



Host sweet host: Rodent communities support similar ectoparasite diversity regardless of anthropogenic disturbance

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Abstract

Rodents are important hosts for ectoparasites, such as fleas, ticks, and mites, which means they are also important intermediate hosts for many zoonotic diseases. As anthropogenic environments bring humans and rodents into closer contact, an understanding of host–ectoparasite ecology is essential to predict and manage disease spillover risks. We aimed to understand how disturbances in vegetation cover affect rodent ectoparasite diversity, prevalence, spatial segregation, host (i.e., sex, genus, size, and habitat domain), and environmental (i.e., vegetation structure, forest cover, and rainfall) variables in the state of Michoacan, Mexico. We investigated these relationships by trapping rodents in five paired disturbed (reduced vegetation cover and regular human activities) and undisturbed (no reduction in vegetation cover) sites in the summer and autumn of 2022. From 110 trapped rodents, we collected 138 ectoparasites on 38 individuals. We found no difference in rodent diversity, ectoparasite diversity, or ectoparasite prevalence between disturbed and undisturbed sites. However, arboreal and male rodents had a higher probability of carrying ectoparasites than ground-dwelling and female rodents. Rodents with ectoparasites were not spatially clustered; rather, they were randomly distributed across trapping grids. We also identified two rodent genera (*Rattus* and *Sigmodon*) that carry ectoparasites of medical importance and that are in close contact with humans. Our results highlight the necessity of constant monitoring of rodents, ectoparasites, and their associated transmittable diseases. Assessing these interactions and how they are affected by anthropogenic disturbance could better inform management decisions and support the need for rodent conservation programmes in the area.

KEYWORDS

ectoparasite communities, ectoparasite prevalence, host–ectoparasite ecology, spatial segregation, transmission, vegetation cover disturbance

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1 | INTRODUCTION

Rodents are the most diverse mammalian order (around 2635 species) representing 40% of all species in the class Mammalia (American Society of Mammalogists, 2022). They carry out a variety of important ecosystem functions, including dispersal and predation of seeds and spores, and pollination (Dickman, 1999). Moreover, rodents occupy a wide range of ecological niches and occur throughout most terrestrial ecosystems, in part, due to their high competitiveness and adaptability to harsh environmental conditions, such as those found at high altitudes or in deserts (Dreiss et al., 2015; Martin-Regalado et al., 2019; Novillo & Ojeda, 2021). Some rodent species also have remarkably broad habitat ranges (e.g., *Rattus rattus*), while others have more specialised habitat requirements (e.g., *Otonyctomys hattii*, a forest dweller with limited dispersal capability) (Banks & Smith, 2015; Zaragoza-Quintana et al., 2021).

Variation in rodent abundance not only affects the ecosystem services they perform but also impacts human well-being, e.g., by acting as disease vectors. This is because rodents are some of the preferred hosts for ectoparasites, such as fleas, ticks, and mites (Dáttilo et al., 2020; Foley et al., 2016; Jayashankar et al., 2016; Mihalca & Sándor, 2013), which are the intermediate hosts for many zoonotic diseases, including viral encephalitis, the plague, Q fever, Lyme disease, and allergic reactions such as dermatitis (Baneth, 2014; Foley et al., 2016; Herrera-Mares et al., 2022; Ho et al., 2021; Hofmeester et al., 2016; Meerburg et al., 2009). Therefore, understanding how anthropogenic disturbance influences rodent–ectoparasite interactions can inform the management of local ecosystems and public health risks.

The two main requirements for ectoparasite persistence are host availability and suitable environmental conditions (Uspensky, 2014). For ectoparasites, living on hosts brings multiple benefits, such as increased access to nutrients and enhanced reproductive success (Luong & Subasinghe, 2017; Raffel et al., 2008). They also use their host as habitat, and therefore, ectoparasite diversity is expected to be driven by host diversity (Walther et al., 1995). Consequently, the composition of host communities, i.e., host richness and abundance, affects the diversity of ectoparasites (Harris et al., 2013).

No generalisations have emerged from studies that have examined how attributes of different rodent species, such as sex, age, and body size, influence ectoparasite diversity (de Mendonça et al., 2020; Kiffner et al., 2011; Krasnov et al., 2005; López-Pérez et al., 2022; Medvedev et al., 2020; Moravvej et al., 2016; Obiegala et al., 2021; Surkova et al., 2018). For body size, most studies show a positive association with ectoparasite load (Butler et al., 2020; Froeschke et al., 2013), while others found no relationship (Maaz et al., 2018; Shuai et al., 2022). Similarly, for host sex, some studies have found a higher ectoparasite load on male rodents (Shilereyo et al., 2022), while others have found no differences in ectoparasite loads between sexes (Kiffner et al., 2011). It may be that other attributes of rodents, such as habitat requirements (e.g., arboreal or ground-dwelling) and spatial distribution (e.g., population density and home range), are more important determinants of the

composition of ectoparasite communities than host size or sex (Buettner et al., 2013; Morand, 2015).

Anthropogenic disturbances often facilitate an increase in the density of generalist rodents (Mendoza et al., 2020). As an example, agricultural crops increase food availability, which in turn can favour an increase in the abundance of pest species (Munawar et al., 2024; Ruscoe et al., 2022). There is often a high prevalence of ectoparasites (i.e., the percentage of rodents carrying ectoparasites) in rodent populations in fragmented and disturbed forests (Ho et al., 2021). Typically, in disturbed forests with low canopy cover, the understorey temperature is higher than in closed-canopy forests (Nowakowski et al., 2018). These changes in microclimatic conditions directly influence ectoparasite diversity, affecting the number of larvae produced and their generation times (Gilbert, 2021; Leal et al., 2020). Furthermore, reduced canopy cover increases light availability in the understorey, which may lead to the thickening of the understorey vegetation (Franklin et al., 2021). Such changes in vegetation structure can lead to an increase in the abundance of generalist rodent species (Adams et al., 2022; Kluever et al., 2019; Thomas et al., 2022). In turn, this higher availability of generalist rodent hosts will lead to higher ectoparasite diversity (BeVier et al., 2022; Eldridge et al., 2011; Kiene et al., 2020; Kiffner et al., 2011; Schwarz et al., 2009; Van Gestel et al., 2021; Williams & Ward, 2010).

An increased likelihood of rodents being ectoparasite hosts in response to anthropogenic disturbance could increase the probability of ectoparasite transmission to other hosts, including humans, which could lead to zoonotic disease outbreaks (Blasdell et al., 2022; Krawczyk et al., 2020; Mendoza et al., 2020). However, it remains unclear if spatial proximity between hosts is a risk factor or whether transmission relies mainly on free-living ectoparasite individuals (Cevitanes et al., 2021). Although it is generally accepted that the potential transfer of ectoparasites from generalist rodents to humans and domesticated animals is greater than from specialist rodents given their more frequent interactions with human populations (Vargas-Sandoval et al., 2014), there is a need to increase our understanding of the spatial dynamics of transmission from host to host. Higher densities of rodents mean closer spatial proximity between individuals, which could lead to host-to-host ectoparasite transmission (Fernandes et al., 2021; Webber et al., 2015). We propose that this could be tested through the spatial segregation patterns of rodents with and without ectoparasites. Spatial segregation, at the species level, occurs when a species is more likely to be in the vicinity of conspecifics (Dixon, 2002). In our case, we will apply the sample principle for rodents with or without ectoparasites.

Despite the importance of rodent–ectoparasite interactions in forest function and human well-being, our understanding of these interactions remains poor (Jayashankar et al., 2016). The overarching aim of this study is to increase our understanding of rodent host–ectoparasite interactions in response to anthropogenic disturbance. As in many places in the world, the forest in our study area is being affected by anthropogenic disturbance caused by forest logging for timber exploitation or conversion to commercial plantations. Our

study aims to: (1) determine the relationship between rodent and ectoparasite diversity in response to anthropogenic disturbance (forest conversion to commercial plantations), (2) determine the relationship between rodent ectoparasite prevalence in response to anthropogenic disturbance, (3) assess the influence of rodent host characteristics (sex, size, and habitat domain) and environmental variables (vegetation structure, forest cover, and rainfall) on ectoparasite presence, and (4) determine the spatial segregation of rodent hosts, i.e., whether rodents with ectoparasites cluster in close proximity, or are randomly distributed. We predicted that the diversity of rodents and their associated ectoparasites will be higher in undisturbed than in disturbed sites, due to the higher diversity of rodent niches in the former. We also hypothesised that the abundance of generalist rodents and the prevalence of ectoparasites will be higher in disturbed sites than in undisturbed sites. For rodent host attributes, we hypothesised that males, i.e., the biggest rodent individuals, and ground-dwelling rodents may be the most prone to present ectoparasites. Also, high shrub density, low forest cover, and higher precipitation may favour the presence of ectoparasites. Regarding spatial segregation, we expect rodents with ectoparasites to be clustered in space due to direct interhost transmission of ectoparasites.

2 | MATERIALS AND METHODS

2.1 | Study sites

Our study sites were in the municipalities of Nuevo San Juan, Tancitaro, and Uruapan in the state of Michoacan, Mexico (Figure 1), in the Trans-Mexican Volcanic Belt. The study sites are close to the

Paricutín volcano that formed in 1942. The geological processes associated with the volcano have significantly influenced the composition of the vegetation in the area (Medina García et al., 2000). The area has a temperate climate, with altitudes ranging between 1800 and 3000 m.a.s.l. The average annual rainfall is between 1000 and 1500 mm (INEGI, 2008). The predominant tree genera in the area are *Pinus*, *Quercus*, and *Abies*, with interspersed grasslands mainly composed by *Trisetum*, *Piptochaetium*, *Festuca*, and *Aegopogon* species (Fregoso et al., 2001). Eight of the sites are within the territory of the Indigenous Community of Nuevo San Juan that is greatly involved in forest management (Fregoso et al., 2001; Velázquez et al., 2015). Extensive and rapid land-use changes have occurred in the area over the last few decades, such as the establishment of avocado orchards and extensive logging in the area are driving local habitat fragmentation (Latorre-Cárdenas et al., 2023). The two remaining sites are located in the municipality of Tancitaro.

We defined the disturbance status of our sampling sites based on their forest structure and cover. Five paired disturbed and undisturbed sampling sites were chosen to be, on average, 300 m apart between sites within a pair. Undisturbed sites had high forest cover (see Section 3 below), while disturbed sites had highly disturbed vegetation due to human activities (Figure 1). At each site, we measured plant (trees and shrubs) height, density, and growth form along three transects. Each transect was 50 m long and 2 m wide (Perkins et al., 2019). Each plant was identified to species level with the help of community professionals from the Forestry Direction of Nuevo San Juan.

As another measure of disturbance, we compared the forest cover between disturbed and undisturbed sites. We created a 30 m buffer around our grid of Sherman traps (Figure 2). The 30 m

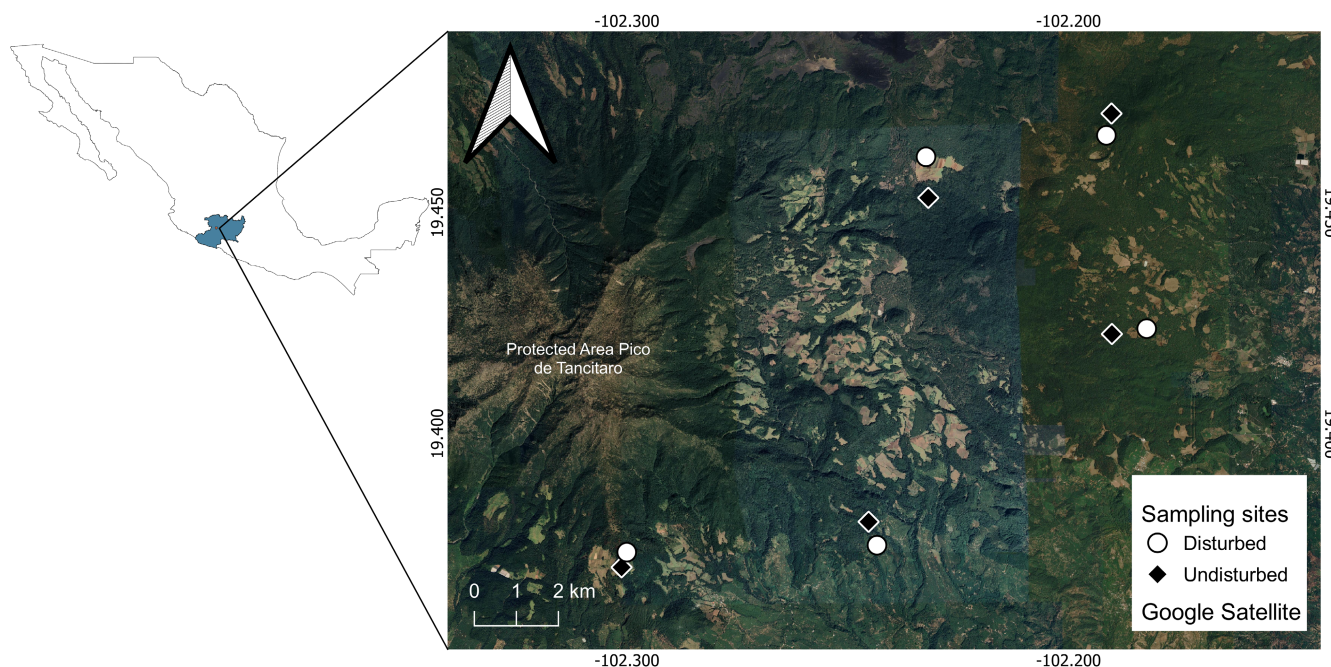


FIGURE 1 Paired disturbed and undisturbed sampling sites used to compare the ectoparasite diversity associated with rodents in Nuevo San Juan, Michoacan, Mexico. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/jen.13299)]

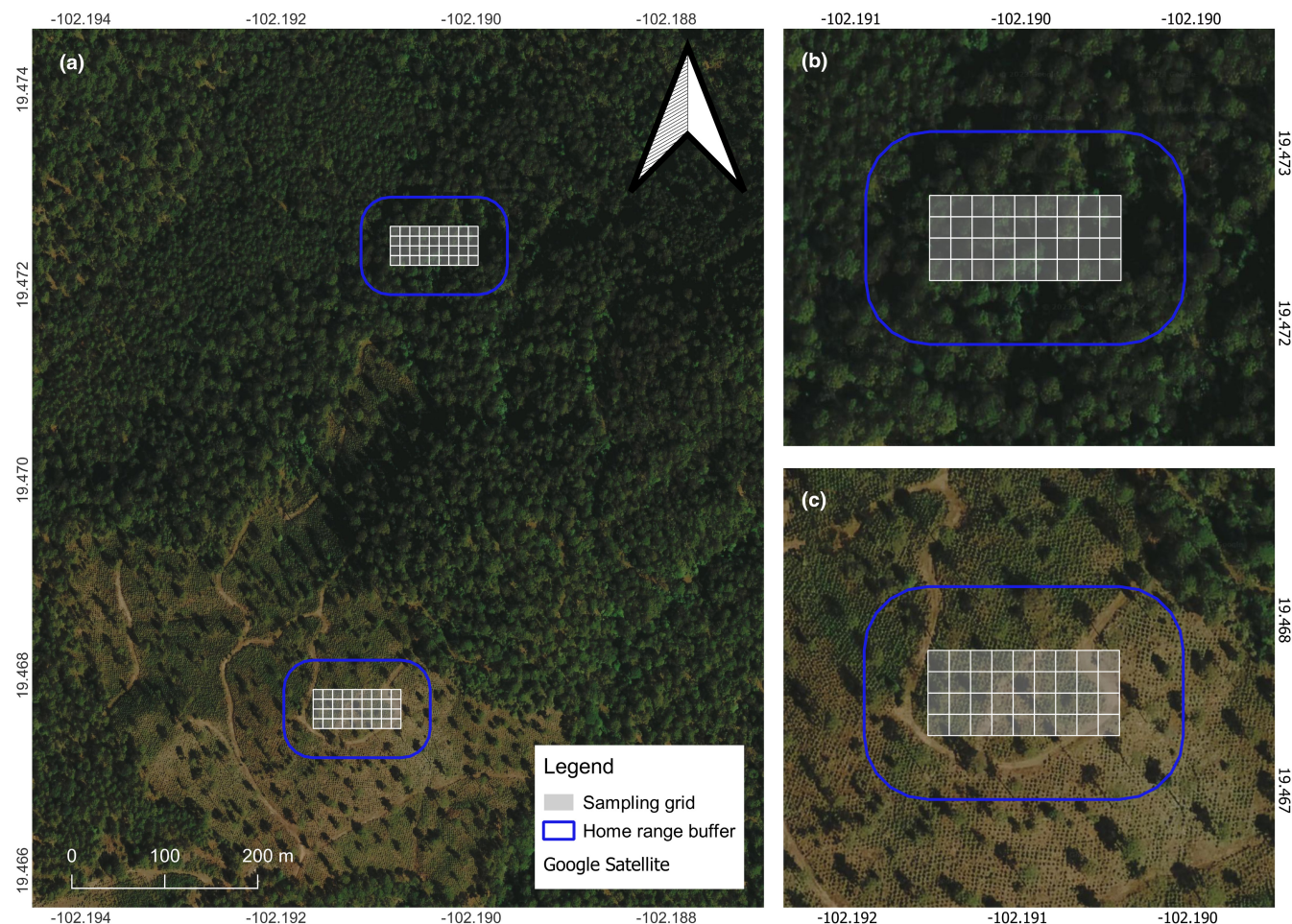


FIGURE 2 Sampling design to compare the diversity of rodent-associated ectoparasites in response to anthropogenic disturbance in Nuevo San Juan, Michoacan, Mexico: (a) example of a sampling block with an undisturbed site (b) and a disturbed site (c), which were sampled simultaneously. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

buffer was determined as the radius of the home range size of *Sigmodon hispidus*, which has the largest home range size among the native rodent species registered in the area (Cameron & Spencer, 1985). We performed a visual classification using ArcGIS software (ESRI, 2015) and distinguished forest and non-forest cover within our buffers. For the classification, we used multi-spectral images from the Sentinel 2 satellite Level 2-A reflectance (bottom-of-atmosphere) with a resolution of 10 m. The Sentinel images were acquired for the April 2023 date and cloud-free from the Copernicus data hub. In addition, we used recent (2022–2023) high-resolution images from Google Earth pro software (Google Inc, 2022). Furthermore, we determined the minimum year of apparent disturbance driven by land cover change at disturbed sites using older high-resolution satellite imagery available in Google Earth Pro (Google Inc, 2022) and Sentinel 2 satellite. Our visual review indicates that the five undisturbed sites have maintained these conditions since at least 2004, four of our disturbed sites have remained so since at least 2004, while one site presented disturbance since 2017 (see Appendix S1). Considering the review of satellite images, the history of land use/cover change (Latorre-Cárdenas et al., 2023; Ramírez-Mejía et al., 2022), and

our experience in the field, we can determine that the disturbance is due to human-induced development activities.

To sample rodents, at each site, we placed 50 Sherman traps in a 5 × 10 grid arrangement (spaced at 10 m). We baited the traps with a mixture of peanut butter, vanilla essence, and oats, which have given good results in similar environments (Vázquez et al., 2000). Paired disturbed and undisturbed sites were sampled simultaneously on each event. Sites were sampled for two nights in both dry (May 2022) and wet (August 2022) seasons. As rodents can be sensitive to light, we avoided sampling on full moon nights. Each captured rodent was identified, photographed, and measured (total length, tail length, ear length, and hind foot length measured in millimetres and weight measured in grams). We inspected the fur of each rodent systematically with entomological tweezers on the dorsal area, the ears, and limbs for approximately 2 min. All observed ectoparasites were removed. The use of anaesthetics during the inspections was not necessary due to the docile nature of the individuals captured. However, signs of distress were assessed prior to inspecting each individual and stressed individuals were immediately released and monitored until recovery. Our procedures were approved by the Secretariat of Environment and

Natural Resources (in Spanish: Secretaría de Medio Ambiente y Recursos Naturales from Mexico, SEMARNAT), under the permit number SGPA/DGVS/02787/22. Collected ectoparasites were preserved in 70% ethanol for later identification and counting. In the laboratory, collected mites (Mesostigmata) and chiggers (Trombidiformes) were submerged in a chloral hydrate solution until translucent and then individually mounted in Hoyer's medium (Moravvej et al., 2016). Fleas were submerged in potassium hydroxide (KOH) until transparent and mounted in Canada balsam (Wirth & Marston, 1968). All ectoparasite species were identified based on taxonomic keys specific for each ectoparasite order, family, or genus, if necessary (Acosta & Morrone, 2003; Hoffmann, 1990; Keirans et al., 1989; Loomis, 1971; McDaniel, 1979; Pratt, 1996).

2.2 | Data analyses

The diversity of rodent and ectoparasite communities was compared between disturbed and undisturbed sites using a Hutcheson's *t*-test (See F1 in Appendix S2) to compare the Shannon Diversity Index performed in the *ecolTest* R package (R Core Team, 2022; Salinas & Ramirez-Delgado, 2021). We compared ectoparasite species richness among site types using species accumulation curves inferred using the *iNEXT* package from R (Hsieh et al., 2016; R Core Team, 2022). We also calculated the sample coverage, defined as a measure of sample completeness, giving the proportion of the total number of individuals in a community that belong to the species represented in the sample (Chao & Jost, 2012). Pielou's evenness index was used to compare ectoparasite communities between site types using a Mann-Whitney test (see F2 in Appendix S2) implemented in the *R base* package (R Core Team, 2022). We compared the relative abundance of ectoparasite orders between site types (i.e., Siphonaptera, Ixodida, Mesostigmata, and Trombidiformes) using a Mann-Whitney test in the *R base* package (R Core Team, 2022). We calculated the prevalence of taxonomic orders of ectoparasites on rodents per sampling event and compared them among disturbed and undisturbed sites using a Mann-Whitney test. To compare beta diversity of ectoparasite communities, we applied a non-metric multidimensional scaling (NMDS) using the 'metaMDS' function in *vegan* (Oksanen et al., 2022; R Core Team, 2022). We used the Bray-Curtis distance, and the treatment factor using 1000 permutations. We then performed an analysis of similarity (ANOSIM) using the 'anosim' function from *vegan* under the same parameters.

We developed binomial generalised linear models to predict the presence of ectoparasites on rodents. We generated a global model in the *MuMIn* (multi-model inference) R package (Barton, 2018) to assess the influence of rodent life-history traits and habitat condition on the presence/absence of ectoparasites on rodents. Rodent host variables included activity patterns (nocturnal/crepuscular), habitat domain (arboreal/ground-dwelling), sex, body mass index (BMI), host genus, and rodent relative abundance per season for each site. The environmental variables included in the global model

were season (wet/dry), shrub density, tree density, and site type (disturbed/undisturbed). As more than one model met the $\Delta AICc < 2$ (second-order Akaike information criterion), we applied a model full averaging to produce an average of the estimates with these models (Burnham & Anderson, 2002).

We calculated the spatial patterns of ectoparasite presence on rodent hosts through the segregation index (*S*, see F3 in Appendix S2) using the *dixon2002* function from the *ecspa* R package (de la Cruz et al., 2023; R Core Team, 2022). This index describes the tendency of one species to be associated with itself or with other species (Dixon, 2002). In the context of this study, we applied the index to know how rodents with and without ectoparasites interact spatially. $S > 0$ indicates that rodents hosting ectoparasites are segregated, whereas $S < 0$ indicates that rodents with ectoparasites are clustered and found near one another. *S* close to 0 suggests a random distribution of rodents with ectoparasites (de la Cruz et al., 2023).

3 | RESULTS

The vegetation diversity (Shannon-Wiener Diversity) was significantly different between disturbed and undisturbed sites ($t=6.245$; $p < 0.001$). Overall, disturbed sites had a total species richness of 17 trees and shrubs, whereas undisturbed sites had 29 species. The most diverse sites were the Undisturbed 2, 3, and 4 (Table 1). The undisturbed sites had a higher tree density and a higher tree height (Table 1). Undisturbed sites had an average of 99.42% (SD=1.3%) forest cover within the 30m buffer around our grid of Sherman traps, whereas forest cover was 46.75% (SD=30.3%) in disturbed sites (Table 1). Disturbed Site 1 consisted of a young pine plantation, which on satellite shows as having high forest cover. However, its structure was highly homogeneous and with a high incidence of shrubs.

3.1 | Ectoparasite species diversity in response to anthropogenic disturbance

The rodent sampling effort was 1997 trap nights. We captured 110 rodents (discarding recaptures), 62 from undisturbed sites and 48 from disturbed sites, resulting in an overall trap success rate of 5.5% (number of captures/total number of traps \times 100). In the wet and dry seasons, trapping success rates were 8.4% and 2.6%, respectively. Captured individuals were from six genera; *Reithrodontomys* ($n=66$), *Microtus* ($n=20$), *Sigmodon* ($n=12$), *Peromyscus* ($n=7$), *Hodomys* ($n=4$), and *Rattus* ($n=1$). The genera *Reithrodontomys*, *Hodomys*, and *Rattus* were classified as arboreal species. The genera *Microtus*, *Sigmodon*, and *Peromyscus* were classified as ground-dwelling. Two out of the six rodent genera were exclusively found in disturbed sites: *Sigmodon* and the introduced genus *Rattus*. *Sigmodon* species hosted two unique genera of ectoparasites, *Xenopsylla* and *Ornithonyssus*. We did not detect any ectoparasites on the *Rattus* individual captured.

We detected 138 ectoparasites on 38 individual rodents. Four orders of ectoparasites were identified at both site types: Ixodida,

TABLE 1 Vegetation structure and forest cover for disturbed and undisturbed sites in Nuevo San Juan, Michoacan, Mexico.

Site type	Pair	Plant species richness ^a	Tree density (ind/transect)	Average tree height	Shrub density (ind/transect)	Forest cover (%)
Undisturbed	1	8	15 ± 5.3	6.4 ± 5.1	2.33 ± 1.53	100
	2	11	8.7 ± 3.8	8.5 ± 9	5.67 ± 2.52	100
	3	12	8.3 ± 3.2	9.4 ± 6.7	4 ± 1.73	97.11
	4	11	18 ± 9.5	9.7 ± 5.6	5 ± 1.41	100
	5	8	7.7 ± 2.1	10.5 ± 8.1	2 ± 1	100
Disturbed	1	7	11 ± 1.4	4 ± 2.4	21.5 ± 0.71	100
	2	6	2.5 ± 2.1	5.1 ± 4.5	10 ± 5.29	34.61
	3	3	1	2	3	29.53
	4	4	6	11.9 ± 11.7	3	27.2
	5	4	2	7.8 ± 6	16	42.41

Note: ± indicates standard deviation.

^aIncludes the richness of shrubs and trees.

Mesostigmata, Trombidiformes, and Siphonaptera. Within these orders, we identified the Acari families like Trombiculidae, Macronyssidae, Leeuwenhoekiidae, Laelapidae, and Ixodidae (Appendix S3). Twelve ectoparasite species of the Acari were identified on 25 individual rodent hosts plus two morphospecies. Moreover, we identified three flea species from the families like Ceratophyllidae, Pulicidae, and Leptopsyllidae; found on 23 rodent hosts. Seventy ectoparasites were collected at disturbed sites and 68 from undisturbed sites. We identified eight ectoparasite species and two morphospecies (Trombiculidae) in the disturbed sites and 12 species in the undisturbed sites.

We found no difference in rodent diversity ($t=1.05$, $df=86.19$, $p=0.26$) or in ectoparasite diversity ($t=-0.03$, $df=48.7$, $p=0.97$) between site types. The species accumulation curve for ectoparasite richness did not reach asymptotes for either site type (Figure 3a). However, the sample coverage was high for both the disturbed (0.80) and the undisturbed (0.73) sites (Figure 3b). The evenness of both the rodent ($W=4$, $p=0.19$) and the ectoparasite ($W=5$, $p=1$) communities was not significantly different among site types. The NMDS showed no difference in the structure of ectoparasite communities between treatments, as points are not clustered per site type (Figure 4). Likewise, the ANOSIM showed no difference between the abundances of ectoparasite species between site types ($R=-0.22$, $p=0.87$).

3.2 | Ectoparasite prevalence

We detected ectoparasites on 32.3% ($n=42$) of captured rodents. In the disturbed sites, 34.5% of the captured rodents had ectoparasites ($n=20$), whereas 30.6% ($n=22$) of the rodents captured at undisturbed sites had ectoparasites. We found no significant difference between the prevalence of ectoparasites among undisturbed and disturbed sites ($W=13$, $p=1$). There was no difference in the prevalence of Siphonaptera ($W=11$, $p=0.46$), Trombidiformes ($W=8$, $p=1$), Mesostigmata ($W=10$, $p=0.66$), or Ixodida ($W=8.5$, $p=1$). Similarly, when present, the relative abundance of Siphonaptera ($W=14$, $p=0.83$), Trombidiformes ($W=11.5$, $p=0.91$), Mesostigmata

($W=13$, $p=1$), and Ixodida ($W=13$, $p=1$) did not differ significantly among site types (Table 2). The ectoparasite order with the highest relative abundance for both the undisturbed and disturbed sites was Siphonaptera (Table 2).

The most prevalent order for both site types was Siphonaptera (Table 2, Figure 5). Siphonapterae were associated with two rodent genera in the disturbed sites and three rodent genera at the undisturbed sites. Trombidiformes were only found associated with *Microtus mexicanus* in undisturbed sites but were associated with three rodent genera in disturbed sites. *Sigmodon* individuals were only found at one disturbed site, in which it hosted Mesostigmata, Trombidiformes, and Siphonaptera ectoparasites (Figure 5).

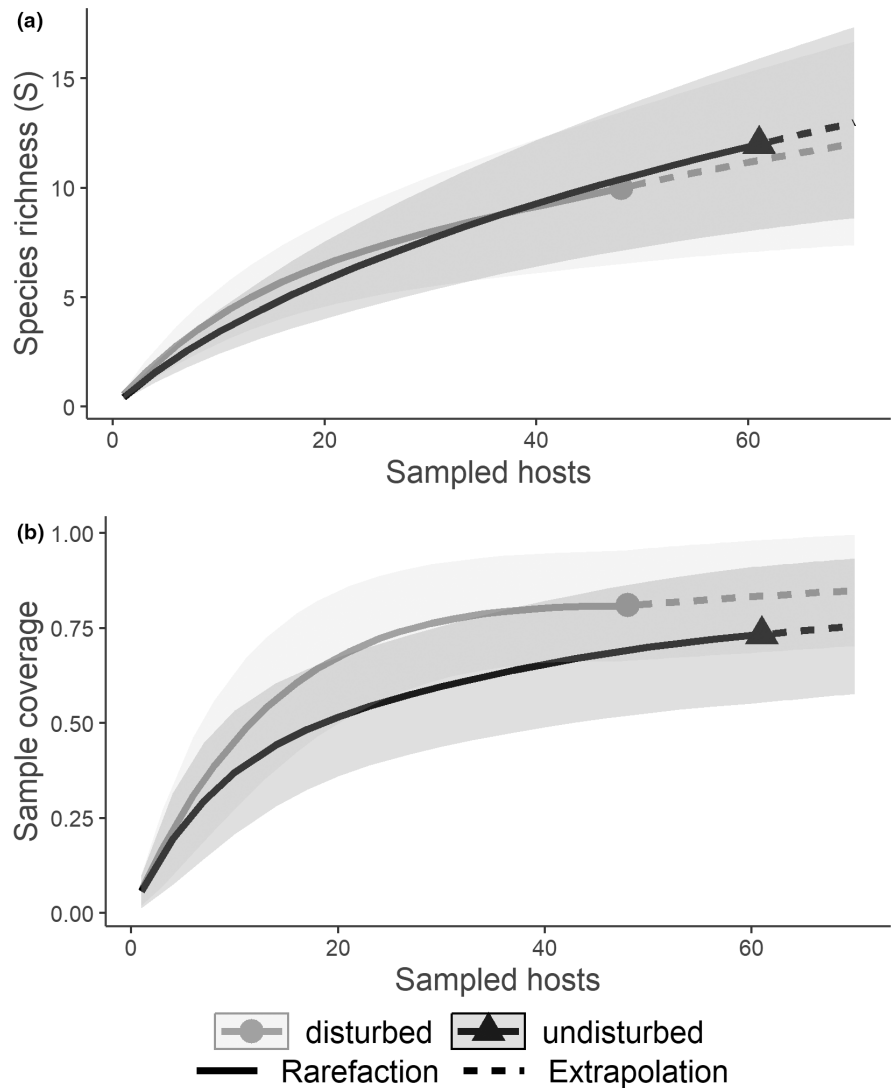
3.3 | Rodent host and environmental variables associated with the presence of ectoparasites

Three models were selected based on the corrected Akaike Information Criterion (AICc) values and a $\Delta AICc < 2$. These models included the host variables of habitat domain (arboreal/ground-dwelling), sex, rodent relative abundance, and body mass index (Table 3). According to the model averaging estimates (Table 4), there was a significant difference between arboreal and ground-dwelling rodent species, where arboreal rodent species have a higher probability of carrying ectoparasites. Males also had a higher probability of carrying ectoparasites than females. Although included within the best models, there were no significant relationships between the presence of ectoparasites and rodent relative abundance, or body mass index. The intercept model had a lower AICc than the best models.

3.4 | Spatial segregation of ectoparasite presence

Due to sparse data, we were only able to analyse data from the wet season for six of the sites for the detection of spatial segregation of ectoparasite prevalence. In the undisturbed sites, the S

FIGURE 3 Species accumulation curve for ectoparasites found on rodents (a) and sample coverage (b) for the overall sampling effort in disturbed and undisturbed sites in Nuevo San Juan, Michoacan, Mexico.



value of rodents with ectoparasites as nearest neighbours of other rodents with ectoparasites ranged from negative infinity (due to zero observations) to 0.9 (Table 5). In disturbed sites, S ranged from negative infinity to 0.18 for rodents with ectoparasites as nearest neighbours of other rodents with ectoparasites. These values are close to zero, suggesting a random spatial distribution. There was no significant difference between the observed and expected counts for neighbouring rodents with absent or present ectoparasites according to the overall segregation chi-square tests performed for each site.

4 | DISCUSSION

Rodents are important forest species that provide many vital ecosystem services (Dickman, 1999; Godó et al., 2022). Understanding the composition of rodent communities may therefore provide us with important insights into forest health and function (Zúñiga et al., 2021). Rodent diversity is often higher in undisturbed areas because of the high presence of habitat specialist species compared

to in disturbed habitats (Palmeirim et al., 2020). As a result, ectoparasite diversity also tends to be higher in these areas (Morand et al., 2019). Contrary to previous research, we found that the rodent diversity in Nuevo San Juan, Mexico, did not differ between disturbed and undisturbed sites. This may be explained by the fact that the rodent species we captured are habitat generalists (Bordes et al., 2015; Franchini et al., 2022; Sánchez-Cordero et al., 2022). Consequently, the lack of difference in rodent diversity between the site types translated into no differences in ectoparasite diversity between them either.

Diversity is made up of two components: abundance and richness (Booth et al., 2003). We found that neither rodent nor ectoparasite abundance differed between disturbed and undisturbed sites. Contrary to our findings, there is evidence of altered ectoparasite communities in response to anthropogenic disturbance, where the abundance of ectoparasites has been reported to be higher in agricultural areas than in reserves, especially among generalist rodent host species (Mendoza et al., 2020; Shilereyo et al., 2022). Similar to abundance, we also found ectoparasite richness to not differ between the site types. These results likely reflect the known strong

correlation between rodent and ectoparasite richness (Walther et al., 1995).

In general, the prevalence of ectoparasites on rodents in disturbed areas (e.g., in cities and agricultural lands) has been reported to range between 23% and 89% (Baak-Baak et al., 2018; Hamidi et al., 2015; Herrero-Cófreces et al., 2021; Moravvej et al., 2016; Teixeira et al., 2019), while in undisturbed areas (e.g., protected areas) this ranges between 57% and 98% (Bohn et al., 2017; Fantozzi et al., 2022; Kiffner et al., 2011; Thaneet et al., 2009). Several studies have compared ectoparasite prevalence between disturbed and undisturbed sites in the same areas (Durden et al., 2004; Kiene et al., 2020; Smith et al., 2021; Veloso-Frías et al., 2019). These comparisons have shown that ectoparasite prevalence is generally lower in disturbed sites compared to undisturbed sites, likely due to the disruption of microhabitats caused by, for example, changes in vegetation structure (Smith et al., 2021). In contrast, we did not

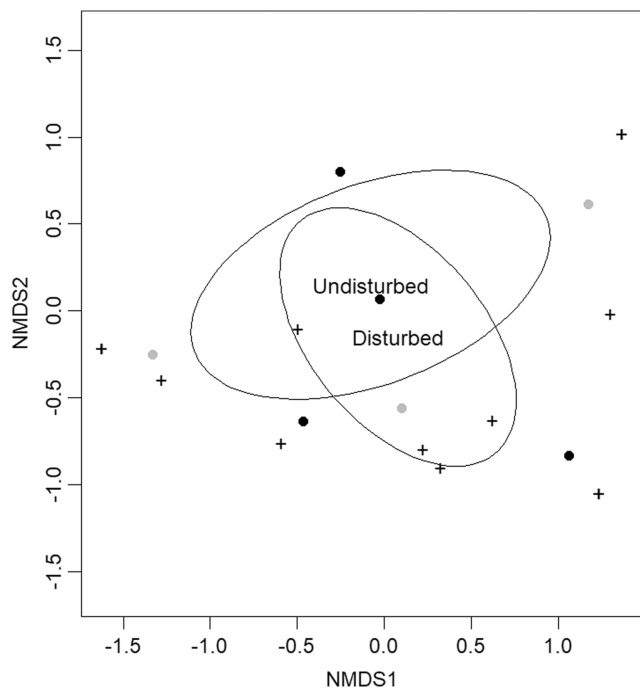


FIGURE 4 Non-metric multidimensional scaling for rodent ectoparasite species abundances in Nuevo San Juan, Michoacan, Mexico. Observations are compared by ectoparasite species (+), disturbed (grey) and undisturbed (black) sites.

find a significant difference in ectoparasite prevalence between our site types. However, it should be acknowledged that comparing ectoparasite prevalence between disturbed and undisturbed sites is often more insightful when examined at the ectoparasite species level (Veloso-Frías et al., 2019). This is because each ectoparasite species can have unique microhabitat requirements and life-history traits (Dowling, 2006; Froeschke et al., 2013; Kiene et al., 2020). Unfortunately, species-level ectoparasite prevalence comparisons were not feasible for our study due to our small sample sizes.

Contrary to previous studies (Durden et al., 2004; Froeschke et al., 2013; Kiene et al., 2020; Smith et al., 2021; Veloso-Frías et al., 2019; Wilder & Meikle, 2004), we found that anthropogenic disturbance did not have a significant effect on the presence of ectoparasites. There is a body of literature that has reported similar findings (Franchini et al., 2022; Renwick & Lambin, 2013). For example, Franchini et al. (2022) found no effect of forest fragmentation on the presence of ectoparasites on red squirrels (*Sciurus vulgaris*). Our study site types were classified based on forest cover and vegetation structure. When selecting sites, a minimum distance of 300m was established between sites, which represents a significant distance for rodent dispersal (Mason et al., 2022). Therefore, it is unlikely that the distance between site types was insufficient to capture differences in rodent host and ectoparasite communities. Instead, we suggest that the similarities in the rodent and ectoparasite communities we observed between the site types are because the undisturbed sites are embedded in a highly fragmented landscape and are also affected by anthropogenic disturbance (Latorre-Cárdenas et al., 2023). Such landscapes can have a profound influence on the animal communities that disperse at smaller spatial scales within forested sites (Mapelli et al., 2020; Morand et al., 2019). It should be acknowledged that historical records indicate that 31 native rodent species exist in the area where our study sites are located (Ceballos & Oliva, 2009; Núñez, 2005), of which we only captured eight species. For this reason, long-term rodent monitoring is needed to better gauge the effects of large-scale disturbance on both rodents and their associated ectoparasite populations.

From the rodent host variables that have been reported to influence the ectoparasite presence, such as sex, age, and size (Hawlena et al., 2005; Krasnov et al., 2005; Moravvej et al., 2016; Surkova et al., 2018), we found only rodent habitat domain (i.e., arboreal or ground-dwelling) and sex to be significantly associated with

Ectoparasite order	Relative abundance ^a		Prevalence (%) ^b	
	Disturbed	Undisturbed	Disturbed	Undisturbed
Siphonaptera	45.0 ± 44.3	35.1 ± 38.7	18.4 ± 8.5	16.5 ± 3.5
Mesostigmata	19.4 ± 22.5	19.7 ± 32	10.6 ± 8	6.9 ± 11.2
Trombidiformes	9.8 ± 16.8	22.3 ± 37.6	5.5 ± 7.3	8.4 ± 14.1
Ixodida	6 ± 13.4	3.8 ± 8.4	3.3 ± 6.7	3.1 ± 6.3

Note: ± indicates standard deviation.

^aAverage of the percentage of the total number of ectoparasites per site.

^bIndividuals with co-occurrence of different ectoparasite orders were recounted for each order.

TABLE 2 Relative abundance and prevalence of ectoparasite orders detected in disturbed and undisturbed sites in Nuevo San Juan, Michoacan, Mexico.

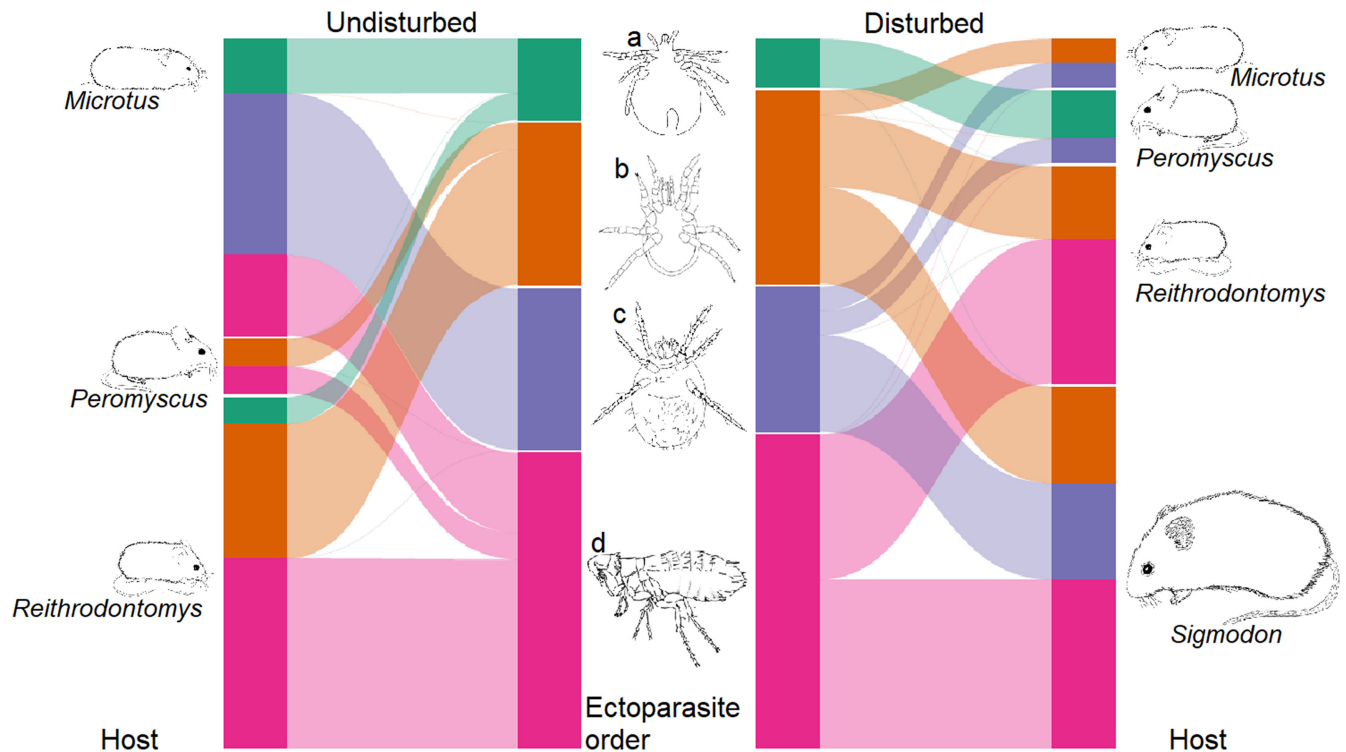


FIGURE 5 Rodent–ectoparasite associations based on the total prevalence of ectoparasite orders detected on rodent hosts in disturbed and undisturbed sites in Nuevo San Juan, Michoacan, Mexico. The studied ectoparasite orders are (a) Ixodida, (b) Mesostigmata, (c) Trombidiformes, and (d) Siphonaptera. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/jen.13249)]

TABLE 3 Model selection results for the generalised linear models selected according to the AICc ($\Delta\text{AICc} < 2$) for the presence of ectoparasites in rodents captured in Nuevo San Juan, Michoacan, Mexico.

Model set	Variables	df	AICc	ΔAICc	Weight
1	Habitat ^a + Sex ^b	3	128.6	0.00	0.047
2	Habitat ^a + Sex ^b + RRA ^c	4	130.3	1.77	0.019
3	Habitat ^a + Sex ^b + BMI	4	130.4	1.86	0.018

Abbreviation: BMI, body mass index.

^aHost habitat domain: ground-dwelling, arboreal.

^bHost sex: female, male.

^cRodent relative abundance obtained per season at each site.

TABLE 4 Estimates of the full averaging of the best generalised linear models for the presence of ectoparasites in rodents captured in Nuevo San Juan, Michoacan, Mexico.

Fixed effect	Estimate	SE	Z value	p	CI 95%
Intercept _{Arboreal female}	-1.613	0.557	2.863	0.004**	-2.717 -0.509
Habit _{Ground-dwelling}	1.470	0.478	3.038	0.002**	0.522 2.418
Sex _{Male}	0.964	0.471	2.021	0.043*	0.029 1.899
RRA ^a	-0.012	0.046	0.259	0.796	-0.219 0.114
BMI	-0.162	0.710	0.225	0.822	-3.464 1.983

Abbreviation: BMI, body mass index.

^aRodent relative abundance obtained per season at each site.

* $p < 0.05$. ** $p < 0.005$.

ectoparasite presence. Ground-dwelling rodent species had a higher probability of having ectoparasites. The ectoparasites we obtained from the rodents tended to be ground-dwelling too, with several of

them (e.g., fleas and mites) living in the underground nests of the rodent hosts (Baláz et al., 2022; Dowling, 2006; Krasnov et al., 2021). Similarly, ticks spend their intermediate moulting stages on the

TABLE 5 Nearest-neighbour count and related statistics for the absence or presence of ectoparasites on captured rodents.

Site	From	To	Observed count	Expected count	S	Z	p-Value	
							Normal	Random
Undisturbed 2	Absent	Absent	8	6.88	0.2	0.71	0.4747	0.5669
	Absent	Present	3	4.12	-0.2	-0.71	0.4747	0.3957
	Present	Absent	4	4.12	-0.04	-0.1	0.9229	0.5987
	Present	Present	2	1.88	0.04	0.1	0.9229	0.8368
Undisturbed 4	Absent	Absent	7	5.6	0.48	1.06	0.2873	0.3531
	Absent	Present	1	2.4	-0.48	-1.06	0.2873	0.5885
	Present	Absent	1	2.4	-0.9	-1.6	0.1086	0.244
	Present	Present	2	0.6	0.9	1.6	0.1086	0.3581
Undisturbed 5	Absent	Absent	3	4.67	-0.37	-1.28	0.1993	0.3705
	Absent	Present	5	3.33	0.37	1.28	0.1993	0.2076
	Present	Absent	5	3.33	Inf	1.34	0.1801	0.3439
	Present	Present	0	1.67	-Inf	-1.34	0.1801	0.5615
	Absent	Absent	8	7.2	0.3	0.53	0.5954	0.4971
Disturbed 1	Absent	Present	1	1.8	-0.3	-0.53	0.5954	0.6845
	Present	Absent	2	1.8	Inf	0.41	0.6785	0.9642
	Present	Present	0	0.2	-Inf	-0.41	0.6785	1.6605
	Absent	Absent	4	3.75	0.08	0.21	0.8299	0.837
Disturbed 2	Absent	Present	2	2.25	-0.08	-0.21	0.8299	0.6543
	Present	Absent	2	2.25	-0.18	-0.3	0.7669	0.5295
	Present	Present	1	0.75	0.18	0.3	0.7669	0.5295
	Absent	Absent	1	0.6	0.3	0.49	0.6236	0.3989
Disturbed 3	Absent	Present	2	2.4	-0.3	-0.49	0.6236	0.3989
	Present	Absent	3	2.4	0.15	0.51	0.611	0.6189
	Present	Present	5	5.6	-0.15	-0.51	0.611	0.5887

Note: "From" is the label of the point and "To" is the label of the nearest neighbour. S is the segregation index, and Z is the z-score for testing whether the observed count equals the expected count. p-values are based on the asymptotic normal distribution of the Z statistic and the randomisation distribution estimated by 5000 randomisations.

ground after they have detached from their hosts (Durden, 2006; Leal et al., 2020). Therefore, the habits and life cycles of both the hosts and the ectoparasites overlap (Kiene et al., 2020). However, generalist ectoparasites can also infest arboreal rodent species when they visit the ground, but the probability of this occurring is lower compared to transfer between ground-dwelling host species (Buettner et al., 2013).

We also found a higher probability of ectoparasite presence in male rodent hosts, which may be due to the levels of several steroid hormones (e.g., testosterone, progesterone, and estrogens, which affect immunocompetence) and the greater mobility of males (Argaez et al., 2021; Krasnov et al., 2005; Obiegala et al., 2021; Rosà et al., 2006; Shilereyo et al., 2022). Contrarily, other studies have found little support for this 'sex-biased' hypothesis (Kiffner et al., 2011). As mentioned previously, the lack of consistent results may be due to ectoparasite species host selection (de Mendonça et al., 2020; Moravvej et al., 2016; Webber et al., 2015).

In contrast to the habitat domain and sex of rodents, their relative abundance and body mass index did not significantly influence ectoparasites' presence. Although, these variables were included in the best models explaining ectoparasite presence, they were not associated with an important variation in ectoparasite presence/absence data. For rodent relative abundance, a weak negative trend was observed regarding ectoparasite presence. Although previous studies have reported a positive relationship between the relative abundances of rodents and ectoparasites (Alkathiry et al., 2022; Baláž et al., 2022), this does not always translate into increased ectoparasite presence, particularly for fleas and ticks (Hawlena et al., 2005; Krasnov et al., 2007).

Ectoparasites tend to aggregate on single hosts (Lareschi et al., 2019), however, this trend has not been widely examined in sympatric mammal hosts such as rodents. We found evidence to suggest that ectoparasites aggregate on individual rodent hosts. It has been shown that the intraspecific transmission of ectoparasites between sympatric individuals is infrequent (Cevitanes et al., 2021). Therefore, we can suggest that the aggregation we observed was related to factors associated with rodents obtaining ectoparasites from the environment and not from other rodents. Ectoparasites are generally very small and have a very limited dispersal ability when not in association with hosts (Calabrese et al., 2011). This means it is unlikely that an ectoparasite can reach a host using its mobility. Rather, they would depend on the mobility of their host. As many of the ectoparasites we obtained from the rodents tend to live in clusters when not on a host, there is an element of chance with a potential host contacting the ectoparasite nest. However, when contact is made, there is a higher chance of the host obtaining multiple ectoparasites, thus explaining the aggregation we observed. Furthermore, our results highlight the potential importance of individual-level variables of the hosts in ectoparasite aggregation. Variables, such as immunocompetence, hormone levels, stress levels, and metabolism, can determine the incidence of ectoparasites, regardless of close contact with infested rodents (Morand et al., 2006; Smith et al., 2021).

Rodents can be important vectors of zoonoses associated with ectoparasites. It has been reported that rodent

transmission of zoonoses increases in response to disturbance (White & Razgour, 2020). Rather than being related to rodent and ectoparasite diversity, this increased transmission risk may be due to the characteristics of the rodent host species that tend to inhabit disturbed sites (Mendoza et al., 2020; Morand et al., 2019). Generalist rodents are associated with fragmented and human-dominated landscapes and tend to have more contact with humans (Morand et al., 2019). This was the case in our study, with *Sigmodon* and *Rattus* only being found in disturbed sites. Both genera are associated with human agricultural activities (Hermira & Michalski, 2022) and have been identified as reservoirs of multiple zoonotic diseases carried by ectoparasites, such as Lyme disease (Lee & Williams, 2006; Rodríguez-Rojas et al., 2020; Roque & Jansen, 2014). Of the two synanthropic rodent species found at the disturbed sites, only *S. hispidus* had ectoparasites. The genera of ectoparasites found on *Sigmodon*, namely *Ornithonyssus* and *Xenopsylla*, are also frequently found in anthropogenic environments (Velo-so-Frías et al., 2019) and can transmit human diseases including dermatitis (*Ornithonyssus*), or the plague and bartonellosis (*Xenopsylla*) (Bassini-Silva et al., 2022; Beck, 2008; Cheslock & Embers, 2019; Rajamannar et al., 2022; Ramalho-Ortigao & Gubler, 2020).

We found no significant differences between ectoparasite diversity, abundance, prevalence, or presence in relation to anthropogenic disturbance. Nevertheless, when examining the species of both rodent hosts and ectoparasites that we found on each site type, we were able to identify rodent genera (*Rattus* and *Sigmodon*) that carry ectoparasites of medical importance and that are in close contact with humans. Our results highlight the necessity of constant monitoring of rodents, ectoparasites, and their associated transmittable diseases. Assessing these interactions and how they are affected by anthropogenic disturbance could better inform management decisions and support the need for rodent conservation programmes in the area. This must be accompanied by outreach interventions in the region that inform the public about the presence of rodent hosts and their ectoparasites.

AUTHOR CONTRIBUTIONS

Margarita Gil-Fernández: Conceptualization; data curation; formal analysis; visualization; writing – original draft; methodology; investigation; project administration; writing – review and editing; software; resources; funding acquisition. **Margarita Vargas-Sandoval:** Writing – review and editing; supervision; validation; methodology; data curation; formal analysis. **Christian A. Delfín-Alfonso:** Writing – review and editing; supervision; validation; conceptualization; methodology. **Eduardo Mendoza:** Visualization; methodology; formal analysis; software; writing – review and editing; project administration. **Oscar Godínez-Gómez:** Writing – review and editing; project administration; formal analysis; visualization; software; methodology. **Nancy K. Jiménez-Lara:** Methodology; investigation. **M. Cristina MacSwiney G.:** Writing – review and editing; supervision; methodology; conceptualization; validation. **Alexandra Carthey:** Validation; methodology; writing – review and editing; supervision; visualization. **Arnulfo Blanco-García:** Methodology; project administration; investigation.

Johannes J. Le Roux: Supervision; project administration; methodology; conceptualization; validation; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

None of the authors have a conflict of interest to disclose.

DATA AVAILABILITY STATEMENT

We have submitted our data in [DRYAD.org](https://www.dryad.org), under the doi:10.5061/dryad.g1jwstqvx. The following link can be used to download the data files only: <https://datadryad.org/stash/share/QbULe5pfsAbdxBAcWtYc4Zy-ivTBU7Xnc4E1o8eumWc>. The data analysed in this paper are publicly available in doi:10.5061/dryad.g1jwstqvx.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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