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A framework to interpret co-occurrence patterns from camera trap data: The case of the gray fox, the bobcat, and the eastern cottontail rabbit in a tropical dry habitat

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Abstract

In mammals, ecological interactions are difficult to observe directly, so they are usually inferred from co-occurrence data. Direct interpretation of co-occurrence patterns can be complicated since they may be the result of different processes such as habitat selection. We propose a logical framework along with multispecies occupancy models, to distinguish which process or interaction of processes gives rise to co-occurrence patterns. We also used temporal kernel density estimates to explore the overlap in diel activity patterns, and ecological knowledge of the species as a complement to explain the drivers that generate co-occurrence. To test our framework, we analyzed three mammal species: the bobcat (*Lynx rufus*), the gray fox (*Urocyon cinereoargenteus*), and their potential prey, the eastern cottontail rabbit (*Sylvilagus floridanus*), in a tropical dry habitat at Tehuacán-Cuicatlán Biosphere Reserve, Mexico. Data were collected across 67 camera trap stations that operated from February to August 2018. The best-fitted model described the spatial interaction between *U. cinereoargenteus* and *L. rufus* with *S. floridanus*; in both cases, the occupancy probability of the predatory species was higher in the presence of their prey than in their absence. Additionally, the three species presented a high overlap in their temporal activity patterns. Based on the knowledge of the species' ecology and our results, we identified that trophic interactions could be an important process shaping the co-occurrence patterns of these species. In short, our framework highlights that it is possible to discern among the processes that influence the co-occurrence patterns for species with well-defined ecological roles, such as in our study system.

Introduction

Biotic interactions are among the most important elements of biodiversity, influencing the functioning and stability of ecological communities (Andresen et al., 2018), as well as the distribution, behavior, and population dynamics of species (Kelt et al., 2019; Ritchie & Johnson, 2009; Schoener, 1988). For several groups of organisms, direct observation of interactions in the field can be a complicated or logistically challenging task (Hines et al., 2010; Karanth & Nichols, 1998), limiting the empirical knowledge of their ecological relationships. In such cases, a common alternative is the use of co-occurrence patterns to infer biotic interactions (Morueta-Holme et al., 2016).

The goal of co-occurrence analysis is to determine the probability that two or more species occur together in a spatial unit (Morueta-Holme et al., 2016), finding three possible patterns: co-occurrence more than expected by chance (i.e. aggregation), less than expected by chance (i.e. segregation), or a random distribution (Veech, 2006). The main idea behind the study of these patterns is that they are the consequence of ecological interactions (Morueta-Holme et al., 2016). Thus, two species with similar niche requirements tend to avoid each other, generating a segregation pattern through competitive interactions

(Diamond, 1975; Gotelli & McCabe, 2002). However, co-occurrence patterns are not always the result of an ecological interaction; they can arise from different habitat requirements of the species, or change with the scale and resolution of the analysis (Blanchet et al., 2020; Cazelles et al., 2016; Thurman et al., 2019). Due to the difficulty of distinguishing the process or interaction of processes that originates co-occurrence patterns, the use of this approach as a surrogate for interactions has been the subject of past debate (Blanchet et al., 2020; Cazelles et al., 2016; Gotelli & McCabe, 2002; Stephens et al., 2020), and remains to be elucidated in detail.

In the case of mammals, camera traps have become the main monitoring tool in use worldwide (Kays et al., 2020; Steenweg et al., 2017), with an increasing number of studies focused on evaluating ecological interactions through co-occurrence (Delisle et al., 2021; Frey et al., 2017). However, there are still challenges to be met regarding the process that generates a pattern of co-occurrence (Blanchet et al., 2020; Thurman et al., 2019). One way to elucidate which mechanisms may influence a co-occurrence pattern is through a logical sequence-based framework (D'Amen et al., 2018; Farris et al., 2020; Kohli et al., 2018). Here, we generate a framework for interpreting co-occurrence patterns from camera trap data, based on multispecies occupancy models (Fig. 1). This analytical procedure allows us to compare the relative importance of habitat filters (e.g. habitat, environmental, topographic, or disturbance drivers) and ecological interactions (e.g. predation, competition, or commensalism) in shaping the species co-occurrence patterns (D'Amen et al., 2018; Morueta-Holme et al., 2016). We complemented the interpretation of co-occurrence by assessing the overlap in daily temporal activity patterns of the species, to ensure that they share the same activity periods. Finally, we verified the results with previous knowledge of the ecology and natural history of the species (Holt, 2020; Stephens et al., 2020).

We used the logical framework to analyze the co-occurrence patterns of three mammal species, the bobcat (*Lynx rufus*), the gray fox (*Urocyon cinereoargenteus*), and their potential prey, the eastern cottontail rabbit (*Sylvilagus floridanus*), inhabiting tropical dry forest in central Mexico. All of the three mammals are common in arid and temperate mammal communities in North America and there is a large amount of information available on their ecology and life history (Armenta Méndez et al., 2018; Dunagan et al., 2019; Farías et al., 2012; Hansen, 2007; Lesmeister et al., 2015). Moreover, previous surveys conducted in our study region have shown that these three mammal species are among the most frequently recorded throughout the entire year (Cruz-Jácome et al., 2015), and thus provide a suitable study system with which to empirically investigate co-occurrence patterns from camera trap data.

For this three species system, we initially evaluated the effect of habitat type, topographic, and disturbance variables to verify the importance of habitat filters for species occurrence. We then postulated two possible interaction hypotheses and their associated co-occurrence patterns. The first was segregation by competition, in which the bobcat, being a larger carnivorous species (mean body mass = 9.6 kg; Larivière & Walton, 1997) than the

gray fox (mean body mass = 5.6 kg; Fritzell & Haroldson, 1982), would generate a pattern of spatial segregation due to interference competition. The second hypothesis was based on aggregation by trophic interaction, in which we expected that the presence of the eastern cottontail rabbit would have a positive influence on the occurrence of the bobcat and, to a lesser extent, the gray fox. We compare the importance of these hypotheses with the modeling framework and discuss the results based on the ecological knowledge of the species.

Materials and methods

Study area and data collection

The study was conducted in San Gabriel Casa Blanca (17°39′N, 96°55′W), located in the municipality of San Antonio Nanahuatipam, in the state of Oaxaca, Mexico (Fig. 2). The study area forms part of the central-eastern part of the Tehuacán Cuicatlán Biosphere Reserve (TCBR). It is approximately 59 km² in area and is characterized by a rugged terrain of hills ranging from 700 to 800 m a.s.l in elevation (Mandujano et al., 2016). The climate is arid, with a mean annual temperature of 21°C and annual precipitation ranging between 50 and 250 mm occurring from September to December (CONANP, 2013). The vegetation cover is mainly composed of low dry deciduous forest with a predominance of columnar cacti (*Neobuxbaumia tetetzo*), spiny shrub vegetation such as *Mimosa* sp., and areas in use for agriculture, mainly for sugar cane and melon cultivation (Fig. 2; Barrera-Salazar et al., 2015; Villaseñor et al., 1990).

Sampling was conducted from February to August 2018 using 40 camera traps (Moultrie A30, Primos Truth Cam35, and Moultrie D55IR) located at 67 stations within the study area. The main objective of this design was to estimate the density and abundance of bobcats (Velásquez-C, 2020), for which camera trapping surveys were established in six quadrat arrangements. Each quadrat was composed of nine cameras deployed in lines of three, at 500 m apart (Fig. 2). To maximize the number of sites sampled, the quadrats were relocated to other sites after 3 months of sampling. Thus three quadrats were in operation from February to April and three from May to August. Furthermore, 13 independent cameras were installed at least 1 km away from the established quadrats and were in continuous operation from February to August (Fig. 2). The total extension (maximum distance between stations) of the study was 8 km and the resolution (minimum distance in observation) was 500 m to 1 km, representing a fine-scale for camera trap research.

The total sampling effort was 6025 trapping nights, with an average of 92.36 nights of operation per camera trap (minimum of 27 and maximum of 130 nights). The information obtained from the camera sampling was organized within the open-access photo manager software DigiKam, where each species photographed was identified and labeled through the EXIF metadata of each image (López-Tello & Mandujano, 2017). Subsequently, we used the "camtrapR" package (Niedballa et al., 2016) to organize and process the species records for each analysis.
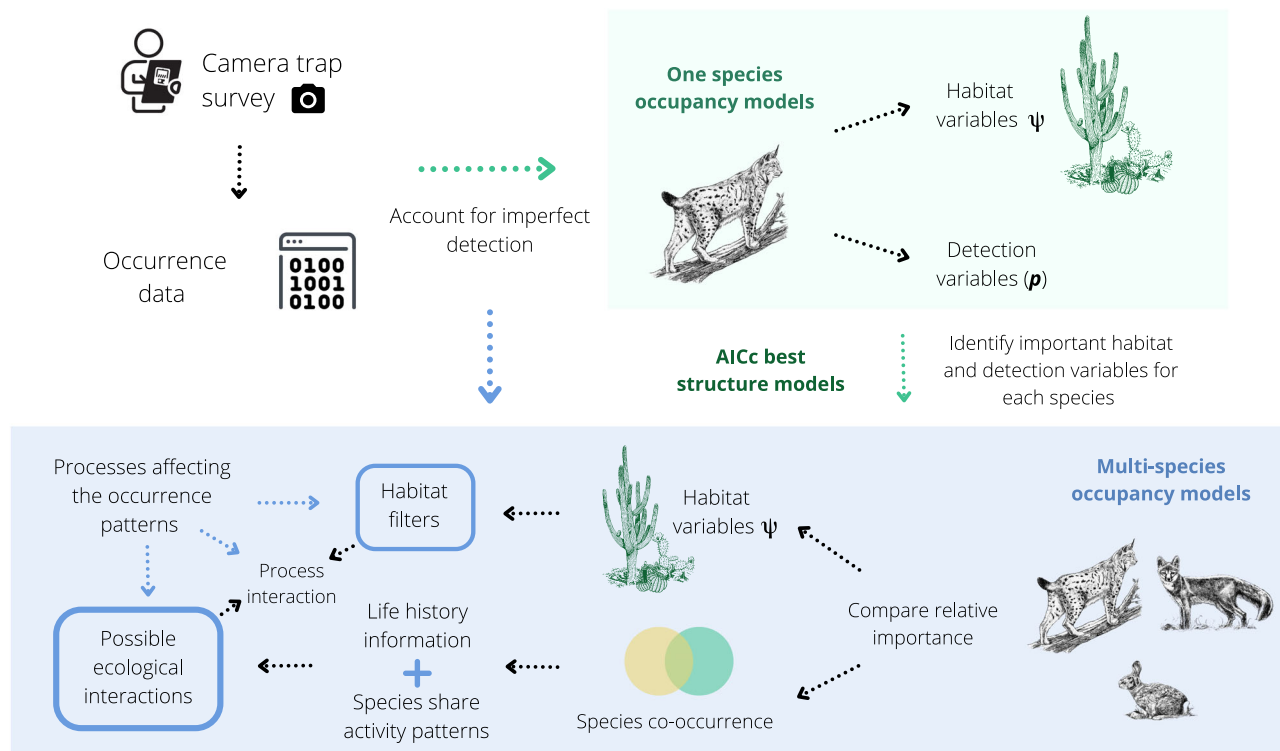
Figure 1 Logical framework for the interpretation of camera trap co-occurrence patterns. Co-occurrence patterns can be caused by different processes such as habitat filters (e.g. habitat requirements, disturbance tolerance of the species) or by ecological interactions (e.g. competition). To distinguish between these two processes, we first identified the possible habitat variables that influence species occurrence (ψ) using one species on season occupancy models. Once the variables were identified, they were used to construct multispecies occupancy models to compare their importance and the presence of other species in species distribution patterns. The best-performing models present evidence in favor of the process or interaction of processes that originate co-occurrence patterns. To confirm the importance of the ecological interactions, we analyzed the daily temporal activity patterns of the species, so that there would be a high probability that the species are active during the same hours of the day. In addition, we used ecological and life history information to allow us to conclude the existence of ecological interactions between the species.

Habitat and detection drivers

To analyze the effect of habitat filters on species occurrence, we used five variables: habitat type, modified soil-adjusted vegetation index (MSAVI2), terrain slope, linear distance to human settlement, and the crops (Table 1). The habitat type at each sampling station was obtained from the San Gabriel Casa Blanca vegetation cover map, elaborated by Barrera-Salazar et al. (2015) (Fig. 2). This variable consisted of four categories: habitat dominated by columnar cacti (*N. tetetzo*), scrub vegetation (*Mimosa* spp. and crassicaule scrub dominated by *Parkinsonia praecox*), crops, and abandoned salt extraction areas. The MSAVI2 (Qi et al., 1994) was calculated from Sentinel 2 satellite images obtained by Global Visualization (GloVis; U.S. Dept. of the Interior, U.S. Geological Survey, 2005). This variable is a representation of plant productivity which can influence the foraging patterns of leporids in arid areas, as well as being a proxy for the abundance of rodent species that are the prey of bobcats and gray foxes (Hernández, Laundré, González-Romero, et al., 2011; Hernández, Laundré, Grajales,

et al., 2011). The slope covariate was calculated from a digital elevation map constructed using elevation data recorded with a Garmin GPS (etrex 20×; maximum precision of 3 m) in the field. Finally, to determine whether there was an effect of human disturbance on the presence of the species, we measured the linear distances from each sampling station to the crops and the urban areas of San Gabriel Casa Blanca, using QGIS (QGIS Development Team, 2018).

Additionally, we considered vertical vegetation cover, sampling effort, and the camera trap model used (Table 1), since they can influence the detection probability of the study species. Vertical vegetation cover was included in the detection process because plant obstruction decreases the range of vision of the camera traps (Glen et al., 2013). This variable was measured using a 1-m wooden ruler subdivided into four sections of 25 cm each. The ruler was placed at a distance of 10 m in front of the focus zone of each camera, where the same observer checked the number of visible sections to estimate the percentage of visibility at each sampling station. The value was 0 when the vegetation did not obstruct visibility and 100 when it
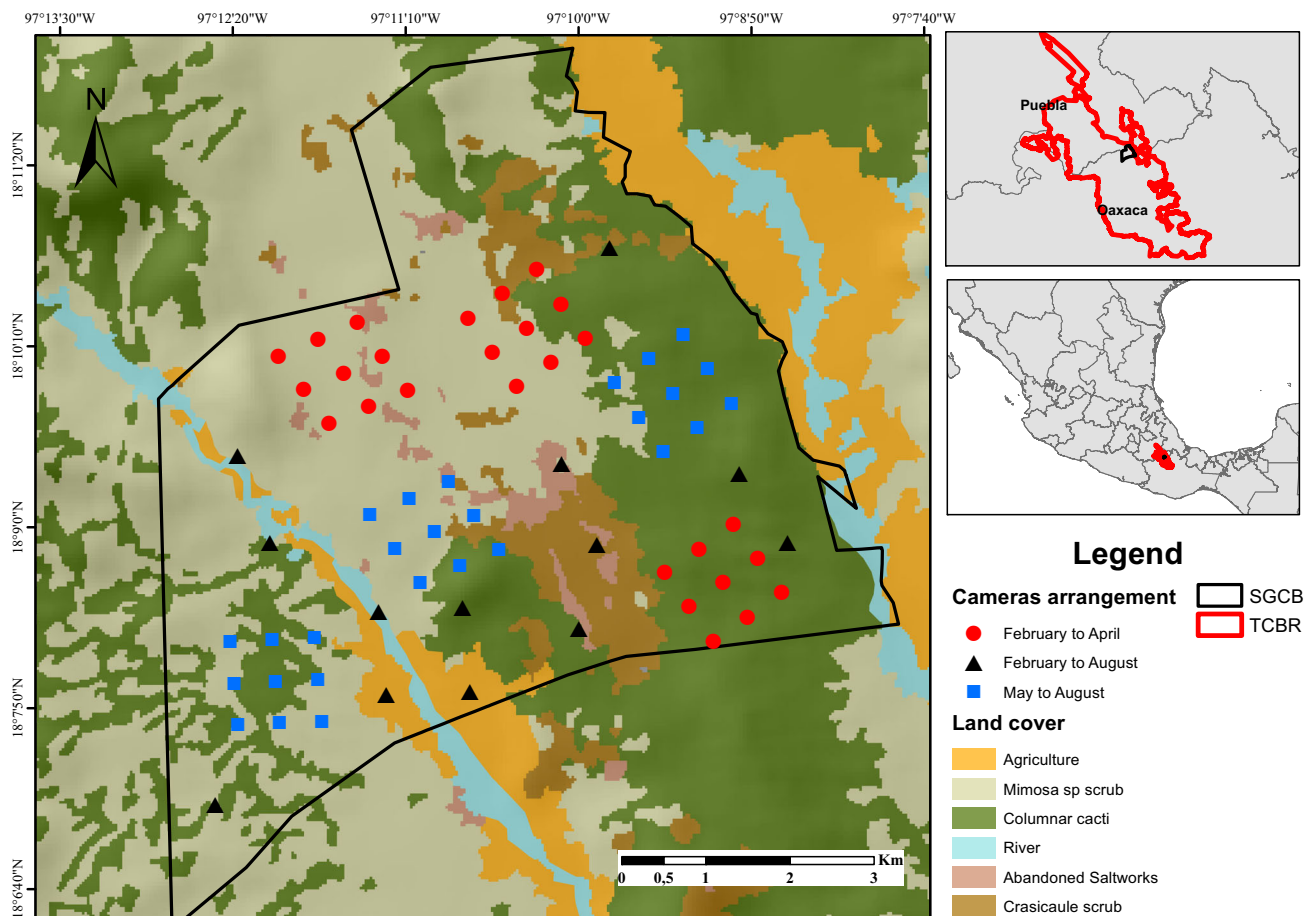
Figure 2 Map of San Gabriel Casa Blanca's communal areas (SGBC), with camera trap arrangements and locations, and land cover categories. TCBR, Tehuacán Cuicatlán Biosphere Reserve.

completely obstructed visibility. Sampling effort was measured as the number of days in operation for each camera trap station. This was included as a detection covariate since the detection of elusive species such as the bobcat may require a greater effort (Shannon et al., 2014). Finally, the camera trap model was also used as a detection covariate, given that characteristics such as shutter speed and sensitivity can influence the camera's ability to detect species (Findlay et al., 2020). This study used three different camera models: Moultrie A30 (*n*: 28; optical field of view: 56 degrees (estimated); Trigger speed: ~0.7 s), Primos Truth Cam35 (*n*: 26; optical field of view: 45 degrees Trigger speed: ~1.5 s), and Moultrie D55IR (*n*: 11; optical field of view: 52 degrees; Trigger speed: ~4 s).

Prior to statistical modeling, the continuous covariates were standardized as mean 0 and variance 1 to facilitate model convergence. A summary of the continuous variables at their real scale can be found in Table S1. Furthermore, to evaluate possible multicollinearity between the continuous variables, we used a Variance Inflation Factor analysis (VIF) using the "usdm" R package (Naimi et al., 2014). Since none of the variables presented high multicollinearity (VIF > 3; Zuur et al., 2010), all

of them were included in the statistical modeling process (Table S2).

Modeling spatial co-occurrence

To analyze the spatial co-occurrence patterns and the influence of habitat on species occurrence while accounting for imperfect detection, we used a multispecies occupancy model (Rota et al., 2016). Although we use the term occupancy, the estimate obtained from the models is interpreted as "use" since the detection area of the camera is small relative to the movement of the species (Efford & Dawson, 2012). To reduce the complexity of multispecies models, we used a two-step approach. First, we fitted single-species occupancy models (MacKenzie, et al., 2017b) to identify the relevant variables that drive occupancy and detection probability for each species. We then used multispecies occupancy models (Rota et al., 2016) to compare the relative importance of species spatial interactions and the previously identified variables. Single-species and multispecies models are composed of two submodels; one for occupancy (ψ) and the other for detection (p). The

Table 1 Habitat and detection drivers used to model the occupancy (ψ) and the detection (p) processes

Variable	Description	Parameter	Source
Habitat type (Habitat)	Habitat type at each sampling station	ψ	Vegetation map (Barrera-Salazar et al., 2015)
Modified soil adjusted vegetation index (MSAVI)	MSAVI index value	ψ	Sentinel 2 Satellite image
Distance to human settlement (Dpop)	Linear distance in meters to human settlement San Gabriel Casa Blanca	ψ	derived from geographic information
Distance to crops (Dcrops)	Linear distance in meters to the nearest crop of each sampling station	ψ	derived from geographic information
Slope	Slope value in degrees of each sampling point	ψ	Calculated with GPS elevation values
Vertical vegetation cover (Ver.cover)	Percentage of obstruction of visibility given by vegetation at each sampling point	p	Field
Sampling effort (Effort)	Number of operational days of each camera trap	p	Sampling data
Camera trap model (Cam)	Camera trap model deployed at each sampling station	p	Sampling data

detection submodel describes the observational process undertaken to estimate the detection probability for each site and survey event, following a Bernoulli distribution probability and conditional to the species presence (MacKenzie, et al., 2017b). The occupancy submodel describes the ecological process of the probability of use for each site, following a Bernoulli distribution for the single-species model and a multivariate Bernoulli for the multispecies model. For occupancy modeling, we defined each camera trap sampling station as the analysis site and each sampling event as five consecutive days of operation for each camera. Detection matrices were constructed for each species, with 66 sites (excluding those cameras with less than two sampling events) and 36 sampling events.

For the first step, we identified the best covariate structure for single-species occupancy models following a secondary candidate modeling selection strategy (Bromaghin et al., 2013; Morin et al., 2020). In this strategy, we used the Akaike Information Criterion corrected for small samples (AICc; Anderson, 2008), to rank the possible candidate models for each submodel (detection and occupancy) independently. The best ranking models (ΔAICc < 2) for each process were combined in a final selection stage.

In the second step, we used the multispecies occupancy model (Rota et al., 2016) to test the species co-occurrence hypotheses, along with the covariates identified in the first step. For detection modeling, we conserved the detection covariates selected in single-occupancy modeling. We fitted candidate models representing nonspecies interactions (first-order natural parameter), paired interactions of species, for example, gray fox occupancy in the presence or absence of bobcat (second-order natural parameter), and triple interaction of species (third-order natural parameter), for example, gray fox occupancy in the presence or absence of both bobcat and cottontail rabbit. Moreover, we fitted models with habitat variables with and without species spatial interactions. We ranked

all candidate models with AICc and selected the best models using ΔAICc < 2 (Anderson, 2008).

To evaluate the goodness of fit of the best single and multispecies models, we used a parametric bootstrap approach that simulates datasets based upon a fitted model, refits the model, and evaluates a user-specified fit-statistic for each simulation. Comparing this sampling distribution to the observed statistic provides a means of evaluating goodness-of-fit (Fiske & Chandler, 2011). In addition, the dispersion parameter (c-hat) was calculated as the ratio of the observed Chi-Square statistic value over the mean of the simulated distribution. The entire procedure for adjusting single and multispecies occupancy models was conducted with a maximum likelihood approach using the "unmarked" package (Fiske & Chandler, 2011) in R 4.0.1 (R Core Team, 2017). The code for the entire procedure is provided in Appendix S2.

Since the distance between camera traps was shorter compared to the scale of the estimated home ranges for the gray fox (0.69–6.69 km^2; Allen et al., 2021) and the bobcat (11.29–34.0 km^2; Elizalde-Arellano et al., 2012; Monroy & Briones-Salas, 2012), and to a lesser extent for the cottontail rabbit (0.01–0.9 km^2; Trent & Rongstad, 1974), there was a possibility of violating the assumption of spatial independence between sampling units (MacKenzie et al., 2017a, 2017b). To verify spatial autocorrelation, we applied Moran's I index to the single-species occupancy model residuals for each species (Legendre & Legendre, 2012) and visually examined patterns of correlations across the distance unit using splines correlograms. The single-species occupancy model residuals were defined following Warton et al. (2017).

Activity pattern overlap

To quantitate the overlap in the temporal diel activity of species, we estimated the activity patterns using the kernel density

estimation method, with the von Mises distribution for circular data (Ridout & Linkie, 2009). To ensure the temporal independence of the records, only those of the same species separated by more than 30 min were used (Rovero & Zimmermann, 2016). The activity patterns estimated for each pair of species were compared using the overlap coefficient (Δ; Ridout & Linkie, 2009), which quantitates the area of overlap under the density curves. Values of the overlap coefficient close to one indicated total overlap in the activity patterns of the species, while values close to zero indicated total differentiation in activity patterns. Different nonparametric estimators were used for small (Δ_1 for <50 records; bobcat) and large samples (Δ_4 for >75 records; gray fox and eastern cottontail rabbit). Moreover, we calculated the 95% CI for each overlap coefficient using 10 000 bootstrap samples (Ridout & Linkie, 2009). The temporal overlap coefficient was calculated using the "overlap" package (Ridout & Linkie, 2009). To test whether the pattern of overlap for each pair of species was significant, we used a randomization test with the activity package (Rowcliffe, 2021). If the *P*-value of this test is less than 0.05 it is possible to interpret that the kernel circular probability distributions differ, and that overlapping patterns could, therefore, be the consequence of chance. The R-code for activity pattern overlap is provided in Appendix S2.

Results

The cottontail rabbit presented the highest number of independent records, with the total of 492, and was detected in 55% ($n = 37$) of the sampling stations. This was followed by the gray fox with 174 photographic records and detections at 46% ($n = 31$) of the sampling stations. Finally, the bobcat presented 50 photographic records and was detected at 35% ($n = 24$) of the sampling stations.

Spatial co-occurrence

For single-species occupancy models, we adjusted a total of 12 candidate models for the cottontail rabbit, 11 for the gray fox, and 9 for the bobcat (Table S3, S5 and S7). In the case of the gray fox, the best models indicated that the species most frequently used areas far from the human settlement ($\beta_{Dpop} = 0.60 \pm 0.28$; Fig. 3b) and the scrub habitats ($\beta_{H\_scrubs} = 1.67 \pm 0.58$), but with poor informative intervals for the saltworks and the crop zones (Fig. 3c; Table S4). We also had a lower ability to detect gray foxes in sites with high vertical vegetation cover ($\beta_{Vert.cover} = -0.20 \pm 0.10$; Fig. 3a). For the bobcat, we only identified informative covariates associated with the observational process, with higher detection probability for cameras with a higher sampling effort ($\beta_{Effort} = 0.45 \pm 0.18$; Fig. 3d; Table S6). The best model for the cottontail rabbit indicated higher habitat use in sites far from cultivated areas ($\beta_{Dcrops} = -5.50 \pm 16.11$; Fig. 3f) and a lower detectability in sites with the Primos camera model ($\beta_{Primos} = -0.76 \pm 0.09$; Fig. 3e; Table S8). All of the best models showed a good fit for the three statistics used and a dispersion parameter that was close to one (Fig. S1). In addition, we found no evidence

of spatial autocorrelation in the probability of occupancy in any of the species (Fig. S2).

We fitted 12 multispecies occupancy models integrating models with species spatial interactions, habitat drivers only, and species interactions with habitat drivers. The best-fitting model was the one in which the conditional occupancy probability of both the bobcat and the gray fox was affected by the presence of cottontail rabbits (Table 2). For both predators, we found a higher habitat use probability in the presence of cottontail rabbits ($\psi_{gray\ fox|\ cottontail\ presence} = 0.76 \pm 0.08$; $\psi_{bobcat|\ cottontail\ presence} = 0.73 \pm 0.14$) than in its absence ($\psi_{gray\ fox|\ cottontail\ absence} = 0.17 \pm 0.08$; $\psi_{bobcat|\ cottontail\ absence} = 0.30 \pm 0.12$; Fig. 4). The goodness of fit test showed that the best model fitted the data, with a dispersion parameter close to one (c-hat = 1.01; Fig. S3).

Activity patterns overlap

We observed a predominantly nocturnal activity pattern for both the gray fox and the bobcat (20:00 to 05:00 h; Fig. 5a,b) and, although active during the same hours as the other species, for the cottontail rabbit the period with the highest number of records was dawn (05:00 to 06:00 h; Fig. 5c). We found a high overlap in diel temporal activity among all three species ($\Delta > 0.7$), with a significant overlap coefficient between the bobcat and the gray fox, and between the bobcat and the cottontail rabbit (Fig. 5e,f). However, the overlap coefficient was not significant between the cottontail rabbit and the gray fox (*P*-value > 0.05; Fig. 5d).

Discussion

Despite the difficulties in distinguishing the processes that originate the co-occurrence patterns (Blanchet et al., 2020), by using our framework, we were able to verify for our three species system in San Gabriel Casa Blanca, that the co-occurrence patterns were not a consequence of the habitat filter process. Accordingly, we found evidence in favor of our hypothesis of trophic interaction since the bobcat and the gray fox co-occurred with their potential prey, the cottontail rabbit. However, the competition hypothesis of spatial segregation was not fulfilled since the gray fox and the bobcat occurred independently in the study area.

For our study conducted in a relatively small area, habitat, topography, or disturbance drivers did not limit the space use of the studied predator species. The crop areas were only a detriment for the cottontail rabbit, which was probably because the sugarcane fields are sparsely populated with herbaceous plants that are important in the diet of lagomorphs (Althoff et al., 1997). The gray fox and the bobcat are reported to use a variety of habitat types and environments, including those present in our study area (Allen et al., 2021; Hansen, 2007). Even in the case of the gray fox, for which we found drivers such as habitat types or distance to human settlement affecting habitat use, these lose importance compared to the cottontail rabbit presence (Table 2). Thus, in our case, interaction emerges as the process shaping the co-occurrence patterns.

The hypothesis of trophic interaction is supported by the life history of the species as well as the similarity in their activity patterns found in this study, thus making interaction feasible (possibility of meeting during the period of activity of the species). Cottontail rabbits and other *Sylvilagus* species form part of the diets of the gray fox and the bobcat throughout their distribution (Aranda et al., 2002; Arnaud & Acevedo, 1990; Delibes et al., 1997; Matlack & Evans, 2011; Meyer et al., 2020; Sánchez-González et al., 2018). In particular, bobcats are considered to be specialist rabbit predators (López-Vidal et al., 2014), the spatial or temporal activity patterns of which could be influenced by the availability of lagomorphs (Dunagan et al., 2019), even at a continental scale (Stephens et al., 2017). Gray foxes, on the other hand, are opportunistic predators that can access several types of resources (Arnaud & Acevedo, 1990; Neale & Sacks, 2001), that can be founded in our study site (e.g. insects, fruits, small mammals). However, rabbits are not only one of the most frequently recorded species (Cruz-Jácome et al., 2015) but also one of the highest biomass prey items (~1.2 kg; Chapman et al., 1980). Because of the availability of rabbits and the cost-energetic benefit of consuming them (MacCracken & Hansen, 1987), gray foxes are likely to favor rabbit foraging. This is congruent with the strong spatial association of gray foxes and rabbits in our study zone (Fig. 4).

We did not find any pattern of spatial segregation between the bobcat and the gray fox in our study area, even though they share the same diel activity periods. The absence of segregation patterns for these species has also been reported in other studies using camera traps and occupancy models (Lesmeister et al., 2015; Lombardi et al., 2017; Reed, 2011), and seems to be a constant in carnivorous mammal assemblages (Davis et al., 2018; Gompper et al., 2016). However, studies conducted at a finer scale have reported avoidance patterns between the two predators. For example, Atwood et al. (2011) found that gray foxes avoided using watering sites that had recently been used by coyotes and bobcats. Also, although gray fox territories overlap with those of bobcats, telemetry studies have revealed that these species did not overlap in their core areas (where 95% of individual activity is recorded) (Chamberlain & Leopold, 2005). Since cases of fox mortality due to bobcats have been reported in the literature (Farías et al., 2005), in this case, the absence of a negative co-occurrence pattern does not imply the absence of competitive interaction. The above suggests that the interference competition between the gray fox and the bobcat is not strong enough to influence the occurrence pattern of the subordinate species at a population level, where our analysis is conducted.

Although we were able to discern among the processes underlying the co-occurrence patterns of the three species in our system, there are limitations to be considered when applying the proposed framework. In our approach, the temporal activity pattern of the species was analyzed through the activity overlap estimator which lacks conditional structure, making it difficult to infer the causality of the resulting patterns (Blanchet et al., 2020). For example, it is not possible to discern whether the difference in the fox and the rabbit activity patterns (Fig. 5d) is due to the rabbits minimizing the risk of predation by avoiding the peak activity of gray foxes, or whether it corresponds to the natural circadian cycle of rabbits (Abu
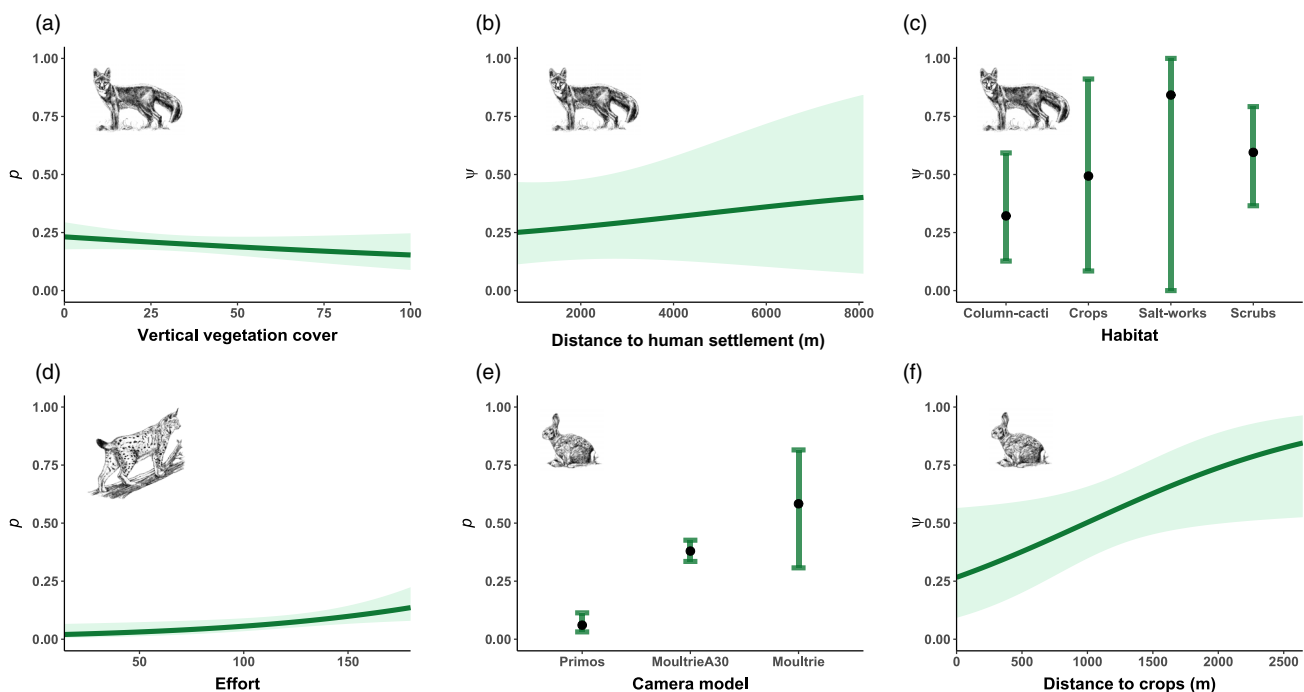

Figure 3 Prediction plots with 95% confidence intervals for occupancy probability (ψ) and detection probability (*P*) variables of one species *occupancy models*. Best model prediction plots for gray fox (a, b, c), bobcat (d), and cottontail rabbit (e, f).

Table 2 Model selection result for multispecies occupancy models

Models	nPars	AICc	dAICc	AICcWt	cltvWt
Pr(Gf|Cr) + Pr(Bc|Cr)	12	1767.26	0.00	0.58	0.58
Pr(Gf|Cr)	11	1769.57	2.31	0.18	0.76
Pr(Gf|Bc) + Pr(Gf|Cr) + Pr(Bc|Cr)	13	1769.98	2.72	0.15	0.90
Pr(Gf|Bc) + Pr(Gf|Cr) + Pr(Bc|Cr) + Pr(Gf|Bc|Cr)	14	1772.52	5.26	0.04	0.95
Pr(Gf|Cr)*(Dcrops) + Pr(Bc|Cr)	15	1772.57	5.31	0.04	0.99
Pr(Gf|Bc) + Pr(Bc|Cr)	12	1775.81	8.55	0.01	0.99
Pr(Gf|Cr)*(Dpop+Habitat) + Pr(Bc|Cr)	20	1776.56	9.30	0.01	1.00
Pr(Bc|Cr)	11	1782.49	15.23	0.00	1.00
Habitat covariates	15	1784.67	17.41	0.00	1.00
Only detection covariates	10	1785.01	17.75	0.00	1.00
Pr(Gf|Bc)	11	1787.60	20.34	0.00	1.00
Null model	6	1838.90	71.64	0.00	1.00

"I", Indicated spatial interaction between pairs of species; AICc, Akaike's Information Criterion for small samples; AICcwt, model weights; Bc, bobcat; cltvWt, Cumulative model weights; Cr, eastern cottontail rabbit; Gf, gray fox; nPars, number of parameters.
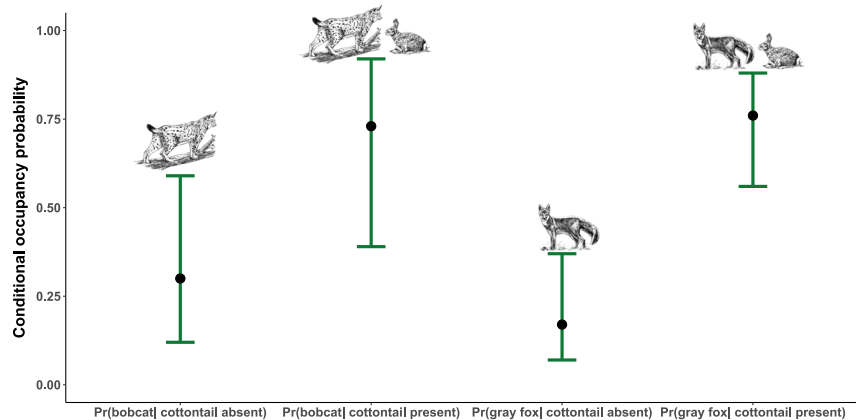All models included detection covariates for each species, except for the "Null model."

Figure 4 Conditional occupancy probability estimates (Pr) with 95% confidence intervals for both gray fox and bobcat in the presence and absence of cottontail rabbit.

Baker et al., 2015; Monroy-Vilchis et al., 2011). Because of the difficulty in explaining temporal occurrence patterns, we prefer to interpret the activity patterns as the possibility of species meeting throughout the diel activity, thus making their interaction possible.

The use of other approaches that present a conditional estimation of temporal or spatio-temporal parameters can be included in our framework (e.g. time interval or time lag between species records (Louvrier et al., 2022; Niedballa et al., 2019)), and would allow a more direct interpretation of the temporal co-occurrence patterns of the species. Another alternative is the use of recent approaches that include the temporal and spatial dimensions within a hierarchical model approach (Kellner et al., 2022). This allows to consider the effect of imperfect detection along with the spatial and temporal relationships of species within the same model, and also permits the evaluation of the spatio-temporal co-occurrence patterns of the species along with temporal and spatial environmental drivers (Kellner et al., 2022).

An additional methodological limitation of our framework is that the relative nature of the analytical approach (AICc) can lead to different results or interpretations if important habitat drivers or other interacting species are omitted in the modeling process (Arnold, 2010). For example, the omission of the rabbit from the analyses would lead us to conclude that the gray fox is distributed according to habitat drivers, rather than interactions. This point highlights the importance of choosing carefully the possible drivers and interacting species within the framework (Morin et al., 2020), which should be based on ecological knowledge of the species. Even when important potential interacting species are identified, their inclusion in the analysis is limited by the number of records obtained. In our case, pumas (*Puma concolor*) and coyotes (*Canis latrans*) could influence bobcat or gray fox occurrence patterns through competitive interference (Fleming et al., 2017; Hass, 2009). However, the pumas and the coyotes are historically rare (Cruz-Jácome et al., 2015) and presented very few records in the study area (1 and 6 records, respectively), making it
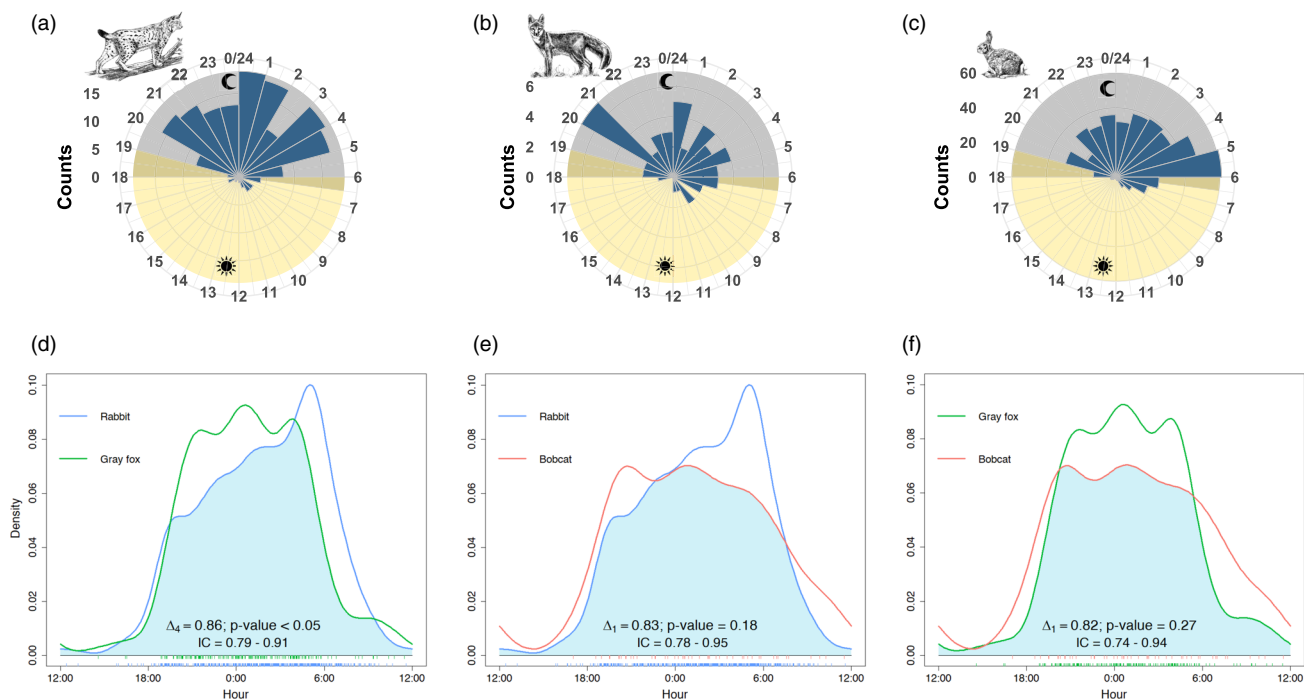
Figure 5 (a-c) Number of records per hour for each species. (d-f) Kernel activity patterns overlap for each pair of species with its significance *P*-values and 95% confidence intervals.

impossible to analyze their effect on the species examined here. Despite this, for our study, the existence of other important variables or interacting species influencing the occurrence of bobcats, gray fox, or cottontail rabbits is unlikely, since their omission would have been reflected in a substantial lack of goodness of fit of the occupancy models (additional variation in the data that is not explained by the model (Kéry & Royle, 2015)). Moreover, the inclusion of additional species in the analyses might have affected the precision and performance of the occupancy models (Rota et al., 2016) because multispecies occupancy models require a large amount of information (sites and records) to correctly estimate conditional occupancy parameters (Clipp et al., 2021; Kéry & Royle, 2021). The sensitivity of multispecies occupancy models to sample size and the number of records has not been formally tested and therefore requires more studies to check model performance and ability to detect co-occurrence patterns under different sampling scenarios.

Our framework proved to be a suitable analytical tool to discern among the different processes that may give rise to co-occurrence patterns in our three-species system. These results and their interpretation should be limited to the spatial and temporal window in which the study was conducted. Variations in the extent of the spatial or temporal scale of subsequent studies using our framework may identify how the importance of environmental filters and interactions changes with the scale (King et al., 2021). Therefore, at the scale of the analysis used in the present study, we found evidence that the bobcat and the gray fox distributions can be explained by trophic interactions with cottontail rabbits, which is confirmed by prior knowledge of the species' ecology. Consistent with other camera-trapping studies (Gompper et al., 2016; Lesmeister et al., 2015), a pattern of segregation between the gray fox and the bobcat was not evident in our study. We interpret this not as an absence of interaction, but rather that the intensity of the competitive interaction occurring between these species is of insufficient strength to be detectable at the population level. This may be important when interpreting the effect of the occurrence of exotic species on the distribution of native species (Farris et al., 2020; Zapata-Ríos & Branch, 2018). In this sense, we found that in species with clearly defined ecological and trophic roles, co-occurrence patterns could provide information on how ecological interactions are expressed at the scale and level of analysis utilized in the sampling design (Thurman et al., 2019). We believe that the logical framework we propose allows a better understanding of the processes underlying species co-occurrence patterns and, therefore, may be useful for future studies aimed at analyzing mammal co-occurrence using camera traps.

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Conflict of interests

All authors declare no competing interests.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Summary table of the continuous covariates used in the modeling process. Variables values are in their original scale.

Table S2. Variance inflation factor (VIF) values for covariates used in the statistical modeling process.

Table S3. Model selection results for one species occupancy models of a gray fox. AICcWt, model weights; cltvWt, Cumulative model weights; dQAICc, delta QAICc values; nPars, number of parameters; QAICc, Quasi Akaike's Information Criterion for small samples.

Table S4. Estimated parameters and standard error for gray fox average model.

Table S5. Model selection results for one species occupancy models of the bobcat. AICc, Akaike´s Information Criterion for small samples; AICcWt, model weights; cltvWt, Cumulative model weights; dAICc, Delta values of AICc; nPars: number of parameters.

Table S6. Estimated parameters and standard errors for bobcat best model.

Table S7. Model selection results for one species occupancy models of the eastern cottontail rabbit. AICc, Akaike's Information Criterion for small samples; AICcWt, model weights; cltvWt, Cumulative model; dAICc, Delta values of AICc; nPars, number of parameters.

Table S8. Estimated parameters and standard error for eastern cottontail rabbit best model.

Fig. S1. Goodness of fit tests for the best occupancy model for each species. (a-c) gray fox best model Goodness of fit tests; (d-f) bobcat best model Goodness of fit tests; (g-i) cottontail rabbit best model Goodness of fit tests.

Fig. S2. Moran's I spatial correlograms for single-species occupancy model residuals.

Fig. S3. Goodness of fit test for the best multi-species occupancy model. (a) sum of squared errors statistic; (b) Chi-square statistic; (c) Freeman-Tukey.

Appendix S2. R–Code of occupancy and activity pattern analysis.

Translated abstract