

Research Article

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Abundance-occupancy relationships drive core-satellite structure in helminth metacommunities of a Neotropical cichlid

Vianey Rodríguez-Alvarado^{1,2} , Jesús Montoya-Mendoza³ , Juan Manuel Caspeta-Mandujano⁴ ,
Ivonne López-del-Monte^{1,2}  and Guillermo Salgado-Maldonado² 

¹ Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico;

² Laboratorio de Helmintología, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico;

³ Laboratorio de Ecología y Helmintología, Tecnológico Nacional de México, Instituto Tecnológico de Boca del Río, Boca del Río, Veracruz, Mexico;

⁴ Laboratorio de Parasitología de Animales Silvestres, Facultad de Ciencias Biológicas y Centro de Investigación Biológicas, Universidad Autónoma del Estado de Morelos, Cuernavaca, Morelos, Mexico.

Abstract: Understanding how parasite communities are structured across spatial scales is a central challenge in parasite ecology. A widespread macroecological pattern is the positive relationship between local abundance and regional occurrence (abundance–occupancy relationship), yet its role in shaping parasite assemblages remains incompletely understood. In this study, we analysed helminth communities of 247 specimens of the Neotropical cichlid *Vieja fenestrata* (Günther) (with a size range of 38–194 mm) across 13 localities in two river basins in Mexico, integrating local (component community) and regional (metacommunity) scales. We evaluated (i) the relationship between local abundance and regional occurrence, (ii) the presence of core-satellite structure, and (iii) the contribution of spatial processes to community organisation. A total of 16 helminth taxa were recorded. Most species exhibited low prevalence and restricted distributions, whereas a small subset of taxa reached high prevalence and occurred across multiple localities. The relationship between abundance and prevalence revealed a clear positive association, supporting the existence of an abundance-occupancy pattern. This pattern was accompanied by a well-defined core-satellite structure, with a few widespread and abundant species coexisting with many rare and spatially restricted taxa. Spatial analyses indicated high heterogeneity among component communities and only weak structuring across environmental gradients, suggesting that local ecological filtering and transmission dynamics play a stronger role than broad-scale spatial segregation. Our results demonstrate that helminth communities in *V. fenestrata* are structured by macroecological processes that link local infection dynamics to regional distribution patterns. The core-satellite organisation arises from the abundance-occupancy relationship, highlighting the importance of integrating metacommunity theory into parasite ecology.

Keywords: Helminth communities, local and regional scale, freshwater fish parasites, community ecology, *Vieja fenestrata*.

This article contains supporting files (Tables S1, S2; Figs S1–S6) online at <http://folia.paru.cas.cz/suppl/2026-73-010.pdf>

Parasite communities are structured by the interaction of ecological, evolutionary and spatial processes operating across multiple scales, rather than being randomly assembled (Holmes and Price 1986, Esch et al. 1990, Kennedy 1990, Ieshko et al. 2025). One of the most consistent macroecological patterns is the abundance-range relationship, which predicts that locally abundant species tend to have wider distributions, while rare species are typically spatially restricted. This has been linked to transmission efficiency, host specificity and ecological constraints (Brown 1984, Gaston 2000, Gaston and Lawton 1990). However, the mechanisms generating this relationship in host-parasite systems remain incompletely understood, particularly in communities dominated by parasite species with complex life cycles.

A related and widely documented pattern in parasite ecology is the core-satellite structure, in which a small number of species are both locally abundant and regionally widespread (core species), while the majority are rare and occur in few localities (satellite species) (Hanski 1982, Holmes and Price 1986, Esch et al. 1990, Chugunova et al. 2024, Pelegrini et al. 2024, Ieshko et al. 2025). Although traditionally treated as a distinct framework, increasing evidence suggests that core-satellite organisation may emerge as a consequence of the abundance-occupancy relationship, reflecting differences in transmission success, persistence and spatial dynamics (Brown 1984, Gaston 2000, da Fonte et al. 2021, Stadler et al. 2023).

Address for correspondence: V. Rodríguez-Alvarado, Universidad Nacional Autónoma de México, Instituto de Biología, Laboratorio de Helmintología, Ciudad Universitaria, Coyoacán C.P. 04510, Ciudad de México, Mexico. Tel.: +52-555 622 8222 (ext. 46421); E-mail vianrnav@gmail.com, ORCID: [0009-0005-5807-3573](https://orcid.org/0009-0005-5807-3573)

At the same time, parasite communities are increasingly interpreted within a metacommunity framework, in which community structure arises from the interaction between regional dispersal and local ecological filtering (Leibold et al. 2004, Logue et al. 2011, Blasco-Costa et al. 2015, López-del-Monte et al. 2025). Under this perspective, parasite species may be present in a regional species pool but differ markedly in their ability to establish and persist within local host populations. This can generate strong spatial heterogeneity and, in some cases, a decoupling between regional occurrences and local success.

In Neotropical river systems, where environmental heterogeneity and trophic complexity are high, parasite communities provide an excellent model for integrating local infection dynamics with regional-scale processes. Examining the relationship between abundance and occupancy across multiple localities offers a powerful approach to understanding how transmission processes scale up to shape community structure.

In freshwater fish, helminth assemblages typically exhibit high unevenness, with a few dominant species coexisting with a large number of rare taxa. This pattern is particularly evident in cichlid fishes, which harbour a rich and well-documented parasite fauna (Pariselle et al. 2011, Vanhove et al. 2016). Previous studies have proposed that cichlids support a characteristic helminth fauna that recurs across geographic regions.

Helminths widely distributed across various cichlid species include monogeneans of the genus *Sciadicleithrum* Kritsky, Thatcher et Boeger, 1989, trematodes such as *Crassicutis cichlasomae* Manter, 1936 and *Oligogonotylus manteri* Watson, 1976, acanthocephalan *Neoechinorhynchus golvani* Salgado-Maldonado, 1978, and nematodes such as *Procamallanus rebecca* (Andrade-Salas, Pineda-López et García-Magaña, 1994) and *Rhabdochona kidderi* Pearse, 1936, suggesting that host phylogenetic lineage acts as a strong ecological filter shaping parasite assemblages (Pérez-Ponce de León and Choudhury 2005, Salgado-Maldonado et al. 2005, Salgado-Maldonado 2006, 2008). However, empirical evaluations of how these host-related constraints interact with spatial processes to generate macroecological patterns remain limited.

In this study, we analyse helminth communities of the cichlid *Vieja fenestrata* (Günther) across 13 localities in two Neotropical river basins in Mexico. Using a hierarchical framework that integrates local (component community) and regional (metacommunity) scales. Our objectives were: 1) Evaluate the relationship between local abundance and regional occurrence of parasite species (abundance-occupancy relationship). 2) Determine whether helminth assemblages exhibit a core-satellite structure as an emergent property of this relationship. 3) Assess the extent to which community structure reflects spatial processes and host-related filtering. We predict that parasite assemblages will exhibit a positive abundance-occupancy relationship, resulting in a small subset of widespread, locally abundant core species coexisting with a larger number of rare, spatially restricted satellite taxa. Additionally, we expect that spatial variation among communities will reflect the interaction between regional

dispersal and local ecological constraints, consistent with a metacommunity framework.

MATERIALS AND METHODS

Study area

The study was carried out in 13 sampling sites established, 11 in the Papaloapan River basin (Collection Sites (CS) 1–11) and two on the neighbouring La Antigua River basin (CS 12, 13) (Fig. 1). In 2023, two sampling campaigns were carried out: one in July and August in the Los Tuxtlas region and Lake Catemaco, and the other in September in the areas surrounding the Jamapa River and the border with the La Antigua River basin. Both hydrological systems are in the southern part of the state of Veracruz and flow into the Gulf of Mexico (DOF 2018).

Data collection

The fish were caught using nets and electrofishing, and they were immediately placed in containers filled with environmental water and kept oxygenated with portable pumps until their helminthological examination. Immediately after capture, the fish were euthanised by an overdose of the anaesthetic 2-phenoxyethanol (García-Vásquez et al. 2019). Using a stereoscopic microscope Leica Zomm 2000, the skin and fins were examined in Petri dishes containing water from the environment, and each internal organ and muscle was carefully inspected for helminths (Salgado-Maldonado et al. 2014).

The recovered helminths were separated and fixed in two ways: half of the individuals of each species were put directly in 96% alcohol for molecular processing. In contrast, the other half was fixed in hot 4% formalin and processed for morphological identification. Trematodes and acanthocephalans were stained with Mayer's paracarmine and Ehrlich's haematoxylin and mounted whole in permanent preparations with Canada balsam (Lamothe-Argumedo 1997). Nematodes were studied morphologically in temporary preparations rinsed with glycerine after dehydration in a graded glycerine-ethanol series (Caspeta-Mandujano et al. 2009). All helminths were identified to the lowest taxonomic level possible using specialised and primary literature.

Reference specimens were deposited in the National Helminth Collection (CNHE) of the Institute of Biology, UNAM. The taxonomic identification of most (12) helminth taxa recovered was assessed by means of molecular tools; this information will form part of a taxonomic report to be published elsewhere.

Analytical framework: local vs regional scale

To explicitly link local processes with regional patterns, analyses were conducted at two complementary spatial scales. At the *local scale*, each sampling site was considered a *component community*, where parasite assemblages were described in terms of species richness, prevalence, abundance, and dominance structure. At the *regional scale*, all 13 component communities were integrated into a *metacommunity framework*, allowing evaluation of large-scale patterns such as the relationship between local abundance and regional occurrence, the emergence of core-satellite structure, and spatial organisation of assemblages. This hierarchical approach allowed us to test whether local infection dynamics scale up to produce consistent macroecological patterns across the study region.

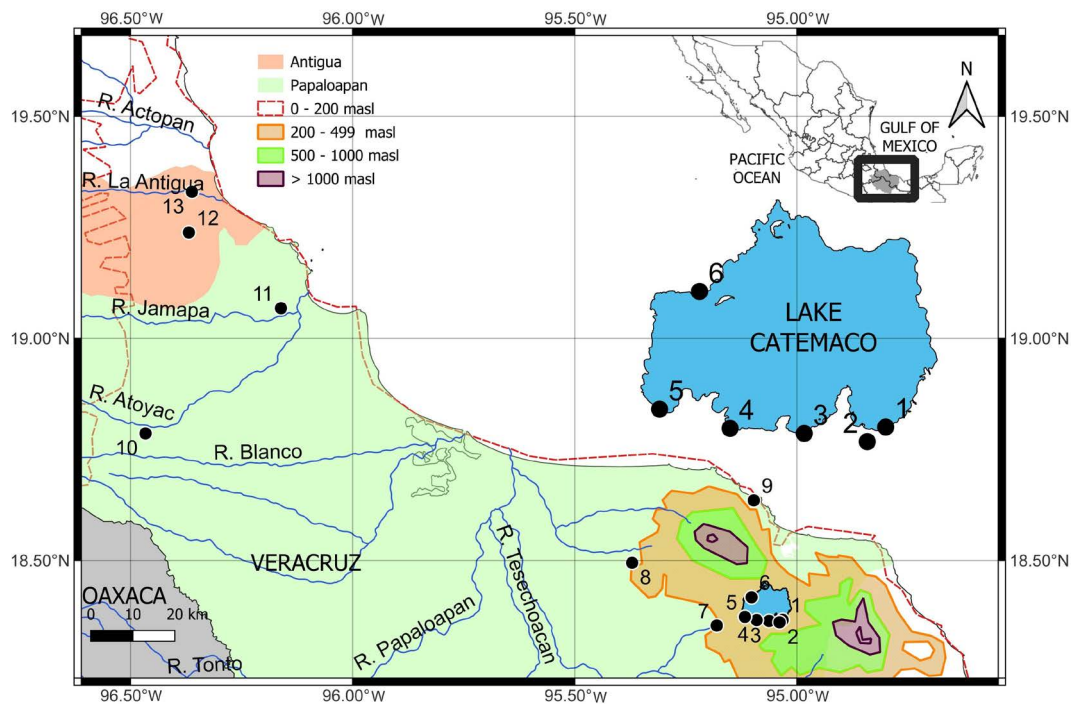


Fig. 1. Geographical location of the 13 sampling sites of *Vieja fenestrata* in the Papaloapan and La Antigua river basins, Veracruz, Mexico. Colours indicate hydrological basins. CS1 (18.3662N, -95.0320W), CS2 (18.3607N, -95.0389W), CS3 (18.3637N, -95.0626W), CS4 (18.3657N, -95.0904W), CS5 (18.3729N, -95.1169W), CS6 (18.4170N, -95.1018W), CS7 (18.3534N, -95.1802W), CS8 (18.4947N, -95.3709W), CS9 (18.6353N, -95.0969W), CS10 (18.7861N, -96.4663W), CS11 (19.0680N, -96.1612W), CS12 (19.2385N, -96.3687W), CS13 (19.3302N, -96.3617W).

Sampling completeness

To evaluate sampling effectiveness in recovering helminth diversity, three complementary approaches were used: 1) species accumulation curves, 2) clench asymptotic model was fitted using the equation: $V_2 = (a * V_1) / (1 + (b * V_1))$, where V_2 is observed richness, V_1 is the number of examined hosts, and a and b are fitted parameters, total expected richness was estimated as a/b , and the slope of the curve was calculated as $a / (1 + b * n)^2$; 3) bootstrap non-parametric richness estimator was calculated as: $S_b = S_o + \sum [1 - (h_j/H)]^H$, where S_o is the number of species observed in the original sample, h_j is the frequency of species j in the bootstrap sample, and H is the total sample size (Poulin 1998, Jiménez-Valverde and Hortal 2003, Salgado-Maldonado et al. 2014).

Abundance-occupancy relationship

To evaluate whether helminth assemblages follow a macroecological abundance-occupancy relationship, species were characterised by their *mean abundance* and *prevalence across component communities*. The relationship between these variables was explored using a bivariate approach based on log-transformed abundance ($\ln X + 1$) and prevalence (%). This analysis allowed identification of dominant versus rare species and assessment of whether widely distributed species tend to reach higher local abundances (Salgado-Maldonado et al. 2014).

Core-satellite classification

To classify species into central and satellite categories, the Partitioning Around Medoids (PAM) algorithm (Kaufman and Rousseeuw 1990) was used, with Manhattan distance as the dissimilarity measure (Legendre and de Cáceres 2013). A species $\times$ variable

matrix was constructed with two descriptors per species: (1) occupancy frequency (proportion of sites where the species was present) and (2) mean abundance per site (log-transformed to base 10). The variables were standardised (mean = 0, standard deviation = 1) to avoid biases due to differences in scale and 95% confidence intervals (Sarabeev et al. 2018). To determine the optimal number of clusters, we used the average silhouette width (Rousseeuw 1987). In addition, we assessed the quality of the clustering using the Davies-Bouldin Index (DBI), where lower values indicate a better clustering structure (Davies and Bouldin 1979, Anfossi and Chicco 2026), making it suitable for ecological data with high variability.

Local community structure

At the component community level, infection parameters were calculated following Bush et al. (1997): 1) prevalence, 2) mean intensity and 3) mean abundance. Community structure was further explored using: 1) rank-abundance curves (Whittaker), 2) frequency distributions of prevalence and 3) graphical representations of species dominance patterns. Prevalence values are presented with 95% confidence intervals.

Spatial structure of helminth assemblages

To evaluate the spatial organisation of parasite communities, we performed NMDS ordination based on Bray-Curtis dissimilarity (Clarke and Warwick 2001, Anderson 2017).

To assess the contribution of each site to regional community structure, we followed the key β -diversity partition framework proposed by Legendre and de Cáceres (2013). This decomposition breaks down the variation into two components: 1) the local contribution to β -diversity (LCBD), which allows the uniqueness of

a site's helminth composition to be estimated in relation to another site; and 2) the species contribution (SCBD). This partition was analysed using abundance data with the Hellinger transformation.

All analyses were carried out in R version 4.3.1. (R Core Team 2023) within the RStudio environment. The following packages were used: BiodiversityR (rankabundance; Kindt 2025), vegan (metaMDS, adonis2; Oksanen et al. 2025), adespatial (beta.div; Dray et al. 2026), cluster (pam; Maechler et al. 2026) and factoextra (fviz_cluster; Kassambara et al. 2026).

RESULTS

Regional richness and sampling completeness

A total of 16 helminth taxa were recorded across 13 component communities of *Vieja fenestrata* (Table 1). We analysed 247 specimens of *V. fenestrata* ranging in size from 38 to 194 mm; the specimens with the largest average size were found at CS9 (169 mm), while the smallest were found in CS11 (73 mm) (Table 2). Local species richness ranged from 2 to 9 taxa per site, with the highest values observed in sites CS5, CS8 and CS11 (Fig. 1, Table 2).

Species accumulation curves approached asymptotes in most communities (Fig. 2), and both Clench and Bootstrap estimators indicated that observed richness represented a high proportion of expected richness (Table 2). However, some sites (e.g., CS3 and CS6) showed steeper slopes and discrepancies between observed and estimated richness, suggesting incomplete sampling.

Abundance-occupancy relationship at the regional scale

Across the regional metacommunity, parasite species exhibited a highly uneven distribution in both prevalence and abundance. The majority of taxa showed low prevalence (<30%), while only a few species reaching moderate to high values (Figs. S1, S2). The bivariate relationship between mean abundance and prevalence (Fig. 3) revealed a clear positive association, with a subset of eight species, including *Crassicutis cichlasomae*, *Rhabdochona kidderi*,

Proterodiplostomum sp.), occupying the high-abundance/high-prevalence region, whereas most species clustered at low values of both parameters.

This pattern supports the existence of an abundance-occupancy relationship structuring the helminth metacommunity.

Emergence of a core-satellite structure

Medoid-based cluster analysis (PAM) revealed a structure comprising two distinct groups: core and satellite. This partition was validated by the average silhouette width and the DBI value ($k = 2$, DBI = 0.861) (Table S1 and Fig. S3). The first group, core species, which had the highest abundances and high occupancy frequencies: *C. cichlasomae* (77%), *Proterodiplostomum* (69 %) and *R. kidderi* (46%). The second group, satellite species, included the remaining 13 species, characterised by low total abundances (≤ 110 individuals) and occupancy frequencies of less than 40% (Figs. 4, S4, Table S2).

Core species were widespread and locally abundant, occurring in multiple component communities and reaching the highest prevalence values. In contrast, satellite species were restricted to one or a few localities and exhibited consistently low prevalence and abundance.

The strongly right-skewed distribution of prevalence (Fig. S5) and the clustering pattern observed in ordination of species support the existence of a core-satellite structure emerging from the uneven distribution of species across the region (Fig. 4).

Local community variation (site-level patterns)

At the component community level, parasite assemblages were characterised by low median prevalence and high variability among sites (Fig. S6). Occasional high-prevalence values corresponded to core species dominating specific communities.

Rank-abundance curves (Fig. 5) showed steep slopes across sites, indicating low evenness and dominance by one or a few species, followed by a long tail of rare taxa.

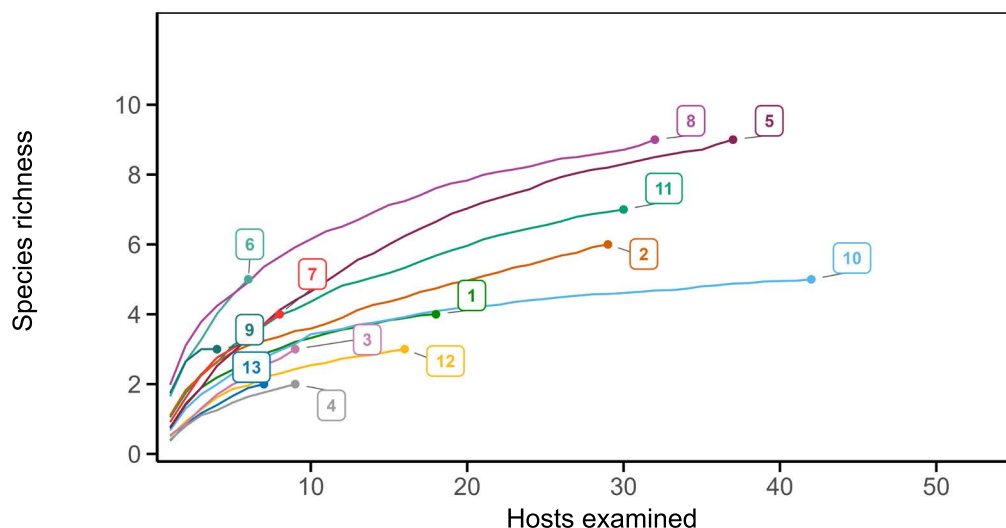


Fig. 2. Species accumulation curves for helminth assemblages across 13 component communities. Curves represent the increase in species richness as a function of the number of hosts examined. Numbers correspond to sampling sites.

Table 1. Helminth parasites of *Vieja fenestrata* (Günther) across 13 sampling sites (CS) in the Papaloapan and La Antigua River basins. For each species at each site, infection parameters are shown as prevalence (PR % with 95% confidence intervals), mean intensity (MI $\pm$ SD), and mean abundance (MA $\pm$ SD with 95% confidence intervals).

Helminth Phylum Platyhelminthes Monogenea	CNHE catalog number	Site of infection	CS	No. of in- fected hosts/ examined	No. of individual parasites	PR (%)	MI $\pm$ SD	MA $\pm$ SD
<i>Sciadicleithrum bravohollisae</i> Kritsky, Vidal-Martinez et Rodríguez-Canul, 1994		Gills	8	3/32	5	9 (0.02–0.25)	1.6 $\pm$ 1.2	0.15 $\pm$ 0.57 (0.03–0.46)
			10	1/42	4	2 (0.001–0.13)	4	0.09 $\pm$ 0.61 (0–0.29)
			11	8/30	15	27 (0.12–0.50)	1.9 $\pm$ 2.1	0.5 $\pm$ 1.33 (0.2–1.21)
Trematoda (Adults)								
<i>Oligogonotylus manteri</i> Wat- son, 1976	12610	Intestine	5	1/37	2	3 (0.001–0.14)	2	0.05 $\pm$ 0.32 (0–0.16)
	12611		7	1/8	6	13 (0.003–0.52)	6	0.75 $\pm$ 2.12 (0–2.25)
	12612		8	3/32	12	9 (0.02–0.25)	4.0 $\pm$ 1.7	0.37 $\pm$ 1.26 (0–0.94)
			10	5/42	15	12 (0.04–0.26)	3 $\pm$ 2.7	0.35 $\pm$ 1.30 (0.07–1)
			13	2/7	5	29 (0.04–0.71)	2.5 $\pm$ 2.1	0.71 $\pm$ 1.49 (0–1.86)
<i>Crassicutis cichlasomae</i> Manter, 1936		Intestine	1	5/18	9	28 (0.09–0.54)	1.8 $\pm$ 0.4	0.5 $\pm$ 0.85 (0.11–0.88)
	12613		2	12/29	29	41 (0.23–0.61)	2.4 $\pm$ 2.1	1.0 $\pm$ 1.7 (0.51–1.79)
	12615		5	2/37	2	5 (0.07–0.18)	1 $\pm$ 0	0.05 $\pm$ 0.22 (0–0.14)
	12616		6	4/6	26	67 (0.22–0.96)	6.5 $\pm$ 3.4	4.3 $\pm$ 4.3 (1.33–7.67)
			7	2/8	4	25 (0.03–0.65)	2 $\pm$ 0	0.5 $\pm$ 0.92 (0–1)
			8	25/32	222	78 (0.60–0.90)	8.9 $\pm$ 8.0	6.9 $\pm$ 7.9 (4.84–10.6)
			9	2/4	3	50 (0.07–0.93)	1.5 $\pm$ 0.7	0.75 $\pm$ 0.95 (0–1.5)
			10	2/42	2	5 (0.01–0.16)	1	0.04 $\pm$ 0.21 (0–0.12)
			12	4/16	13	25 (0.07–0.52)	3.3 $\pm$ 1.3	0.81 $\pm$ 1.55 (0.18–1.62)
			13	1/7	5	14 (0.004–0.58)	4	0.50 $\pm$ 1.51 (0–0.17)
<i>Genarchella isabellae</i> Lam- othe-Argumedo, 1977	12617	Stomach	8	11/32	42	34 (0.19–0.52)	3.8 $\pm$ 4.0	1.3 $\pm$ 2.92 (0.62–2.91)
<i>Phyllodistomum</i> sp.	12618	Intestine	5	1/37	1	3 (0.001–0.142)	1	0.02 $\pm$ 0.16 (0–0.08)
			12	3/16	32	19 (0.04–0.46)	10.7 $\pm$ 14.2	2 $\pm$ 6.7 (0.19–11.8)
Trematoda (larvae)								
<i>Clinostomum</i> sp.	12619	Intestine, operculum and mesenteries	10	6/42	16	14 (0.05–0.29)	2.7 $\pm$ 3.1	0.38 $\pm$ 1.44 (0.11–1.16)
	12620		11	1/30	2	3 (0.001–0.17)	2	0.07 $\pm$ 0.36 (0–0.20)
	12621	Intestine	1	1/18	1	6 (0.001–0.27)	1	0.055 $\pm$ 0.23
<i>Posthodiplostomum</i> sp.			3	1/9	1	11 (0.003–0.48)	1	0.11 $\pm$ 0.33 (0–0.33)
			4	1/9	1	11 (0.003–0.48)	1	0.11 $\pm$ 0.33 (0–0.33)
			5	1/37	1	3 (0.001–0.14)	1	0.02 $\pm$ 0.16 (0–0.08)
			8	1/32	1	3 (0.001–0.16)	1	0.03 $\pm$ 0.17 (0–0.094)
			11	1/30	1	3 (0.001–0.17)	1	0.033 $\pm$ 0.18 (0–0.1)
<i>Proterodiplostomum</i> sp.	12622	Gills	1	2/18	6	11 (0.01–0.34)	3.0 $\pm$ 2.8	0.30 $\pm$ 1.18 (0–1.61)
	12623		2	1/29	2	3 (0.001–0.18)	2	0.06 $\pm$ 0.37 (0–0.21)
			3	1/9	9	11 (0.003–0.48)	9	1 $\pm$ 3 (0–3)
			5	5/37	10	14 (0.04–0.28)	2 $\pm$ 1	0.27 $\pm$ 0.76 (0.05–0.57)
			6	2/6	106	33 (0.04–0.77)	53.0 $\pm$ 66.4	17.7 $\pm$ 40.4 (0–52)
			7	4/8	118	50 (0.16–0.84)	29.5 $\pm$ 43.7	14.8 $\pm$ 32.7 (1.93–49)
			8	1/32	1	3 (0.001–0.162)	1	0.03 $\pm$ 0.17 (0–0.09)
			9	3/4	75	75 (0.19–0.99)	25.0 $\pm$ 23.6	18.8 $\pm$ 23.0 (1.5–38.2)
			11	3/30	75	10 (0.02–0.27)	25.0 $\pm$ 24.5	2.5 $\pm$ 10.0 (0.03–9.93)
<i>Centrocestus formosanus</i> Nishigori, 1924		Gills	5	3/37	4	8 (0.017–0.219)	1.3 $\pm$ 0.6	0.10 $\pm$ 0.39 (0–0.27)
			8	1/32	1	3 (0.001–0.16)	1	0.03 $\pm$ 0.17 (0.03–0.09)
		Gills	2	1/29	3	3 (0.001–0.18)	3	0.10 $\pm$ 0.55 (0–0.31)
<i>Ascoctyle</i> sp.			5	2/37	4	5 (0.07–0.18)	2 $\pm$ 1	0.27 $\pm$ 0.76 (0–0.27)
			6	1/6	6	17 (0.004–0.64)	6	1 $\pm$ 2.45 (0–2)
			7	1/8	4	13 (0.003–0.52)	4	0.5 $\pm$ 1.4 (0–1.5)
			11	1/30	4	3 (0.001–0.17)	4	0.13 $\pm$ 0.73 (0–0.4)
Nematoda (Adults)								
<i>Rhabdochona kidderi</i> Pearse, 1936	12624	Intestine	2	16/29	90	55 (0.35–0.74)	5.6 $\pm$ 10.1	3.10 $\pm$ 7.90 (1.45–10.7)
			6	1/6	3	17 (0.004–0.64)	4	0.6 $\pm$ 1.6 (0–2)
	12625		8	18/32	213	56 (0.38–0.74)	11.8 $\pm$ 12.3	6.7 $\pm$ 10.9 (4.04–12.7)
			9	2/4	31	50 (0.07–0.93)	15.5 $\pm$ 19.0	7.8 $\pm$ 14.2 (0–21.8)
			11	2/30	3	7 (0.01–0.22)	1.5 $\pm$ 0.70	0.1 $\pm$ 0.4 (0–0.33)
<i>Procamallanus rebecca</i> An- drade-Salas, Pineda-López et. García-Magaña, 1994	12626	Intestine	2	1/29	2	3 (0.001–0.18)	2	0.06 $\pm$ 0.25 (0–0.18)
								0.07 $\pm$ 0.37 (0–0.20)
Larvae								
<i>Contracaecum</i> sp.	12627	Mesenteries	2	2/29	3	7 (0.01–0.23)	1.5 $\pm$ 0.70	0.10 $\pm$ 0.40 (0–0.32)
			8	5/32	9	16 (0.05–0.39)	1.8 $\pm$ 1.3	0.28 $\pm$ 0.81 (0.09–0.70)
			10	14/42	23	33 (0.20–0.50)	1.64 $\pm$ 1.08	0.55 $\pm$ 0.99 (0.31–0.92)
			11	15/30	19	50 (0.13–0.69)	1.26 $\pm$ 0.45	0.63 $\pm$ 0.71 (0.37–0.87)
<i>Spiroxyx</i> sp.		Intestine	6	1/6	3	17 (0.004–0.64)	3	0.5 $\pm$ 1.2 (0–1)

Table 1. continued

Acanthocephala								
<i>Neoechinorhynchus golvani</i> Salgado-Maldonado, 1978	12628	Intestine	1	6/18	55	33 (0.13–0.59)	9.2±8.2	3.05±6.28 (1.17–7.97)
	12629		3	3/9	9	33 (0.08–0.70)	3±1	1.0±1.58 (0.22–2.19)
			4	3/9	6	33 (0.08–0.70)	2±1	0.67±1.11 (0.005–1.44)
			5	9/37	40	24 (0.12–0.41)	4.4±4.0	1.08±2.71 (0.46–2.49)
Cystacanth								
<i>Southwellina hispida</i> Van Cleave, 1925		Mesentery	5	3/37	6	8 (0.01–0.21)	2	0.16±0.55 (0–0.32)

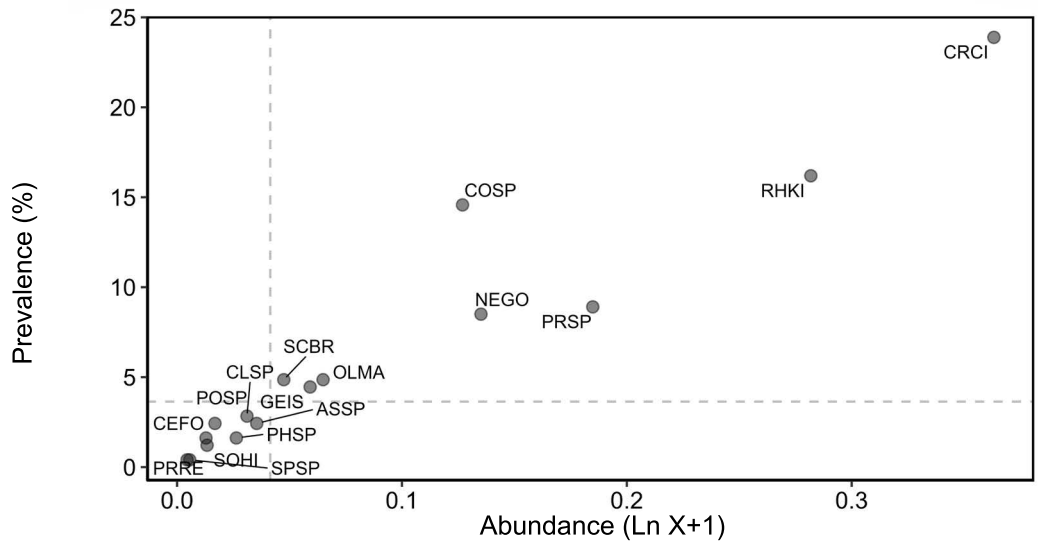


Fig. 3. Relationship between mean abundance (Ln X+1) and prevalence (%) of helminth species across the regional metacommunity. Dashed lines indicate mean values, separating dominant (high abundance–high prevalence) from rare species. Abbreviations of helminth species: ASSP – *Ascocotyle* sp.; CEFO – *Centrocestus formosanus*; CLSP – *Clinostomum* sp.; COSP – *Contracaecum* sp.; CROI – *Crassicutis cichlasomae*; GEIS – *Genarchella isabellae*; NEG – *Neoechinorhynchus golvani*; OLMA – *Oligogonotylus manteri*; PHSP – *Phyllodistomum* sp.; POSP – *Posthodiplostomum* sp.; PRRE – *Procamallanus rebeae*; PRSP – *Proterodiplostomum* sp.; RHKI – *Rhabdochona kidderi*; SCBR – *Sciadicleithrum bravohollisae*; SOHI – *Southwellina hispida*; SPSP – *Spiroxys* sp.

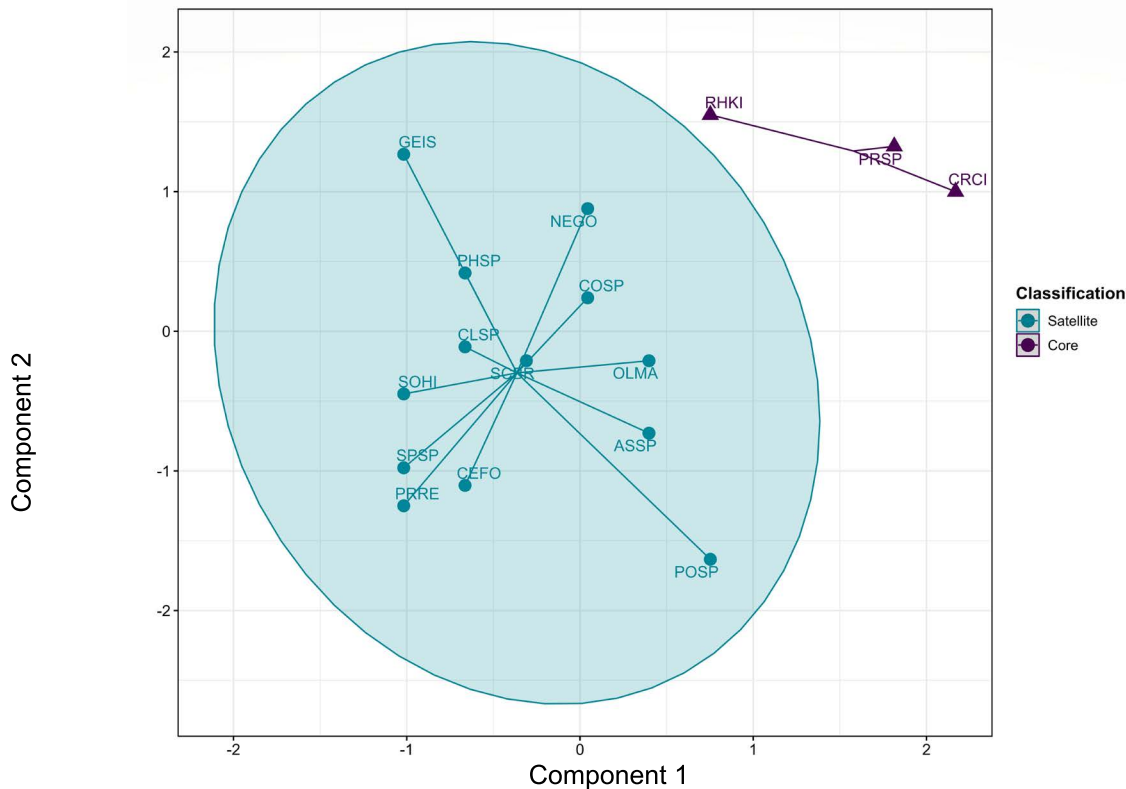


Fig. 4. Cluster plots of core and satellite species based on occupancy frequency (proportion of sites where the species was present) and mean abundance per site (log-transformed to base 10). For abbreviations of helminth species, see Fig. 3. The ellipse represents the 95% confidence intervals.

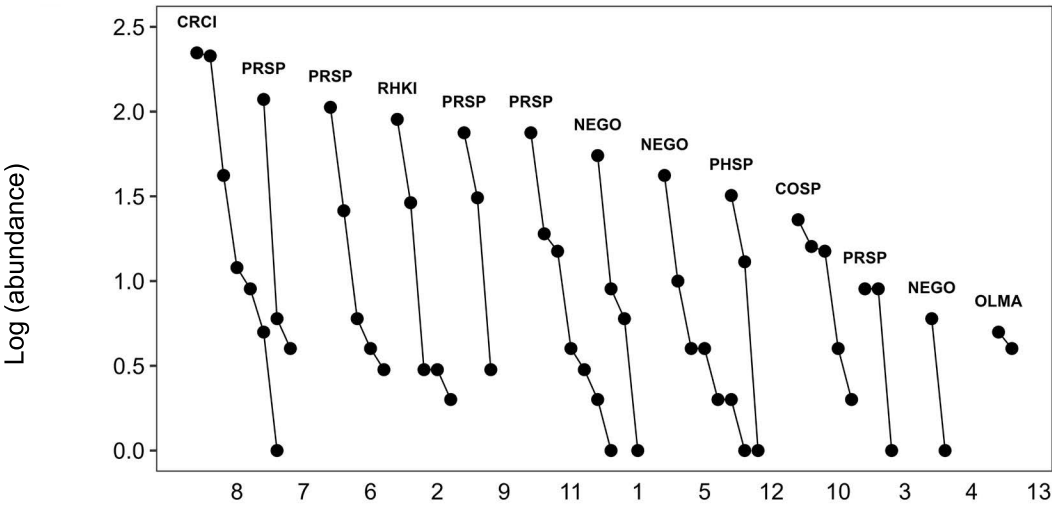


Fig. 5. Rank–abundance (Whittaker) curves for helminth assemblages across component communities. Species are ordered from most to least abundant, illustrating dominance patterns and low evenness. For abbreviations of helminth species, see Fig. 3.

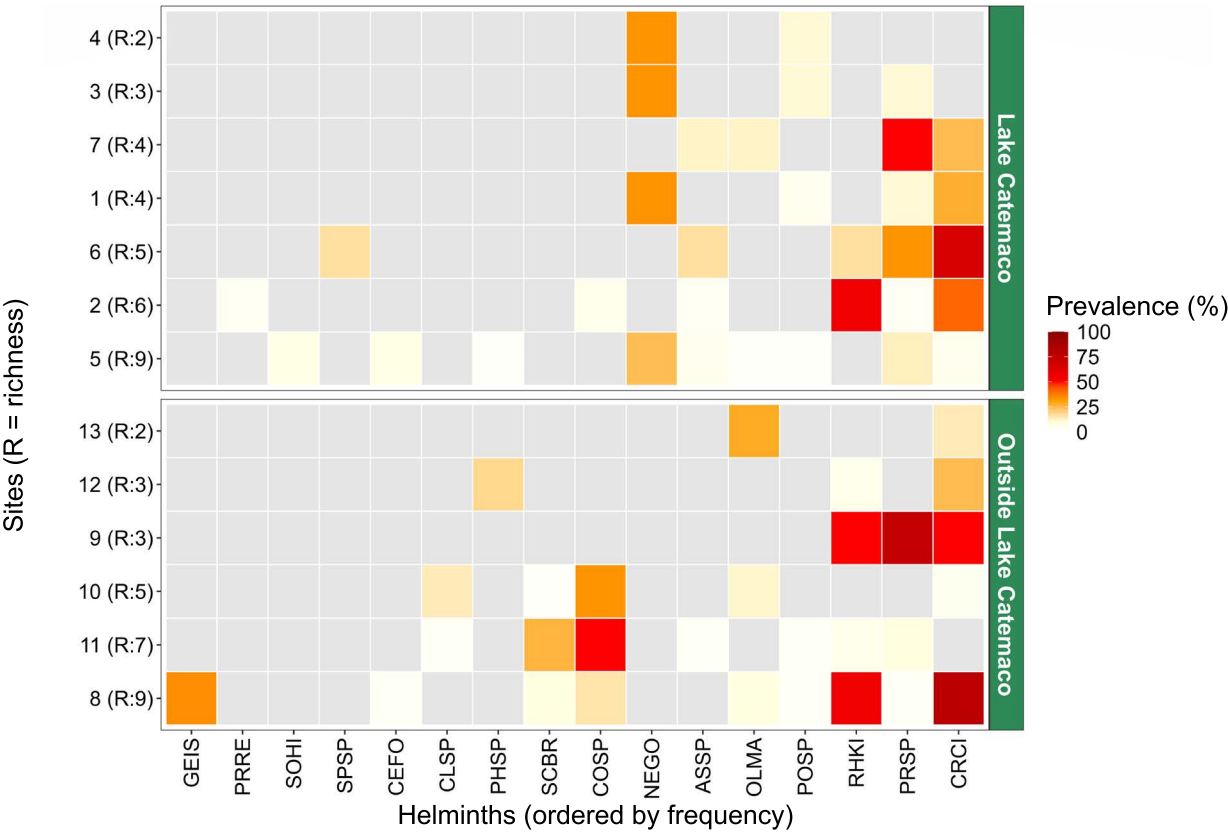


Fig. 6. Heatmap showing spatial variation in helminth prevalence across component communities. Rows represent sites and columns represent helminth taxa. Colour intensity indicates prevalence (%), highlighting heterogeneous spatial occupancy patterns. For abbreviations of helminth taxa, see Fig. 3.

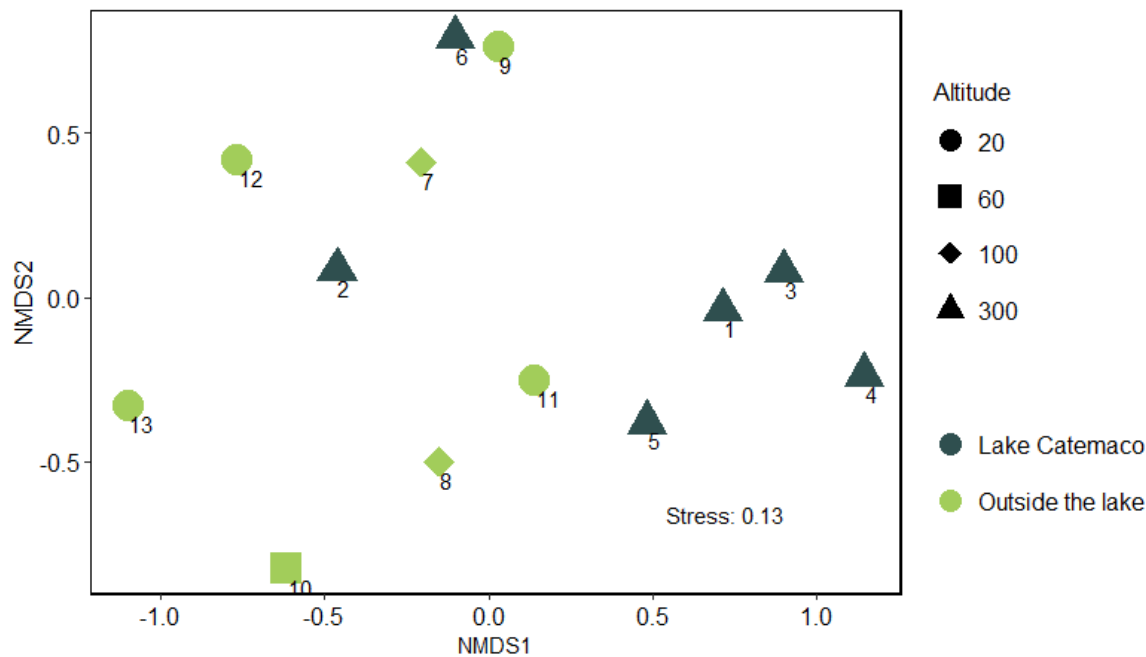


Fig. 7. NMDS ordination of component communities based on Bray–Curtis similarity. Symbol colour indicates proximity to Lake Catemaco, and shape represents altitude categories.

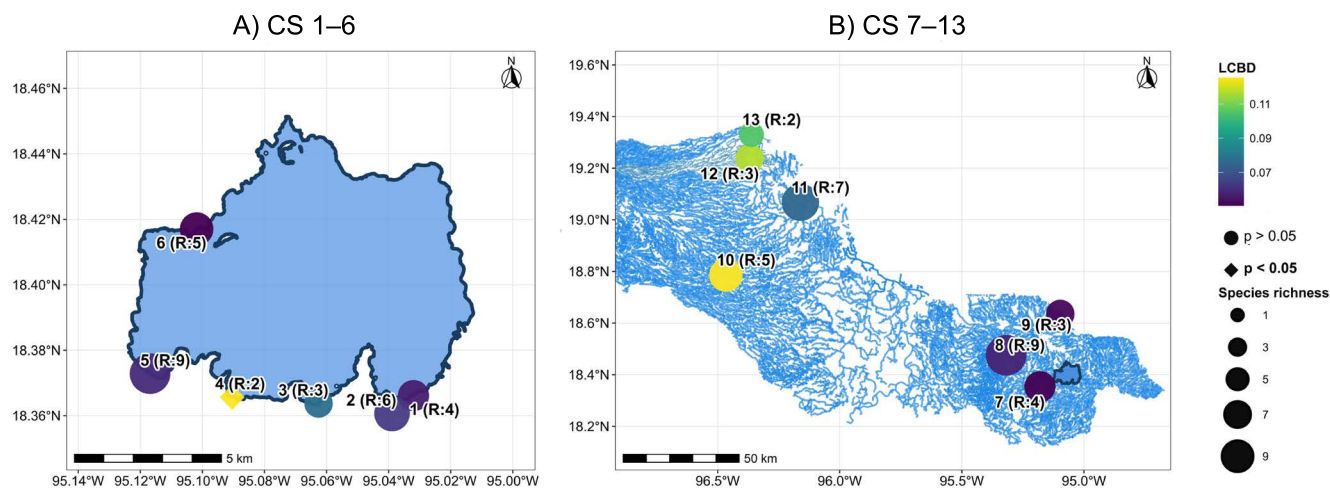


Fig. 8. LCBD values at 13 CS collection sites in Papaloapan River basin.

Table 2. Observed and estimated species richness of helminth assemblages across component communities. Estimates are based on the Clench model and the Bootstrap estimator. The slope of the species accumulation curve is included as an indicator of sampling completeness.

CS	No. of hosts examined	Total length (mm) $\bar{x}$ (min–max)	S Observed	Clench’s model parameters		Richness estimated (Clench a/b)	Slope	Bootstrap
				a	b			
1	18	81 (41–125)	4	1.75	0.37	5	0.03	4.48
2	29	100 (66–180)	6	0.53	0.07	8	0.06	7.21
3	9	112 (100–128)	3	0.86	0.14	6	0.16	3.71
4	9	116 (90–145)	2	0.49	0.15	3	0.09	2.37
5	37	103 (42–157)	9	0.31	0.03	10	0.07	10.8
6	6	97 (70–120)	5	1.21	0.28	6	0.17	6.09
7	8	74 (40–121)	4	3.59	0.73	5	0.07	4.79
8	32	104 (38–194)	9	3.43	0.33	10	0.06	10.2
9	4	169 (142–183)	3	5.09	1.37	4	0.12	3.12
10	42	82 (53–183)	5	6.83	1.32	5	0.002	5.49
11	30	73 (55–163)	7	7.05	0.74	10	0.01	8.25
12	16	89 (52–189)	3	0.68	0.18	4	0.045	3.4
13	7	101 (75–129)	2	0.9	0.29	3	0.09	2.43

CS – Collection sites; S – Richness

The heatmap representation (Fig. 6) revealed high spatial heterogeneity, with most species absent from many sites and only a small subset consistently presents across multiple localities.

Spatial structure and environmental gradients

NMDS ordination of component communities (Fig. 7) suggested partial spatial structuring, with sites near Lake Catemaco clustering together and some separation along an altitudinal gradient. Of the 13 sampling points, four stood out for contributing most to β -diversity (LCBD); three sites (CS 10, 12 and 13) were remote, and one on Lake Catemaco (CS 4) made a significant contribution to regional β -diversity (LCBD = 0.1254, $p = 0.034$) (Fig. 8).

The species with the highest SCBD values were three species from different groups: the acanthocephalan *Neoechinorhynchus golvani* (0.26), the trematode *Proterodiplostomum* (0.22) and the nematode *Rhabdochona kidderi* (0.18); these species can be considered the main drivers of β -diversity patterns in the basin.

A relationship was observed between SCBD and species occupancy ($R^2 = 0.42$, Fig. 9). Whilst *N. golvani* and *Proterodiplostomum* exhibited intermediate occupancy, *R. kidderi* showed high occupancy but maintained a high SCBD (0.18).

These results suggest that helminth community structure is influenced by environmental gradients but largely dominated by stochastic or host-related processes at the regional scale.

DISCUSSION

Our results provide clear evidence that helminth communities of *Vieja fenestrata* are structured by a positive relationship between local abundance and regional occurrence, consistent with the abundance-occupancy pattern widely documented in parasite systems (Brown 1984, Gaston 2000, Blasco-Costa et al. 2015, Ieshko et al. 2022, Sarabeev et al. 2022, Silva et al. 2022, Plaksina et al. 2023, Chugunova et al. 2024).

The majority of parasite taxa exhibited low prevalence and low abundance, whereas a small subset of species reached both high prevalence and high abundance across multiple component communities. Parasites do not remain constant across space and time; population success depends on both abiotic and biotic factors (Choudhury and Dick 2000, Poulin 2006, Blasco-Costa et al. 2015). Variability across localities within the same region is very common in helminth populations. This is the case with the helminths of *V. fenestrata* in southeast Mexico; there is marked variability in infection parameters. For example, Jiménez-García (1993) recorded the nematode *Rhabdochona kidderi* in Lake Catemaco with a prevalence of 13%, while Salgado-Maldonado et al. (2005) recorded it in the Papaloapan River basin with a prevalence ranging from 13 to 69%. This pattern indicates that widely distributed species tend to achieve higher local success, suggesting that transmission efficiency and establishment probability scale positively across spatial levels.

Importantly, this macroecological relationship provides the mechanistic basis for the emergence of uneven community structure, linking local infection dynamics with regional distribution patterns.

The observed abundance-occupancy relationship gives rise to a clear core-satellite structure, characterised by a small number of widespread and abundant species and a large pool of rare, spatially restricted taxa.

This pattern is consistent with the core-satellite hypothesis (Hanski 1982) and its application to parasite systems (da Fonte et al. 2021, Stadler et al. 2023) and is supported here by the convergence of multiple analytical approaches, including prevalence distributions, rank-abundance curves, and ordination analyses.

Rather than representing independent processes, our results suggest that the core-satellite structure is an emergent property of the abundance-occupancy relationship (Brown 1984, Gaston 2000), reflecting underlying differences in transmission success, host compatibility, and persistence across spatial scales. The consistent presence of a subset of core species across localities supports the existence of a characteristic helminth fauna associated with cichlid hosts, as previously proposed (Salgado-Maldonado 2006, 2008).

Core species such as *Crassicutis cichlasomae*, *Proterodiplostomum* sp., and *R. kidderi* were widely distributed and reached high prevalence, suggesting strong adaptation to cichlid hosts. This pattern highlights the role of host phylogenetic lineage as a primary ecological filter structuring parasite assemblages at regional scales (Pariselle et al. 2011, Vanhove et al. 2016). Thus, the metacommunity structure observed here reflects the interaction between evolutionary constraints imposed by host lineage and ecological processes governing parasite transmission.

The predominance of satellite species with low prevalence can be largely attributed to the complex life cycles of helminths, which depend on trophic transmission involving multiple hosts. Such complexity imposes strong constraints on successful transmission, reducing the probability of establishment in any given locality and leading to sporadic occurrences (Esch et al. 1990, Marcogliese 2023).

In this context, variation in prevalence and abundance reflects not only ecological specialisation but also stochastic and demographic processes associated with transmission dynamics (Morand and Guégan 2000). Moreover, parasite populations may exhibit temporal variability linked to host availability and environmental conditions, potentially shifting species along the core-satellite continuum (Muñoz and Delorme 2011).

The strong spatial heterogeneity observed among component communities indicates that parasite assemblages are not uniformly distributed across the region. Instead, most species occur in a limited number of sites, while only a few are widely distributed. This pattern supports a metacommunity framework in which community structure emerges from the interplay between regional dispersal and local ecological filtering (Holmes and Price 1986, Kennedy 1990, Leibold et al. 2004, Logue et al. 2011, Blasco-Costa et al. 2015, López-del-Monte et al. 2025).

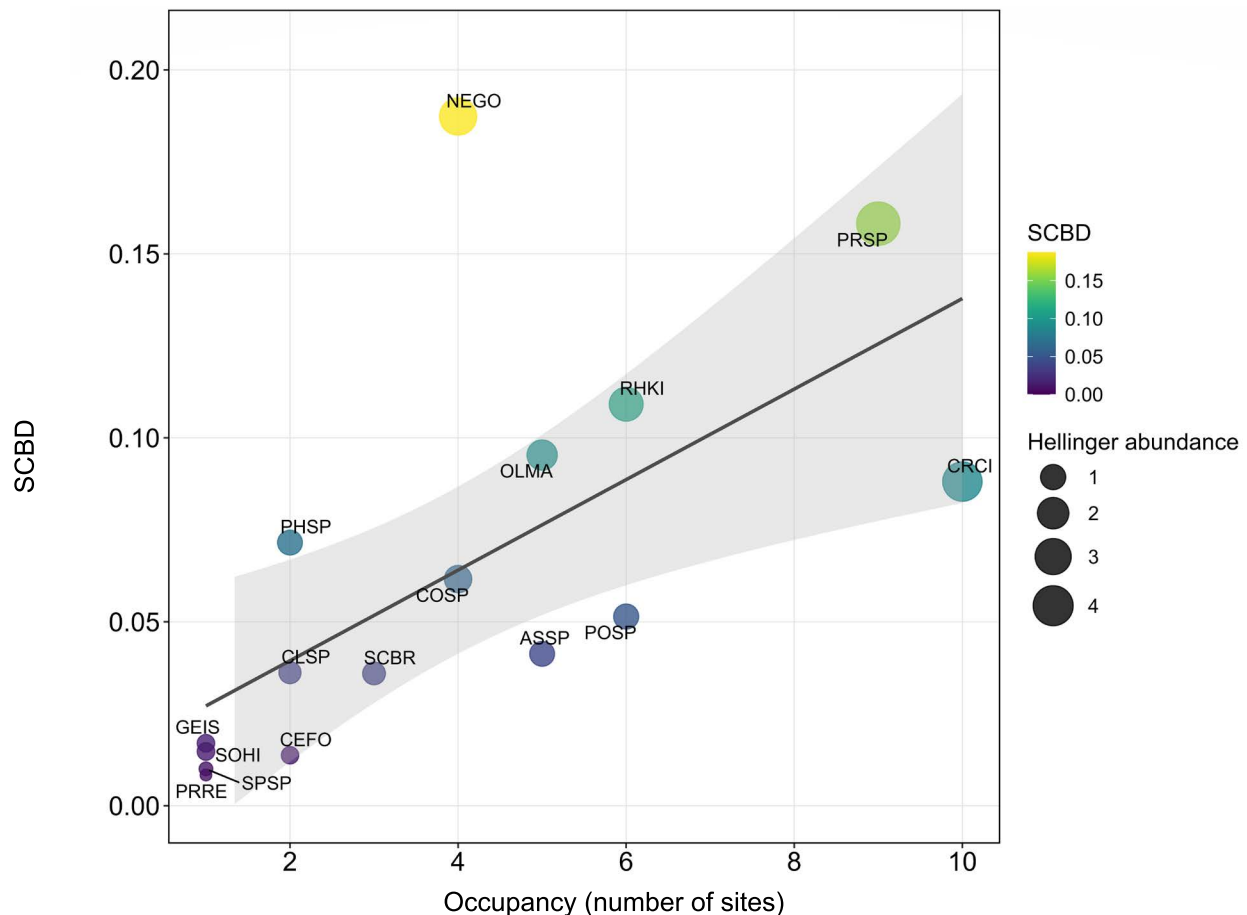


Fig. 9. Relationship between the number of sites occupied by each helminth taxon and the SCBD value. For abbreviations of helminth taxa, see Fig. 3.

The establishment of parasite species at both local and regional scales depends on the availability of hosts, trophic interactions and environmental conditions. Core species likely represent taxa with high dispersal ability and broad ecological tolerance, whereas satellite species reflect limited dispersal, strong environmental filtering, or low host compatibility (da Fonte et al. 2021, Stadler et al. 2023). Among cichlid helminths, *C. cichlasomae* and *R. kidderi* have been reported as widely distributed species (Salgado-Maldonado et al. 2005, Salgado-Maldonado 2006, 2008), whereas *Proterodiplostomum* sp. was not previously considered among these species. However, in the present study, its consistent presence at sampling sites confirms its high dispersal capacity, characteristics typical of keystone species.

LCBD values were not correlated with species richness, which is consistent with previous studies (Legendre and De Cáceres 2013, Pozzobom et al. 2020), indicating that the contribution to β -diversity depends more on species identity. Despite the overall abundance-occupancy relationship, our results also suggest a partial decoupling between regional occurrence and local success. Many species were present in the region but exhibited low prevalence and restricted distributions.

This indicates that dispersal alone is insufficient to determine parasite success and highlights the importance of local ecological constraints in shaping infection patterns. Such decoupling is consistent with metacommunity theo-

ry, where species presence does not necessarily imply successful establishment or persistence, particularly in systems with strong environmental filtering and complex life cycles, as predicted by metacommunity theory (Leibold et al. 2004, Logue et al. 2011).

The coexistence of a few dominant species and a large number of rare taxa reflect contrasting transmission strategies and ecological roles within parasite communities. Core species, characterised by high prevalence and wide distribution, likely contribute disproportionately to transmission dynamics and represent stable host-parasite associations (Ieshko et al. 2022, Sarabeev et al. 2022, Silva et al. 2022, Plaksina et al. 2023, Chugunova et al. 2024). These species are typically associated with cichlids and exploit consistent ecological pathways (Salgado-Maldonado 2006).

In contrast, satellite species appear to represent transient or opportunistic infections, influenced by stochastic colonisation events, environmental variability, and host feeding behaviour (Stock and Holmes 1987, Esch et al. 1990, Plaksina et al. 2023). Overall, these findings highlight the importance of integrating local infection processes with regional-scale dynamics to understand parasite biodiversity.

In conclusion, our study demonstrates that helminth communities of *Vieja fenestrata* are structured by the interaction of macroecological, ecological, and evolutionary processes. The abundance-occupancy relationship emerges as a central organising principle, generating a core-satellite

structure that reflects differences in transmission success and host association. At the same time, spatial heterogeneity and partial decoupling between occurrence and abundance indicate the importance of local ecological filtering within a metacommunity framework.

These results provide empirical support for the idea that parasite communities are shaped by hierarchical processes operating across spatial scales and reinforce the role of host phylogeny as a key determinant of parasite community structure in Neotropical freshwater systems.

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Author contributions statement. GSM and VRA (research design, research execution, data analysis, and manuscript writing), GSM, VRA, JMM, JMCM and ILdM (sample processing and collection). All authors provided commentary throughout the manuscript process.

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