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A matter of time not of co-occurrence: temporal partitioning facilitates coexistence between coyotes (*Canis latrans*) and gray foxes (*Urocyon cinereoargenteus*) in temperate forests of Mexico

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Abstract

Sympatric species reduce competitive interactions by segregating their ecological niche as a strategy that promotes coexistence. The main dimensions in which niche differentiation occurs are spatial, trophic, and temporal axes. Thus, describing the spatiotemporal patterns of sympatric species help us better grasp how species coexist. In Mexico, coyotes (*Canis latrans*) and gray foxes (*Urocyon cinereoargenteus*) are sympatric and widely distributed, and information about their temporal and spatiotemporal interactions is still needed to explain their coexistence throughout their distribution. The evaluation of the ecological niche in temperate forests where both species coexist has shown high spatial and trophic overlap. Therefore, more pronounced segregation must occur in other niche dimensions, such as temporal and spatiotemporal axes, to maintain the coexistence between coyotes and gray foxes. As an approach to exploring the coexistence between these species in temperate forests, we pose the following question: Is there temporal or spatiotemporal segregation between sympatric coyotes and gray foxes? We hypothesized that both species maintain coexistence due to differences in their daily activity patterns (temporal segregation) and the presence of avoidance behaviors at the spatiotemporal level (spatiotemporal segregation), thereby reducing agonistic interactions. We aimed to evaluate indicators of niche segregation through two approaches: (i) temporal niche partitioning, measuring the overlap of the daily activity patterns and activity levels; and (ii) spatiotemporal niche partitioning, through temporal co-occurrence analysis and time to encounter analysis. In 2018, we used a camera-trap array ($n=43$) to evaluate spatiotemporal interactions of coyotes and gray foxes in temperate forests of northern Mexico. We found that coyotes exhibited a diurnal daily activity pattern, whereas gray foxes were nocturnal, showing low overlap between daily activity patterns. Temporal co-occurrence and time to encounter analysis showed that coyotes and gray foxes occurred independently of each other. Therefore, we demonstrated that the spatiotemporal interactions between both species is a result of random species associations. In conclusion, here we provide evidence that ecological segregation occurred in the temporal niche and not in the spatiotemporal niche of the species. Thus, the temporal niche segregation represents one of the ecological strategies that facilitates the coexistence between coyotes and gray foxes and therefore promotes their sympatry in the temperate forests of northern Mexico.

Keywords Activity pattern · Camera traps · Coexistence · Niche overlap · Niche segregation · Sympatry · Wild canids

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Introduction

Understanding processes that maintain the structure of ecological communities is crucial for wildlife conservation programs (Glen and Dickman 2005; Vellend 2016). Inter-specific competition is an important species interaction factor that structures ecological communities (Rosenzweig 1966; Sommer and Worm 2002) and can take two forms: interference and exploitative competition (Case and Gilpin 1974; Schoener 1983). Interference competition can be considered one of the main factors determining intraguild relationships among mammalian species belonging to the order Carnivora (Rosenzweig 1966; Palomares and Caro 1999; Linnell and Strand 2000). These competitive interactions are usually more intense among sympatric species with similar ecological niches (MacArthur and Levins 1967; Morin 1999); therefore, the strategy to promote their coexistence is niche segregation to minimize competition (MacArthur and Levins 1967; Pianka 1969; Schoener 1974a).

Ecological niche segregation has mainly been studied in terms of three axes: spatial, trophic, and temporal (Pianka 1973; Schoener 1974a). Potential competition between sympatric species is largely determined by spatial niche segregation (Kitchen et al. 1999; Palomares and Caro 1999; Grasset et al. 2015) because the development of interactions between species that share the same distribution area involves accessibility to the resources found there (Schoener 1974a; Sih 2005). The trophic niche segregation and distribution of food resources can determine the structure of ecological communities, as well as they provide insight into the potential for intra- and interspecific competition among sympatric species, given the importance of food resources for the species (Colwell and Futuyma 1971; Schoener 1974a; Taper and Marquet 1996; Jones and Barmuta 1998; Costa-Pereira et al. 2019). On the other hand, temporal segregation is important to reduce competitive interactions (Schoener 1974b; Kronfeld-Schor and Dayan 2003) because the species can reduce intraguild competition and predation risk by minimizing temporal overlap with ecologically similar species or with sympatric predators (Schoener 1974b; Carothers and Jakšić 1984). Consequently, spatiotemporal niche partitioning research enables a better understanding of the coexistence mechanisms among wildlife species (Sommer and Worm 2002; Kronfeld-Schor and Dayan 2003; Watabe et al. 2022). Hence, our aim here was to analyze the spatial and temporal axes of the ecological niche for two sympatric species, with the objective of quantifying their segregation and clarifying the mechanisms supporting their coexistence.

In Mexico, coyotes (*Canis latrans*) and gray foxes (*Urocyon cinereoargenteus*) are abundant and widely

distributed; both species are sympatric throughout much of their distribution range in the country (Servín and Chacón 2014; Servín et al. 2014a). Both species belong to the same taxonomic family (*Canidae*) and have similar feeding habits (Bekoff 1977; Fritzell and Haroldson 1982). Studies of intraguild interactions between coyotes and gray foxes in North America have primarily focused on the spatial and trophic axes of their ecological niches, but recently more attention has been directed toward the temporal niche due to advancements in technology, such as camera traps and accelerometers, which enable the definition of the temporal activity patterns of wild animals (Sanchez-Ferrer et al. 2016; Zimmermann et al. 2016; Frey et al. 2017).

The studies on the spatial niche interactions between coyotes and gray foxes have reported both the absence (Neale and Sacks 2001; Chamberlain and Leopold 2005; Parsons et al. 2019, 2022; Rodríguez-Luna et al. 2021a; Allen et al. 2022; Morin et al. 2022) and presence (Fedriani et al. 2000; Farías et al. 2012) of spatial segregation between species. The studies focused on the trophic niche interactions have shown high similarity in feeding habits; the primary difference lies in the fact that coyotes can access larger prey types than gray foxes (Delibes et al. 1989; Fedriani et al. 2000; Neale and Sacks 2001; Larson et al. 2015; Smith et al. 2018; Rodríguez-Luna et al. 2021b; Masters and Maher 2022). In the case of the research focused on the temporal niche interactions between both species, it has been primarily studied in forested and urban systems in North America, reaching divergent conclusions. In studies conducted in natural environments, where human intervention is low or absent, temporal segregation between coyotes and gray foxes was observed (Farías et al. 2012; Lesmeister et al. 2015; Hall et al. 2021; Branney et al. 2023), whereas in areas where anthropogenic influence is evident, temporal activity tends to overlap (LeFlore et al. 2019; Morin et al. 2022; Parsons et al. 2022; Soccorsi and LaPoint 2023; Avrin et al. 2023).

In some cases, temporal interactions between species are inconclusive (Branney et al. 2023) and we still lack a comprehensive understanding of the spatiotemporal niche partitioning between coyotes and gray foxes, which could potentially explain how the coexistence of these species is facilitated in areas where they are sympatric (Kronfeld-Schor and Dayan 2003). Therefore, here we analyzed information generated in 2018 to assess the spatiotemporal interactions between sympatric coyotes and gray foxes in temperate forests in the Sierra Madre Occidental of Durango, Northern Mexico. We aimed to evaluate indicators of ecological niche segregation through two approaches: (i) temporal niche partitioning, measuring the overlap of the daily activity patterns and activity levels; and (ii) spatiotemporal niche partitioning, through temporal co-occurrence analysis and time to encounter analysis. We hypothesized that the temporal and

spatiotemporal niche segregation between coyotes and gray foxes acts as an ecological mechanism that facilitates the coexistence of both species in the study area (Kronfeld-Schor and Dayan 2003; Lesmeister et al. 2015). Thus, we expected a low overlap degree between the daily activity patterns of the species and the emergence of a segregation pattern at the spatiotemporal level, as evidence of the avoidance of agonistic interactions between foxes and coyotes that could promote coexistence.

Materials and methods

Study area

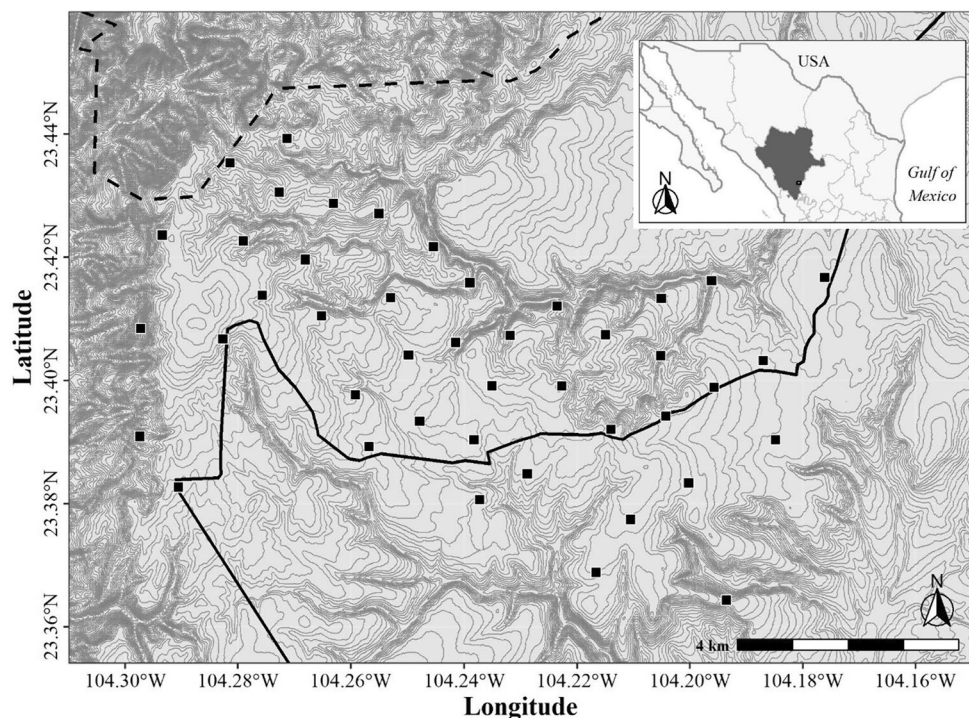
We carried out the fieldwork in the mountain region on the buffer area of La Michilía Biosphere Reserve (MBR), municipality of SÚchil, Durango, Mexico; between the coordinates 23°21'00"–23°28'00" N and 104°09'00"–104°21'00" W (Fig. 1). The MBR is located on the southeastern of the Sierra Madre Occidental and covers *ca.* 70,000 ha, with altitudes that range between 2000 and 2985 m a.s.l. (Halffter 1978). In the MBR sub-humid temperate (Cw) climate predominates, average annual rainfall fluctuates between 700 to 900 mm, and the mean annual minimum and maximum temperatures are 2 °C (in winter) and 22 °C (in summer), respectively (Gadsden and Reyes-Castillo 1991; INEGI 2017). Dominant vegetation types in the MBR are the coniferous forest (*Pinus* spp.) and oak forest (*Quercus* spp.), with areas of natural grasslands (*Bouteloua* spp.), xerophilous

scrubs (dominated by two species: *Arctostaphylos pungens* and *Acacia schaffneri*), and transition zones for these types of vegetation where dominant species vary depending on altitude, geomorphology, and microclimatic conditions (González-Elizondo et al. 1993).

Camera-traps survey

During 2018, we considered four biological seasons described for both species for the implementation of the camera traps survey (Servín and Huxley 1995; Smith et al. 1981): breeding (January–March 15), gestation (March 16–April 30), pup rearing (May 1–July 31), and dispersal or pups' independence (August 1–December 31). At the end of each season, we checked the camera traps, downloaded the images, and replaced the batteries. We set and geo-referenced 43 infrared-triggered camera-trap sites (Cuddeback™ mod E3 Long Range, WI, USA, and Bushnell™ mod HD Essential, KS, USA), we determined the spatial arrangement of the camera traps sites based on the average home range size of focal species (Rovero and Spitalé 2016) in the study area: for coyotes $12.20 \pm 1.74 \text{ km}^2$ (Servín and Huxley 1995; Rodríguez-Luna et al. 2021a) and for gray foxes $5.30 \pm 0.67 \text{ km}^2$ (Servín et al. 2014a; Rodríguez-Luna et al. 2021a). As a result, camera traps were distributed at an average distance of $1.14 \pm 0.20 \text{ km}$ between them, considering a regular grid (Fig. 1). During the fieldwork, we placed camera traps sites at locations with signs of wildlife presence to maximize the capture probability of the target species (Zimmermann and Rovero 2016) and we attached the camera traps to trees at

Fig. 1 Camera-traps array (black squares) in La Michilía Biosphere Reserve (MBR), Durango, Mexico. MBR buffer zone is denoted with black-solid line, MBR core zone is denoted with black dashed line, and contour lines (15 m) are represented by gray solid lines



30–60 cm above ground level. We programmed all camera traps to be active 24 h a day and to burn three images for each trigger, with a 60 s of delay between them. We recorded the species, time, date, and camera-trap site for all images. To maintain statistical independence, we considered as independent events all photographic records of the same species when multiple individuals appeared in the same image or when they were ≥ 30 min apart (Ridout and Linkie 2009).

Data analysis

Factors affecting species interactions may differ depending on the temporal scales; therefore, we evaluated temporal and spatiotemporal niche partitioning through multiple analytical methods (*sensu* Watabe et al. 2022). We evaluated the temporal niche partitioning through the overlap of daily activity patterns and daily activity levels (Ridout and Linkie 2009; Rowcliffe et al. 2014). Besides, we evaluated the spatiotemporal niche partitioning based on: *i*) temporal co-occurrence analysis (Veech 2013), a method that allows evaluating the spatiotemporal responses of species focusing on the date rather than the time of the day by using detection and non-detection data (Watabe et al. 2022); and *ii*) time to encounter analysis (Karanth et al. 2017), which evaluates data with multiple temporal scales (e.g., hours, days, weeks; Watabe et al. 2022) and is conditional on observed space use and temporal activity patterns of the focal species, and thus allows to infer fine-scale behavioral segregation/aggregation patterns (Karanth et al. 2017; Balme et al. 2019).

Overlap of daily activity patterns and daily activity levels. In the tropics, the clock time of sunrise and sunset changes slightly over the year, depending on the distance from the equator and time of year; however, behavior timing should be recorded relative to these events to avoid biased conclusions (Nouvellet et al. 2011). Thus, we used solar time rather than clock time to analyze daily activity patterns. To account for successive changes in the solar position throughout the year, we corrected the clock time of each photographic record with reference to the solar time, according to its specific geographic position and date (*sensu* Nouvellet et al. 2011). Sunrise and sunset times for each survey day were established using information from the United States Naval Observatory (USNO; <https://aa.usno.navy.mil/>). We considered: *(i)* sunrise and sunset, when the geometric center of the sun was on the horizon; *(ii)* twilight, as the average duration of this period throughout the 365 days of the year in the study area, so morning twilight was 1.32 ± 0.07 h before sunrise and evening twilight was 1.32 ± 0.07 h after sunset; *(iii)* daylight period, the time span between sunrise and sunset; and *(iv)* night period, the time span that occurred after the end of evening twilight until morning twilight (Seidelmann and Wilkins 2006). We classified the records as diurnal if they were obtained during daylight hours; nocturnal, if they

were obtained during the night period; or, crepuscular, if they were obtained during morning or evening twilight. To determine the main activity period over 24 h, we counted the number of independent photographic records obtained for each period of the day in the entire sample. We then conducted a Chi-square goodness-of-fit test (McDonald 2014) to examine the null hypothesis of no significant difference between the observed number of records and the expected values, which were based on the proportion of time occupied by each period of the day: 50% diurnal, 39% nocturnal, and 11% crepuscular. When necessary, we performed a post hoc Chi-square goodness-of-fit test (Zar 2013).

To represent daily activity patterns, we converted solar time to radians and represented data using circular statistics. We estimated the daily activity patterns of focal species as a probability density function using kernel density estimation, and then we adjusted the sunrise, noon, and sunset to $\pi/2$, π , and $3\pi/2$, respectively (Ridout and Linkie 2009). Daily activity levels were defined as the proportion of a 24-h daily cycle during which the species appeared to be active, and it is equal to the area under the capture rate curve (Rowcliffe et al. 2014). We determined interspecific temporal overlap using the delta coefficient Δ , which acquires values between 0 (no overlap between density curves) and 1 (complete overlap; Ridout and Linkie 2009). We considered the overlap proportion of daily activity patterns “low” when $\Delta \leq 0.50$ (i.e., partitioning), “moderate” when $0.50 < \Delta \leq 0.75$, and $\Delta > 0.75$ as “high” (Monterroso et al. 2014). Due to the large number of records obtained for both species, we estimated the specific overlap coefficient through the Δ_4 method, which more robustly estimates overlap for samples ≥ 75 registers (see Ridout and Linkie 2009), and we calculated 95% confidence intervals ($CI_{95\%}$) for each Δ value using the bootstrap method with 10,000 repetitions. To statistically evaluate daily activity patterns data, we performed a Rao’s spacing test of uniformity to test whether each underlying distribution appears to deviate from circular uniformity (Rao 1976); we used a non-parametric Mardia-Watson-Wheeler test (MWW) to assess interspecific and intraspecific variation and to determine whether two circular distributions differ significantly from each other (Batschelet 1981), and we performed a Wald Chi-squared to test for significant differences in the activity levels of each pair of distributions (Rowcliffe et al. 2014).

Temporal co-occurrence analysis. We used camera-trap data to test for statistically significant temporal co-occurrence patterns between coyotes and gray foxes by using a matrix containing the detection-non-detection data per night at each camera site for each species (*sensu* Veech 2013). The probabilistic model of species temporal co-occurrence measures the daily co-occurrence as the number of sampling sites where two species co-occur (Griffith et al. 2016). This method employs combinatorics to analytically determine the

probability that the observed frequency of co-occurrence of two species is (i) less than the expected frequency by chance (P_l), (ii) greater than the expected frequency by chance (P_{gt}), or (iii) not different from the expected frequency by chance, if the two species occurred independently from each other in units of one day (Griffith et al. 2016). The observed probability that the two species co-occur at exactly j number of sites is given by the following equation (Griffith et al. 2016):

$$P_j = \frac{\binom{N_1}{j} \times \binom{N - N_1}{N_2 - j}}{\binom{N}{N_2}}$$

For $j=1$ to N_j sites, N_j =number of sites where species #1 occurs, N_2 =number of sites where species #2 occurs, and N =total number of sites that were surveyed (where both species could occur). The observed co-occurrence can be compared to the expected co-occurrence where the latter is the product of the two species' probability of occurrence multiplied by the number of sampling sites (Griffith et al. 2016): $E(N_{j,2})=P(1) \times P(2) \times N$. Probability values can be utilized to determine whether species co-occur significantly less often or significantly more often than expected by chance, according to the following criteria: $P_l < 0.05$ values indicates negative species associations (i.e., partitioning), $P_{gt} < 0.05$ values indicates positive species associations (i.e., co-occurrence), and p -values ≥ 0.05 of any of these parameters indicates random species associations (i.e., species occurred independently from each other; Veech 2013; Griffith et al. 2016; Watabe et al. 2022).

Time to encounter analysis. Following Karanth et al. (2017), we used multi-response permutation procedures to assess the overall behavioral segregation between coyotes and gray foxes. To do this, we analyzed the entire data from 2018. Multiple captures of the same individual less than 30 min apart were collapsed into a single record (sensu Li et al. 2018). For each coyote-detection record, we calculated the minimum time for the subsequent gray fox encounter and vice versa. Thus, for the species pair, a set of observed times to encounter was obtained. To compare this to a random expectation (i.e., a null model representative of neither segregation nor aggregation), we used standard permutation tests (Zar 2013) to compare whether the median-observed time to encounter differed from a simulated distribution of expected time to encounter, calculated by randomly attributing a capture time to each detection of the species at each camera-trap site with the same survey duration (Karanth et al. 2017; Balme et al. 2019; Watabe et al. 2022). We then used this random permutation to re-calculate the time to encounter and repeated this process 10,000 times (Karanth et al. 2017; Watabe et al. 2022). This resulted in 10,000 expected values of detection, which we compared to the

observed value using a standard permutation test. The latter computed the two-tailed probability $P=(n_e + 1) / N$ of getting a value that was more or less than the observed value, where N is the total number expected values and n_e is the number of values lesser or greater than the observed (Cusack et al. 2017). An observed time to encounter larger than expected (assuming species independence) suggests species spatiotemporal segregation, while a smaller value implies species spatiotemporal aggregation (Karanth et al. 2017; Balme et al. 2019).

We considered a significance level of $\alpha=0.05$ for all statistical analyses that considered the overall (annual) data, except for the two-tailed permutation test, where we used a significance level of $\alpha=0.025$. Whenever it was necessary to conduct multiple comparisons (i.e., by biological season), we conducted paired analyses. In these cases, we performed an alpha value correction using the Bonferroni method (Shaffer 1995), based on the number of comparisons tested. We also reported the effect size values (d) as a complement to the statistical significance tests that required such analysis. The effect size expresses the difference between two means in terms of standard deviations and allows for assessing their relevance; the reference values are as follows: low, $d \leq 0.20$; moderate, $0.20 < d \leq 0.50$; high, $0.50 < d \leq 1.30$; very high, $d > 1.30$ (Cohen 1988). We used R version 4.0.2 software (R Core Team 2022) for all statistical analyses. We used “overlap” (Ridout and Linkie 2009), “activity” (Rowcliffe 2022), “circular” (Agostinelli and Lund 2022), and “cooccur” (Griffith et al. 2016) R packages to estimate daily activity patterns and overlap, activity levels, circular statistical analyses, and temporal co-occurrence, respectively.

Results

Throughout the year 2018, we obtained a total sampling effort of 11,814 camera-trap-days. We obtained a total of 1569 independent records for both species combined throughout the entire study: 1041 records for coyotes and 528 records for gray foxes. We presented a detailed description of independent records obtained for both species per biological season in Table 1.

Overlap of daily activity patterns and daily activity levels

For coyotes, we obtained 602 (57.83%) diurnal records, 313 (30.07%) nocturnal records, and 126 (12.10%) crepuscular records. The frequency of records across the 24-h period differed significantly, although the value of the effect size was low ($\chi^2_{(2)}=35.21$, $p < 0.001$; $d=0.18$); diurnal records were greater than expected by chance (post hoc $\chi^2_{(1)}=25.52$, $p < 0.001$; $d=0.17$). In the case of gray foxes, we obtained

Table 1 Results of the Mardia-Watson-Wheeler test for the intra- and interspecific comparison of kernel density distributions of the daily activity patterns of coyotes and gray foxes among biological seasons

in 2018, within temperate forests of La Michilía Biosphere Reserve, Durango, Mexico

		Coyotes				Gray foxes			
		Breeding	Gestation	Pup-rearing	Dispersal	Breeding	Gestation	Pup-rearing	Dispersal
		<i>n</i> = 213	<i>n</i> = 252	<i>n</i> = 341	<i>n</i> = 235	<i>n</i> = 80	<i>n</i> = 100	<i>n</i> = 88	<i>n</i> = 260
Coyotes	Breeding	–							
	Gestation	<i>p</i> = 0.33 <i>d</i> = 4.08	–						
	Pup-rearing	<i>p</i> < 0.001 <i>d</i> = 2.39	<i>p</i> = 0.02 <i>d</i> = 6.77	–					
	Dispersal	<i>p</i> = 0.16 <i>d</i> = 1.83	<i>p</i> = 0.58 <i>d</i> = 2.31	<i>p</i> < 0.001 <i>d</i> = 4.39	–				
Gray foxes	Breeding	<i>p</i> < 0.001 <i>d</i> = 3.03	<i>p</i> < 0.001 <i>d</i> = 0.63	<i>p</i> < 0.001 <i>d</i> = 5.63	<i>p</i> < 0.001 <i>d</i> = 1.46	–			
	Gestation	<i>p</i> < 0.001 <i>d</i> = 5.99	<i>p</i> < 0.001 <i>d</i> = 2.40	<i>p</i> < 0.001 <i>d</i> = 8.89	<i>p</i> < 0.001 <i>d</i> = 4.50	<i>p</i> = 0.17 <i>d</i> = 2.49	–		
	Pup-rearing	<i>p</i> < 0.001 <i>d</i> = 1.39	<i>p</i> < 0.001 <i>d</i> = 5.23	<i>p</i> < 0.001 <i>d</i> = 0.72	<i>p</i> < 0.001 <i>d</i> = 3.13	<i>p</i> = 0.66 <i>d</i> = 3.70	<i>p</i> = 0.31 <i>d</i> = 6.31	–	
	Dispersal	<i>p</i> < 0.001 <i>d</i> = 2.78	<i>p</i> < 0.001 <i>d</i> = 0.68	<i>p</i> < 0.001 <i>d</i> = 5.09	<i>p</i> < 0.001 <i>d</i> = 1.27	<i>p</i> = 0.18 <i>d</i> = 0.80	<i>p</i> = 1.46 <i>d</i> = 2.60	<i>p</i> = 0.23 <i>d</i> = 3.71	–

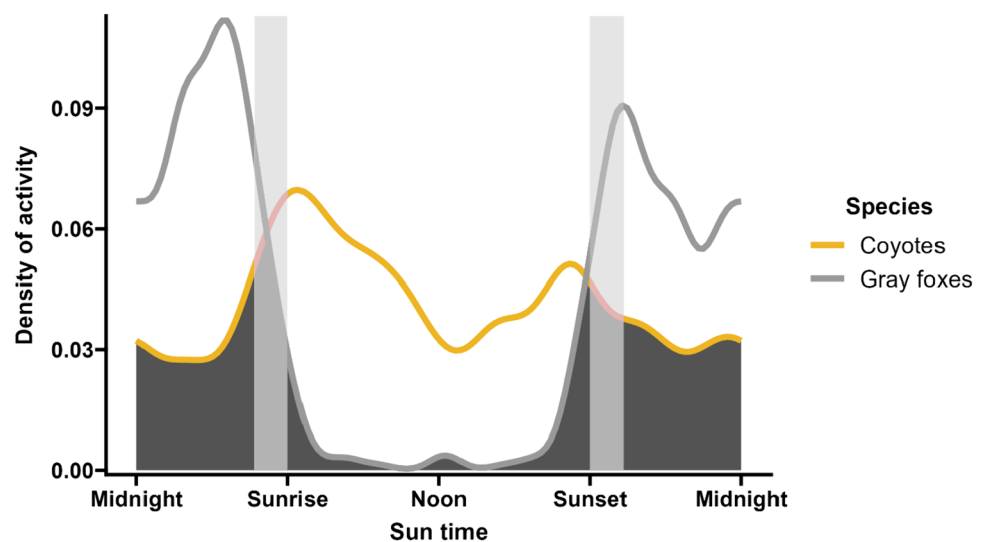
The sample size is denoted with *n* symbol. A Bonferroni-adjusted alpha value was used based on the correction for the number of comparisons tested. Statistically significant values ($p \leq 0.002$) were indicated in bold. The reference values for Cohen's effect size (*d*), which expresses the difference between two means in terms of standard deviations, are as follows: low, $d \leq 0.20$; moderate, $0.20 < d \leq 0.50$; high, $0.50 < d \leq 1.30$; very high, $d > 1.30$.

37 (7.01%) diurnal records, 409 (77.46%) nocturnal records, and 82 (15.53%) crepuscular records. The frequency of records across the 24-h periods varied significantly, revealing a high effect size ($\chi^2_{(2)} = 405.32$, $p < 0.001$; $d = 0.62$); specifically, nocturnal records were greater than expected by chance in the comparison (post hoc $\chi^2_{(1)} = 328.33$, $p < 0.001$; $d = 0.56$).

Overall daily activity pattern for coyotes was not uniform (Rao's test; $U = 158.75$, $p < 0.001$), it displayed two

activity peaks (bimodal) during the daylight period and showed lesser activity during the night period (Fig. 2). The gray foxes drastically restricted its activity during daylight period, the overall daily activity pattern of the species was not uniform (Rao's test; $U = 203.02$, $p < 0.001$) and it was also bimodal, with two activity peaks during the night period (Fig. 2). The MWW test indicated significant differences between daily activity patterns from both species ($W = 373.83$, $d.f. = 2$, $p < 0.001$), with a very high effect size

Fig. 2 Daily activity patterns and overlap (dark gray area) between coyotes (yellow line) and gray foxes (light gray line) in 2018 in temperate forests in La Michilía Biosphere Reserve, Durango, Mexico. Overlap index was $\Delta_4 = 0.49$ ($CI_{95\%}$: 0.45–0.53). The light-gray area indicates morning and evening twilight periods



($d=2.27$). The overlap of the daily activity patterns from coyotes and gray foxes was low: $\Delta_4=0.49$ ($CI_{95\%}$: 0.45–0.53; Fig. 2). Overall daily activity levels of coyotes were higher ($Act=0.60$; $CI_{95\%}$: 0.52–0.67) and differed significantly (Wald test; $Dif.=0.23$, $W=22.44$, $p<0.001$) with very high effect size ($d=2.25$) from those of gray foxes ($Act=0.37$; $CI_{95\%}$: 0.31–0.42). That is, we detected segregation in the temporal niche between both species.

We performed the Rao's spacing test to assess the uniformity of the distributions of daily activity patterns for both species in each of the biological seasons. In all cases, the test values were highly significant ($p<0.001$), indicating non-uniform distributions in every season. The (U) values for Rao's test ranged between 151.03 and 171.65 for coyotes and between 205.12 and 220.69 for gray foxes. The intraspecific comparison of the daily activity patterns showed that the coyotes displayed slight variations across biological seasons (Fig. 3). There was no evidence of significant differences between the daily activity patterns among breeding, gestation, and dispersal seasons; however, the pup-rearing season showed significant differences compared with the rest of the biological seasons (Table 1; Fig. 3). In the case

of gray foxes, there was no evidence of significant differences among daily activity patterns throughout biological seasons (Table 1; Fig. 3). On the other hand, the interspecific analysis revealed significant differences between the daily activity patterns of both species under any level of comparison across biological seasons (Table 1). The overlap values of daily activity patterns across biological seasons ranged between 0.44 ($CI_{95\%}$: 0.36–0.51) during pup-rearing season and 0.56 ($CI_{95\%}$: 0.48–0.65) during the breeding season (Fig. 3). Daily activity levels across biological seasons for coyotes ranged from $Act=0.48$ ($CI_{95\%}$: 0.35–0.63) to $Act=0.61$ ($CI_{95\%}$: 0.47–0.71), while for the gray foxes they ranged from $Act=0.35$ ($CI_{95\%}$: 0.25–0.42) to $Act=0.40$ ($CI_{95\%}$: 0.31–0.43; Table 2). For both species, there were no significant differences in intraspecific daily activity levels among biological seasons. However, interspecific comparison revealed that the daily activity levels exhibited by coyotes during the gestation season were significantly higher compared to the daily activity levels of gray foxes throughout all biological seasons (Table 2). In all comparisons, where significant differences were observed at both intra- and interspecific levels for coyotes and gray foxes,

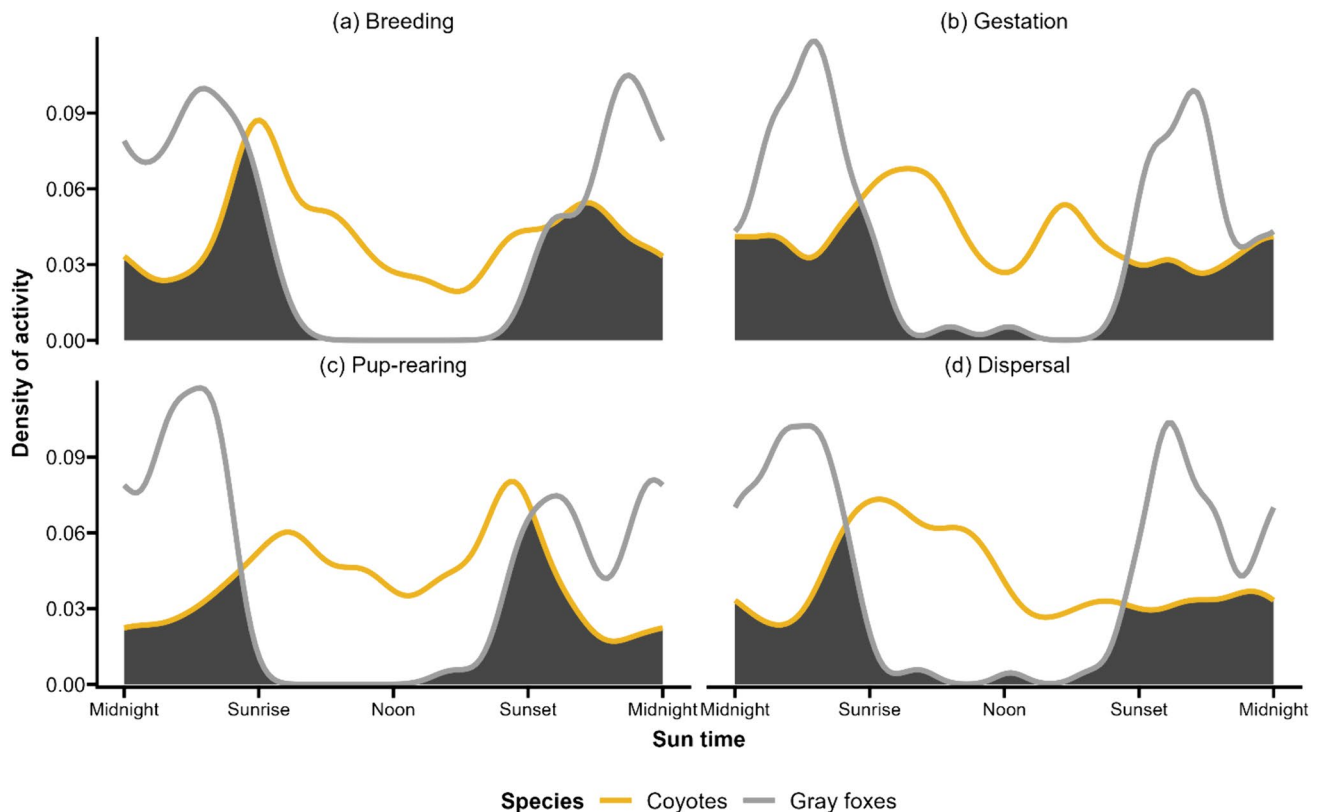


Fig. 3 Daily activity patterns and overlap (dark gray area), through biological seasons in 2018, between coyotes (yellow line) and gray foxes (light gray line) in temperate forests in La Michilía Biosphere Reserve, Durango, Mexico. Overlap values were: **a** breeding

($\Delta_4=0.56$; $CI_{95\%}$: 0.48–0.65); **b** gestation ($\Delta_4=0.50$; $CI_{95\%}$: 0.43–0.59); **c** pup-rearing ($\Delta_4=0.44$; $CI_{95\%}$: 0.41–0.54); and **d** dispersal ($\Delta_4=0.47$; $CI_{95\%}$: 0.36–0.51)

Table 2 Wald Chi-squared test for intraspecific and interspecific variations in activity levels of coyotes and gray foxes in 2018 among biological periods in temperate forests in La Michilía Biosphere Reserve, Durango, Mexico

		Coyotes				Gray foxes			
		Breeding Act=0.48 (0.35–0.63)	Gestation Act=0.61 (0.47–0.71)	Pup-rearing Act=0.52 (0.41–0.64)	Dispersal Act=0.57 (0.44–0.66)	Breeding Act=0.40 (0.27–0.44)	Gestation Act=0.35 (0.25–0.42)	Pup-rearing Act=0.35 (0.25–0.43)	Dispersal Act=0.40 (0.31–0.43)
Coyotes	Breeding	—							
	Gestation	$p=0.16$	—						
	Pup-rearing	$p=0.67$	$p=0.27$	—					
	Dispersal	$p=0.33$	$p=0.60$	$p=0.54$	—				
Gray foxes	Breeding	$p=0.34$	$p=0.002$	$p=0.05$	$p=0.01$	—			
	Gestation	$p=0.14$	$p<0.001$	$p=0.02$	$p=0.006$	$p=0.45$	—		
	Pup-rearing	$p=0.16$	$p<0.001$	$p=0.03$	$p=0.008$	$p=0.50$	$p=0.95$	—	
	Dispersal	$p=0.34$	$p<0.001$	$p=0.05$	$p=0.01$	$p=0.92$	$p=0.34$	$p=0.71$	—

Activity level is denoted by *Act* and 95% confidence intervals are shown in parentheses. The effect size values for this test are the same as those displayed in Table 1. A Bonferroni-adjusted alpha value was used based on the correction for the number of comparisons tested. Statistically significant values ($p \leq 0.002$) were indicated in bold. The reference values for Cohen's effect size (d), which expresses the difference between two means in terms of standard deviations, are as follows: low, $d \leq 0.20$; moderate, $0.20 < d \leq 0.50$; high, $0.50 < d \leq 1.30$; very high, $d > 1.30$

encompassing daily activity patterns and activity levels, the magnitude of the difference was substantial, with high or very high effect size values ($d \geq 0.63$) for the corresponding statistical tests, as depicted in Table 1.

Temporal co-occurrence analysis

For the overall data, the temporal co-occurrence analyses showed that the observed daily co-occurrence of coyotes and gray foxes was not significantly different from that expected by chance, indicating a random species association at the scale of daily visits (Table 3). The random species association was also evident during almost all biological seasons, except for the dispersal season when the daily co-occurrence

pattern showed aggregation ($p=0.001$) at the scale of daily visits, albeit with a low effect size value ($d=0.11$; Table 3).

Time to encounter analysis

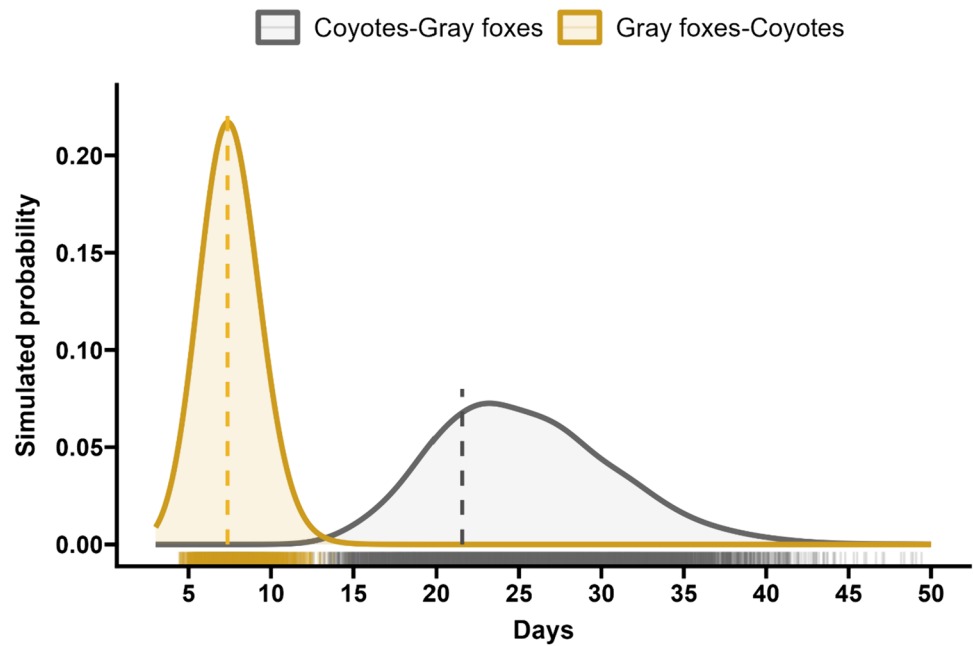
We observed a minimum time to encounter median of 21.56 days ($n=867$) for gray foxes after the detection of coyotes (i.e., coyotes-gray foxes), and a median of 7.37 days ($n=449$) for coyotes after the detection of gray foxes (i.e., gray foxes-coyotes; Fig. 4). On the other hand, the median of the random permutations for coyotes-gray foxes was 24.70 days and for gray foxes-coyotes was 7.43 days. The probability of obtaining a value greater or less than the observed time to encounter median was not significant for both, in the case of the coyotes-gray foxes ($p=0.74$ and

Table 3 Daily temporal co-occurrence analysis between coyotes and gray foxes, for 2018 overall data and by biological seasons, in temperate forests in La Michilía Biosphere Reserve, Durango, Mexico

Comparison level	Observed co-occurrence	Expected co-occurrence	P_{lt}	P_{gt}	Effect size (d)	Pattern
Overall data	33.00	32.98	1.00	0.99	0.28	Random
<i>Biological season</i>						
Breeding	14.00	12.10	0.94	0.18	0.04	Random
Gestation	6.00	6.00	0.67	0.66	0.03	Random
Pup-rearing	9.00	7.40	0.97	0.19	0.04	Random
Dispersal	28.00	23.60	0.99	0.001	0.11	Aggregation

The probability that the observed frequency of co-occurrence of the species is less than the expected frequency by chance (segregation) is denoted with P_{lt} ; the probability that the observed frequency of co-occurrence is greater than the expected (aggregation) is denoted with P_{gt} . If, in any case, no significant differences from the expected frequency by chance are observed, the two species occurred independently from each other. We considered a significance level of $\alpha=0.05$ for the overall data analysis. A Bonferroni-adjusted alpha value was used based on the correction for the number of comparisons tested. Statistically significant values ($p \leq 0.01$) were indicated in bold. The reference values for Cohen's effect size (d), which expresses the difference between two means in terms of standard deviations, are as follows: low, $d \leq 0.20$; moderate, $0.20 < d \leq 0.50$; high, $0.50 < d \leq 1.30$; very high, $d > 1.30$

Fig. 4 Multi-response permutation procedures for time to encounter analysis between coyotes and gray foxes in 2018 in temperate forests in La Michilía Biosphere Reserve, Durango, Mexico. Coyotes-gray foxes (gray) represents that gray foxes were detected after coyotes, and gray foxes-coyotes (yellow) represents the opposite case. The dashed-vertical lines represent the observed time to encounter median between the two species for both cases: Coyotes-gray foxes = 21.56 days ($n = 867$) and gray foxes-coyotes = 7.37 days ($n = 449$). The rug plot illustrates the 10,000 medians of the random permutations, and the area under the curve represents the distribution estimated from them



$p = 0.26$, respectively) and for gray foxes-coyotes ($p = 0.52$ and $p = 0.48$, respectively). Therefore, no behavioral fine-scale spatiotemporal segregation or aggregation was detected.

Discussion

At the scale of our analysis, the intensive sampling with camera traps provided information for a detailed understanding of the spatiotemporal interactions between coyotes and gray foxes by which these sympatric species coexist in temperate forests of northern Mexico.

Considering the temporal partitioning approach, our prediction about a low overlap degree between the daily activity patterns of the species was supported. We found that the daily activity patterns of coyotes and gray foxes were significantly different. In addition, we found that the difference between them was very high, resulting in low overlap, signaling evident temporal segregation between both species. Coyotes have been described to exhibit multiple periods of activity throughout the day with mainly crepuscular and nocturnal activity along its distribution range (Bekoff 1977; Andelt and Gipson 1979; Andelt 1985; Gese et al. 1996; Gese and Bekoff 2004; Young et al. 2006; Servín et al. 2014b). However, here we determined that the daily activity pattern of coyotes was predominantly diurnal, therefore daily activity pattern appears to be context dependent. Daily activity patterns change seasonally, or in response to human disturbance and persecution (Kitchen et al. 2000). In places with significant human presence, coyotes tend to be mainly nocturnal to reduce encounters with humans, whereas in

places with limited or no anthropogenic disturbance coyotes tend to be more active during the daylight period (List 1998; Kitchen et al. 2000; McClellenn et al. 2001; Way et al. 2004; Lendrum et al. 2017; Reilly et al. 2017; Smith et al. 2018; Avrin et al. 2023). We thus consider that the diurnal activity pattern of coyotes in the study area reflects the positive effect of conservation programs implemented in the MBR-protected area, where anthropogenic activities are limited, and the human presence is very reduced. In addition, the diurnal activity patterns of coyotes can be explained by the mesopredator release effect (Crooks and Soulé 1999; Prugh et al. 2009; Avrin et al. 2023). Mesopredators can develop behavioral adaptations that include an expansion of their daily activity patterns in the absence of top predators (Hudgens and Garcelon 2011; Shores et al. 2019; Avrin et al. 2023). This behavioral adaptation by coyotes has been demonstrated in Northamerican areas where wolves (*Canis lupus*) have been reintroduced, as they represent dominant predators (Switalski 2003; Levi and Wilmers 2012; Newsome and Ripple 2014). In areas where both canids coexist, coyotes adjust their daily activity patterns to minimize competitive interactions and reduce the risk of mortality associated with wolves (Arjo and Pletscher 1999; Atwood and Gese 2008; Merkle et al. 2009; Miller et al. 2012; Shores et al. 2019). An important factor to consider in our study is that coyotes do not have to avoid competitive interactions with a top predator that have been extirpated from the temperate forests in the MBR region: the Mexican gray wolf (*Canis lupus baileyi*), extirpated in the 1970s (Ceballos and Navarro 1991). However, it is not possible to probe this hypothesis because there is no available data on the daily activity patterns of the Mexican gray wolf before

the extirpation. When we analyzed seasonally, daily activity patterns of coyotes were similar during three of the four biological seasons and there was no evidence of significant differences among breeding, gestation, and dispersal seasons. However, during the pup-rearing season, the daily activity pattern of coyotes was significantly different from those of the remaining seasons because the coyotes displayed their highest rate of diurnal activity of the year. The increase in diurnal activity during this period is related to reproductive behavior; namely: females entering oestrus, triggering the active search for a mate, courtship behavior, large increase in aggressive behavior, long-distance traveling displayed to provide enough food for pup rearing (Bekoff 1977; Bekoff and Wells 1980; Servín et al. 2003).

Coyotes' diurnal activity contrasts with the nocturnal daily activity pattern of the gray foxes. We observed that daily activity patterns of gray foxes were consistent throughout the biological seasons and there was no evidence of significant differences. Nocturnal activity pattern of gray foxes has been reported throughout its distribution in North America (Fritzell and Haroldson 1982; Harrison 1997; Fedriani et al. 2000; Fuller and Cypher 2004; Farías et al. 2012; Servín and Chacón 2014; Gómez-Ortiz et al. 2019). Evidence supporting the nocturnal activity pattern of gray foxes shows that the presence and abundance of superior competitors, coyotes in this case, limit gray fox abundance and daily activity pattern frame to minimize the likelihood of intra-guild predation (Crooks and Soulé 1999; Henke and Bryant 1999; Atwood et al. 2011; Hudgens and Garcelon 2011; Farías et al. 2012).

The differences between the daily activity patterns of coyotes and gray foxes throughout the year and during biological seasons were substantial and significant, as indicated by the effect size values for the comparisons. The differentiated use of the temporal resource, in this case, during the daylight period, leads to temporal niche segregation between both species. This strategy of temporal partitioning represents a mechanism that promotes the coexistence between the species (Schoener 1974b; Kronfeld-Schor and Dayan 2003), as has also been demonstrated among pairs of other wild canid species in North America: wolves-coyotes (Arjo and Pletscher 1999; Levi and Wilmers 2012; Newsome and Ripple 2014; Shores et al. 2019), wolves-red foxes (*Vulpes vulpes*; Fowler et al. 2021), coyotes-red foxes (Lesmeister et al. 2015; Klauder et al. 2021), and coyotes-kit foxes (*Vulpes macrotis*; Hall et al. 2021; Deatherage et al. 2022).

In the case of coyotes and gray foxes, temporal segregation is likely to occur due to differences in the foraging strategies of both species, dependent on the type and availability of food items (Hunter 2020). However, proving this in future research may be challenging due to the high similarity in their feeding habits in the study area (Delibes et al. 1989; Rodríguez-Luna et al. 2021b). On the other hand,

if we consider that the size of the species involved in the competition process determines the results of competitive interactions, then larger carnivores will dominate smaller carnivores (Polis et al. 1989; Donadio and Buskirk 2006; Ripple et al. 2014; Wallach et al. 2015). Therefore, gray foxes avoid lethal encounters with coyotes through temporal niche segregation, because coyotes can kill sympatric species of foxes to reduce interspecific competition (Johnson et al. 1996; Cypher and Spencer 1998; Sovada et al. 1998; Kitchen et al. 1999; Fedriani et al. 2000; Weston and Brisbin 2003; Farías et al. 2005; Cherry et al. 2016). We observed similarities in the extents of their temporal overlaps across all biological seasons, with a higher occurrence during the breeding season. During this period, both species actively search for mates and engage in courtship behaviors, contributing to the increased temporal overlap (Bekoff 1977; Bekoff and Wells 1980; Servín et al. 2003). On the other hand, during the pup-rearing season, the lowest overlap proportion was observed. This is when both canids are dedicated to caring for and feeding their litters, and females spend a greater amount of time around their dens, traveling with pups across their home ranges (Nicholson et al. 1985; Bekoff and Wells 1980; Servín and Huxley 1995; Chamberlain and Leopold 2002; Gese and Bekoff 2004; Fuller and Cypher 2004; Servín et al. 2003).

The temporal segregation between coyotes and gray foxes, presented as an ecological strategy that reduces agonistic interactions and promotes species coexistence, has been demonstrated in natural environments, primarily in North America, such as deserts (Atwood et al. 2011; Hall et al. 2021), chaparral and scrubland areas (Farías et al. 2012), and forested systems (Lesmeister et al. 2015; Moll et al. 2021; Branney et al. 2023). However, it is important to note that recent studies have provided evidence that the outcome of temporal interactions between coyotes and gray foxes depends on limiting environmental factors. In distribution areas characterized by gradients from natural to urban habitat, with high human presence (i.e., anthropogenic development zones), temporal segregation between coyotes and gray foxes is not observed (LeFlore et al. 2019; Morin et al. 2022; Parsons et al. 2022; Soccorsi and LaPoint 2023; Avrin et al. 2023). The evidence indicates that the presence of human activity (Wang et al. 2015; Soccorsi and LaPoint 2023; Avrin et al. 2023), changes in land use (Morin et al. 2022; Parsons et al. 2022; Soccorsi and LaPoint 2023), and resource limitations (LeFlore et al. 2019; Parsons et al. 2019; Farmer et al. 2021) may lead to an increase in temporal overlap between both species. In the scenario of high-temporal overlap, interspecific competition may be intensified (Parsons et al. 2019). Consequently, species are likely to adopt alternative niche segregation strategies (Schoener 1974b), including fine-scale spatial segregation (Farmer et al. 2021), less territorial behaviors (Parsons et al. 2022), variations

in foraging activities (Hansen et al. 2020), and mobility between habitat patches (Lesmeister et al. 2015). Therefore, it is necessary to continue investigating how habitat variables influence the coexistence between coyotes and gray foxes.

The coyote daily activity level estimated here was within the range reported for the species (38–67%) in Eastern Connecticut (O'Connor and Rittenhouse 2017). In contrast, the daily activity levels of gray foxes that we estimated were much lower than the values reported for Southern California (56–60%) estimated by radiotelemetry (Farías et al. 2012). Although, differences in activity levels between coyotes and gray foxes may also be reflected in temporal segregation, there is still a need for research focused on discerning how potentially the activity levels can be reflected in behaviors that allow niche segregation between sympatric species.

Considering the spatiotemporal approach, we did not find support for the expected results. The spatiotemporal analysis of the overall data indicated that coyotes and gray foxes occurred independently of each other; thus, no segregation was observed at this level. Our findings coincide with information from studies that have noted the absence of segregation at the level of fine-scale co-occurrence patterns, (Lesmeister et al. 2015; Rich et al. 2018; Parsons et al. 2019; Veals et al. 2021). Even the absence of segregation between both species has been demonstrated at a broader spatial scale (Neale and Sacks 2001; Chamberlain and Leopold 2005; Rodríguez-Luna et al. 2021a). In the absence of spatiotemporal segregation, the importance of segregation in other niche axes, such as trophic and temporal dimensions, has been highlighted to promote coexistence between coyotes and gray foxes (Neale and Sacks 2001; Chamberlain and Leopold 2005; Lesmeister et al. 2015; Rich et al. 2018; Parsons et al. 2022; Rodríguez-Luna et al. 2021a). Although no partitioning or aggregation patterns were observed considering the overall data, daily co-occurrence probabilistic analysis detected that both coyotes and gray foxes significantly aggregated only in dispersal season. This observation suggests that specific ecological conditions may emerge during this biological season, potentially enhancing the likelihood of co-occurrence. Potentially, this includes the influx of new individuals from both coyotes and gray foxes traversing the study area, as young individuals disperse from their parental groups, explore new distribution sites, and seek out their own territories.

All our findings about the spatiotemporal interactions between coyotes and gray foxes provide evidence that ecological segregation occurred in the temporal niche rather than in the spatiotemporal niche of species. Thus, the temporal niche segregation represents an ecological strategy that facilitates the coexistence of both species and therefore promotes their sympatry in the temperate forests of Mexico. However, it is important to consider that our conclusions

may have a limited scope because the bounded sampling timeframe of a year is subject to stochastic factors that could affect interspecific relationships between both species. In addition, although we did not identify all factors involved, it should be considered that the coexistence between coyotes and gray foxes can also be facilitated by segregation among different ecological niche dimensions. Identified ecological segregation strategies include differentiated habitat use (Neale and Sacks 2001; Rodríguez-Luna et al. 2021a) and trophic segregation, involving differences in prey type, consumption frequency, and niche breadth (Delibes et al. 1989; Fedriani et al. 2000; Cunningham et al. 2006; Larson et al. 2015; Rodríguez-Luna et al. 2021b).

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by César R. Rodríguez-Luna, Jorge Servín, David Valenzuela-Galván, and Rurik List. The first draft of the manuscript was written by César R. Rodríguez-Luna and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The data set generated and used in this study are available upon reasonable request to the corresponding author.

Declarations

Competing interests The authors have no competing interests to declare.

Ethics approval Camera trapping was conducted under applicable laws, guidelines, and regulations. Fieldwork conducted in La Michilía Biosphere Reserve was covered by scientific research license number SGPA/DGVS/12685/18 granted to the corresponding author (JS) issued by the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT) of México. Whenever necessary, we also had the landowners' written permission to conduct fieldwork on private properties.

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