owls (Flesch et al. 2015). In general, these resources promote habitat quality by reducing risks posed by heterospecific enemies, providing more optimal nesting habitat that better mitigates predation risk, interspecific competition, and thermal stress, and by enhancing food resources (Flesch and Steidl 2010, Flesch et al. 2015). Thus, identifying, protecting, and restoring areas with high woody vegetation cover such as riparian areas and nearby stands of saguaros and large trees can aid conservation efforts. In general, management that promotes the survival and recruitment of saguaros, and mitigates threats to saguaros will benefit pygmy-owls, especially when saguaros are closely associated with xeric or mesic riparian woodlands.

In areas where potential nest cavities are naturally sparse or have been lost due to fire, invasion of non-native grasses, overgrazing, or other stressors, active efforts to augment nest cavities by erecting nest boxes or translocating saguaros (especially those that have been salvaged and already have suitable cavities; Flesch and Steidl 2010) could have major benefits for pygmy-owls. Such techniques can create new habitat in areas where woodlands are already suitable (e.g., in semi-desert and mesquite-invaded grasslands) or enhance existing habitat by augmenting availability of potential nest cavities, which can reduce predation, competition, and interspecific aggression with other species of cavity nesters (Flesch et al. 2015). Although the appropriateness of creating habitat in areas where it may not have been present in the past is debatable, such techniques could augment abundance in areas within close dispersal range (e.g., Avra Valley) of populations that have declined to extinction (e.g., northwest Tucson), and provide source populations of potential immigrants that offset reductions in landscape connectivity.

Historically, many records of pygmy-owls in the Sonoran Desert were from large riparian areas in valley bottoms that have been lost or degraded over the last century (Johnson et al. 2003). Restoring these once extensive desert riparian areas by promoting the establishment and growth of mesquite and other riparian trees will enhance recovery prospects for pygmy-owls while creating habitat for other wildlife. Because increasing woody vegetation cover amplifies the positive effects of favorable weather on reproductive output, and lower woodland fragmentation reduces the negative influence of nearby conspecific competitors (e.g., other pygmy-owls; Flesch et al. 2015), restoring large unfragmented woodlands in valley bottoms where they have been lost or degraded, such as along the Santa Cruz River near Tucson, should have multiplicative benefits.

Despite significant impacts of  $P$  and  $T$  on reproduction and population dynamics of pygmy-owls, recent studies suggest the influence of these climatic attributes depends on habitat quality, which has important management implications. Territories with greater woody vegetation cover, for example, augment the positive influence of precipitation on reproduction (Flesch et al. 2015), and as in other owl systems, high-quality habitat could potentially buffer the negative influence of harsh weather on survival (Franklin et al. 2000). Here, we found  $P$  had increasingly positive effects on occupancy as territory quality increased, due likely to synergistic positive effects of increasing  $P$  and vegetation cover on food abundance (Van Horne et al 1997, Flesch et al. 2017). Again, such patterns indicate the importance of identifying and protecting areas of high-quality habitat, and suggest efforts to enhance vegetation and woodland cover will have multiplicative benefits. Given observed interactions between weather and habitat quality, management focused

on improving habitat quality could offer a promising strategy to mitigate the impacts of climatic flux.

Resources for management and recovery are virtually always limited, and thus focusing on locations and strategies with the highest potential for success is critical. We found that increasing levels of anthropogenic disturbance had negative effects on occupancy on average, and that the negative impacts of increasing  $T_{\min}$  were greater in areas with higher levels of anthropogenic disturbance. Although identifying mechanisms that drove interactions between disturbance and  $T$  will require additional study, such results suggest focusing conservation efforts in areas with little anthropogenic disturbance has the greatest potential for success. Additionally, landscape planning that reduces the footprint of land-cover change is important for conservation and recovery. Understanding critical thresholds in the quantity and arrangement of land-cover types representing disturbance both within and around owl home ranges can aid such planning efforts and be addressed in the future with data gathered during this study.

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Table 1: Parameter estimates from top-ranked models of population dynamics and population structure of ferruginous pygmy-owls in northwest Mexico, 2000–2016. Multivariate state-space models (SSM) estimated population growth rate ( $u$ ), observation variance ( $R$ ), process variance ( $Q$ ), and linear mixed-effects models (LMEM) estimated trend ( $\beta_1$ ), observation variance ( $\sigma^2$ ), and random intercepts for each region ( $b_{0j}$ ) in log transformed time-series abundance data.

Model Type	$u/\beta_1$		$R/\sigma^2$		$Q$	
	Est.	SE	Est.	SE	Est.	SE
<b>SSM</b>						
Regional subpopulations, equal $u$ , equal $Q$ with equal covariance	-0.0056	0.032	0.083	0.0079	0.020	0.0085
Regional subpopulations, varying $u$ , equal $Q$ with covariance			0.088	0.0075	0.017	0.0085
Upper Altar	0.011	0.035				
Middle Rio Sasabe	-0.019	0.034				
Sasabe area	-0.010	0.034				
Upper Rio Plomo	-0.0065	0.035				
<b>LMEM</b>						
Regional subpopulations, equal $\beta_1$ , varying $\sigma^2$ , same $b_{0j}$	-0.0014	0.0054	0.072	0.016		

Table 2: Rankings and descriptions of models of population dynamics and population structure of ferruginous pygmy-owls in northwest Mexico, 2000-2011. Multivariate state-space models (SSM) estimated population growth rate ( $u$ ), observation variance ( $R$ ), process variance ( $Q$ ), and linear mixed-effects models (LMEM) estimated trend ( $\beta_1$ ), observation variance ( $\sigma^2$ ), and random intercepts for each region ( $b_{0j}$ ) in log transformed time-series abundance data. In SSM that considered regional subpopulation structure, each estimated process error and covariance is considered an estimated parameter ( $K$ ).

Model approach			
Description	$K$	$\Delta AIC_c$	$w_i$
<b>SSM</b>			
Regional subpopulations, equal $u$ , equal $Q$ with equal covariance	22	0.00	0.67
Regional subpopulations, varying $u$ , equal $Q$ with covariance	25	1.60	0.30
One population, $Q$ with no covariance	21	2.95	0.15
Regional subpopulations, equal $u$ , varying $Q$ with time-varying covariance	30	3.12	0.14
Regional subpopulations, varying $u$ , varying $Q$ with covariance	33	9.68	0.01
<b>LMEM</b>			
Regional subpopulations, equal $\beta_1$ , varying $\sigma^2$ , same $b_{0j}$	8	0.00	0.72
Regional subpopulations, equal $\beta_1$ , varying $\sigma^2$ , varying $b_{0j}$	9	2.13	0.25
Regional subpopulations, varying $\beta_1$ , varying $\sigma^2$ , varying $b_{0j}$	11	6.44	0.03
One population, equal $\beta_1$ , equal $\sigma^2$ , same $b_{0j}$	5	13.21	0.00
Regional subpopulations, equal $\beta_1$ , equal $\sigma^2$ , varying $b_{0j}$	6	15.29	0.00
Regional subpopulations, varying $\beta_1$ , equal $\sigma^2$ , varying $b_{0j}$	8	19.37	0.00

Table 3: Rankings and descriptions of models of temporal variation in territory occupancy of ferruginous pygmy-owls in 11 watershed regions in northern Sonora, Mexico and 3 watershed region in adjacent southern Arizona, USA between 2001 and 2016. Models are based on generalized linear mixed models with occupancy (occupied or unoccupied) fit as the response variable, territory and landscape identity fit as random intercepts, and year, nation (USA or Mexico), and watershed region fit as fixed effects.

Model	$K$	$\Delta AIC_c$	$w_i$
Regional variation in trends {Year + Region + Region $\times$ Year}	30	0.00	1.00
National variation in trends {Year + Nation + Nation $\times$ Year}	6	63.11	0.00
One population with equal trend {Year}	4	67.30	0.00

Table 4: Parameter estimates from top-ranked models of temporal dynamics in territory occupancy of ferruginous pygmy-owls in 11 watershed regions in northern Sonora, Mexico and 3 watershed region in adjacent southern Arizona, USA between 2001 and 2016. Estimates are from a generalized linear mixed models with occupancy (occupied or unoccupied) fit as the response variable, territory and landscape identity fit as random intercepts, and year, region, and year  $\times$  region fit as fixed effects.  $F$ -statistics are Wald tests. Regions are listed from north to south, and the first 3 regions are in the USA.

Term ( $F$ statistic)	Est.	SE	$ Z $	$P$
Year (0.27)	0.031	0.038	0.82	0.41
Region (2.49)				
Northwest Tucson	-5.33	1.19	4.49	<0.001
Lower Brawley	-1.11	0.50	2.20	0.028
Upper Brawley	-4.27	1.20	3.55	<0.001
Upper Sonoyta	-0.40	0.75	0.54	0.59
Upper Sasabe	-0.98	0.53	1.85	0.064
Upper Altar	-0.70	0.49	1.42	0.15
Lower Plomo	-0.67	0.54	1.24	0.21
Lower Sasabe	-0.24	0.66	0.37	0.71
Lower Altar	-1.17	0.56	2.08	0.037
Lower Busani	-2.29	0.63	3.63	<0.001
Upper Magdalena	-0.65	0.76	0.86	0.39
Magdalena-Coyotillo	-1.43	0.61	2.34	0.019
Upper San Miguel	0.15	0.75	0.20	0.84
Region $\times$ Year (4.15)				
Northwest Tucson $\times$ Year	-0.50	0.17	2.90	0.004
Lower Brawley $\times$ Year	0.13	0.06	2.25	0.024
Upper Brawley $\times$ Year	-0.38	0.18	2.10	0.036
Upper Sonoyta $\times$ Year	-0.066	0.103	0.64	0.52
Upper Sasabe $\times$ Year	-0.088	0.051	1.75	0.081
Upper Altar $\times$ Year	-0.047	0.052	0.91	0.36
Lower Plomo $\times$ Year	0.031	0.065	0.47	0.64
Lower Sasabe $\times$ Year	-0.12	0.07	1.67	0.094
Lower Altar $\times$ Year	-0.14	0.07	2.20	0.028
Lower Busani $\times$ Year	0.13	0.08	1.65	0.098
Upper Magdalena $\times$ Year	0.017	0.082	0.21	0.84
Magdalena-Coyotillo $\times$ Year	-0.008	0.070	0.12	0.91
Upper San Miguel $\times$ Year	-0.38	0.10	3.69	<0.001

Table 5: Rankings and descriptions of models that explained spatiotemporal variation in territory occupancy of ferruginous pygmy-owls in 11 watershed regions in northern Sonora, Mexico and 3 watershed region in adjacent southern Arizona, USA between 2001 and 2016. Models are generalized linear mixed models with occupancy (occupied or unoccupied) fit as the response variable, territory and landscape identity fit as random intercepts, and estimates of landscape disturbance, weather (precipitation and temperature), and habitat quality fit as fixed effects. Parameter estimates for top-ranked models and the full additive model are in Table 6.

Model	$K$	$\Delta AIC_c$	$w_i$
Disturbance $\times$ Weather + Habitat quality $\times$ Weather	9	0.00	1.00
Disturbance $\times$ Weather + Habitat quality	8	1.55	0.46
Disturbance + Weather $\times$ Habitat quality	8	8.43	0.01
Disturbance + Weather + Habitat quality	7	10.07	0.01
Disturbance $\times$ Habitat quality + Weather	8	10.38	0.01
Disturbance + Weather	6	12.41	0.00
Weather + Habitat quality	6	16.21	0.00
Weather	5	18.62	0.00
Disturbance + Habitat quality	5	33.12	0.00
Disturbance	4	36.16	0.00
Habitat quality	4	40.41	0.00
Null {Intercepts only}	3	43.60	0.00

Table 6: Parameter estimates from 2 top-ranked models and the full additive model that explained spatiotemporal variation in territory occupancy of ferruginous pygmy-owls in 11 watershed regions in northern Sonora, Mexico and 3 watershed region in adjacent southern Arizona, USA between 2001 and 2016. Models are generalized linear mixed models with occupancy (occupied or unoccupied) fit as the response variable, territory and landscape identity fit as random intercepts, and estimates of landscape disturbance, weather (precipitation and temperature), and habitat quality fit as fixed effects. Random effects variances were estimated at 1.24 for territory intercept and 0.47 for landscape intercept in the top-ranked model. Sample sizes included 1,634 observations from 151 territories in 39 landscape regions. Scaled estimates from the full additive model are based on  $z$ -scored fixed effects.

Model ( $\Delta$ AICc)				
Term (units)	Est.	SE	Z/	P
Disturbance $\times$ Weather + Weather $\times$ Habitat quality (0.00)				
Disturbance (%)	0.043	0.025	1.70	0.090
$T_{\min}$ ( $^{\circ}$ C)	-0.0067	0.055	0.12	0.90
$P_{\text{year}}$ (mm, ln)	-0.75	0.87	0.86	0.39
Habitat quality (no. young/year)	-2.97	1.81	1.64	0.10
Disturbance $\times T_{\min}$	-0.012	0.0040	3.10	0.002
$P_{\text{year}} \times$ Habitat quality	0.60	0.32	1.91	0.057
Disturbance $\times$ Weather + Habitat quality (1.55)				
Disturbance (%)	0.042	0.025	1.69	0.092
$T_{\min}$ ( $^{\circ}$ C)	-0.0033	0.055	0.06	0.95
$P_{\text{year}}$ (mm, ln)	0.88	0.18	4.91	<0.001
Habitat quality (no. young/year)	0.46	0.22	2.06	0.039
Disturbance $\times T_{\min}$	-0.012	0.0040	3.11	0.002
Disturbance + Weather + Habitat quality (10.07)				
Disturbance (scaled)	-0.36	0.13	2.84	0.004
$T_{\min}$ (scaled)	-0.26	0.12	2.13	0.033
$P_{\text{year}}$ (scaled)	0.35	0.072	4.93	<0.001
Habitat quality (scaled)	0.26	0.12	2.11	0.035

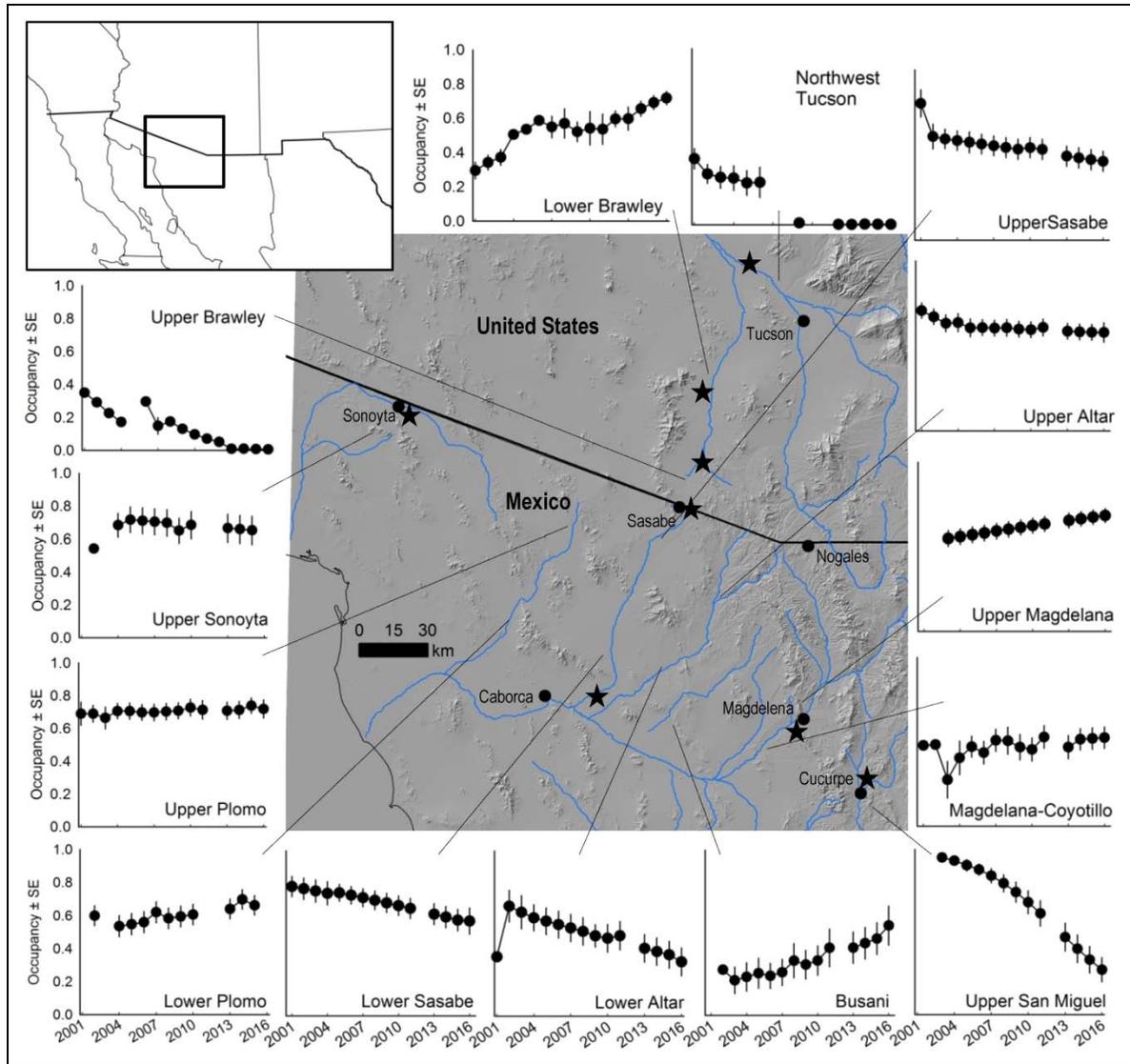


Figure 1. Study area for monitoring territory occupancy of ferruginous pygmy-owls in northern Sonora, Mexico and adjacent southern Arizona, USA between 2001 and 2016. Main map illustrates the location of 14 watershed regions, major cities (circles), weather stations (stars), and drainages (blue lines). Surrounding scatter plots show temporal variation in territory occupancy in each watershed region, and are predictions from a generalized linear mixed model in which occupancy (occupied or unoccupied) was fit as the response variable, year, watershed region, and year  $\times$  region interactions were fit as fixed effects, and territory patch ( $n = 151$ ) and landscape ( $n = 39$ ) identities were fit as random intercepts. Inset map shows the location of the study area with reference to surrounding state and international boundaries.

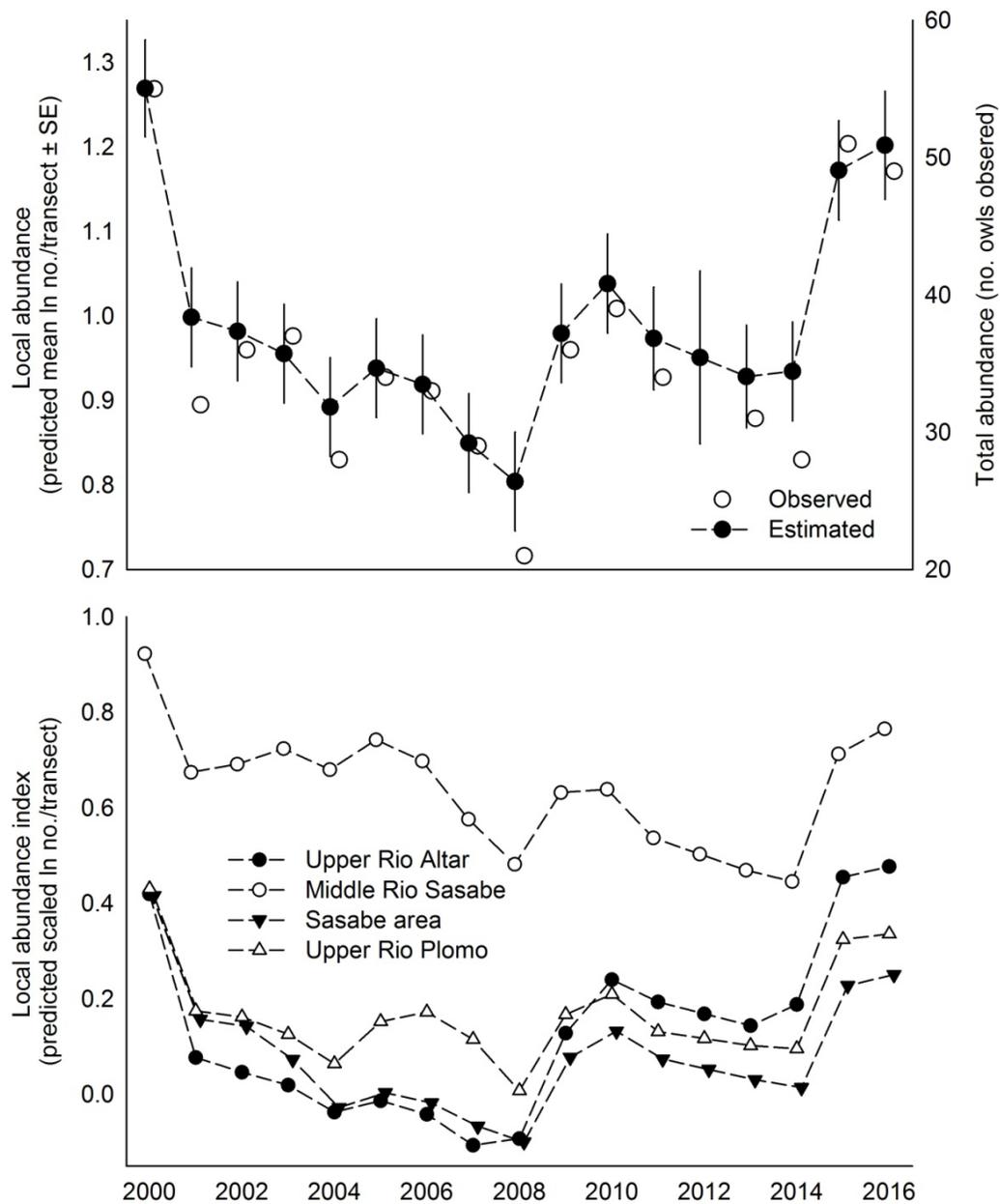


Figure 2. Temporal variation in abundance of ferruginous pygmy-owls along 54 km of transects ( $n = 18$ ) in northern Sonora Mexico between 2000 and 2016. Top figure shows annual estimates of abundance based on the observed data (open points) and smoothed state estimates from a top-ranked multivariate state-space model (black points, dashed line). Bottom figure shows spatiotemporal variation in abundance among four regions based on smoothed state estimates from a state-space model that considered spatial population structure and was parameterized with growth rates for each region, equal process error, and regional covariance in process error among subpopulation units in each region. Spatiotemporal variation in abundance is represented by an abundance index because estimates are scaled to the first observation time series in each region that we selected to be the time series with the lowest mean abundance across time.

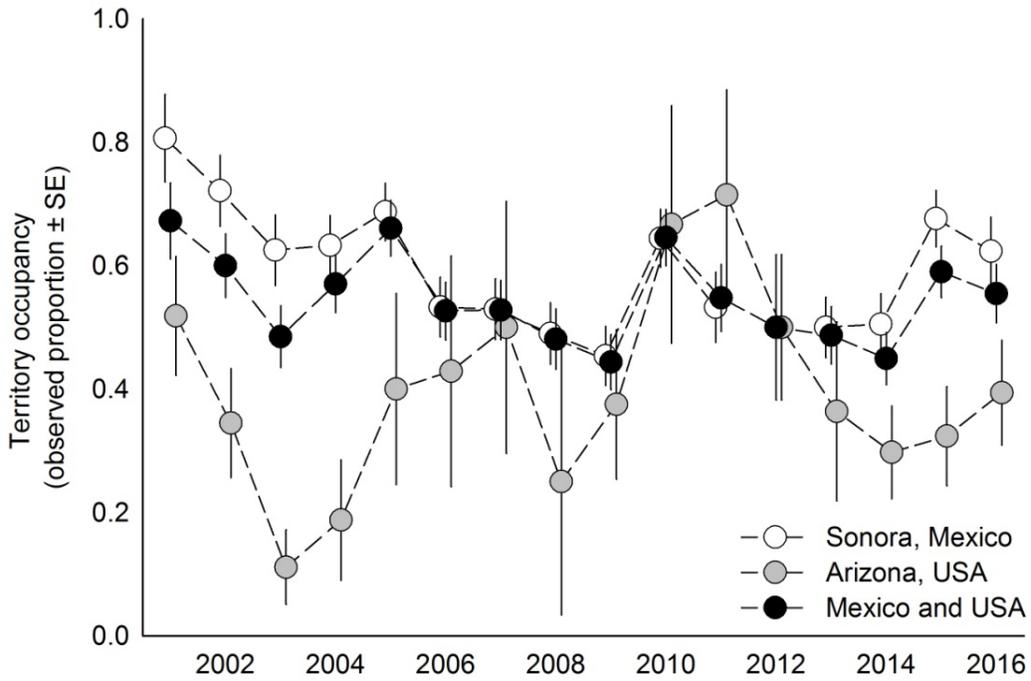


Figure 3. Temporal variation in territory occupancy of ferruginous pygmy-owls in northern Sonora, Mexico and adjacent southern Arizona, USA between 2001 and 2016. Estimates are the proportion of territories that were occupied each year in each nation and overall  $\pm 1$  binomial standard error. In Mexico we considered 112 territory patches and surveyed between 31 and 108 patches per year, except in 2012 when no data were gathered. In the USA we considered 39 territory patches and surveyed between 4 and 37 patches per year.

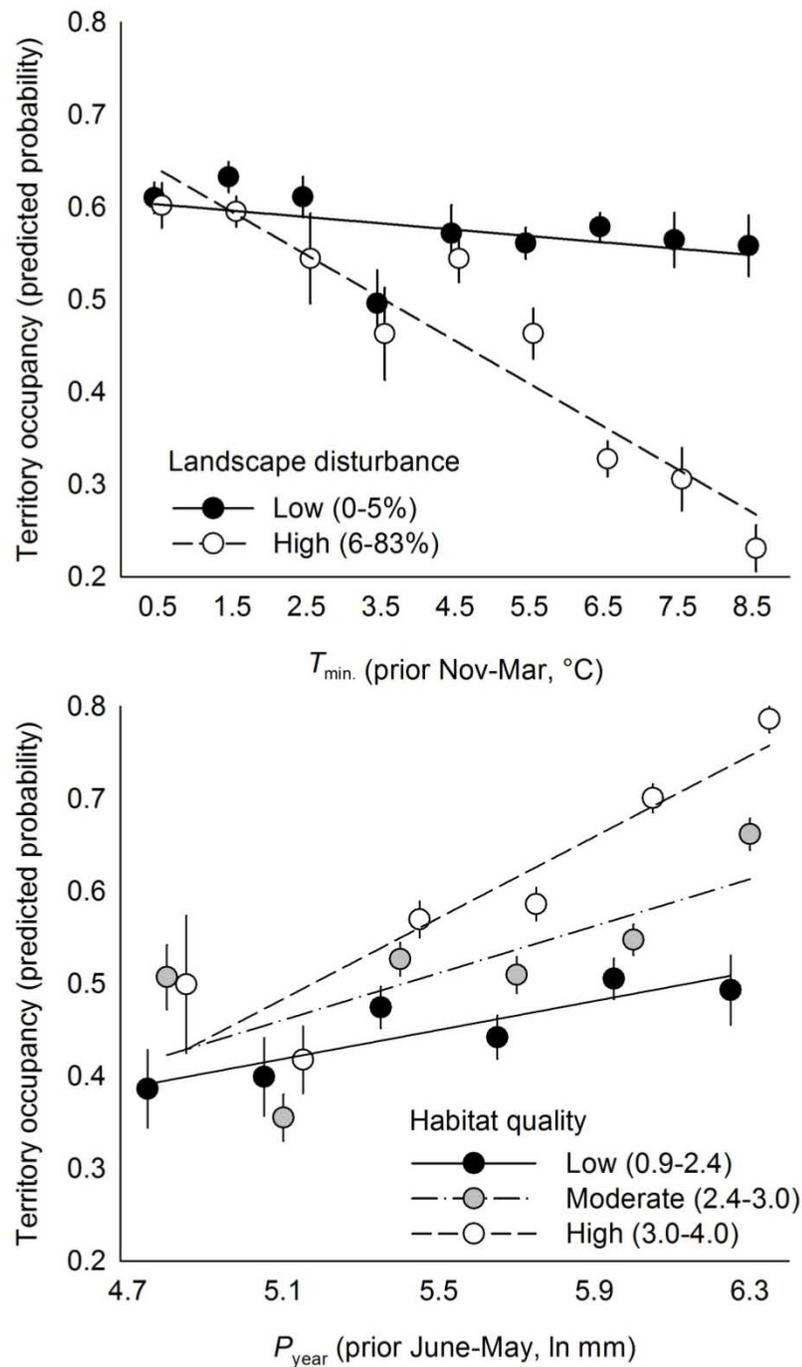
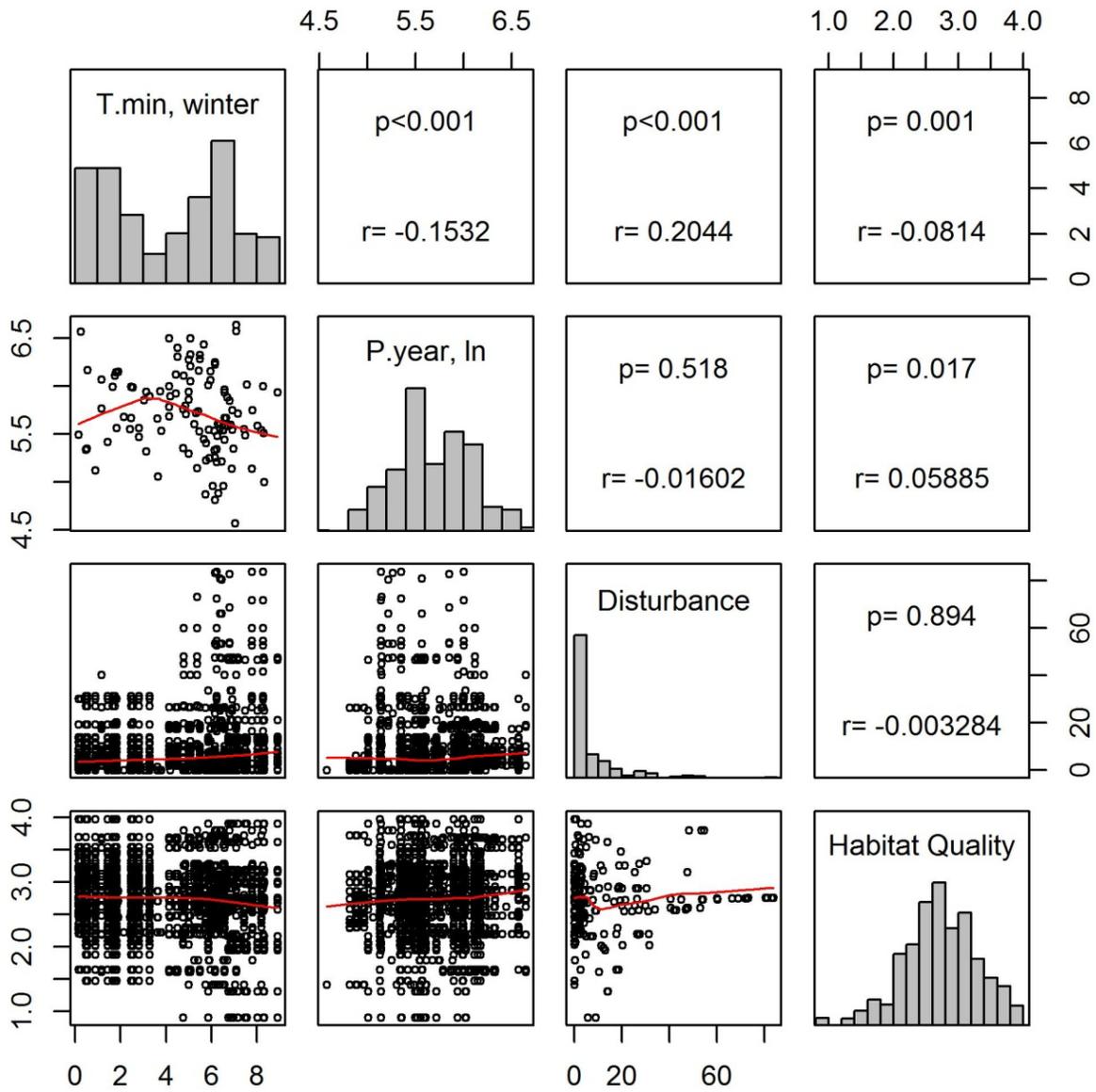


Figure 4. Interactive effects of climatic attributes, anthropogenic disturbance, and spatial variation in habitat quality on territory occupancy dynamics of ferruginous pygmy-owls in northern Sonora, Mexico and adjacent southern Arizona, USA between 2001 and 2016. Estimates are predictions from a top-ranked generalized linear mixed models with occupancy (occupied or unoccupied) fit as the response variable, territory and landscape identity fit as random intercepts, and estimates of landscape disturbance, precipitation ( $P$ ) and temperature ( $T$ ), and habitat quality fit as fixed effects. Temperature is mean minimum daily air temperature between Nov. and March of the prior year ( $T_{\min}$ ), and  $P$  is annual rainfall from June of the prior year through May of the current year ( $P_{\text{year}}$ ).

Appendix A: Correlations among factors linked to the predicted influence of weather, disturbance, and habitat quality on spatiotemporal variation in territory occupancy of ferruginous pygmy-owls.



Appendix B: Sample sizes and regional variation in factors that explained territory occupancy dynamics of ferruginous pygmy-owls in northern Sonora, Mexico and adjacent southern Arizona, USA between 2001 and 2016. Sample sizes show the number of territory patches and total number of occupancy surveys across time within territories in each of 14 watershed regions listed from north to south. Percent differences (% Diff.) are from average values among all 14 regions for annual precipitation (mm; June-May), mean daily minimum air temperature between November and March (°C), disturbance cover (%), and habitat quality (no. young/year).

Watershed region	Sample size		$P_{\text{year}}$		$T_{\text{min}}$		Disturbance		Habitat quality	
	Territories	Surveys	Mean	% Diff.	Mean	% Diff.	Mean	% Diff.	Mean	% Diff.
Northwest Tucson	16	108	265.2	-20.6	6.5	37.2	33.8	307.9	2.8	3.6
Lower Brawley	18	144	272.4	-18.4	6.0	27.7	0.1	-98.7	2.9	5.9
Upper Brawley	5	36	319.0	-4.5	3.2	-33.0	0.5	-93.7	2.5	-9.1
Upper Sonoyta	5	43	217.5	-34.9	6.6	38.8	2.4	-71.2	2.5	-6.8
Upper Sasabe	20	265	334.8	0.3	1.6	-66.7	2.4	-71.3	2.8	4.0
Upper Altar	16	214	336.2	0.7	1.6	-66.7	6.4	-22.6	2.6	-5.2
Upper Plomo	17	205	315.0	-5.7	2.4	-48.5	3.5	-57.2	2.6	-5.7
Lower Plomo	12	125	225.6	-32.4	6.7	42.3	3.9	-52.4	2.7	-1.7
Lower Sasabe	6	81	333.4	-0.2	2.3	-52.0	14.3	72.2	3.3	20.0
Lower Altar	11	119	303.5	-9.1	7.0	48.2	9.8	18.4	2.6	-3.5
Lower Busani	8	93	270.4	-19.0	7.4	56.7	9.3	12.5	2.5	-8.1
Upper Magdalena	4	52	498.9	49.4	5.0	5.5	6.3	-23.5	2.8	3.8
Magdalena-Coyotillo	8	86	473.7	41.9	5.0	5.4	15.5	87.2	2.3	-15.6
Upper San Miguel	5	63	508.8	52.4	5.0	5.2	7.7	-7.5	3.2	18.5