

Landcover change and habitat quality mediate impacts of temperature and precipitation on population dynamics of a threatened aridland predator

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Keywords

climate change; interactive impacts; meta-population; neighborhood effects; pygmy-owl; Sonoran Desert; synergistic effects; temperature.

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Abstract

Climate and landcover change can have synergistic impacts on wildlife populations, but the pervasiveness of these threats and factors that buffer them remain unclear despite important implications for conservation. I evaluated the additive and interactive effects of spatiotemporal variation in temperature, precipitation, and landcover change on annual territory occupancy, colonization, and extinction of a threatened top-predator, the ferruginous pygmy-owl (*Glaucidium brasilianum*), across a vast binational region of the Sonoran Desert over 16 years. I also assessed how local habitat quality and regional population size mediate impacts of these stressors. Despite significant bivariate associations between occupancy and temperature, precipitation, and landcover change, evidence for interactions was much greater than for additive effects. Occupancy of territories imbedded in increasingly disturbed landscapes declined at greater rates with warming winter temperatures, but the temperature had little effect in intact landscapes suggesting they buffer impacts of climate warming. Occupancy increased markedly with precipitation due likely to major positive impacts on prey, but again, interactive effects were stronger given territories of higher quality amplified benefits of precipitation. Impacts of landcover change and habitat quality on extinction depended markedly on regional population sizes. When populations were small and few potential colonists were present, high-quality habitat and low landcover change failed to reduce extinction. When populations were large, however, high-quality habitat and more intact landscapes, which best foster dispersal, reduced extinction. Hence, complex interacting processes linked to the effects of precipitation and habitat quality on carrying capacity, landcover change on habitat connectivity and vulnerability to rising temperatures, and local population sizes simultaneously drove dynamics. Efforts to identify and protect high-quality habitat and limit landcover change can enhance conservation but will be most efficient in intact landscapes. Efforts to enhance local habitat quality and quantity, and directly augment populations should consider broader landscape contexts linked to habitat connectivity and potential source populations.

Introduction

Climate and landcover change can have marked impacts on wildlife populations by altering the quantity, quality, and accessibility of resources and conditions that comprise habitats (Parmesan, 2006; Fischer & Lindenmayer, 2007). When combined, such stressors can impact populations additively, or in ways that are greater than (synergistic) or less than (antagonistic) their individual impacts, but the frequency of these patterns and most vulnerable systems remain unclear despite major implications for conservation (Sala *et al.*, 2000; Mantyka-Pringle, Martin, & Rhodes, 2012). In the case of synergistic impacts, wildlife populations in areas where habitat has been lost or fragmented by anthropogenic landcover change are sometimes found to be more vulnerable to climatic variation

than those in areas where habitats are less disturbed (Travis, 2003; Opdam & Wascher, 2004; Prevalenti *et al.*, 2010; Oliver *et al.*, 2015). Recent reviews, however, indicate the prevalence of these and other synergistically-acting stressors are more limited than they have been emphasized in the literature, suggesting synergies may be focused in specific contexts or require long-term data at local scales to detect (Côté, Darling, & Brown, 2016; Jackson *et al.*, 2016; Greenville *et al.*, 2021). In arid environments, wildlife populations could face greater threats from synergies given the unpredictable, resource-limited nature of these systems, tendency for small changes in precipitation and temperature to have large effects on abundance and vital rates (Lima, Stenseth, & Jaksic, 2002; Holmgren *et al.*, 2006), and because impacts of habitat loss and fragmentation seem to increase with maximum

temperatures (Mantyka-Pringle *et al.*, 2012). Nonetheless, few studies have evaluated the additive and interactive effects of climate and landcover change in arid systems (Previtali *et al.*, 2010; Bennett *et al.*, 2015). Assessing these questions is important for conservation because when present, synergistically-acting stressors can greatly magnify extinction risk, create ecological surprises, and require more complex context-dependent management strategies (Sala *et al.*, 2000; Brook, Sodhi, & Bradshaw, 2008; de Chazal & Rounsevell, 2009; Titeux *et al.*, 2016).

Developing efficient conservation strategies to address the impacts of climate and landcover change can be aided by understanding processes that mediate or buffer their effects. For example, evidence from a growing body of work suggests old-growth forests and climate refugia linked to local topography can function in this capacity by mitigating impacts of climate warming and harsh weather on populations (Franklin *et al.*, 2000; Dobrowski, 2011; Betts *et al.*, 2018; Suggitt *et al.*, 2018), but examples are limited to few systems. Such buffering may be realized when animals select specific resources and conditions linked to high-quality habitat, which promote population growth rates but may be uncommon (Johnson, 2007). If such buffering processes are frequent in nature, then identifying and augmenting resources and conditions that promote them could enhance ecological resiliency and help focus management. Factors that promote buffering and drive habitat quality, however, are unknown in most systems and data on individual responses to these and other stressors across a broad range of environments and variation in weather and landscape structure are needed to address these questions (Jarzyna *et al.*, 2016; Greenville *et al.*, 2021).

Here, I use a long-term (2000–2016), large-scale (>25,000 km²) population study in the Sonoran Desert of North America to assess hypotheses that explain spatiotemporal variation in annual occupancy, colonization, and extinction at territory-specific scales. Hypotheses I consider focus on the potential additive and interactive effects of spatiotemporal variation in precipitation, temperature, landcover change, and habitat quality on annual observations of territory occupancy, colonization, and extinction at scales linked to individual animals, and how spatiotemporal variation in regional population sizes mediate these effects. With regard to regional population sizes, impacts of landcover change on landscape connectivity, dispersal, and ultimately population dynamics may not be detectable unless sufficient numbers of potential colonists are present in surrounding neighborhoods to realize effects (Hanski, 1999; Yackulic *et al.*, 2012). Populations in the focal system are well suited to address these questions because they occupy arid environments where precipitation and temperature have varied widely and unpredictably recently due likely to climate change, and a diversity of landscapes from wild areas to the developing margins of major cities. Moreover, detection probability during surveys is nearly perfect, anthropogenic landscape structures influences movement (Flesch *et al.*, 2010) in ways that make landcover change important, and spatial variation in local habitat quality is already well known from a decade of

demographic monitoring. Finally, the focal species—the ferruginous pygmy-owls (*Glaucidium brasilianum*)—is also of major conservation concern at the northern end of its range, making this work vital for conservation.

Materials and methods

Study system

I considered a ≈20,000 km² region in northwest Mexico and ≈5,000 km² region in the adjacent U.S.A. that spanned 14 watershed regions and both major vegetation communities occupied by pygmy-owls in the northern Sonoran Desert (Fig. 1). Here, pygmy-owls are year-round residents in woodlands associated with giant saguaro cacti (*Carnegiea gigantea*) that provide nest cavities. Arizona Upland desert-scrub is dominated by woodland and scrub of short trees such as mesquite (*Prosopis velutina*) and saguaros. Semi-desert grassland is dominated by open mesquite woodlands, bunchgrasses, and sub-shrubs. Riparian areas are dominated by mesquite woodlands. Annual precipitation is bimodal with a summer monsoon in late June–Sept and occasional winter storms of Pacific origin. Summers are hot with maximum temperatures >40°C and winters are cool with minimum temperatures near 0°C. Pygmy-owls are diurnal generalists that prey largely on lizards in the warm season, and small birds and mammals across the year.

A century ago, pygmy-owls occurred in gallery forests along perennial river valleys in lowland southern Arizona, U.S.A., and in woodlands along ephemeral streams (Phillips, Marshall, & Monson, 1964). By the mid-1900s, clearing of wooded bottomlands for agriculture, water diversion, and other impacts drove widespread habitat loss and population declines (Johnson *et al.*, 2003). As a result, pygmy-owls were listed as endangered in Arizona by the U.S. federal government in 1997, delisted for reasons unrelated to recovery a decade later, but recently proposed for re-listing as threatened (USFWS, 2021). Although populations in Arizona are thought to have declined following listing and climate and landcover change are major threats, no quantitative estimates of population trends or factors that influence them are available. In adjacent northwestern Mexico, pygmy-owls are more common, occupy similar environments, and abundance declines between 2000 and 2011 were associated with drought, extreme temperatures, and land-use intensity (Flesch & Steidl, 2006; Flesch, 2014).

Hypotheses

Conversion of natural vegetation to anthropogenic landcover can diminish the quantity, quality, and connectivity of habitats by eliminating resources, increasing predation risk, and promoting other stressors in ways that reduce abundance and promote extinction (Lindenmayer & Fischer, 2013). Thus, this *landcover change hypothesis* predicts greater conversion of natural vegetation to anthropogenic landcover within territories or surrounding landscapes reduces territory occupancy and colonization by pygmy-owls and increases extinction.

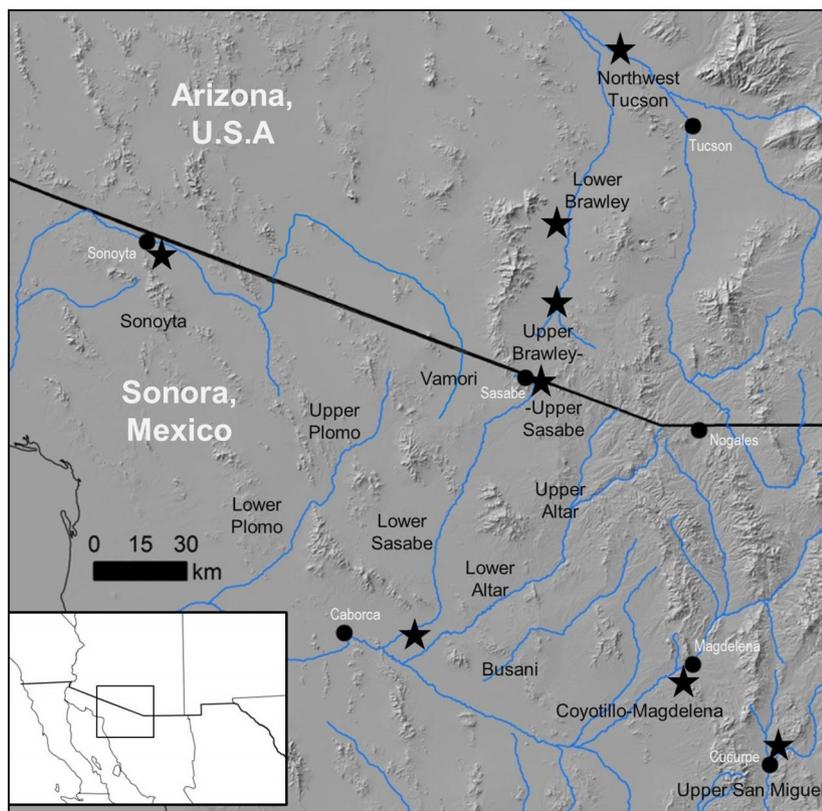


Figure 1 Study area and watershed regions in northern Sonora, Mexico, and adjacent southern Arizona, U.S.A., 2001–2016 noting cities (circles; white font), weather stations (stars), major drainages (blue lines), and state and international boundaries (inset map). Mexico and the U.S. included 12 and two watershed regions, respectively, with one bi-national region spanning the upper Arroyo Sasabe and southern Brawley Valley. Data from Sonoyta and lower Plomo, and lower Magdalena-Coyotillo and upper Magdalena regions were combined to augment precision due to limited samples and similar dynamics. Regions were subdivided based on the upper and lower portions of each secondary watershed.

Spatiotemporal variation in climate can influence individuals directly through energetic and thermoregulatory constraints, or indirectly by affecting prey or other resources in various ways (Stenseth *et al.*, 2002; Holmgren *et al.*, 2006). Low average daily-minimum air temperatures (T_{\min}) during winter could degrade body condition, drive mortality, or reduce reproduction of owls or prey. Moreover, high T_{\min} could reduce abundances of important lizard prey by degrading low-temperature thermoregulatory refugia, increasing costs of maintenance metabolism during dormancy, and reducing prey abundance (Zani, 2008). Thus, these T_{\min} -effects hypotheses, predict decreasing or increasing cool-season (November–March) T_{\min} reduces owl occupancy and colonization and promotes extinction at lag times of ≈ 0.5 –1.5 years. High average daily-maximum temperatures (T_{\max}) during nesting (April–June) can reduce prey abundance or activity or directly degrade owl nestling condition or survival, reduce reproductive output (Flesch *et al.*, 2015) and occupancy and colonization ≈ 1 -year later. Thus, this *temperature-stress hypothesis* predicts high nesting-season T_{\max} reduces owl occupancy and colonization the following year. In arid environments, precipitation can augment prey abundance directly during the same year or indirectly by augmenting resources important to prey creating lagged effects

tied to local food-web structure (Holmgren *et al.*, 2006). Thus, this *prey-enhancement hypothesis* predicts increasing precipitation augments occupancy and colonization, and reduces extinction at lag times of ≈ 0 –2 years.

Habitat-selection theory posits individuals select the highest quality habitat available so that the best territories are selected first and used more consistently (Fretwell & Lucas, 1970). Thus, this *habitat-quality hypothesis* predicts positive associations between habitat quality and owl occupancy and colonization, and negative associations with extinction.

Processes linked to each hypothesis above can interact in complex ways. If populations in areas with greater landcover change are more vulnerable to the direct (e.g., temperature stress) or indirect (e.g., through prey or other resources) effects of climatic variation, or if areas with lower landcover change buffer impacts of climatic variation (Travis, 2003; Opdam & Wascher, 2004), then interactions between weather and landcover change will be present with predictions depending on the form of these relationships. Moreover, if impacts of climate or landcover change are buffered or amplified by high-quality habitat (Franklin *et al.*, 2000), or greater in low-quality habitat, then interactions between these factors will explain occupancy, colonization, and extinction.

Design and surveys

I estimated annual territory occupancy, extinction, and colonization by surveying a large sample of territory patches ($n = 151$) just before or during the nesting season across time (Table S1). Territories were considered occupied if they harbored a territorial male or pair of pygmy-owls with most territories surveyed early in the nesting season. Territory patches were delineated in space based on observed patterns of spatial use by owls across time such that each individual territory patch could be occupied by only single territorial owls or breeding pairs (Flesch *et al.*, 2015). To locate owls and identify territories, I broadcast conspecific territorial vocalizations during and just before the nesting season (April–June) in a manner that yields nearly perfect detection probability (Flesch & Steidl, 2007). In Mexico, I surveyed transects near random and non-random points in spring 2000–2002 and searched for nests in occupied areas until I located the nests of most individuals. From 2001–2011 to 2013–2016, I surveyed areas within ≈ 300 m of past nests (or owl locations if nests were not found initially) at most occupied sites, and through 2010 searched for nests exhaustively. To delineate territories, I plotted nest coordinates across time, identified clusters of use in space, and placed 399-m radius circles (50 ha) around average coordinates of each cluster, which is similar in area to a breeding territory. This approach fostered the identification of discrete territory patches because potential nest cavities were clumped in space, owls used the same general areas over time, and abundance peaked in early years when most habitat was occupied (Flesch, 2014). Methods were similar in the U.S. but surveys were non-random and more sporadic across time.

Environmental measurements

I used satellite imagery, weather-station data, on-the-ground measurements, and models of territory-specific reproductive output to quantify factors linked to hypotheses (Table S1). To assess landcover change within and adjacent to territories, I digitized landcover types linked to human land uses in Google Earth in each year and measured cover within territories and adjacent 1-km radius landscapes across time (see Appendix S1). To quantify climatic variation, I used data from eight weather stations located across the study area (Fig. 1), and matched territories with the closest station based on proximity and elevation. Because the influence of precipitation or temperature can vary seasonally and with different lag times, I quantified various seasonal periods and lag times linked to the biology and past findings in this system (Appendix S1). To measure habitat quality, I modeled the influence of various territory-specific habitat resources on observed annual reproductive output (R) of owls within territories in Mexico from 2001–2010. This procedure yielded precise model-based predictions of R that could be achieved by individuals in each territory across time (see Flesch *et al.*, 2015) and a fitness-based metric of habitat quality, which is more closely linked to habitat-specific population growth rate than indirect measures such as habitat structure (Franklin *et al.*, 2000; Mortelliti, Amori, & Boitani, 2010; Flesch, 2017).

Analyses

To assess hypotheses, I fit generalized linear mixed-effects models (GLMMs) representing each prediction and used model selection based on AIC_c to evaluate support among models (Burnham & Anderson, 2002). GLMMs included territory-specific observations of occupancy, colonization, and extinction in each year as binary response variables and various fixed effects linked to predictions (Table S1). To adjust for correlations among repeated measurements of the same territories, and of territories embedded in the same landscapes and watershed regions, I considered random intercepts for territory, landscape, and watershed region in models of occupancy, and used model selection to assess optimal structures. Region was fit as a random intercept in models of colonization and extinction because data were too sparse for more complex structures. Landscape identities ($n = 39$) grouped territories within ≈ 5 km. I directly modeled responses rather than using dynamic occupancy models because detectability was known *a priori* to be ≈ 1.0 based on experimental trials (Flesch & Steidl, 2007). Observations from territories not visited in year $t-1$ were censored when modeling extinction and colonization, as were observations from the initial year each territory was identified when modeling occupancy.

To develop models to represent hypotheses, I first assessed sets of related models for the same hypothesis to identify the most influential factors. This involved fitting models to assess the influence of each related weather factor during different seasonal periods and lag times, disturbance measured at local and landscape scales, factors on raw and log-transformed scales, and quadratic terms, and selecting models that minimized AIC_c . I then considered all possible additive and interactive combinations of models linked to each hypothesis, after first confirming that pairwise correlations among factors were low ($r < 0.6$; Appendix S2). For models with interactions, I fit sets of preliminary models to assess the best two-way interactions among all possible combinations. Finally, I considered refinements to top-ranked models by assessing the influence of including, excluding, or changing terms. When modeling occupancy, I included a first-order autoregressive term for occupancy state in the prior time step to account for Markovian dependencies inherent in occupancy data. Because local colonization and extinction may depend on abundance of potential colonists in neighborhoods around territories (e.g., Yackulic *et al.*, 2012), I considered regional occupancy (e.g., proportion territories occupied) in the current and prior year as covariates when modeling colonization and extinction. I also fit interactions between regional occupancy and habitat quality and landcover change because effects could depend on having sufficient numbers of potential colonists in neighborhoods surrounding territories.

To provide insight into spatiotemporal trends in landcover, climate, and owl occupancy across the study period, which are important for management and understanding results, I assessed trends at regional and national scales. To assess trends in occupancy, I fit GLMMs representing three population structures: (1) interconnected population with one trend

across the study area, (2) national variation in trends, and (3) varying trends among watershed regions. All models were fit with the lme4 library with predictions and 95% confidence intervals computed with the ggeffects library in R (Bates *et al.*, 2014; Lüdtke, 2018; R Core Team, 2021). To evaluate models, I assessed classification accuracy, overdispersion, and plotted scaled residuals against fitted values. Classification accuracy for all final models was high (0.84–0.92) assuming predictions ≥ 0.5 represented focal events with no evidence of overdispersion.

Results

Effort and observations

Over 16 years, I compiled 1,635 observations of territory occupancy in years following initial discovery of each territory. Most territories (74.2%) and observations (82.4%) were in Mexico. In Mexico, effort increased across the first 4 years as more territories were documented, then reached ≈ 100 territories sampled per year. Time between successive observations of the same territory averaged 1.15 ± 0.01 years with 88.7% sampled at 1-year intervals. In the U.S., effort was more sporadic with 4–37 samples per year, time between estimates averaging 1.85 ± 0.13 years with 81.9% sampled at 1-year intervals. Environmental attributes spanned broad gradients in most factors but there were relatively few territories (13.9%) with moderate ($\geq 20\%$) and high (6.6%, $\geq 40\%$) levels of landcover change.

Occupancy drivers

Support for the landcover change, prey-enhancement, T_{\min} -effects, and habitat quality hypotheses was strong (Table 1 and S1), but there was little evidence for the temperature-stress hypothesis ($\Delta AIC_c \geq 1.09$ for T_{\max} added to top-ranked and full additive models). As predicted, probability of occupancy increased markedly with increasing annual precipitation (P_{year}) and habitat quality and declined with increasing landcover change (Table 1). Importantly, however, evidence for a model that included interactions between landcover change and T_{\min} , and between P_{year} and habitat quality was much greater than for models without interactions (Table 1). Occupancy of territories imbedded in landscapes with high levels of landcover change declined at a much greater rate with warming cool-season T_{\min} than those with moderate landcover change, but T_{\min} had little effect in undisturbed landscapes (Fig. 2f). Moreover, occupancy varied very little with warming T_{\min} (Fig. 2c) unless considered at different levels of landcover change. Occupancy of high-quality territories increased with increasing P_{year} at a much greater rate than in territories of moderate quality, but P_{year} had little effect on occupancy of low-quality territories (Fig. 2e).

Colonization-extinction drivers

For colonization, support was strong for the landcover change and prey-enhancement hypotheses, but there was

little evidence for the habitat quality, T_{\min} -effects, or temperature-stress hypotheses ($\Delta AIC_c \geq 1.53$, Table 1). In contrast to patterns for occupancy, there was no evidence for interactions between factors linked to different hypotheses (Table 1), or with regional occupancy ($\Delta AIC_c \geq 1.73$). Colonization probabilities increased with increasing recent cool-season P and regional occupancy in the current time period (Fig. 3a,b), were highest at low levels of landcover change but declined markedly from moderate to high levels of landcover change (Fig. 3d).

For extinction, support was strong for the landcover change, prey-enhancement, T_{\min} -effects, and habitat quality hypotheses (Table 1), but there was no evidence of temperature stress ($\Delta AIC_c = 9.32$ for substituting T_{\max} for T_{\min} in top-ranked model). Despite little evidence for interactions between factors linked to different hypotheses (Table 1), influence of landcover change and habitat quality depended markedly on regional occupancy ($\Delta AIC_c = 6.89$ for removing interactions from top-ranked model). Extinction probabilities were lowest in high-quality habitat when regional occupancy was high, high in moderate- and high-quality habitat when regional occupancy was low, but varied little with changes in regional occupancy in low-quality habitat (Fig. 4f). Extinction probabilities were low in territories imbedded in undisturbed landscapes when regional occupancy was high, high in undisturbed landscapes when regional occupancy was low, and varied little with changes in regional occupancy in highly disturbed landscapes (Fig. 4g). When evaluated independent of variation in regional occupancy, extinction probability varied little with changes in habitat quality or landcover (Fig. 4c,d).

Regional trends

Evidence for regional variation in occupancy trends was overwhelming compared to that for national variation or for a single trend across the broader population (Appendix S3). Occupancy dynamics were similar across the first decade of study, but then decreased more in the U.S. than in Mexico. Occupancy declined in two regions, increased in two other regions, but fluctuated elsewhere. Populations declined to extinction in two of three regions in the U.S. Regional dynamics seemed linked to local changes in climate and landcover with increasing trends in T_{\min} and landcover change in 83% and 67% of regions, respectively (Appendix S3).

Discussion

I evaluated the additive and interactive effects of temperature, precipitation, landcover change, and local habitat quality on spatiotemporal variation in territory occupancy and colonization-extinction dynamics of an aridland top-predator over 16 years. Although significant bivariate associations between occupancy and each of these factors were observed, evidence for interactions was much greater than for additive relationships, suggesting a range of complex processes simultaneously drove dynamics. Such patterns match similar

Table 1 Rankings and descriptions of models that explained spatiotemporal variation in territory occupancy, colonization, and extinction of ferruginous pygmy-owls across 14 watershed regions in northern Mexico and adjacent Arizona, U.S.A., 2001–2016. Models are generalized linear mixed models with each parameter fit as a response variable. Estimates of landcover change, weather (precipitation- P and temperature- T), and habitat quality were fit as fixed effects to represent five hypotheses (see text), three of which were linked to weather. P_{year} is the log annual precipitation in mm from prior May-current June, $P_{\text{cool season}}$ is the recent cool-season precipitation in mm from October to May, and T_{min} is the mean minimum temperature in °C during the most recent from November to March period. Territory and landscape identities are random intercepts in occupancy models, as is region in colonization and extinction models, and are included as model parameters (K). Occupancy models include a fixed effect for occupancy status in the prior time period, and colonization and extinction models include a fixed effect for regional occupancy in current time period. AIC_c is Akaike's information criterion adjusted for sample size, and w_i are AIC_c weights to compare models. Parameter estimates are in Table S2

Parameter (events, observations)	K	ΔAIC_c	w_i
Occupancy (887, 1635)			
Landcover change $\times T_{\text{min}}$ + Habitat quality \times Prey (P_{year})	10	0.00	0.75
Landcover change $\times T_{\text{min}}$ + Prey (P_{year}) + Habitat quality	9	3.45	0.13
Landcover change + T_{min} + Prey (P_{year}) \times Habitat quality	9	4.30	0.09
Landcover change + T_{min} + Prey (P_{year}) + Habitat quality	8	7.81	0.01
Landcover change \times Habitat quality + T_{min} + Prey (P_{year})	9	8.39	0.01
Landcover change + T_{min} + Prey (P_{year})	7	10.22	0.00
T_{min} + Prey (P_{year}) + Habitat quality	7	10.70	0.00
T_{min} + Prey (P_{year})	6	13.15	0.00
Landcover change + Habitat quality	6	26.63	0.00
Habitat quality	5	29.60	0.00
Landcover change	5	29.72	0.00
Prior occupancy only	4	32.75	0.00
Null {Intercepts only}	3	164.07	0.00
Colonization (175, 1414)			
Landcover change + Prey ($P_{\text{cool season}}$)	6	0.00	0.29
Prey ($P_{\text{cool season}}$)	4	0.16	0.26
Landcover change + Habitat quality + Prey ($P_{\text{cool season}}$)	7	1.72	0.12
Habitat quality + Prey ($P_{\text{cool season}}$)	5	2.00	0.10
Prey ($P_{\text{cool season}}$) + Landcover change \times Habitat quality	8	3.41	0.05
Habitat quality + Landcover change $\times T_{\text{min}}$	8	3.53	0.05
Regional occupancy only	3	4.10	0.04
Landcover change	5	4.29	0.03
Landcover change + T_{min} \times Habitat quality	9	5.36	0.02
Habitat quality	4	5.92	0.01
Landcover change + Habitat quality	6	6.05	0.01
Landcover change $\times T_{\text{min}}$ + Habitat quality \times Prey ($P_{\text{cool season}}$)	10	7.19	0.01
Null {Intercept only}	2	45.96	0.00
Extinction (220, 1414)			
Landcover change* + Habitat quality* + T_{min} + Prey (P_{year})	9	0.00	0.30
Landcover change* + T_{min} + Prey (P_{year}) \times Habitat quality*	10	1.29	0.16
T_{min} + Prey (P_{year}) + Landcover change* \times Habitat quality*	10	1.58	0.14
Habitat quality* + Landcover change* + T_{min} + Prey (P_{year})	10	1.65	0.13
Landcover change* + T_{min} + Prey (P_{year})	7	2.49	0.09
Habitat quality* + T_{min} + Prey (P_{year})	7	2.55	0.08
Landcover change* $\times T_{\text{min}}$ + Habitat quality* \times Prey (P_{year})	11	2.92	0.07
T_{min} + Prey (P_{year})	5	4.28	0.04
Landcover change* + Habitat quality* + T_{min} + Prey (P_{year})	7	8.93	0.00
Landcover change*	5	11.63	0.00
Habitat quality*	5	13.55	0.00
Regional occupancy only	3	15.47	0.00
Null {Intercept only}	2	37.00	0.00

*Includes interaction with regional occupancy.

observations of interactive effects between these and related factors on populations (Previtali *et al.*, 2010; Oliver & Morecroft, 2014; Bennett *et al.*, 2015; Betts *et al.*, 2018), and are

based on long-term data at local territory-specific scales at which the reproductive quality of habitat was known across numerous independent landscapes. Occupancy of territories

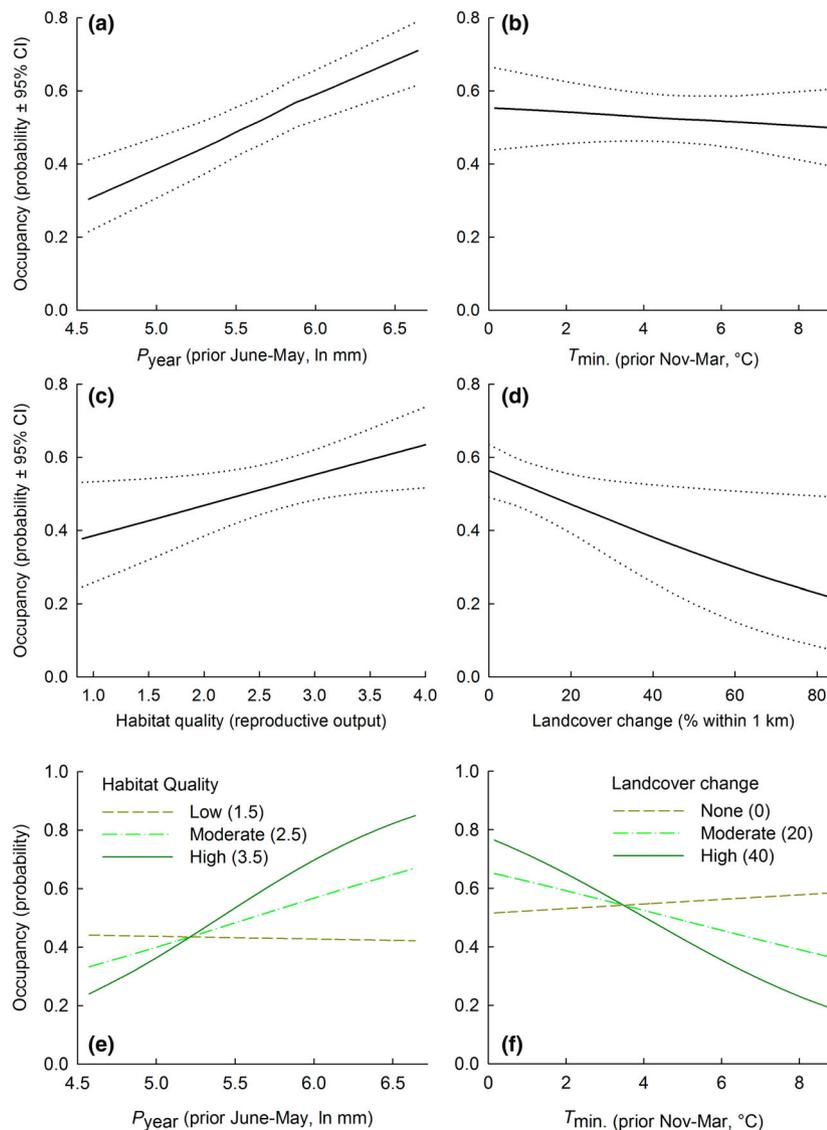


Figure 2 Relationships between precipitation (P ; a) and temperature (T ; b), habitat quality (c), anthropogenic landcover change (d), and interactions between these factors (e, f) on occupancy of individual territory patches by ferruginous pygmy-owls in northern Mexico and adjacent Arizona, U.S.A., 2001–2016. Estimates are predictions from a full additive ($\Delta\text{AIC}_c = 7.81$; a-d) and a top-ranked generalized linear mixed model that included interactions ($\Delta\text{AIC}_c = 0.00$; e, f). Occupancy (occupied or unoccupied) is the response variable, territory, and landscape identities are random intercepts, and factors noted above and occupancy status in the prior time period are fixed effects. Temperature is the mean minimum daily air temperature from November to 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_{year}).

imbedded in landscapes with higher levels of landcover change declined at greater rates with warming mean minimum air temperatures (T_{min}), but warming T_{min} had no effect on occupancy of territories with little to no adjacent landcover change (Fig. 2f), or across the broader population when assessed independent of landcover change (Fig. 2b). Hence, intact landscapes seemed to buffer the impacts of climate warming on populations (e.g., Gaüzère, Jiguet, & Devictor, 2016; Betts *et al.*, 2018) and recent warming was not the dominant stressor in this system. In contrast, although occupancy increased markedly with annual

precipitation on average (Fig. 2a), precipitation had increasingly positive effects in territories of higher quality (Fig. 2e), which was estimated directly based on observed reproductive output (Flesch *et al.*, 2015). Such results illustrate important interactions among stressors and the ability of high-quality habitat to amplify the benefits of favorable weather on populations, which have received little attention in arid systems (Previtali *et al.*, 2010; Bennett *et al.*, 2015).

In contrast to patterns for occupancy, there was no evidence for interactive effects of weather and landcover change on colonization or extinction, although lower

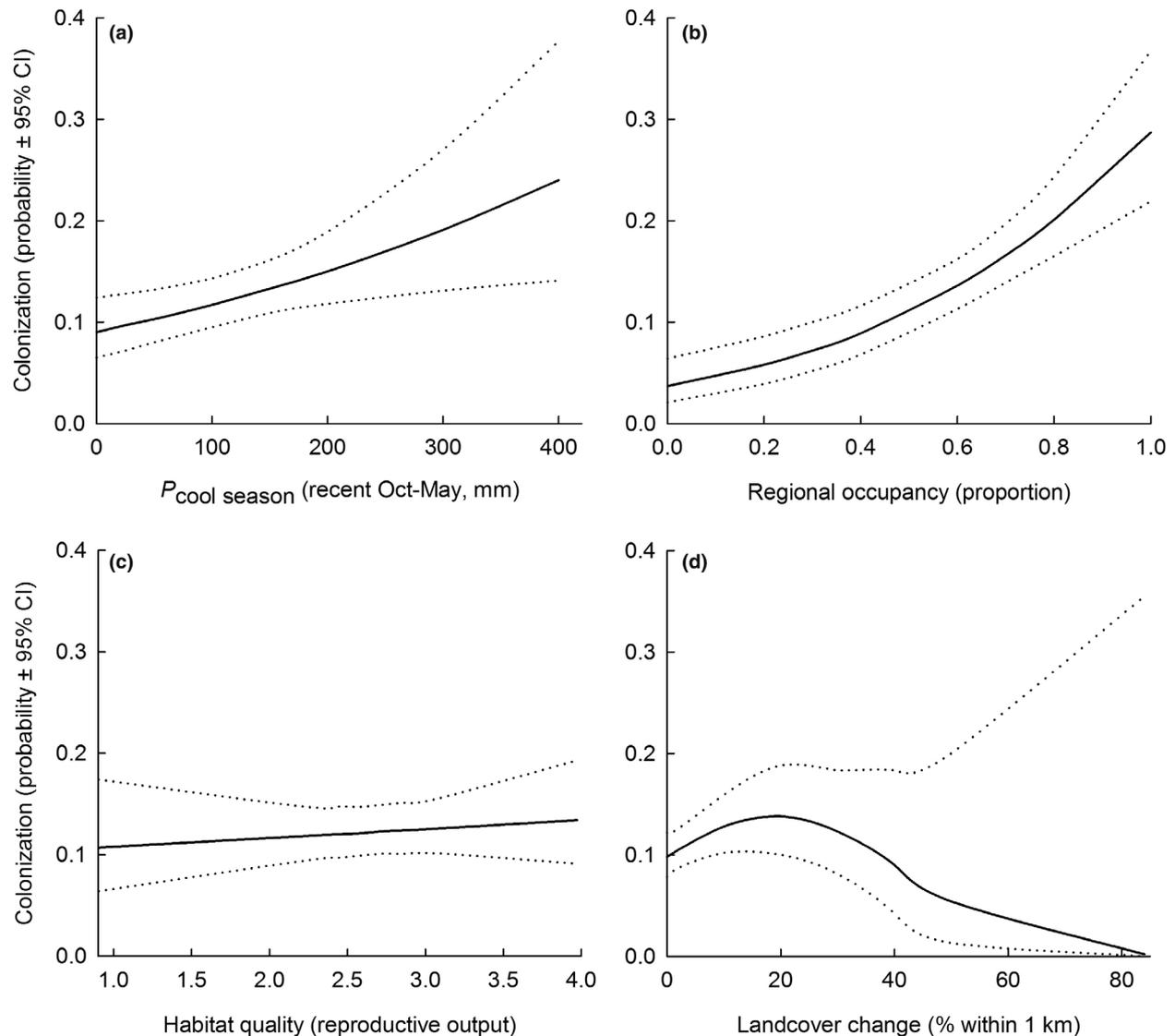


Figure 3 Relationships between precipitation (a), regional occupancy (b), habitat quality (c), and anthropogenic landcover change (d) on colonization probability of individual territory patches by ferruginous pygmy-owls in northern Mexico and adjacent Arizona, U.S.A., 2001–2016. Estimates are predictions from a full additive model ($\Delta AIC_c = 1.72$). Colonization events (transitions from unoccupied in year $t - 1$ to occupied in current year) was the response variable, region identity was a random intercept, factors noted above are fixed effects, and regional occupancy (proportion of territories occupied in surrounding region) is a fixed covariate. P is cool-season rainfall Oct of the prior year through May of the current year ($P_{cool\ season}$). A total of 175 colonization events were observed across 1,414 territory years.

frequency of these events limited evaluations somewhat. Impacts of landcover change and habitat quality on extinction, however, were strongly mediated by variation in regional population sizes around focal territories. When populations were small and few potential colonists present, high-quality habitat failed to buffer extinction risks, but not at moderate to high population sizes when extinction was lowest in high-quality habitat (Fig. 4f). Extinction also declined with increasing regional population size but only in landscapes with little to no landcover change (Fig. 4g) that best foster dispersal movements and colonization success in this and other systems (Flesch *et al.*, 2010; Driscoll

et al., 2013; Flesch, 2017). Importantly, impacts of landcover change and habitat quality on extinction were not apparent unless evaluated at different levels of regional population size (Fig. 4d,e). When populations were small, high habitat quality and low landcover change did not reduce extinction likely because potential colonists were too few to realize such effects and given overarching impacts of drought on carrying capacity. Hence, the effects of important stressors and resource levels were masked by population processes at broader scales, which are rarely considered in threat assessments despite their importance to dynamics of spatially structured (Hanski, 1999; Yackulic *et al.*, 2012)

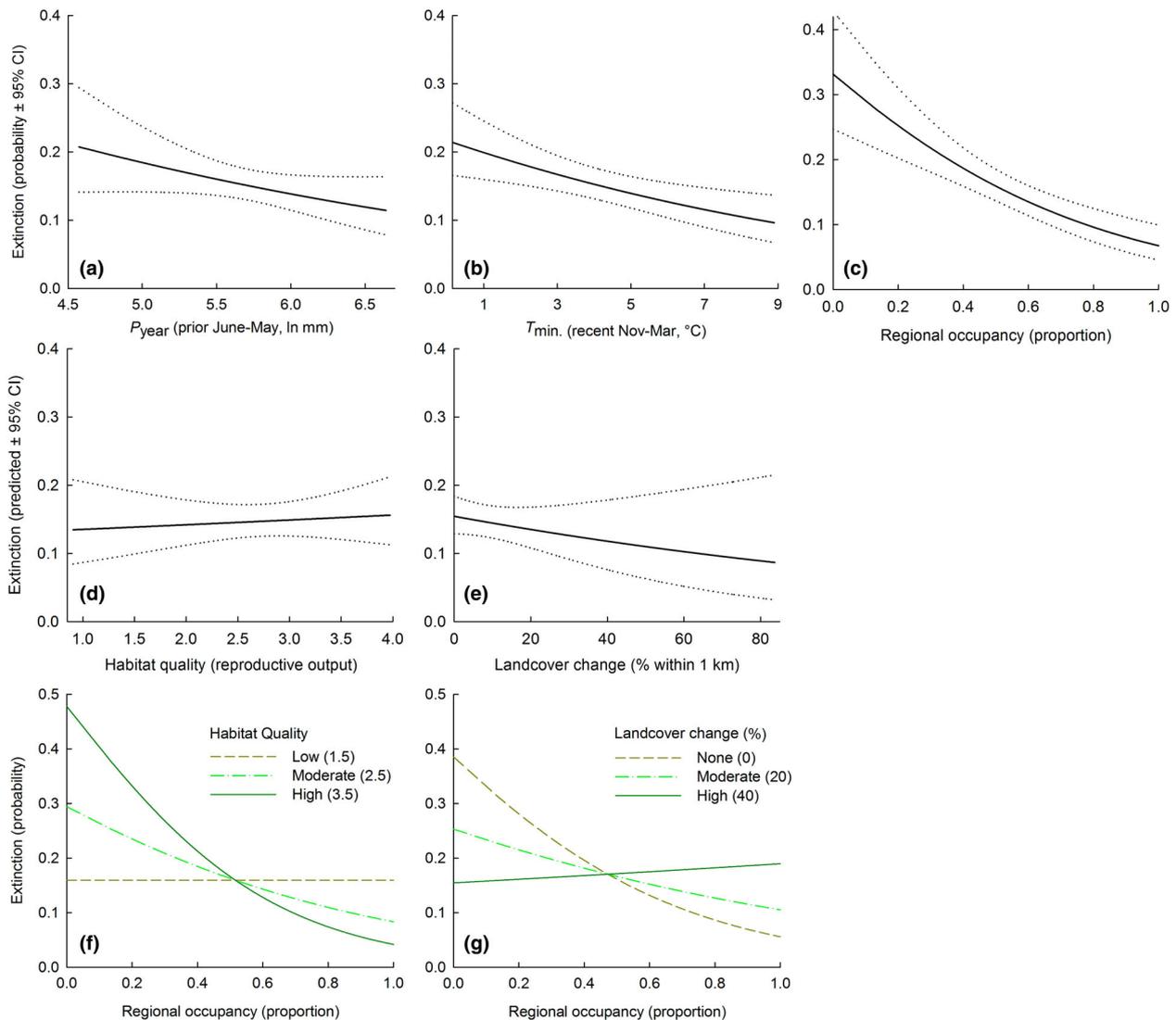


Figure 4 Relationships between precipitation (P ; a), temperature (T ; b), regional occupancy (c), habitat quality (d), anthropogenic landcover change (e), and interactions between some of these factors (F, g), on extinction probability of individual territory patches by ferruginous pygmy-owls in northern Mexico and adjacent Arizona, U.S.A., 2001–2016. Estimates are predictions from a top-ranked model that included interactions between two terms and regional occupancy (a, b, f, g) and a full additive model with no interactions with regional occupancy ($\Delta AIC_1 = 6.89$; c-e). Extinction events (transitions from occupied in year $t - 1$ to unoccupied in current year) was the response variable, region identity was a random intercept, factors noted above are fixed effects, and regional occupancy (proportion of territories occupied in surrounding region) is a fixed covariate. Temperature is mean minimum daily air temperature Nov.-March of prior year (T_{min}) and P is annual rainfall from June of the prior year to May of current year (P_{year}). A total of 220 extinction events were observed across 1,414 territory years.

and density-dependent (Coulson *et al.*, 1997; Bonenfant *et al.*, 2009) populations.

Environmental drivers

In arid regions of southwestern North America, recent evidence of climate change is pervasive, expected to intensify, and drought and extreme temperatures are linked to declines of numerous taxa (Lovich *et al.*, 2014; Cook, Ault, & Smerdon, 2015; Cruz-McDonnell & Wolf, 2016; Williams

et al., 2020). In aridlands, the positive bottom-up effects of precipitation on vertebrate populations have been observed nearly worldwide (Lima *et al.*, 2002; Holmgren *et al.*, 2006). In these systems, precipitation drives rapid increases in plant productivity, insects, and other resources that directly bolster food availability for small consumers, augmenting their reproductive output and abundances at fairly short lag times (Jaksic, 2001; Lima *et al.*, 2002, 2008) and predator populations at somewhat longer lag times (Dennis & Otten, 2000; Letnic, Tamayo, & Dickman, 2005). Such resource pulses

drive major increases in carrying capacity that is the foundation of the prey-enhancement hypotheses, which was supported by strong associations between precipitation and all three population attributes I considered. But why were the positive effects of precipitation magnified by territories of greater habitat quality? In this system, territories with higher woody vegetation cover magnify the benefits of precipitation on reproduction likely by amplifying prey abundance so that when conditions are favorable occupants attain multiplicative benefits (Flesch *et al.*, 2015). When predictable, such patterns should reinforce the selection of high-quality territories and produce the interactive effects observed here and elsewhere (Van Horne *et al.*, 1997). In contrast, the inability of high-quality habitat to buffer impacts of low precipitation likely reflect short-term reductions in carrying capacity linked to drought that have more similar negative impacts across space.

Anthropogenic landcover change can affect the quantity, quality, and connectivity of habitats in ways that reduce abundance and colonization and promote extinction (Fischer & Lindenmayer, 2007; Lindenmayer & Fischer, 2013). Lower occupancy of territories in landscapes with greater landcover change, and lower colonization at moderate and especially high levels of landcover change are thus consistent with well-known impacts of landscape disturbance on wildlife that embody the landcover change hypotheses. In this system, such patterns are likely driven directly by habitat loss and degradation, and by negative impacts of vegetation clearings and roadways on movement, colonization success during dispersal, and hence habitat connectivity (Flesch *et al.*, 2010). Although the landcover change hypotheses evaluated here did not attempt to disentangle the effects of habitat degradation, habitat quantity, and habitat connectivity, recent work combined with stronger associations with landcover change at landscape versus local scales observed here, indicate the importance of habitat connectivity for pygmy-owl populations (Flesch, 2017). Interestingly, associations between extinction and landcover change were mediated by regional population sizes, which are closely tied to abundance of potential colonists in neighborhoods around territories. Whereas such patterns are uncommon in the literature, they are not surprising given the impacts of reduced landscape connectivity may not be realized unless sufficient source populations of colonists are present. When regional population sizes were small, higher extinction rates were likely also linked to short-term reductions in carrying capacity due to drought. Regardless, such neighborhood effects are important for threat assessments but rarely considered due likely to challenges in sampling large areas.

Warming temperatures linked to climate change can have pervasive impacts on populations, especially in aridlands, but most studies focus on rising mean maximum air temperatures (T_{max}) and not T_{min} (Stenseth *et al.*, 2002; Holmgren *et al.*, 2006; McKechnie & Wolf, 2010). Although drought and high T_{max} synergistically depress reproductive output in this system (Flesch *et al.*, 2015), there was little evidence T_{max} influenced populations but marked negative associations with T_{min} in areas with moderate to high levels of landcover

change. Observed interactions between T_{min} and landcover change could be driven by numerous potential mechanisms linked to prey abundance, prey diversity, habitat-mediated predation risk, microclimates, and other processes. In the Sonoran Desert, diurnal lizards are the main prey of owls during the warm season, but owls are generalists that consume other small vertebrates and large arthropods. As ectotherms, metabolic activity of lizards rises exponentially with temperature, which if high during periods of cool-season dormancy can consume energy important for growth and reproduction (Adolph & Porter, 1993). If dormant lizards experience unusually warm conditions that degrade low-temperature thermal refugia and trigger metabolic activity, more foraging and risk would be required to replace lost energy, maintain body condition, and reproduce (Zani, 2008; Clarke & Zani, 2012). Strong negative associations between abundances of five lizard species that are owl prey and increasing winter T_{min} over 25 years in the Sonoran Desert suggest cool-season warming reduces prey abundance (Flesch, Rosen, & Holm, 2017). Such processes could impact owls more in disturbed landscapes where prey communities may be less diverse than in intact landscapes where higher prey diversity compensates for lower lizard abundance. Moreover, warming T_{min} could degrade vegetation cover and augment predation risk, and have greater impacts in disturbed landscapes where native and non-native mesopredators are often more abundant (Crooks & Soulé, 1999). Finally, in disturbed landscapes, temperature effects could be magnified by urban heat-island effects (Arnfield, 2003) whereas intact landscapes offer microclimates that buffer temperature impacts (Frey *et al.*, 2016), patterns that may not be detectable with coarse-grained weather-station data. Although identifying the roles of these and other potential mechanisms will require additional study and more observations in disturbed landscapes, patterns observed here suggest anthropogenic landcover change can magnify impacts of climate warming, which has important implications for the design of urban areas and conservation (Opdam & Wascher, 2004; Brook *et al.*, 2008; Mantyka-Pringle *et al.*, 2012). This is especially true in aridlands like the Sonoran Desert where rising winter T_{min} is among the most pervasive trends linked to climate change (Weiss & Overpeck, 2005).

Implications

Understanding the degree to which variation in habitats and landcover can mediate climate impacts and promote resilience is important for guiding conservation and management. I found that increasing landcover change magnified the impacts of climate warming on populations, whereas intact landscapes buffered these impacts. Although mechanisms that cause these patterns remain unclear, my results suggest protecting natural intact landscapes can limit impacts of climate warming on wildlife populations (e.g., Güzère *et al.*, 2016; Lehikoinen *et al.*, 2019). In the case of interacting stressors, focusing management on local threats such as landcover change offer better potential strategies for addressing climate

change and promoting ecological resilience due to complexities of addressing global stressors (Brown *et al.*, 2013).

Compared to more localized and context-dependent impacts of temperature, precipitation had widespread positive effects on populations that were magnified in territories of higher reproductive quality. Hence, identifying areas and protecting resources that promote habitat quality, and enhancing poor or degraded habitats are important conservation strategies that should have multiplicative benefits when weather conditions are favorable. In theory, augmenting habitat quality can mitigate climate-change impacts on populations more than bolstering habitat amount (Jeltsch *et al.*, 2011), which is supported empirically in this system given local territory quality has greater effects on distributional dynamics than landscape habitat amount (Flesch, 2017). For pygmy-owls, high-quality territories tend to support larger and less fragmented woodlands and have high abundance of potential nest cavities (Flesch *et al.*, 2015) that are important targets for conservation and augmentation. Moreover, protecting intact bottomland forests, restoring desert riparian areas by promoting the establishment and growth of mesquite and other riparian trees, and supplementing natural cavities with nest boxes and salvaged saguaros will promote conservation in a changing climate. Ongoing drought, however, is predicted to increase in southwestern North America (Cook *et al.*, 2015; Pascale *et al.*, 2017; Williams *et al.*, 2020), and could drive prolonged ecological crunches that augment extinction risk, especially in disturbed landscapes (Flesch, 2014; Maron *et al.*, 2015). To help guide management, future efforts should identify specific resources that mitigate impacts of drought and extreme temperatures on populations.

Data on the combined and potential synergistic impacts of climate and landcover change are essential for threat assessments and avoiding ecological surprises, but knowledge of processes that buffer or mediate these threats are needed to guide management responses. My results suggest local efforts to protect high-quality habitat and limit landcover change will be most efficient in intact landscapes. Efforts to increase local habitat quality and habitat amount, or directly augment populations, however, should consider connectivity and potential source populations at broader landscape scales.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Detailed descriptions of methods used to measure environmental variables and definitions of variables considered.

Appendix S2. Correlations among factors linked to the predicted influence of weather, landcover change, and habitat quality on spatiotemporal variation in territory occupancy of ferruginous pygmy-owls.

Appendix S3. Occupancy dynamics and regional variation in occupancy trends and environmental attributes.