Spatiotemporal Coexistence of Mesopredators and Their Prey in a Defaunated Neotropical Rainforest

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Abstract

Background and Research Aims: Forest loss and fragmentation have a negative impact on large-sized predators and prey, whose populations are reduced or extirpated locally. We explored the spatiotemporal coexistence of the mesopredators (< 15 kg) coyote, ocelot, and white-nosed coati, with their potential prey (< 15 kg) Mexican agouti, lowland paca, and collared peccary in a defaunated rainforest.

Methods: We used two-species occupancy-detection models between mesopredators and their potential prey, overlap index of circular models, and latency time measurements to evaluate temporal and spatial segregation and habitat use of species.

Results: Presence of ocelot and coyote was influenced by an increase in the detectability and occupancy of the Mexican agouti. Among most mesopredator–prey species pairs, the correlation for both the capture rates at camera-trap stations and the 1-hr intervals were mainly moderate or low. Some mesopredator–prey species pairs showed low or inverse correlations suggesting species avoidance. The Mexican agouti exhibited a significant negative correlation with the presence of mesopredators. The coyote and ocelot showed a positive correlation with their use of low use trails by people.

Conclusions: Spatiotemporal tolerance was observed among mesopredator omnivores and prey herbivores. High temporal overlap of ocelots and potential prey (lowland paca) was observed compared to other tropical forests holding large-sized predators, suggesting behavioral shifts for increasing mesopredator–prey encounters. Furthermore, mesopredator coexistence was mediated by a displacement in the temporal peaks of activity and spatial segregation among species.

Implications for Conservation: Defaunated tropical forests need protection to ensure the conservation of remaining species and their ecological interactions.

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Keywords
activity patterns, habitat fragmentation, Mexico, mesopredator–prey interactions, species coexistence, terrestrial mammals

Introduction

Species interactions are one of the main factors that influence the coexistence of species, community structure, and ecosystem functioning (Futuyma & Agrawal, 2009; Levin, 2009; Thompson, 1999). Although individual interactions in animals occur frequently in small time lapses, they have a great impact on population dynamics and the behavior of interacting species (Schmitz & Suttle, 2001; Werner, 1992). Predation is a common interaction that has a direct impact on populations of predators and prey, including complex behaviors between these species (Mittelbach, 1986; Saul & Jeschke, 2015). For instance, in terrestrial mammal communities, it has been observed that prey species accommodate their daily schedule to avoid activity peaks of predators (Di Bitetti et al., 2010; Harmsen et al., 2011; Herrera et al., 2018; Hernández-SaintMartín et al., 2013; Massara et al., 2015; Massara et al., 2018; Santos et al., 2019). Prey species also frequently avoid sites where predators occur (Boron et al., 2020; Davis et al., 2011). Such spatial and temporal segregation is stronger between predators and their main prey (Ávila-Nájera et al., 2016).

The temporal and spatial coexistence and the use of habitats involving predator and prey species have been explored in well-conserved Neotropical forests, which hold adequate completeness of their species composition and trophic guilds, for example, communities structured with large-sized predators and prey, and mesopredators (< 15 kg) and medium-sized prey (< 15 kg) (Buskirk, 1999; Gehrt & Clark, 2003). On the other hand, defaunated Neotropical forests show reduced terrestrial mammal communities of predator and prey species (Bogoni et al., 2020a, 2020b). In the absence of large-sized predator and prey species, it is expected that interactions between mesopredators and prey will increase, likely resulting in differences in their spatiotemporal use of habitat (Crooks & Soulé, 1999; Massara et al., 2015, 2016). Further, it has been proposed that human presence (e.g., trails and dirt roads) and habitat disturbances (e.g., logging) affect the presence of mesopredator species and prey in defaunated forest compared to well-conserved Neotropical forest (Gutiérrez-Granados & Dirzo, 2021).

The Los Tuxtlas region located in southeastern Mexico is the northernmost tropical rainforest in the Americas. This region has experienced elevated deforestation rates for decades leading to high habitat loss and fragmentation. For example, it is estimated that only 42% of the region still holds rainforest (Von Thaden et al., 2020). The reduction and fragmentation of rainforests have also resulted in high defaunation, where large-sized mammals have been regionally extirpated or show low population abundances (Estrada et al., 1994; Flores-Martínez et al., 2014; Ríos-Solís et al., 2021). Recent studies on mammal surveys have failed to record jaguar (*Panthera onca*), puma (*Puma concolor*), white-lipped collared peccary (*Tayassu pecari*), and Central American tapir (*Tapirella bairdii*), that once commonly occurred at Los Tuxtlas (Dirzo & Mendoza, 2007; Estrada et al., 1994; González-Christen & Coates, 2019). Other large-sized prey such as white-tailed deer (*Odocoileus virginianus*) and mazama (*Mazama temama*) show low population abundances (González-Christen & Coates, 2019).

The establishment of the Los Tuxtlas Tropical Biological Station (LTBS) of the Institute of Biology, UNAM in the 1960s, has provided protection for a large remaining rainforest fragment and its biodiversity, although large-sized predators and prey are regionally extinct due to high habitat loss and fragmentation in the surrounding areas (Ríos-Solís et al., 2021). Thus, LTBS provides an adequate site to explore the effects on the spatiotemporal coexistence of remaining mesopredator species and prey, in the absence of large-sized species of predators and prey. Here we assessed the detection and occupancy of mesopredators and compared the spatiotemporal co-occurrence with potential prey. We evaluated latency times in the detection and occurrence of species influencing the presence of mesopredators and their potential prey, as have been observed in other Neotropical forests (Briceño-Méndez et al., 2017). We were interested in determining if the habitat occupancy of mesopredator species will be influenced by their potential prey and the proximity to the LTBS and sources of disturbance. We hypothesized that LTBS provides higher protection to species (e.g., low use trails by people), in contrast to the rainforest borders (e.g., high use trails by people), where high habitat degradation and human activities are expected to negatively affect the presence of mesopredators. We also tested if elevation influences mesopredator and their potential prey species habitat use, as higher elevations have a low human presence at LTBS.

Methods

Study site

The study site is located in the protected tropical rainforest at the LTBS (95°04.45′ W 18°35.18′ N; 120 masl), a field station located within Los Tuxtlas Biosphere Reserve in southern Veracruz, Mexico (Figure 1). The Los Tuxtlas Biosphere Reserve includes 155,122 ha, of which the LTBS includes 640 ha of rainforests. The LTBS still holds a high diversity of terrestrial vertebrates including 166 species of amphibians and reptiles, 565 species of birds, and 139 species of mammals (Estrada et al., 1994). The LTBS is surrounded by forest fragments and deforested areas with cattle raising and agriculture (Figure 1). Settlements located inside the Los Tuxtlas Biosphere Reserve

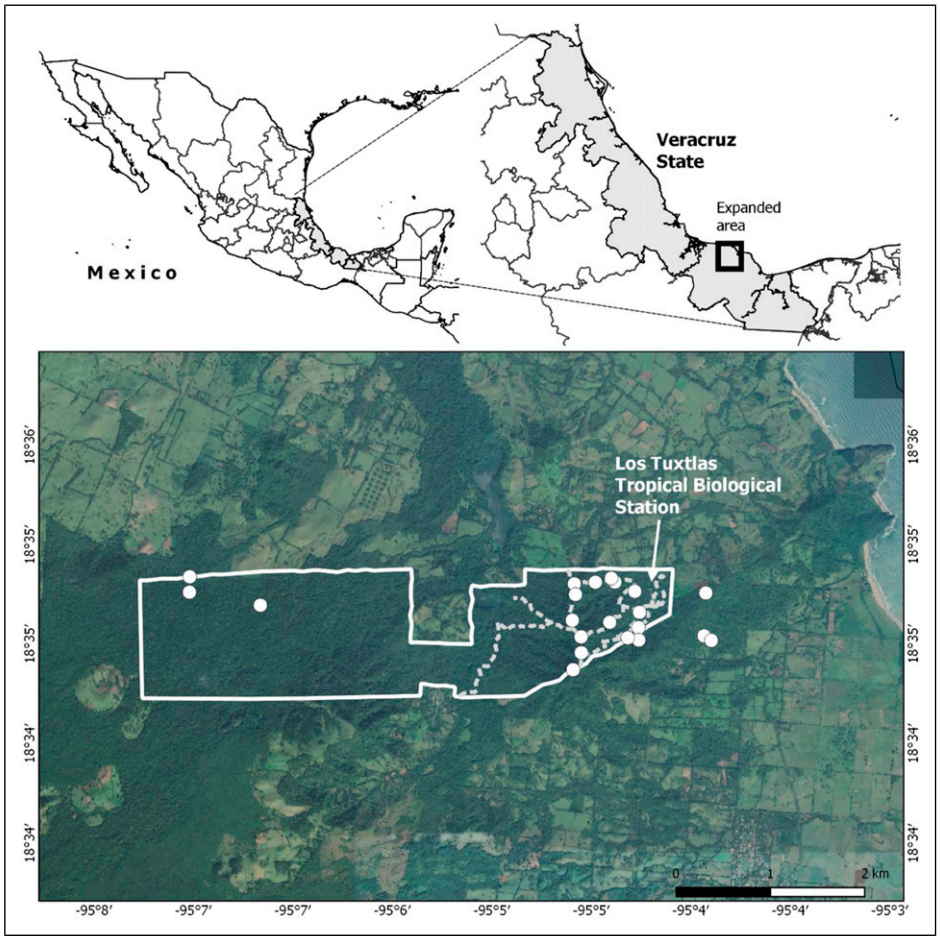

Figure 1. Location of camera-trap stations (white dots) and trails (gray dot lines) within the rainforest fragment at the LTBS (white polygon) located in southern Veracruz, Mexico. Note that three camera-trap stations were located in the surroundings of the polygon of the Los Tuxtlas Biological Station (LTBS).

are mostly inhabited by indigenous communities belonging to the Nahuas, and Zoques-Popolucas. Climate is humid-warm, characterized by an average temperature higher than 22°C (temperature range is 19–30°C); and the elevation range is from 100 to 700 masl (García, 2004). The average annual precipitation ranges from 2000 to 4000 mm (Vidal-Zepeda, 1990).

Data collection and analyses

We set 21 camera traps (LTL ACORN 12MP HUNTING TRAIL and LTL ACORD LTL-6210Mc 12MP FHD models) in trees at 30 cm aboveground and deployed 1–1.5 m from walking trails, between July 2012 and June 2013. A total of 18 camera traps were set inside the LTBS, and three camera traps were set in the surroundings of the LTBS, inside the Los Tuxtlas Biosphere Reserve (Figure 1). Camera traps were set to operate for 24 h at day, shooting one photograph each 40 s. The mean distance among cameras was 1.66 km (range was 0.06–5.57 km). Camera traps were in operation for 44.6 days on average (range was 27–60 days). Four camera traps were set from August to September 2012; five camera traps, from October to December 2012; four camera traps, from November 2012 to January 2013; three camera traps, from January to March 2013; one camera trap, from February to March 2013; one camera trap from March to May 2013, and three cameras from April to May 2013. The total trapping effort was 936 camera traps/days. Independent records were considered to be those of species of those photographs separated by 24 h or more. The capture rate was calculated as the number of independent records of each species multiplied by 100 and dividided by the total camera trapping effort. Species category of risk was obtained from the NOM-059-SEMARNAT (Secretaria de Medio Ambiente y Recursos Naturales, 2020) and of the Red List of the International Union for Conservation of Nature (IUCN, 2020) (Table 1). We followed Álvarez-Castañeda et al. (2017) species nomenclature.

Spatial and temporal species co-occurrence

We analyzed species pairs composed of a mesopredator species and a potential prey to test their spatial and temporal

Table 1. Mammals species recorded with camera traps at the Los Tuxtlas Tropical Biological Station (LTBS).

Species	*N*	CR	IUCN	NOM
Canis latrans	49	5.23	LC	—
Conepatus semistriatus	6	0.64	LC	—
Cuniculus paca	74	7.90	LC	—
Dasyprocta mexicana	318	33.97	CR	—
Dasypus novemcinctus	18	1.92	LC	—
Didelphis sp.	8	0.85	LC	—
Eira barbara	7	0.75	LC	P
Galictis vittata	1	0.11	LC	A
Leopardus pardalis	21	2.24	LC	P
Leopardus wiedii	12	1.28	NT	P
Nasua narica	127	13.57	LC	—
Dicotyles angulatus	33	3.52	VU	—
Procyon lotor	7	0.75	LC	—
Herpailurus yagouaroundi	3	0.32	LC	A
Sciurus deppei	41	4.38	LC	—
Tamandua mexicana	1	0.11	LC	—

Number of records during survey (N), and capture rate (CR). Conservation status of species correspond to the IUCN Red List categories (IUCN, 2020): (LC) Least Concern, (CR) Critically Endangered, (NT) Near Threatened, (VU) Vulnerable, and to the Mexican regulation norm categories (NOM; SEMARNAT, 2020): (P) Endangered, (A) Threatened, and Not included in the lists (—).

coexistence, using two-species and single-season occupancy models, Spearman's correlation coefficient, temporal overlap in circular models, and the measuring of latency times. Two-species and single-season occupancy models incorporate detection values related to presence or absence of species in samples (occasions) at same sites with: temporal repetitions, site variables, variables that affect detection, and the detection histories of a second species (Mackenzie et al., 2002). We followed Richmond et al. (2010) parameterization, in which occupancy and detection values of one subordinate species (species B) is influenced by a dominant species (species A). We included probabilities of occupancy of species A (ψA), probability of occupancy of B if A is absent (ψBA), probability of detection of species A if B is absent (pA), probability of detection of species B if A is absent (pB), probability of detection of species A if both species are present (rA), probability of detection of species B if both are present but A was not detected (rBa), and probability of detection of species B if both are present, and A was detected (rBA). For each site, days of operation were divided into 8 day-occasions. The analyses were implemented in the package rPRESENCE (MacKenzie & Hines, 2021) for the R environment (R Core Team., 2014), including a species effect on occupancy (SP), and an occurrence-level interaction between species (INT).

We tested specific interaction effects and covariates effects on probabilities of occupancy and detection, respectively. Models were fitted with a maximum likelihood approach (Mackenzie et al., 2002). Occupancy models operate with two components, each one with independent variables. One component models probabilities of detection (p); the other component models probabilities of occupancy (ψ) of species taking into account detection. For each site, and as co-variables influencing occupancy, we calculated the Euclidean distance to LTBS facilities, the Euclidean distance to nearest human settlement, and elevation (masl). The covariables affecting detection were the sampling effort measured as the number of days that each camera trap operated, and trails where cameras were placed, differentiated by the intensity of use by field station researchers: vigilantes (low use trails by people, covered by herbaceous plants) and pathways (highly used trails by people); both were approximately 1 m wide. All trails had a natural soil substrate. These covariables were used to model occupancy and detection probabilities of species pairs between mesocarnivores and their potential prey. For each species pair, we tested 55 models with different co-variables combinations. The best competitive models were selected with the Akaike information criterion estimator adjusted for small samples, for example, ΔAICc was < 2.0 (Burnham & Anderson, 2002). When two or more models were ΔAICc < 2.0, real parameters were averaged.

We used Spearman's correlation coefficient to measure the relationship between species pairs in capture rates at stations, and total sums of occurrences within 24 intervals of 1 h (Chaudhary et al., 2020; Harmsen et al., 2011; Vinitpornsawan & Fuller, 2020). We assumed that high and positive correlations (~ 1) indicated tolerance within species pairs, while high and negative correlations (~ -1) indicated species pairs avoidances. Daily temporal overlap was compared against the fit of a smooth circular model using Kernel density (Meredith & Ridout, 2021; Sollmann, 2018). We also calculated an overlap index between the adjusted models, where a value near to 0 indicated a low daily temporal overlap, and values near to one indicated a high temporal overlap. Model fit and overlap index were calculated with overlap package (Meredith & Ridout, 2021).

Lastly, we analyzed the latency times within species pairs between mesopredators and their potential prey, using their occurrence in the same camera trap station in 1-day intervals (24 h). Through binary matrices, we obtained species pair co-occurrences in a station on the same day, 1 day later, 2 days later, and so on up to 20 days later (latency times; Galindo-Aquilar et al., 2022). The observed latency times were contrasted against 10 runs of random models obtained by 100 iteration bootstraps; significant ($p < 0.05$) latency times were shown in a species ecological network. Before conducting the analyses, we checked the similarity of data between stations and found a low value ($< 47\%$).

Results

We obtained 726 independent records of 16 species of terrestrial mammals (Table 1), of which we analyzed three

Table 2. Beta coefficients of two species occupancy models for mesopredators and their potential prey in LTBS.

Model	ψA	ψBA	pA	pB	pA: low use trails	rA
Coyote and Mexican agouti						
ψ(SP)p(SP + INT_o + low use trails)	0.934 (0.539)	1.367 (0.933)	0.444 (1.031)	2.123 (0.406	1.311 (0.372)	−1.797 (1.006)
ψ(SP)p(SP + low use trails)	1.172 (0.632)	1.102 (0.987)	−1.393 (0.363)	2.451 (0.385)	1.416 (0.381)	
Ocelot and Mexican agouti						
ψ(SP)p(SP + INT_o + low use trails)	0.903 (0.595)	1.410 (0.998)	−0.919 (0.679)	3.340 (0.539)	1.990 (0.490	

Parameters: probability of occupancy of species A (ψA), probability of occupancy of B if A is present (ψBA), probability of detection of species A if B is absent (pA), probability of detection of species B if A is absent (pB), and probability of detection of species A if both are present (rA). Standard error in parenthesis. In the species pairs models, SP = species effect on detection or occupancy; INT_o = the occurrence of dominant species changes the detection or occupancy probability of the other subordinate species.

mesopredator species (coyote *Canis latrans*, white-nosed coati *Nasua narica*, and ocelot *Leopardus pardalis*) and three potential preys (lowland paca *Cuniculus paca*, Mexican agouti *Dasyprocta mexicana*, and collared peccary *Dicotyles angulatus*). Mesocarnivore species registered with a low number of records were margay *Leopardus wiedii* (12), striped hog-nosed skunk *Conepatus semistriatus* (12), tayra *Eira barbara* (9), racoon *Procyon lotor* (8), jaguarundi *Herpailurus yagouaroundi* (4), and grison *Galictis vittata* (1). The Mexican agouti was the prey species with the highest capture rate (33.97), followed by the lowland paca (7.91). Of the 16 species recorded, 7 species showed conservation risk categories assigned by the IUCN and the Mexican norm (Table 1).

Species pairs and single-season occupancy

Models perform well for the species pairs of coyote and Mexican agouti, and ocelot and Mexican agouti. For the coyote and Mexican agouti species pair, two models were well supported (ΔAICc < 0.2) (Supplemental Material 1). We found a SP on probability of occupancy for both models. In the detection probabilities, we observed a SP plus type of trails (low use trails), although an occurrence-level INT was only present in the first best model (Table 2). For ocelot and the Mexican agouti species pairs, only one model was supported, with a species effect on probability of occupancy SP, and SP INT and type of trails (low use trails) in the probability of detection (Table 2).

We found that the probability of detection of coyotes was positively influenced by type of trail (low use trails by people) and was higher in the absence than in the presence of the Mexican agouti (p = 0.646, and p = 0.369, respectively). Conversely, the probability of detection of the Mexican agouti was high in the absence and slightly lower in the presence of the coyote (p = 0.927, and p = 0.812, respectively). The probability of detection of the ocelot was also influenced by low use trails by people, and was higher in the absence than in the presence of the Mexican agouti (p = 0.547, and p = 0.170, respectively). The probability of detection of the Mexican agouti was higher in the absence than in the presence of the ocelot (p = 0.958, and p = 0.768, respectively). Further, the probability of occupancy was moderate for coyote (ψ = 0.730) and for ocelot (ψ = 0.711). The probability of occupancy for the Mexican agouti was high in the presence of coyote (ψ = 0.908) or of the ocelot (ψ = 0.910). We did not observe a relationship between probabilities of occupancy of species pairs between mesopredators and their potential prey with distance to human settlements, distance to LTBS or elevation (Tables 2 and 3).

Species capture rates

The white-nosed coati and the coyote showed significant ($p < 0.05$) and moderate positive correlations in their capture rates in relation to the ocelot (r = 0.46 and r = 0.40, respectively). There was a significant ($p < 0.05$) and moderate positive correlation between the coyote and the white-nosed coati (r = 0.48). The Mexican agouti had significant ($p < 0.05$) low inverse correlations with the white-nosed coati (r = −0.05), the coyote (r = −0.14), and the ocelot (r = −0.18) suggesting that sites with a high record rate of these species were avoided by the Mexican agouti. In their daily temporal activity, we observed significant ($p < 0.05$) high correlation values between the white-nosed coati and the Mexican agouti (r = 0.72), and between the white-nosed coati and the collared peccary (r = 0.58). On the other hand, there were significant ($p < 0.05$) negative temporal correlations between the white-nosed coati and the ocelot (r = −0.35), the ocelot and the Mexican agouti (r = −0.23), the Mexican agouti and the lowland paca (r = −0.31), and the white-nosed coati and the lowland paca (r = −0.05).

Most species pairs showed positive spatiotemporal correlations, but we found opposite significant ($p < 0.05$) spatial and temporal values between the coyote and Mexican agouti (spatial r = −0.14; temporal r = 0.41), and between the white-nosed coati and Mexican agouti (spatial r = −0.05; temporal r = 0.72). Conversely, the white-nosed coati and ocelot (spatial r = 0.46; temporal r = −0.35), white-nosed coati and lowland paca (spatial r = 0.23; temporal r = −0.05), and lowland paca and Mexican agouti (spatial r = 0.22; temporal r = −0.31) species pairs showed an opposite trend. No species pairs

Table 3. Real estimates of two species occupancy and detection models for mesopredators and their potential prey in LTBS.

Species pairs	ψA	ψBA	pA	pB	rA	rBA
Coyote and Mexican agouti	0.730 (0.112; 0.469–0.892)	0.908 (0.064; 0.685–0.978)	0.646 (0.229; 0.208–0.934)	0.927 (0.064; 0.677–0.988)	0.369 (0.064; 0.255–0.503)	0.812 (0.054; 0.691–0.894)
Ocelot and Mexican agouti	0.711 (0.122; 0.434–0.888)	0.910 (0.645; 0.684–0.979)	0.547 (0.131; 0.295–0.779)	0.958 (0.026; 0.866–0.988)	0.170 (0.047; 0.097–0.284)	0.768 (0.064–0.873)

Parameters: occupancy of species A (ψA), occupancy of species B if species A is present (ψBA), detection of species A if species B is absent (pA), detection of species B if species A is absent (pB), detection of species A if both species are present (rA), and detection of species B if both species are present (rBA). Standard error, and 95% confidence intervals are in parenthesis.

Table 4. Temporal overlap index between species pairs of mesopredators and their potential prey in the LTBS rainforest. Confidence intervals at 95% are in parenthesis.

Species	White-nosed coati	Coyote	Lowland paca	Mexican agouti	Collared peccary
Coyote	0.85 (0.76–0.96)	0.58 (0.40–0.73)	0.51 (0.34–0.62)	0.73 (0.62–0.82)	0.68 (0.49–0.79)
White–nosed coati		0.49 (0.32–0.62)	0.41 (0.26–0.46)	0.84 (0.77–0.90)	0.80 (0.70–0.93)
Ocelot			0.81 (0.69–0.98)	0.40 (0.22–0.50)	0.46 (0.26–0.63)

between mesopredators and their potential prey showed a negative relationship in both spatial and temporal dimensions. Likewise, the Kernell circular models overlap index showed that the highest daily temporal overlap were between the coyote and white-nosed coati, and the white-nosed coati and Mexican agouti, and the lowest were between the ocelot and Mexican agouti, and the white-nosed coati and lowland paca species pairs, respectively (Table 4; Supplemental Material 2).

Latency times

From the 10 runs in the random models comparing species co-occurrences, we found high consistency (96.41%), i.e. almost all significant latencies were similar among runs. The latency times shown in the species ecological network exhibited that some species occurred only several days after the occurrence of other species (Figure 2). For example, we found 4 days of latency between the occurrence of coyote and white-nosed coati, and between ocelot and white-nosed coati. Five days of latency were observed between the Mexican agouti and coyote, the lowland paca and white-nosed coati, and the white-nosed coati and Mexican agouti. The longest latency time was observed between the coyote and the collared peccary, with a 13-day difference. On the other hand, species exhibiting a high coexistence were the white-nosed coati and the collared peccary, that occurred on the same day at the same sites. We found that ocelots appeared 3–4 days after white-nose coati, and white-nose coati appeared 5–6 days after the Mexican agouti (Figure 2).

Discussion

Our study provides information on species coexistence of the mesopredators and their potential prey in a defaunated rainforest, where populations of large-sized predators (e.g., jaguar and puma) and their main prey (tapir, white-tailed deer, mazama, and white-lipped peccary) have been extirpated or occur at low numbers (Ríos-Solís et al., 2021). Overall, distance to the LTBS did not emerge as a variable explaining the probability of occupancy of mesopredators. These species used the rainforest fragments surrounding LTBS, irrespectively, neither considering it as a facility providing protection nor as a risky zone. It is possible that this fragmented landscape area is part of their home ranges (Ríos-Solís et al., 2021). The probability of occupancy of coyote and ocelot was associated with the covariable of low use trails by people, which may be explained by a preference to avoid human presence (Salom-Pérez et al., 2021).

The best-supported occupancy models showed that low use trails by people were positively correlated with the detection of ocelots. Ocelot occupancy showed no correlation with elevation, which has been documented positive and negative in other tropical forests (García-R et al., 2019; Nagy-Reis et al., 2017; Santos et al., 2019;

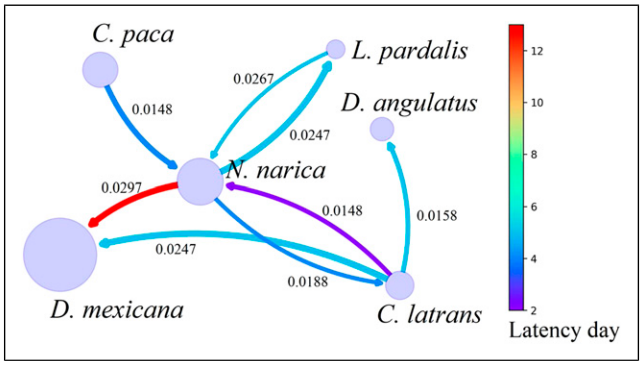

Figure 2. Ecological network of latency times between species pairs of mesopredators and their potential prey in the LTBS rainforest. The arrow-head indicates the first occurring species, and the arrow foot indicates the later occurring species. The color of the arrow indicates latency times in days, as indicated in the colored sidebar. Line thickness indicates average significance ($p < 0.05$); a wide arrow corresponds to a higher average significance.

Wang et al., 2019). We also observed that occupancy models showed that the probability of detection of the Mexican agouti decreased in the presence of coyote and ocelot likely to avoid encounters with these potential predator species.

Potential prey species were not related to the habitat use of mesopredators. Such findings could be explained by the fact that coyotes and white-nosed coatis are omnivorous species that do not strictly depend on vertebrates as their main food source (Bekoff, 1977; Gompper, 1995). Ocelots frequently visited sites where lowland pacas were common, although this species is not among their main prey (Murray & Gardner, 1997). The importance of lowland pacas on the feeding habits of ocelots in the defaunated LTBS rainforest deserves further study (see Moreno et al., 2006; Oliveira et al., 2010). In the absence of large-sized predators and prey, it is likely to expect a rearrangement of the spatiotemporal coexistence between mesopredators and potential prey. This hypothesis can be further tested by comparing well-conserved with defaunated tropical forests and quantitatively determined expected shifts in predator–prey interactions.

We observed that ocelots and lowland pacas were mainly nocturnal, whereas collared peccaries, white-nosed coatis, and the Mexican agoutis were diurnal, and the coyote was cathemeral. These daily activity patterns were in accordance with reports for these species in other Neotropical forests (Lira-Torres & Briones-Salas, 2012; Marqués & Fábian, 2018; Porfirio et al., 2016). However, we found slight differences in the daily activity patterns between ocelot and its potential prey, suggesting that changes in their activity have occurred due to the absence of large predators. Ocelots had high and low temporal overlaps with lowland paca and the Mexican agouti, respectively, which coincides with patterns observed in other Neotropical forests, even with the presence of large-sized predators and prey (de Matos et al., 2018; García-R et al., 2019; Herrera et al., 2018). Nonetheless, such temporal overlap was slightly higher in LTBS (0.81 with the lowland paca, and 0.40 with the Mexican agouti) than in sites of Brazil, Colombia, or Costa Rica, where the overlap ranged 0.67–0.80 for lowland paca, and 0.23–0.36 for *Dasyprocta* spp. (Botts et al., 2020; de Matos et al., 2018; García-R et al., 2019; Herrera et al., 2018; Porfirio et al., 2016). We also found that ocelots showed a higher temporal overlap with collared peccaries (0.46) and with white-nosed coatis (0.49) than reported for Costa Rica (0.36–41 and 0.25–0.39, respectively) (Botts et al., 2020; Herrera et al., 2018). Such higher temporal overlap with potential prey at the LTBS could indicate that ocelots are expanding their activity to increase the chances of encountering these potential prey species in this defaunated rainforest (Ríos-Solís et al., 2021). Changes in prey selection have been observed in ocelots in Barro Colorado Island, where they hunt frequently larger prey such as collared peccaries *Dicotyles* sp., once jaguar populations become extremely rare or locally extirpated (Moreno et al., 2006).

Further, the relationship between the capture rate of ocelots was low with lowland pacas, and negative with the Mexican agouti. In addition, we did not find any significant latency time between ocelots and lowland pacas or the Mexican agouti, suggesting that ocelots randomly visited the same sites of these potential prey. An alternate explanation is that the spatial overlap is occurring in sites not sampled in our camera traps design, such as refuges that ocelot usually visit to prey on *Dasyprocta* sp. (Emsens et al., 2014). This was also the case between ocelots and collared peccaries, where the spatial correlation was low and did not have latency times. Conversely, we observed a negative temporal correlation between ocelots and white-nosed coatis. Further, the analysis of latency times showed that white-nosed coatis took 3 days to occur after ocelots, but ocelots only took 1 day to appear in the same site as the white-nosed coati. Ocelots may seek out white-nosed coatis to prey on them (Bianchi et al., 2014; Oliveira et al., 2010), which may explain our observations of co-occurrence.

We observed low values of correlation between coyotes with lowland pacas and collared peccaries suggesting that these prey species avoid coyotes spatially and temporally. However, latency times did not provide evidence of any predatory behavior of coyotes over lowland pacas. Interestingly, we observed that coyotes and collared peccaries co-occurred in the same sites for long periods. Coyotes and white-nosed coatis showed a higher spatiotemporal overlap (0.36) than in other tropical forests (Botts et al., 2020). There was a moderate correlation between coyotes and white-nosed coatis in the capture rate in camera-trap stations and the 1-hour intervals, and the latency times showed that these species co-occurred cyclically in the same sites with a difference of 3 or 4 days. While white-nosed coatis are preyed upon by large-sized predators such as pumas and jaguars, no evidence exists of coyotes preying on them (Hass & Valenzuela, 2002). We did not find latency times co-

occurrences between coyotes and ocelots, and the correlation indices showed a low spatial and temporal relationship. We also observed a moderate temporal overlap, similar to that reported in Costa Rica for both species (Herrera et al., 2018). It seems that coyotes spatially and temporally avoided ocelots at LTBS, where they are mainly seed predators competing with seed dispersers in our study site (Zambrano et al., 2015). Coyotes are opportunists concerning habitat use and feeding habits, they have been expanding their distribution in the Neotropics as a consequence of forest loss due to cattle ranching (Cove et al., 2012).

Overall, pairs of mesopredator species such as the coyote and white-nosed coatis, and coyotes and ocelots showed an intraguild tolerance behavior driven by a displacement on peaks of activity time and spatial segregation, allowing their coexistence in this defaunated rainforest. In another defaunated site in the Brazilian Atlantic forest, Massara et al. (2016) did not find changes in the spatial use and activity patterns of mesopredators as a response to ocelots. Although confidence intervals of the temporal overlap between species pairs did not differ, we found a slightly higher value at the LTBS rainforest than at the Atlantic forest site, suggesting that behavioral changes are likely occurring due to the absence of large-sized predators. Future studies in other defaunated Neotropical forests should address whether or not these behavioral shifts in mesopredators' spatiotemporal patterns are consistent with our observations.

Implications for Conservation

Deforestation is a major cause of habitat loss and fragmentation in tropical forests leading to biodiversity loss worldwide (Bogoni et al., 2020a, 2020b; Dirzo et al., 2014; Dirzo & Miranda, 1990; Galetti & Dirzo, 2013). As a consequence, many species in tropical forests have become extinct or their populations have been extirpated regionally. This is the case of the Los Tuxtlas Biosphere Reserve, where large-sized species of terrestrial mammals (e.g., jaguar, puma, tapir, white-tailed deer, mazama, and white-lipped peccary) have become extinct or their populations occur in low abundances (Flores-Martínez et al., 2014; Ríos-Solís et al., 2021). It is likely that remaining medium-to-small-sized predators and prey interactions in the defaunated tropical forests will modify spatially and temporally their coexistence (Massara et al., 2016). We studied interactions between mesopredators and their potential prey in the defaunated LTBR and observed spatial and temporal shifts leading to high overlap between ocelots and other mesopredators and their potential prey. Defaunated forests such as LTBR provide excellent sites to conduct long-term research to determine the impact of habitat loss and fragmentation of predator–prey interactions compared to non-defaunated tropical forests. Documenting spatiotemporal shifts in species co-occurrences in defaunated habitats contributes to determining adjustments of predator–prey interactions. Further, of the 16 species recorded in our study, 7 showed a conservation risk category assigned by the IUCN Red List (International Union for Conservation of Nature (IUCN), 2020) and the Mexican norm (Secretaria de Medio Ambiente y Recursos Naturales (SEMARNAT), 2020), which highlights the importance of their conservation. Defaunated tropical forests should also be prioritized to ensure the conservation of remaining species and their ecological interactions.

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Supplemental Material

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