Influence of local and landscape factors on distributional dynamics: a species-centered, fitness-based approach

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In spatially-structured populations, distributional dynamics are driven by the quantity, connectivity, and quality of habitat. Because these drivers are rarely measured directly and simultaneously at relevant scales, information on their relative importance remains unclear. I assessed the influence of both direct and indirect measures of local habitat quality, and of landscape habitat amount and connectivity on long-term territory occupancy dynamics of non-migratory pygmy-owls. Direct measures of local habitat quality based on territory-specific reproductive output had greater effects on distribution than landscape factors, but only when spatiotemporal fluxes in performance linked to environmental stochasticity and intraspecific competition were considered. When habitat quality was measured indirectly based on habitat structure, however, landscape factors had greater effects. Although all landscape factors were important, measures of landscape connectivity that were uncorrelated with habitat amount and based on attributes of matrix structure and habitat configuration that influence dispersal movements had greater effects than habitat effective area (amount weighted by quality). Moreover, the influence of connectivity but not habitat effective area depended on local habitat quality. Such results suggest the relative importance of local habitat quality in driving distribution has been underestimated and that conservation strategies should vary spatially depending on both local and landscape contexts.

1. Introduction

Understanding processes that drive the distribution and persistence of animal populations is a core aspect of ecology with major implications for conservation. In spatially-structured populations that occupy habitat networks distinct from an intervening matrix of non-habitat, distributional dynamics are driven by the quantity, connectivity, and quality of habitat [1-3].

Consequently, habitat loss, habitat fragmentation, and habitat degradation are among the foremost threats to populations and biodiversity worldwide [4]. Addressing these threats requires understanding the relative and combined effects of those drivers across contexts and scales, so that conservation strategies can be focused on the most threatening processes [5].

Studies of spatially-structured populations have produced a vast body of work on how habitat amount and connectivity influence distributional dynamics often at large spatial scales [2,6,7]. Collectively, these studies show that the effects of habitat amount often exceed those of connectivity, that habitat connectivity depends on how matrix structure and landscape habitat configuration affect movement and colonization, and that habitat fragmentation *per se* (e.g., breaking apart of habitat independent of amount) can have positive or negative effects depending on the context [3,8,9]. Despite these general patterns, understanding the independent and relative influence of habitat amount and connectivity has been challenging for several reasons. First, because habitat often becomes less fragmented as habitat amounts increase, and because immigration rates are higher in landscapes with more habitat and thus more potential colonists, inferences on the effects of each factor are often confounded [8-12]. Second, because movement behaviors are species specific and difficult to observe, functional landscape connectivity can be challenging to measure precisely especially when matrix structure is ignored [3,13,14]. Finally, because habitat is typically comprised of numerous resources and conditions that depend on the focal species, habitat can be difficult to delineate from non-habitat based on human-defined landcover types and the habitat-patch concept that dominates many approaches [12,15].

The influence of habitat quality on distributional dynamics has received increasing attention recently but often only at local scales [16,17]. Although initially assumed to be homogenous, increasing numbers of studies within the framework of the metapopulation paradigm show that

aspects of habitat heterogeneity can have important and sometimes greater influence on distribution than habitat amount or connectivity [18-20]. Most studies however, consider elements of habitat structure that are presumably linked to habitat quality given the biology of a system, or rarely, density of a focal species rather than direct measures of quality based on vital rates [20, but see 21]. Because habitat quality represents habitat-specific population growth rates that depend on the reproduction and survival of individuals in a specific habitat, and because density can be a misleading indicator of habitat quality [22-24], our understanding of the relative importance of various distributional drivers and the implications for management remains unclear [25]. Moreover, habitat quality at a given point in space can fluctuate across time due to environmental stochasticity and variation in conspecific densities [26,27], but such spatiotemporal fluxes in quality are rarely considered despite evidence they influence distribution [28,29]. Regardless, by influencing the attractiveness of space to individuals and their demographic contribution to populations, habitat quality should affect distribution at a range of scales [18,30]. Further, if animals can target high-quality habitat during dispersal where they persist longer, the effects of landscape habitat connectivity may depend on local habitat quality [31]. Thus, despite a strong theoretical basis, our understanding of the influence of habitat quality *per se* on the dynamics of spatially-structured populations remains incomplete.

Integrating aspects of habitat selection theory and more species-centered approaches into studies of spatially-structured populations can enhance our understanding of distributional dynamics [15,25,32]. This is because when the quantity, configuration, and quality of habitat are defined explicitly from the perspective of a focal species, and attributes of landscape structure known to affect movements index connectivity, the influence of various distributional drivers should be more detectable and precise [25,33]. In explaining how environmental variation at

small spatial scales affects settlement choices by individuals, habitat selection theory predicts that habitat quality drives distribution because such choices have major fitness consequences [34]. Hence, animals are thought to select territory patches (habitat patches large enough to support a breeding pair) in an ideal manner so that distribution precisely reflects habitat quality [35]. Field studies generally conform to that ideal expectation because when the proportion of years a territory is occupied is plotted against estimates of its quality, there is virtually always a positive relationship [36,37]. Nonetheless, there are also distributional mismatches characterized by territories with lower or higher use than expected based on their quality. Although explanations of these mismatches include local, and rarely, landscape processes [37], our understanding of their relative roles is limited. At small scales, perceptual errors in assessing quality can decouple settlement choices from their fitness consequences and create non-ideal distribution patterns if: (1) cues used by animals to assess habitat quality are unavailable, (2) future conditions associated with cues are not realized due to environmental stochasticity, or (3) evolutionarily novel cues promote poor choices [38,39]. As scale increases from groups of nearby territory patches to complex landscapes, however, constraints on detecting high-quality patches, fitness tradeoffs associated with colonizing them, or regional abundances of potential colonists may cause some patches to be occupied more or less than expected based on their qualities [40,41].

Here, I evaluate hypotheses derived from first principles of spatially-structured population biology and habitat selection theory to explain long-term territory occupancy dynamics of non-migratory, ferruginous pygmy-owls (*Glaucidium brasilianum*). First, I assessed the degree to which occupancy dynamics matched ideal expectations from habitat selection theory, and how spatiotemporal fluxes in quality driven by environmental stochasticity and variation in local

conspecific densities influenced that relationship. Next, I assessed the influence of landscape habitat amount, habitat effective area (amount weighted by quality), matrix structure, and habitat configuration, and whether associations depended on local factors. Finally, I compared relative effect magnitudes of local and landscape factors, and of direct and indirect estimates of local habitat quality. To address those questions, I delineated habitat based on observed patterns of space use by owls, and considered direct measures of habitat quality based on territory-specific reproductive output monitored over 10 years. Moreover, I quantified matrix structure and habitat configuration based on landscape attributes known to influence movement behavior, and assessed the independent effects of habitat amount and connectivity by considering metrics that were uncorrelated.

(a) Hypotheses

If animals distribute themselves ideally in space, then variation in occupancy should precisely reflect habitat quality. Thus, the *habitat-quality hypothesis* states that spatial variation in important resources that drive individual performance explains distribution and predicts positive associations between occupancy probability and habitat quality. When this expectation is not met, three general explanations of distributional mismatches exist: (1) animals make errors assessing habitat quality, (2) researchers estimate habitat quality inaccurately, or (3) landscape factors influence distribution. If animals make errors assessing quality, cues that promote settlement may not be well matched with their fitness consequences for at least two reasons. First, the *environmental-stochasticity hypothesis* states unpredictable events such as harsh weather, which can temporarily reduce performance even in otherwise good habitat, explain distribution, and predicts estimates of habitat quality adjusted for the effects of weather and

temporal variation in primary productivity better explain distribution. Second, the *ecological-trap hypothesis* states evolutionarily novel cues created by humans [39] explains distribution, and predicts prevalence of traps increases with anthropogenic disturbance within territories. If researchers estimate quality inaccurately, one possibility is the *density-dependence hypothesis*, which states the negative influence of intraspecific competition must be considered, and predicts estimates of habitat quality adjusted for the effects of local conspecific densities better explain distribution. If landscape factors drive distribution, several additional non-mutually exclusive explanations are possible. If populations occupying adjacent landscape habitat influence local colonization and extinction probabilities, or if individuals preferentially settle near conspecifics, the *habitat-amount hypothesis* states the area or effective area [*sensu* 42] of landscape habitat explain distribution, and predicts positive associations between occupancy probability and landscape habitat amount. If movement and colonization are influenced by landscape structure, the *matrix-structure hypothesis* states matrix attributes that influence movement explain distribution, whereas the *habitat-configuration hypothesis* states that habitat fragmentation explains distribution, with predictions varying depending on the functional forms of these relationships. Finally, if habitat configuration is important only below some threshold in habitat amount (*nonlinear-configuration hypothesis*, [43]), interactions between those factors explain distribution. More broadly, if patch choices by individuals or local extinction probabilities depend on landscape context, interactions between local and landscape factors explain distribution.

2. Material and methods

(a) Study system

Ferruginous pygmy-owls are residents across the lowland Neotropics. In the Sonoran Desert, territories include riparian woodlands, one or more saguaro cacti (*Carnegiea gigantea*) that provide nest cavities, and uplands of desert-scrub or semi-desert grassland. Thus, as in many systems, habitat consists of multiple vegetation types, is difficult to delineate into discrete patches based on human-defined landcover types, and is best defined by how individuals utilize and partition space across time. Important properties of this system include: (1) nearly perfect detection probability when estimating occupancy with standardized survey methods [44], (2) variable but relatively low amounts of landscape habitat that make connectivity relevant to distribution [43], and (3) high levels of natural and anthropogenic habitat fragmentation. Moreover, because landscape structures such as large vegetation gaps affect dispersal movements and colonization success [45], they should also influence distribution.

(b) Design

I considered a sample of territory patches of varying quality that were imbedded in numerous landscapes of varying structure across a large region of northwest Mexico (Fig. S1). To delineate territories, I surveyed transects near random and non-random points in years 2000 and 2001, and searched for nests along occupied transects until I located nests of most individuals [44]. From 2002-2011 and in 2013, I surveyed areas around nests (or occupied areas if nests were not located initially) from prior years, and through 2010 searched for nests exhaustively at occupied sites. To delineate territory patches, 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 are similar in area to breeding territories [27]. This approach allowed easy identification of habitat across a broad gradient of qualities because distributions of potential nests were clumped, owls used the same general areas over time, and abundance peaked during early years [46] when presumably most habitat was occupied. I defined landscapes by placing 5-km radius plots around patches, which is an appropriate landscape scale given observed dispersal distances (median=5.0 km; range=1.1-19.2) and density-dependent habitat selection and gap avoidance during dispersal [45,47].

(c) Local factors

I measured habitat quality by monitoring annual reproductive output (R; no. of young survived to within 1 week of fledging) in each occupied territory over 10 years. Although R is only one component of territory-specific population growth rate (λ_h), it provides a useful index of habitat quality because R was highly correlated with adult and juvenile survival in a subset of territories I monitored intensively, and because in similar systems adult survival is high and nearly constant except at low λ_h, which is highly correlated with R [26,27]. Thus, I measured habitat quality by modeling the effects of habitat resources, stochastic factors (weather and primary productivity), and local conspecific densities on R, which I quantified in and around each territory over time in a separate study (Appendix S1). This approach yielded precise predictions of R that could be achieved by individuals in each territory based on the observed effects of those factors, and inferences to territories that were rarely occupied and to the quality of landscape habitat. In this system, R increases with nest-site abundance and woodland aggregation within territories, woody vegetation cover has increasingly positive effects as nest-site abundance increases, R

declines with increasing hot dry conditions and local conspecific densities, and anthropogenic disturbance surrounding territories has no influence [27].

Most studies of the influence of local and landscape factors on distribution measure habitat quality indirectly based on habitat structure, which could underestimate its importance [20]. Thus, I compared the influence of direct measures of habitat quality based on R with indirect measures based on habitat structure. In this system, owls select nest areas with higher abundance of potential nest cavities and greater woody vegetation cover [48], which I measured in each territory and computed an index of quality by summing standardized values.

(d) Landscape factors

To quantify habitat amount, I used data on owl, woodland, and saguaro distribution to estimate the number of actual or potential territory patches within landscapes. To quantify woodland cover, I used 30-m-resolution Landsat imagery and classified pixels with ≥20% woody cover as woodland [27]. These data enabled easy estimation of habitat amount because woodlands were often arranged linearly along drainages and only areas with woodlands and saguaros provide habitat. To quantify habitat effective area, I multiplied habitat amount by the quality of landscape habitat and scaled by maximum quality [42]. To estimate landscape habitat quality, I used the same model-based approach from local scales but based predictions on habitat covariates measured within landscapes. To quantify matrix structure and habitat configuration, I used data obtained while tracking dispersing radio-marked pygmy-owls to ensure landscape attributes I considered were linked to functional connectivity. Dispersing pygmy-owls fly short distances from tree to tree, avoid large vegetation gaps such as major roadways and agricultural fields, and colonization success declines as anthropogenic landscape disturbance increases [45]. Thus, to

quantify matrix structure, I used satellite imagery and computed the area, edge length, and largest patch indices (% landscape of largest patch) of three landcover types representing disturbance (agriculture/other man-made vegetation clearing, housing/urban development, roadway corridor). To quantify habitat configuration, I measured an index of woodland aggregation termed the "clumpiness" index that ranges from -1 (maximal fragmentation) to 1 (maximal aggregation) [49]. I used program Fragstats [49] to estimate landscape metrics. Importantly, landscape metrics were largely uncorrelated, and attributes of matrix structure and landscape habitat configuration were uncorrelated with estimates of local habitat quality (Fig. S2).

(e) Statistical analyses

I developed statistical models to represent hypotheses and used Bayesian information criterion (BIC) to evaluate support among models. To represent distributional dynamics, I used a binomial response equaled to the number of years a territory was occupied divided by the number of years it was surveyed. To represent the *habitat-quality hypothesis*, I used predictions of R that considered the estimated effects of important resources as an explanatory factor. To represent the *stochasticity* and *density-dependence hypotheses*, I used predictions of R that considered the estimated effects of important resources and either stochastic factors or local conspecific densities. Because the influence of resources, stochastic factors, and conspecifics on R interact in complex ways [26,27], I also considered predictions based on the multiplicative effects of those factors. For the *habitat-amount hypotheses*, I considered estimates of habitat amount and habitat effective area, and used the top-ranked model. To assess the *matrix-structure hypothesis*, I fit models with each matrix factor alone, combinations of factors, and used the top-ranked model.

To fit models, I used mixed-effects logistic regression for binomial counts and the *lme4* library in R [50]. To adjust for correlations among nearby territories, I assigned territories to regions based on their proximity and fit region as a random intercept. Variograms confirmed residuals were not spatially autocorrelated. As a modeling strategy, I first considered the effects of local factors, and then evaluated combined effects. In modeling local factors, I first considered the *habitat*, *stochasticity,* and *density-dependence hypotheses* to identify the best overall predictor of occupancy dynamics, then considered the trap hypotheses. To model landscape factors, I considered each hypothesis separately and additive combinations of hypotheses. To evaluate the combined effects of local and landscape factors, I considered the best model of local factors with all possible additive and interactive combinations of factors from supported landscape models. To assess relative effect magnitudes of local and landscape factors, and of direct and indirect measures of local habitat quality, I compared standardized regression coefficients. Because connectivity was represented by multiple factors, I summed their standardized values before comparing standardized coefficients to evaluate the overall importance of connectivity versus habitat quality and amount.

3. Results

I monitored 112 territory patches in 29 regions for an average of 10.2±0.2 (±SE; range = 2-12) years following their year of initial detection. On average, patches were occupied for 6.1±0.3 years (range = 1-12). Habitat amounts ranged from 1-17% of landscapes (mean±SE = 6.9±0.4%), anthropogenic disturbance ranged from 0-29% of landscapes (4.5±0.5%), and local habitat quality ranged from 0.9-4.0 young produced/year (2.7±0.1).

(a) Local effects

Occupancy increased with all measures of local habitat quality in the predicted direction (Fig. 1). Occupancy was best explained, however, by direct measures of quality that considered the interactive effects of important resources, stochastic factors, and local conspecific densities on R (Table S3). In contrast, support for the influence of important habitat resources alone on R was low (ΔBIC = 5.27) and considering spatiotemporal fluxes linked to stochastic factors and intraspecific competition greatly improved correspondence between observed and ideal distribution patterns (Fig. 1). Despite strong positive associations with occupancy ($\beta \pm$SE = 0.18±0.06), there was no support for a model that included indirect measures of habitat quality based on habitat structure. There was also no support for the ecological-trap hypothesis.

(b) Landscape effects

Occupancy varied markedly with all landscape factors (Fig. 1). Evidence for the habitat-amount hypothesis was strongest overall and better represented by habitat effective area than by unadjusted estimates of habitat amount (ΔBIC = 4.71) because occupancy increased with the quality of landscape habitat at greater rates where habitat was common (Fig. 1). Matrix structure and habitat configuration had significant effects on occupancy that did not depend on habitat amount (Table S3). Occupancy decreased as area of agriculture ($\beta \pm$SE = -0.068±0.027) and of the largest roadway corridor (-0.74±0.38) increased within landscape, but decreased as woodlands became increasingly aggregated (-2.8±1.3).

(c) Integrated effects

When considered together, local habitat quality and landscape habitat effective area, matrix structure, and habitat configuration all had significant effects on occupancy dynamics (Table 1). Evidence for cross-scale interactions between local habitat quality and both matrix structure and landscape habitat configuration was high, whereas habitat effective area had positive effects regardless of local habitat quality (Table 1, Fig. 2). As area of landscape agriculture increased, occupancy of low-quality patches declined at a much greater rate than those of moderate quality, whereas occupancy of high-quality patches increased (Fig. 2). As woodlands became increasingly aggregated within landscapes, occupancy of low-quality patches increased, whereas occupancy of high-quality patches decreased.

Relative effect magnitudes of local and landscape factors depended on the processes and measurement procedure considered. When local habitat quality was measured directly based on the influence of resources, stochastic factors, and conspecifics on R, the effect of habitat quality was 1.5-times greater than habitat effective area and >2-times greater than elements of matrix structure or habitat configuration (Table 2). When local habitat quality was measured directly based only on the influence of resources, however, effect sizes declined to 1.2- and ≥1.7-times greater, respectively. In contrast, when quality was measured indirectly based on habitat structure, landscape habitat effective area had greater effects. Among landscape factors, the influence of habitat effective area was 1.4-1.7-times greater than that of indices of matrix structure or landscape habitat configuration. However, when all three factors representing landscape connectivity were considered together, the effect of connectivity was 1.5-times greater

than habitat effective area and only 6% lower than the best measure of local habitat quality (Table 2).

4. Discussion

I integrated core aspects of habitat selection theory and spatially-structured population biology to explain long-term territory occupancy dynamics of ferruginous pygmy-owls across broad gradients in habitat quality and landscape structure. Although all landscape factors influenced local occupancy, habitat effective area had greater effects than matrix structure or habitat configuration, which corresponds generally with past studies [3,8,9]. When landscape connectivity was measured based on all important elements of matrix structure and habitat configuration combined, however, connectivity had greater effects than habitat effective area, likely due to low amounts of landscape habitat and behavioral attributes of pygmy-owls. Regardless, local habitat quality had greater effects than landscape factors, but only when quality was measured directly based on fitness components and spatiotemporal fluxes in quality linked to environmental stochasticity and intraspecific competition were considered. Moreover, there was also evidence the influence of landscape connectivity depended on local habitat quality suggesting important cross-scale interactions. Although the relative influence of landscape factors could vary somewhat with spatial scale and based on more direct measures of actual functional connectivity, my findings indicate important roles of local and landscape processes in driving distribution, and suggest the influence of local processes are mediated by landscape context. Importantly, because measures of habitat configuration were uncorrelated with habitat amount, and because local habitat quality is not influenced by [27] or correlated with (Fig. S2) adjacent matrix structure or landscape habitat configuration, and only weakly correlated with

landscape habitat amount, inferences I report are largely unconfounded. To my knowledge, this is the first study to compare the relative influence of local habitat quality, and of landscape habitat effective area, matrix structure, and habitat configuration on distributional dynamics based on direct measures of the fitness potential of space to individual animals.

Habitat selection theory is based on the expectation that patch choices by individuals are adaptive and driven by the fitness potential of space [34,35]. Hence, habitat patches that confer the highest fitness on occupants are thought to be selected first and used more consistently across time so that distribution precisely reflects patch quality. Although distribution patterns often conform generally to this ideal expectation, mismatches characterized by patches with lower or higher use than expected based on their qualities are common in nature [36], and were clearly evident here. Such mismatches are not merely theoretical curiosities because management efforts that reduce them can augment population growth rates and thus conservation prospects [37]. Whereas natural selection should enhance the ability to accurately assess habitat quality, settlement choices are often triggered by cues associated with future conditions that may not be realized due to environmental stochasticity, especially in seasonal environments [38]. In the Sonoran Desert, pygmy-owls select territories with high woody vegetation cover because it provides habitat for prey and amplifies the benefits of favorable weather on reproduction [27]. Hot dry conditions, however, reduce both prey abundance and activity and can cause poor performance during some years in otherwise good habitat [27], and drive population declines [46]. Thus, considering spatiotemporal fluxes in habitat quality due to weather and the interactive effects of weather and resources better explained distribution. Although evolutionarily novel cues created by humans can promote selection of poor habitat [39], there

was no evidence of this behavior likely because most owls occupied areas with little anthropogenic modification.

Distributional mismatches can also result from inaccurate measurements of habitat quality by researchers. The influence of conspecifics, for example, is rarely considered when estimating habitat quality despite broad recognition that individual performance is density dependent. Moreover, because the negative influence of conspecifics often declines as resource quality increases, and because intraspecific competition can mediate the influence of weather on performance [27,51], considering these relationships best explained variation in space use across time. Because habitat quality represents individual contributions to population growth from a specific habitat [23,26], considering both reproduction and survival should provide even higher conformance with ideal expectations than observed here.

Studies of spatially-structured populations indicate important effects of habitat amount and sometimes connectivity on distributional dynamics at scales often larger than individual territory patches [2,8,9]. Hence, when processes that drive distribution are integrated across scales and viewed from a behavioral perspective, landscape attributes should influence distribution at local scales and help explain patterns of non-ideal habitat selection that are suggested by distributional mismatches. This is especially true for populations occupying complex landscapes where habitat varies widely in quality, quantity, and configuration, and is surrounded by matrices of varying permeability to organisms [2,13]. In such cases, perceptual barriers, dispersal limitation, fitness trade-offs associated with movement, and abundances of potential colonists at larger scales, can influence distribution independent of local processes [40,41]. Accordingly, all landscape attributes I considered had important effects on occupancy, even after controlling for local factors. Habitat amount, however, had greater effects than elements of matrix structure or habitat

configuration, and was best represented by habitat effective area likely because it scales habitat quantity by overall landscape quality thus better representing abundances of potential colonists [52]. Because habitat effective area is closely linked to carrying capacity, and because production of new individuals occurs only within habitat, habitat amount often has greater effects on distribution than connectivity [3,11]. Nonetheless, when important attributes of matrix structure (roadway size, agricultural area) and habitat configuration (woodland aggregation) were considered together to index overall connectivity, that index had greater relative effects than habitat effective area. Although connectivity is typically measured with greater uncertainty than habitat amount [3,53], connectivity should be generally important in systems where landscape habitat is limited in area, highly fragmented, and landscape structure influences dispersal movements [8,43,54,55]. In this system, habitat comprises relatively small proportions of landscapes (≤17%) and is fragmented naturally by moisture and topographic gradients and anthropogenically by disturbance in important wooded bottomlands. Additionally, as for other species of non-migratory woodland birds, dispersing pygmy-owls rarely leave areas of dense cover, fly short distances under but not over canopy trees, and movements and colonization success are affected by large vegetation gaps such as agricultural fields [45,55]. These factors and the ability of more dispersed woodlands to better foster dispersal, explain why increasing woodland fragmentation largely had positive effects and the broader significance of landscape connectivity in this system.

My findings add to a small but growing literature indicating the influence of landscape connectivity depends on local processes [28,31]. The effects of matrix structure and landscape habitat configuration on occupancy depended on local habitat quality, whereas increasing habitat amount had the same positive effect on occupancy at all levels of local habitat quality. Because

dispersers may have the ability to target high-quality habitat where they often persist longer, the influence of connectivity may generally depend on local processes. In this system, occupancy declined markedly with increasing area of agriculture within landscapes, but only in low-quality territories where lower colonization rates likely fail to keep pace with higher local extinction rates. Although habitat fragmentation can have positive or negative influences on distribution [8], which were positive on average here, associations with fragmentation were negative in low-quality habitat and positive in high-quality habitat likely due variation in extinction and colonization rates.

The ability of local habitat quality to explain distributional dynamics depended on how it was defined and measured. When habitat quality was measured indirectly based on important attributes of habitat structure, landscape factors had greater relative effects on distribution. However, when quality was measured directly based on the influence of habitat resources, stochastic factors, and conspecifics on territory-specific reproductive output, the effect of habitat quality nearly doubled and was greater than landscape factors. Because habitat quality depends on how the environment affects the vital rates of individuals occupying a specific habitat [26], fitness components are essential for quantifying habitat quality and evaluating its role in driving distribution [25]. Nonetheless, because virtually all studies of the relative influence of local and landscape factors on distribution measure the quality of local focal patches and regional source patches indirectly [18,20,31], likely due to logistical constraints, its overall role in driving distribution has likely been underestimated.

Animal distribution patterns represent sums of individual choices projected onto landscapes [32]. Thus, explaining distributions depends on understanding how settlement choices by individuals are mediated by landscape context. Although efforts to integrate behavioral and

landscape approaches for explaining distribution are not new, few studies consider scales relevant to individual animals [15,25]. From a landscape perspective, general support for the importance of habitat amount and connectivity provide a useful framework to explain distributions, but that generality may limit more mechanistic understandings. From a behavioral perspective, variation in habitat quality should influence patch choices because high-quality habitats confers greater fitness on occupants, which affects distributions across scales. This is because by augmenting population growth rates and attracting more immigrants, high-quality habitats have lower extinction probabilities, contribute more individuals to regional populations, and enhance colonization prospects.

As threats to biodiversity accelerate, identifying key factors that drive distribution and the spatial scales at which they operate is critical for guiding conservation [5,25]. My results suggest augmenting local habitat quality will be more efficient for promoting occupancy than management focused only on landscape factors, especially given potential for lower economic costs. Landscape factors, however, had major effects on distribution that sometimes depended on local habitat quality, indicating managers must also consider landscape context. Thus, augmenting amounts of high-quality habitat in landscapes where habitat is accessible to individuals should bolster occupancy the most while also promoting colonization at larger scales. Moreover, simultaneously augmenting both local habitat quality and landscape connectivity could have multiplicative benefits. In contrast, strategies focused only on matrix structure or habitat configuration are likely to be less efficient, except in situations where anthropogenic habitat loss and fragmentation have created population networks close to extinction thresholds, where restoring connectivity may be critical [3,54]. For pygmy-owls, this may be the case in the adjacent USA where populations have declined markedly, high-quality habitat in many large

wooded bottomlands has been lost, remaining habitat patches on outwash plains are typically smaller, more isolated, and of lower quality, and transboundary development is degrading connectivity with larger populations in Mexico [45,46]. Determining optimal levels of habitat quality, quantity, and connectivity across systems and contexts, and integrating those targets with economic and social considerations are vital questions for conservation.

Data accessibility. The dataset supporting this article can be accessed in the following digital repository: 10.6084/m9.figshare.4290377

Authors' contributions. Not applicable

Competing interests. I have no competing interests.

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Table 1. Models of the influence of local and landscape factors on territory occupancy dynamics of ferruginous pygmy-owls in northwest, Mexico 2001-2013. Estimates of local habitat quality considered the influence of important habitat resources, stochastic factors (weather and primary productivity), and local conspecific densities on observed annual reproductive output within territory patches over 10 years. Landscape factors include habitat effective area (amount weighted by quality), habitat configuration, and two attributes of matrix structure within surrounding landscapes.

Factors	K	BIC	ΔBIC	w_i
Hab. Quality + Hab. Amount + Hab. Configuration	5	275.54	0.00	0.25
Hab. Quality + Hab. Amount + Matrix Structure	6	275.58	0.04	0.24
Hab. Quality + Hab. Amount + Hab. Quality × Hab. Configuration + Hab. Quality × Matrix Structure	9	276.07	0.53	0.19
Hab. Quality + Hab. Amount	4	277.05	1.51	0.12
Hab. Quality + Hab. Amount + Hab. Configuration + Matrix Structure	7	277.65	2.11	0.09
Hab. Quality + Hab. Quality × Hab. Amount + Hab. Quality × Hab. Configuration	6	277.78	2.24	0.08
Hab. Quality + Hab. Quality × Hab. Amount + Hab. Quality × Hab. Configuration + Hab. Quality × Matrix Structure	10	280.77	5.23	0.02
Hab. Quality × Hab. Amount	5	281.75	6.20	0.01
Hab. Quality × Hab. Amount + Hab. Quality × Matrix Structure	8	283.51	7.97	0.00

Table 2. Standardized regression coefficients from models that described the influence of local and landscape factors on territory occupancy dynamics of ferruginous pygmy-owls in northwest, Mexico 2001-2013. Columns show coefficients and standard errors from models based on different definitions of local habitat quality. Indirect estimates were based on important attributes of habitat structure; direct estimates considered the effects of important habitat resources only, and of habitat resources, stochastic factors, and local conspecific densities on observed reproductive output. Model with all connectivity metrics combined considered the sum of standardized values of landscape habitat configuration and matrix structure.

Model	Indirect - Habitat Structure		Direct - Habitat Only		Direct – Habitat, Stochasticity, Conspecifics	
Scale – Factor	β	SE	β	SE	β	SE
All metrics individually						
Local - Habitat quality	0.191	0.086	0.319	0.075	0.360	0.076
Landscape - Habitat effective area (amount weighted by quality)	0.284	0.100	0.258	0.092	0.248	0.090
- Habitat configuration (clumpiness index)	-0.149	0.097	-0.177	0.092	-0.146	0.089
- Matrix structure (largest road index)	-0.137	0.088	-0.139	0.085	-0.151	0.084
- Matrix structure (area of agriculture)	-0.240	0.111	-0.188	0.103	-0.177	0.100
Connectivity metrics combined						
Local - Habitat quality	0.194	0.090	0.320	0.075	0.362	0.076
Landscape - Habitat effective area (amount weighted by quality)	0.272	0.105	0.253	0.092	0.244	0.091
- Habitat connectivity (habitat configuration + matrix structure)	-0.368	0.104	-0.360	0.095	-0.341	0.093

Figure 1. Effects of local and landscape factors on territory occupancy dynamics of ferruginous pygmy-owls in northwest, Mexico, 2001-2013. Local factors are represented by five definitions of habitat quality that considered the effects of additive and interactive combinations of habitat resources, stochastic factors, and local conspecific densities on observed annual reproductive output measured over 10 years within territories. Landscape factors are represented by habitat effective area, landscape habitat quality, two indices of matrix structure, and habitat configuration within landscapes.

Figure 2. Interactive effects of local and landscape factors on long-term territory occupancy dynamics of ferruginous pygmy-owls in northwest, Mexico, 2001-2013. Effects of agriculture and habitat configuration are based on the 3rd model in Table 1 whereas effect of habitat effective area is based on 6th model. Lines show changes in predicted occupancy based on models at average values of all other covariates; direction and magnitude of effects were unaffected by changing covariates values.

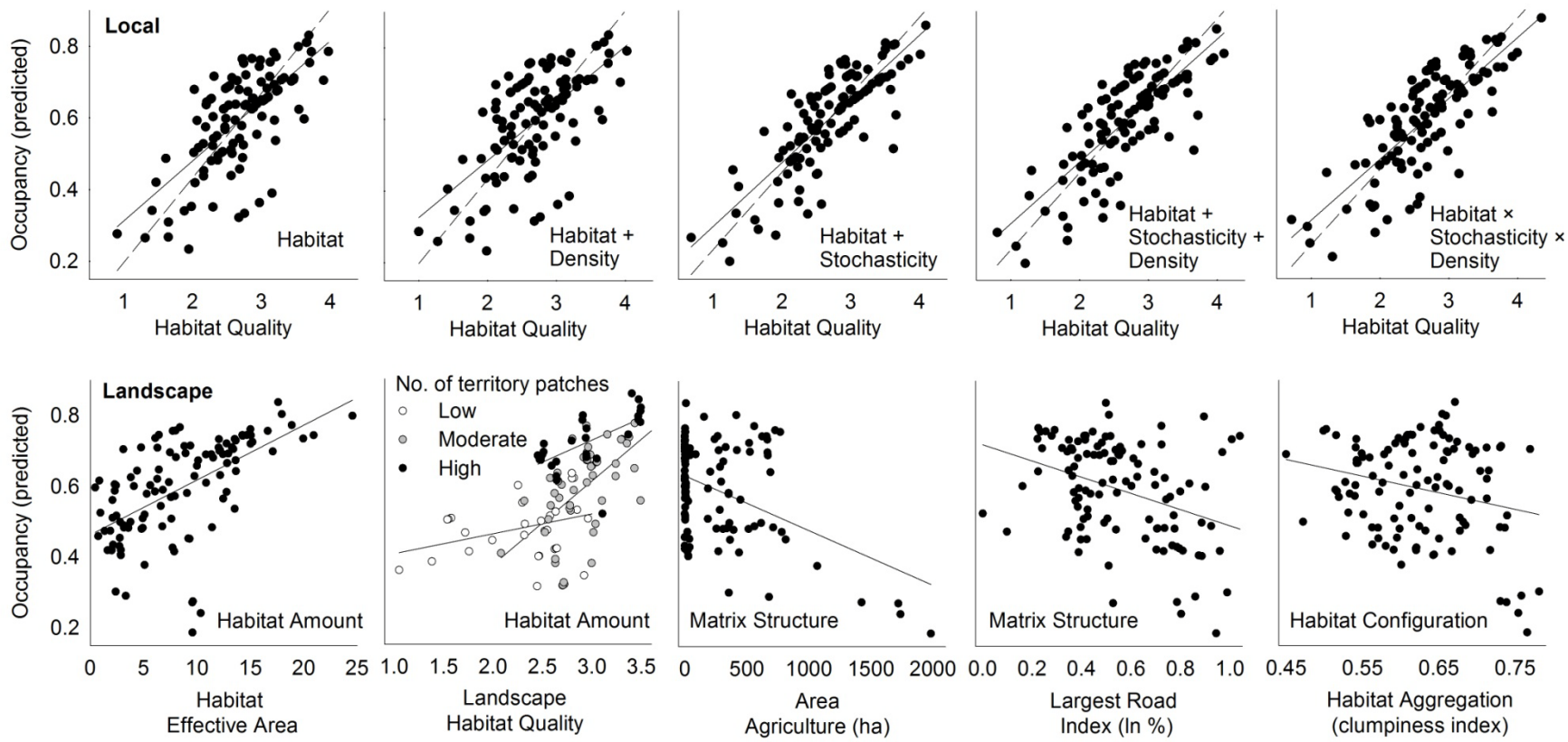
Local
Occupancy (predicted)
0.8
0.6
0.4
0.2
Habitat
Habitat +
Density
Habitat +
Stochasticity
Habitat +
Stochasticity +
Density
Habitat ×
Stochasticity ×
Density
1
2
3
4
Habitat Quality
Landscape
No. of territory patches
Low
Moderate
High
Habitat Amount
Matrix Structure
Habitat Configuration
0
5
10
15
20
25
Habitat
Effective Area
1.0
1.5
2.0
2.5
3.0
3.5
Landscape
Habitat Quality
500
1000
1500
2000
Area
Agriculture (ha)
0.0
0.2
0.4
0.6
0.8
1.0
Largest Road
Index (ln %)
0.45
0.55
0.65
0.75
Habitat Aggregation
(clumpiness index)

Fig. 1

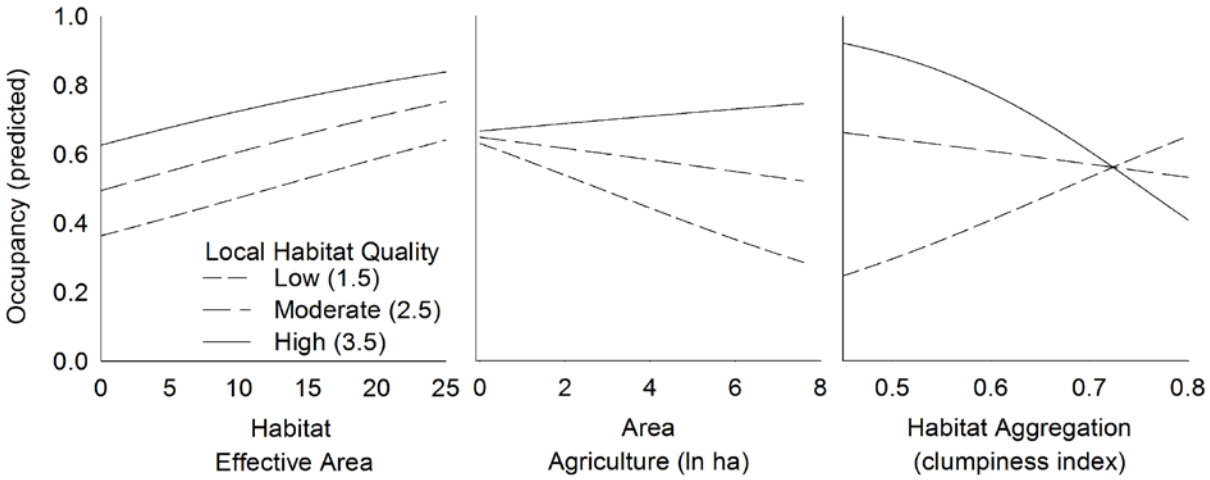
Occupancy (predicted)
1.0
0.8
0.6
0.4
0.2
0.0
Local Habitat Quality
Low (1.5)
Moderate (2.5)
High (3.5)
0
5
10
15
20
25
Habitat
Effective Area
0
2
4
6
8
Area
Agriculture (ln ha)
0.5
0.6
0.7
0.8
Habitat Aggregation
(clumpiness index)

Fig. 2