

HABITAT USE BY GRAY FOX (Urocyon cinereoargenteus, CARNIVORA: CANIDAE) IN AN ANTHROPIZED TROPICAL ECOSYSTEM †

[USO DE HÁBITAT POR ZORRO GRIS (Urocyon cinereoargenteus, CARNIVORA: CANIDAE) EN UN ECOSISTEMA TROPICAL ANTROPIZADO]

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SUMMARY

Background. Gray fox, *Urocyon cinereoargenteus* is tolerant to habitat disturbance, but the biotic and abiotic factors that determine the selection of space in the subperennial medium forest (SMF) with different degrees of anthropization are not known, which is relevant to explain a fraction of an animal's niche. **Objective.** We described the use of habitat by the gray fox, in four habitat units in the SMF, with different degrees of anthropization. **Methodology.** We classified four habitat units with vegetation structure criteria: Sugar canecoffee plantation, Coffee plantation-forest, forest and Coffee plantation, where we evaluated parameters such as number of carnivores and potential prey and plant cover. In addition, we evaluated the altitude, temperature, precipitation and evaporation. Using indirect techniques, we obtained gray fox records in each habitat unit, which we related to biotic and abiotic parameters through a χ^2 test and a partial least squares analysis; we applied a dendrogram to estimate the similarity of use of the habitats; and a response surface-based model to describe habitat use. **Results.** We associated fourteen independent records of gray fox and six of them with the Coffee plantation-SMF habitat, where it was correlated with temperature. **Implications.** Shrub coverage, the number of competitors and evaporation in SMF and Coffee plantation-SMF are factors correlated with a low number of gray fox may be using open habitats for hunting and closed habitats to seek refuge while it is not active.

Key words: agroecosystems; abiotic and biotic conditions; coffee plantation; response surface-based model.

RESUMEN

Antecedentes. El zorro gris, *Urocyon cinereoargenteus* es tolerante a la perturbación del hábitat, pero no se conocen los factores bióticos y abióticos que determinan la selección del espacio en la selva mediana subperennifolia (SMS) con distinto grado de antropización, lo cual es relevante para explicar una fracción de su nicho. Objetivo. Se describió el uso de hábitat por el zorro gris en cuatro unidades de hábitat en la SMS con distinto grado de antropización. Metodología. Se clasificaron cuatro unidades de hábitat mediante criterios de la estructura de la vegetación: Cañal-Cafetal, Cafetal-Selva, Selva y Cafetal, donde se evaluaron los parámetros como número de carnívoros, presas potenciales y cobertura vegetal; la altitud, temperatura, precipitación y evaporación fueron parámetros abióticos evaluados. Usando técnicas indirectas, en cada unidad de hábitat se obtuvieron registros del zorro gris que se relacionaron con los parámetros bióticos y abióticos mediante una prueba

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Copyright © the authors. Work licensed under a CC-BY 4.0 License. https://creativecommons.org/licenses/by/4.0/ ISSN: 1870-0462. de χ^2 y un análisis de mínimos cuadrados parciales; un dendograma fue aplicado para estimar la similitud del uso de los hábitats; un modelo basado en superficie de respuesta fue aplicado para describir el uso de hábitat. **Resultados.** Catorce registros independientes de zorro gris (seis de ellos se asociaron al hábitat cafetal-selva), estuvieron correlacionados con la temperatura del hábitat. **Implicaciones.** La cobertura arbustiva, el número de competidores, la evaporación en la selva y en el cafetal-selva, fueron factores donde se registró un bajo número de presencias del zorro gris. **Conclusión.** El zorro gris en este ecosistema antropizado usa espacios abiertos para cazar y áreas cerradas para buscar refugio mientras no está activo.

Palabras clave: agroecosistemas; condiciones abióticas y bióticas; plantación de café; modelo basado en superficie-respuesta.

INTRODUCTION

We defined habitat as the space that meets the biotic conditions necessary and abiotic for the development of a population (Storch, 2002). Habitat use refers to the physical space where the species is present, while the potential habitat is the physical space with suitable conditions, but the species is not present either due to environmental, demographic, biogeographic or vagility factors (Cooperrider et al., 1986). Studies of habitat use by a species include examining the environmental conditions (Chamberlain and Leopold, 2000). The overlap of space with other predators (Chamberlain and Leopold, 2005), changes in the ecological niche (Armenta-Méndez et al., 2018), landscape structure and Fritzell, 1984), (Haroldson habitat fragmentation (Hernández-Camacho and López-González, 2009) and anthropogenic intervention (Harrison, 1993; Lombardi et al., 2017), can affect the behavior pattern and population dynamics of the species in its habitat (Farías et al., 2012) and, consequently, changes in the selection and use of spaces in its distribution area (Cooper et al., 2012).

For a population of wildlife to survive in natural conditions it is necessary to search for resources that can be granted by habitat components: abiotic (physicochemical component such as temperature, moisture, precipitation, sunlight, atmospheric pressure, altitude, type of soil, pH, water, CO₂, minerals, among others) and biotic (microorganisms, microalgae, fungi, plants, animals and their interactions) (Delfín-Alfonso et al., 2014). These components are closely related to each other and their fluctuations can induce changes that affect the structure and availability of resources in the habitat (Storch, 2002). Understanding how a population selects (Farías et al., 2012) and uses the space based on the disposition and availability of biotic and abiotic resources (Chamberlain and Leopold, 2000), is essential information in the design of conservation plans (Storch, 2002).

To carry out studies on the use of the habitat of a population, a significant sampling is required over a considerable time, to obtain an appropriate sample size that allows making inferences towards the population and its relationship with the components of the habitat (Gallina, 1993). It is important that the preselection of the variables to be measured in the

habitat is based on biological characteristics, population aspects and the role that the species plays in the ecosystem, since these will improve the estimation of habitat preference for the species (Hernández-Camacho and López-González, 2009). For example, availability and disposition of food resources, competition (inter and intraspecific), altitude, temperature, moisture, vegetation cover, are habitat components that can determine how the presence, absence or abundance of an animal is associated with spaces where the habitat favors ideal conditions for its development and survival (Cooperrider, 1986).

The gray fox (Urocyon cinereoargenteus) is a mesocarnivore (Lesmeister et al., 2015) that has been little studied in México (Aranda, 2012). Studies of this specie have focused on their ecology, parasitology, home environment, diet and abundance (Arnaud and Acevedo, 1990; Castellanos et al., 2003; Gallina et al., 2016; Servín et al., 2014). This specie is a habitat generalist, since its presence has been recorded in a broader dimension of the types of habitat that occur in Mexico and throughout its range in the Americas, due to its plasticity to adapt to different habitats (Kapfer and Kirk, 2012) and can expand its feeding spectrum (Hockman and This Chapman, 1983). has made U. cinereoargenteus to be an opportunistic carnivore, because it eats domestic animals (chickens, mainly), and human organic waste in urban areas, but this generates human-mesocarnivore conflicts (Clark, 2011) and, consequently, this specie can present patterns of space selection depending on the level of disturbance of its habitat and human presence (Temple et al., 2010).

To study the use of the gray fox habitat, we recorded a series of habitat components and we related to the frequency/presence of the specie. These measurements could describe the way in which individuals from а population of U. cinereoargenteus use space according to the characteristics of the abiotic-biotic component of the habitat to meet their biological needs (Cooper et al., 2012; Deuel et al., 2017a). Registering the habitat use pattern of this specie contributes to the knowledge about the basic conditions of its ecological niche in a locality inside its geographic range (Deuel et al., 2017a; Deuel et al., 2017b; Armenta-Méndez et al., 2018). We described the use of habitat of *U. cinereoargenteus* in a fraction of the Selva Mediana Subperennifolia (SMF or Medium Sub-evergreen Forest) with different degrees of human intervention, in Atoyac, Veracruz, Mexico.

MATERIAL AND METHODS

Description of the study area

This study was carried out in the locality Rancho San Fermín, municipality of Atoyac, Veracruz, Mexico, located at the coordinates of 18°54'03.29" N and 96°48'21.40" W, with an average altitude of 537 metres above mean sea level (mamsl), during 10 field trips from December 2018 to May 2019. It has a warm-humid climate with abundant rains in summer and an average annual temperature of 26°C and precipitation of 1,882 mm. The region has geological irregularities such as cliffs and ravines forming the watershed of the Atoyac River, which joins the Chiquihuite River (INEGI, 2015). The predominant vegetation of biogeographic region Sierra Madre Oriental where the study area is located, is mainly composed of SMF (Rzedowski, 1988), which is characterized by the presence of abundant populations of lichens, mosses, pteridophytes, phanerogams plants, epiphytic lianas and ferns. Among the upper floors are red cedar (Cedrela odorata), white oak (Quercus virginiana), mulatto stick (Bursera simaruba), jocote (Spondias purpurea), ficus tree (Ficus carica), ramón (Brosimum alicastrum), rubber (Castilla elastica),

izote (*Yucca elephantipes*) and fruit trees such as mango tree (*Mangifera indica*), orange (*Citrus x aurantium*), mamey (*Pouteria sapota*), avocado (*Persea americana*), pomarosa (*Syzygium jambos*), among others (Rzedowski, 1988). The surface of this type of vegetation in the study region has decreased considerably due to the progress of agricultural activities, mainly for the establishment of coffee and sugarcane crops (INEGI, 2015), due to the immoderate logging of timber species for domestic use (firewood, housing construction, fence posts) and for the manufacture of furniture (Guzmán-Pacheco, 2014).

Delimitation of habitat units

We made a classification of habitat units based on criteria of vegetation structure and composition (Haroldson and Fritzell, 1984). In this sense, we classified four habitat units (Fig. 1): a) Sugar cane-Coffee plantation (5 hectares), grouped as an area with presence of sugarcane crops and coffee cultivation (Fig. 2 a, b) Coffee plantation-SMF (2 hectares): area with presence of coffee cultivation and presence of trees representative of the SMF used as shade (Fig. 2 b); c) SMF (8 hectares): area with exclusive presence of SMF flora and with minimal anthropogenic activity (Fig. 2c); d) Coffee plantation (*Coffee canephora*) 20 years old since its plantation (Fig. 2d).

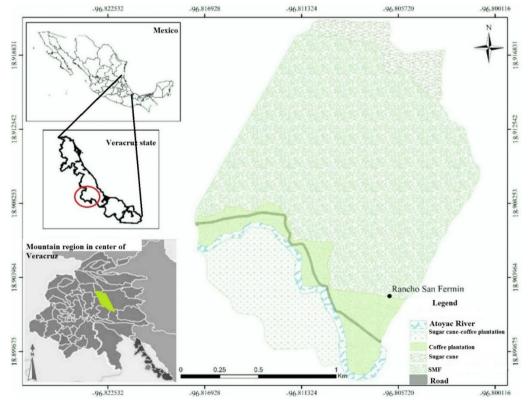


Fig. 1. Location map of the study area and classification of the types of coverage characterized in Rancho San Fermín, Atoyac, Veracruz.



Fig. 2. General characteristics of the landscape of each habitat unit: a) Sugar cane-Coffee plantation, b) Coffee plantation-SMF, c) SMF, d) Coffee plantation. Photographs taken in the field by the first and second authors of the article.

Determination of the presence of gray fox in habitat units

We configured over a period of seven months, from December 2018-June 2019, two trap cameras (Suntekcam HC-300A brand) to take three consecutive photographs with a 30 second interval when motion was detected and a 30 second video later following the photographs. We paired the cameras, each one was held on the shaft of a tree 50 cm from the ground, we activated for 24 h for 53 days, this represent out the monitoring effort per habitat unit. After this period, we moved the same two cameras to another habitat unit, until complete coverage the four habitat units (Díaz-Pulido and Payán-Garrido, 2012). We achieved the photocaptures obtained from the gray and were classified as independent records (presences), when between photocaptures there was more than 24 hours difference, when two or more specimens were fully distinguishable in the same photocapture, or when two or more individuals were photocaptured on the same day, but that by external characteristics (brands) could be differentiated (Serna-Lagunes et al., 2019).



Fig. 3. Photocapture (left) and excreta (right) of gray fox, U. cinereoargenteus recorded in this study.

During the same period that the photo traps remained active (December 2018-June 2019), 10 field trips with a duration of 2 days each and with an interval of 15 days between exits (phototramps were active in each habitat unit at the same time the field trips), with the aim of recording the presence of U. cinereoargenteus through the strip transect technique (Mandujano-Rodríguez, 2011). During the morning (0900 h-1400 h) and in the afternoon (1700 h-2000 h), we covered transects of 50 m at least 10% of the surface of each habitat unit (Gallina-Tessaro and López-González, 2011), to record the presence of excreta, traces, footprints, dumps, burrows, vocalizations or sightings of the gray fox, and other wildlife species (Aranda, 2012). We obtained from each record the type of trail, and we score the species and the geographic coordinate for the corresponding habitat unit.

We installed during one day in the month of February 2019, an olfactory station of approximately 1 m^2 in each habitat unit, which contained a layer of fine and moist sand, and in the center of the station, we placed an attractant (sardine). The following morning, we checked the stations for records of gray fox and other mammalian species (Gallina-Tessaro and Lopez-Gonzalez, 2011), which we identified based on the trail (Aranda, 2012).

We classified the other photocaptured mammal's species based on their trophic guild, since the presence of other carnivores in the same habitat determines the presence/absence of the gray fox (Palomares and Caro, 1999). We considered the records of birds, amphibians and reptiles in each habitat unit as potential prey for Ucinereoargenteus, when comparing the diet records of the species that have been reported in other studies (Arnaud and Acevedo, 1990; Hockman and Chapman, 1993; Sheldon, 2013).

Estimation of forest cover

We determined the percentage of forest cover how a variable that determines habitat use (Gallina-Tessaro, 2011). In each habitat unit, we traced one transect per landscape unit for estimated the forest cover of the herbaceous stratum (from ground level-80 cm high), shrub (80-200 cm) and arboreal (> 200 cm), using the Intersect Line technique (Canfield, 1941). The plant canopy fragment that were intercepted with the line, we recorded with a 50 meter long of line by two meters wide. With this information, for each habitat unit, we obtained the Linear Coverage Index (LCI) = $\sum Li / L \ge 100$, where Li is the sum of the average length of all the intersections of the species(i) divided by L (50 m) and multiplied by 100 (Canfield, 1941).

Obtaining climatic variables

In the QGIS program, through a process of extracting values from the environmental layers of the Digital Climate Atlas of Mexico (Fernández-Eguiarte *et al.*, 2012), from the centroid niche of each habitat unit, we obtained values the annual average temperature, precipitation, evaporation and altitude.

Development of habitat occupation model

In each habitat unit, we counted the number of independent records of U. cinereoargenteus obtained through photocaptures, transects and olfactory stations. With SUPRA software (Response Surface; López-Collado, 2004), which is based on a continuous non-parametric distribution (inverse distance weighting), which analyzes data with a negative binomial or Poisson distribution (López-Collado, 2004) and which it has been used in species with grouped space-time dynamics (Flota-Bañuelos et al., 2013), we constructed the habitat occupation model by U. cinereoargenteus. Associated with the construction of the model, we calculated the aggregation index (minimum and maximum value of records observed per sample). In this model, we used the geographic coordinates (x = latitude, y =longitude) of the center of the habitat unit and (z) the number of independent gray fox records in each habitat unit.

We applied a χ^2 test to determine the association between the number of gray fox records obtained in the dry and wet season based on their frequency in each habitat unit, since this allows identifying the distribution of gray foxes of the year and if these are altered by changes in habitat components (Farías et al., 2012). In addition, we drawn up a dendrogram with squared distances [(sqrt (1-S)] and the cophenetic correlation index, with to objective determine the similarity between pairs of habitat units with to gray fox records. We applied a partial least squares regression analysis (PLS; Di Rienzo et al., 2018), to explain the interaction of gray fox records with the components of their habitat. In this analysis, the abiotic covariates used in the model were the annual average temperature, annual average precipitation, annual average evaporation altitude, the percentage of coverage and (herbaceous, shrubby and arboreal). The number of species classified as carnivores and the number of species classified as potential prey of the gray fox were used as biotic covariates in the analysis The response variable was the number of independent gray fox records obtained in the dry season (December-mid-March) and rains (mid-March-June). We considered the habitat unit (jungle, coffee-jungle, cane-coffee and coffee) as the factor. These analyzes independent were implemented in the InfoStat software (Di Rienzo et al., 2018).

RESULTS

With a sampling time of seven months, 10 field trips and using three recording techniques, we obtained 14 independent records (12 excreta records and 2 photocaptures) from U_{\cdot} cinereoargenteus, distributed on the 4 habitat units. The Coffee plantation-SMF and Sugar cane-Coffee plantation habitat were the habitat unit that presented 6 and 5 gray fox records, respectively that exceeded the records in the Coffee plantation and SMF (Table 1). The values of the biotic and abiotic variables recorded in each habitat unit are presented in Table 1. SMF recorded an annual average temperature (21° C) and evaporation (1214 mm) lower than the other habitat units, but the values of precipitation (2156 mm) and altitude (854 mamsl) were higher than those presented by the three habitat units.

The Coffee plantation-SMF and Sugar cane-Coffee plantation habitat unit presented similar values of temperature, precipitation, evaporation, a greater number of potential dams and a lower number of competitors (Fig. 4); coincidentally, it was in these units that a greater number of gray fox records were recorded (Table 1). The χ^2 test did not show an association between the gray fox records and the habitat unit (Pearson's $\chi^2 = 5.47$, d.f = 3, P = 0.1406). The dendrogram showed the grouping of two landscape units (co-phenetic correlation index = 0.92) with the largest (Sugar cane-Coffee plantation and Coffee plantation) number of records (Fig. 4).

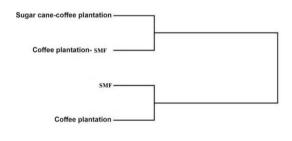


Fig. 4. Dendrogram of similarity / dissimilarity of the use of habitat by gray fox in different habitat covers in Atoyac, Veracruz, Mexico.

We corroborated this inference with the habitat occupation model (Fig. 5): the color scale shows: a) red-orange quadrants in the Coffee plantation-SMF unit where the largest number of gray fox records was presented with a total of six individuals and, b) quadrants with green-blue color in SMF and Coffee plantation unit where three records were obtained, and SMF (blue color) with one record.

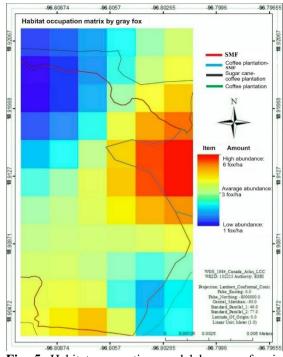


Fig. 5. Habitat occupation model by gray fox in Rancho San Fermín, Atoyac, Veracruz.

The PLS analysis explained 89% (value resulting from the sum explained in the regression by factor 1 = 53.8%, plus factor 2 = 35.2%) of the association of the records with respect to the variables under study (Fig. 6). We correlated the gray fox presence records with the temperature of the Sugar cane-Coffee plantation habitat in both factors of the PLS. In factor 2, gray fox presence records were positively correlated with evaporation, but in factor 1, the percentage of shrub cover and number of carnivores was negatively correlated with fox records in SMF habitat unit and Coffee plantation-SMF. On the other hand, the altitude, precipitation and the percentage of tree cover were correlated with a low number of fox records obtained in Coffee plantation unit (Fig. 6).

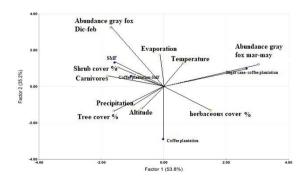


Fig. 6. Partial least squares analysis that determines the variables of importance in the use of habitat by gray fox.

Table 1. Average annual values of temperature (°C), precipitation (mm) and evaporation (mm); altitude (mamsl), percentage of coverage of the herbaceous, shrub and arboreal strata; carnivores number (CN); potential dams number (PDN) and number of gray fox records in the dry and wet season per habitat unit in subperennial medium forest (SMF), in the locality Rancho San Fermín, Atoyac, Veracruz.

Units	Abiotic variables				Forest Coverage			Biotic variables		Season	
Hábitat	Temp (°C)	Pp (mm)	Evaporation	Altitude	Herbaceous	Arbustive	Arboreal	CN	PDN	Dry	Wet
SMF	20.9	2,156	1,214	854	100	5	85	2	1	0	1
Coffee plantation- SMF	21.9	2,058	1,256	729	19	27	59	3	6*	4	2
Sugar cane-Coffe plantation	23	1,850	1,263	561	89	10	10	1	2	1	4
Coffee plantation	22.4	1,985	1,266	655	5	37	100	3	1	2	0

*Sceloporus variabilis, Anolis tropidonotus, Incillius valliceps, Sciurus aureogaster, rodents, and birds of the family Columbidae.

DISCUSION

Gallina *et al.* (2016) indicated that Coffee plantation is a habitat where the gray fox finds a greater supply of food and temporary protection compared to Selva. Foxes can use crop areas (Sugar cane and Coffee plantation) as a space where they can diversify their diet with other vertebrates and arthropods (Villalobos-Escalante *et al.*, 2014). In the intraspecific competition of fox and other carnivores can influence the food, space and time in which they use these resources, which can result in a segregation of resources, activity patterns and behavior changes, which allow coexistence balanced between the carnivorous community (Barravientos and Virgós 2006; Bianchi *et al.*, 2016). The presence of other mammals considered as copredators or competitors, did not affect the abundance-presence of the gray fox in Coffee plantation-Selva unit where there was the greatest presence of the species, where interactions in the community are increased (Deuel et al., 2017a). It is very probable that this habitat provide a greater supply, availability and spatial arrangement of resources (Deuel et al., 2017b), among which the presence of potential mates such as Sciurus aureogaster, Dasypus novemcinctus, rodents, amphibians, reptiles and birds observed in the study area (these species have been registered as potential prey; Fig. 7), compared to the other habitat units. Therefore, the different species of carnivores that we recorded in this study may coexist in the studied locality such as Canis latrans, Conepatus semistriatus (Farías-González and Vega-Flores 2019) and Procyon lotor (these species have been



Fig. 7. Photocaptures of predators-competitors and potential gray fox dam, recorded in the study area.

registered as potential competitors) because they may use different resources (Farías et al., 2012), resulting in competition (Barravientos and Virgós 2006). The semi-arboreal behavior of grav fox can provide an effective escape against coyotes, also their activity patterns can be spatially and temporarily different. which would allow coexisting (Chamberlain and Leopold, 2005). In this study, we found that there was the presence of covotes and gray fox in Coffee plantation-Selva and Sugar cane-Coffee plantation habitat, an indicator of coexistence between these species (Davis et al., 2011), but future studies should evaluate temporal overlap and diet overlap among these spatially overlapping species.

Due to the duration of the sampling carried out in this study, the results of habitat use by the gray fox, may vary if an annual or biannual sampling cycle is covered. However, the period where we carry out the samplings cover the dry and rainy season, where the greatest climatic variability occurs when dispersal processes and, reproductive behavior of the gray fox occur (Mella-Méndez et al., 2019). The average annual rainfall and the percentage of tree cover, are variables that are not important in the selection of the habitat by the gray fox in Coffee plantation unit, while the average annual temperature is an abiotic factor that determined a greater number of fox records in Sugar cane-Coffee plantation, in the dry season, where the average temperature of the season was 21.9 °C (Harmsen et al., 2019). These conditions would be delimiting the environmental niche of gray foxes in the locality studied, but it may be affected by global climate change and modify its range of distribution by promoting movements to areas where it finds conditions similar to those of its natural habitat (McAlpine et al., 2008). On the other hand, these conditions can support the argument that foxes increase their activity in spaces where the probability of finding resources is high, particularly where habitat conditions provide the necessary resources for the species (Farías et al., 2012).

The use of habitat by the gray fox in the SMF with different degrees of anthropogenic intervention showed patterns that support the hypothesis about the general use of the habitat by the species (Harrison, 1997), regardless of their degree of anthropization or human disturbances that affect their habitat (Markovchick-Nicholls et al., 2008). Studies have determined that the gray fox prefers habitats with closed, dense and rocky vegetation cover and avoids areas with high risk of predation (Sillero-Zubiri, 2009). Likewise, Servín et al. (2014) mention that, throughout the year, the gray fox uses habitats such as forests more frequently (especially in the spring, summer and autumn season), since it provides them with food and shelter sources, instead it uses smaller farmland. In our study, the greater preference of gray fox habitat was associated with open areas, with some degree of anthropogenic

intervention and crop cover has replaced a habitat disturbed by changes in the original forest cover and that. In this sense, it can be inferred that the population of foxes of this locality may be adapting or being tolerant of these conditions (Temple *et al.*, 2010).

The SMF is in constant threat in the central region of Veracruz, due to the sugar cane and coffee activities that are the most economically important crops in the region, which affects the biodiversity that inhabits this type of vegetation (Manson *et al.*, 2008). Through an agroecological zoning for the organized planning of these crops, you can identify those areas where they can be grown without affecting the surface of the SMF and conserve the biodiversity in this agroecosystems (Manson *et al.*, 2008).

CONCLUSIONS

The fox prefers the coffee plantation-SMF habitat, so a recommendation is to implement agroecological strategies to increase the productivity of this plant cover, which would increase the availability of resources for the biodiversity of the area under study.

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Conflict of interests. The authors declare that there is no conflict of interest. The funding sources had no role in the study design, in the data collection, analysis or interpretation, in the writing of the manuscript or in the decision to publish the results.

Compliance with ethical standards. The research did not include measurements with humans or animals. The study site is not considered a protected area nor is the species under study protected or in danger of extinction, therefore, its use has negligible effects on the broader functioning of the ecosystem.

Data availability. Data is available with Dr. Ricardo Serna Lagunes, at the email <u>rserna@uv.mx</u> upon reasonable request.

Author contribution statement (CRediT). Serna-Lagunes, Alejandro-Hernández, Torres Cantú established the approach of the study, developed the field work and wrote the manuscript. Ávila-Nájera, Andrés-Meza and Gastelum-Mendoza analyzed the versions of the manuscript, contributed to the discussion and conceptual feedback of the study. Salazar-Ortiz and Ocaña-Parada managed funding for field expenses and publication costs, and also reviewed and provided substantial written comments on the manuscript.

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