

Ecology

## Community structure of the helminths of *Lithobates spectabilis* (Anura: Ranidae) from two localities in the Biosphere Reserve Barranca de Metztitlán, Hidalgo, Mexico

### *Estructura de la comunidad de helmintos de Lithobates spectabilis* (Anura: Ranidae) de dos localidades en la Reserva de la Biosfera Barranca de Metztitlán, Hidalgo, México

Edgar S. Ramírez-Cruz <sup>a</sup>, Scott Monks <sup>a</sup>, Elizabeth A. Martínez-Salazar <sup>b</sup>,  
Jorge Falcón-Ordaz <sup>a</sup>, Griselda Pulido-Flores <sup>a, \*</sup>

<sup>a</sup> Universidad Autónoma del Estado de Hidalgo, Centro de Investigaciones Biológicas, Laboratorio de Morfología Animal, Carretera Pachuca - Tulancingo Km 4.5, Col. Carboneras, 42184 Mineral de la Reforma, Hidalgo, Mexico

<sup>b</sup> Universidad Autónoma de Zacatecas, Unidad Académica de Ciencias Biológicas, Laboratorio de Colecciones Biológicas y Sistemática Molecular, Av. Preparatoria s/n, Campus Universitario II, Col. Agronómica, 98066 Zacatecas, Zacatecas, Mexico

\*Corresponding author: gpulido@uaeh.edu.mx (G. Pulido-Flores)

Received: 5 August 2022; accepted: 10 November 2022

#### Abstract

The helminth community of *Lithobates spectabilis* ( $n=77$ ) was studied from Las Pilas (low altitude) and Metznoxtla (high altitude), Biosphere Reserve Barranca de Metztitlán, Hidalgo, Mexico. Species diversity was compared at the infracommunity and the component community level using Hill numbers, and the beta diversity was calculated. Five species of Digenea, 5 of Nematoda, and 2 of Acanthocephala were found in the frogs from the 2 localities. The species richness of parasites in Las Pilas (9 species) was higher than that of Metznoxtla (7 species). The helminth community in Las Pilas was dominated by nematodes and, in Metznoxtla, it was dominated by digeneans. The most prevalent species in Las Pilas was *Foleyellides* cf. *flexicauda* (65% of frogs were infected) and, in Metznoxtla, it was *Megalodiscus americanus* (76% were infected). *Glypthelmins quieta* was the species with the highest mean abundance in both localities (Las Pilas = 4.5; Metznoxtla = 11.0). The difference in species composition between the 2 localities was significant (Anosim;  $R = 0.54$ ,  $p < 0.05$ ). The differences in the composition of species of helminths between the 2 localities suggest that local environmental conditions are different, which may reflect differences in local host diet.

**Keywords:** Helminth diversity; Infracommunity; Component community; Environmental conditions; Metztitlán

## Resumen

Se estudió la comunidad de helmintos de *Lithobates spectabilis* (n = 77) de Las Pilas (altitud baja) y Metznoxtla (altitud alta), Reserva de la Biosfera Barranca de Metztitlán, Hidalgo, México. Se comparó la diversidad de especies mediante los números de Hill a nivel de la infracomunidad y del componente de comunidad, y se calculó la diversidad beta. Se encontraron 5 especies de Digenea, 5 de Nematoda y 2 de Acanthocephala en las ranas de las 2 localidades. La riqueza de especies de parásitos en Las Pilas (9 especies) fue mayor que la de Metznoxtla (7 especies). La comunidad de helmintos en Las Pilas estuvo dominada por nemátodos y en Metznoxtla por digéneos. La especie más prevalente en Las Pilas fue *Foleyellides* cf. *flexicauda* (65% de las ranas estaban infectadas) y en Metznoxtla fue *Megalodiscus americanus* (76% estaban infectadas). *Glypthelmins quieta* fue la especie con mayor abundancia media en ambas localidades (Las Pilas = 4.5; Metznoxtla = 11.0). La diferencia en la composición de especies entre las 2 localidades fue significativa (Anosim; R = 0.54,  $p > 0.05$ ). Las diferencias en la composición de especies de helmintos entre las 2 localidades sugieren que las condiciones ambientales locales son diferentes, lo que puede reflejar diferencias en la dieta de los hospederos a nivel local.

*Palabras clave:* Diversidad de helmintos; Infracomunidad; Componente de comunidad; Condiciones ambientales; Metztitlán

## Introduction

Helminths (parasitic worms) do not form a monophyletic group; the assemblage consists of members of the phyla Platyhelminthes, Nematoda, Acanthocephala and Annelida (subclass Euhirudinea). Helminths parasitize all classes of vertebrates and invertebrates (Pérez-Ponce de León et al., 2011). They are important as parasites of wild and domestic animals, and they also provide ecological, biogeographical, and evolutionary information on host-parasite relationships (Horwitz & Wilcox, 2005; Mejía-Madrid, 2013).

Approximately, 402 species of amphibians have been described from Mexico (Frots, 2018; Parra-Olea et al., 2014), of which only 66 have been studied from a helminthological perspective; this number represents only about 18% of all Mexican species (Cabrera-Guzmán et al., 2021). Most of those works have focused mainly on taxonomic descriptions, lists of species, or population level studies (Cabrera-Guzmán, 2002; Cabrera-Guzmán et al., 2007, 2010; Galicia-Guerrero et al., 2000; Goldberg & Bursey, 2002; León-Régagnon et al., 2005; Velázquez-Urrieta & León-Régagnon, 2018), and only a few reports of the ecological structure of helminth communities (Adán-Torres et al., 2018; Espínola-Novelo et al., 2017; Goldberg et al., 2001; Mata-López et al., 2013; Paredes-Calderón et al., 2004; Ruiz-Torres et al., 2017; Zelmer et al., 2004). The only helminthological studies of amphibians from Hidalgo state are the helminth fauna of *Ambystoma velasci* (Dugès, 1888), *Lithobates spectabilis* Hillis and Frost, 1985 and *Rhinella horribilis* (Wiegmann, 1833) (Falcón-Ordaz et al., 2014, 2015; Pulido-Flores et al., 2009; Rodríguez-Amador et al., 2013). However, most of the works in Hidalgo have focused on a single locality

and none have carried out the analysis of the structure of helminths communities.

*Lithobates spectabilis* (showy leopard frog) is endemic to the central region of Mexico. Adults inhabit rivers, streams, lagoons, and ponds in ecosystems of mesophilic forests, coniferous forests, sub-montane scrub, and xerophilous habitats with an altitudinal interval of 1,200 m and 3,000 m. They are relatively small, with an average snout to cloaca length (SVL) of 69 mm. Common food habits include organisms belonging to the orders Coleoptera, Hymenoptera, Hemiptera, Diptera and Odonata (Canseco-Márquez & Gutiérrez-Mayén, 2010; Hillis & Frost, 1985; Ramírez-Bautista et al., 2014).

The aim of this study was to analyze the structure of the helminth community at the infracommunity level (community of helminth infrapopulations in a single species of host) and at the component community level (all infrapopulations of helminths associated with some subset of a host species) (Bush et al., 1997) in order to better understand the patterns and processes of the helminth communities of *L. spectabilis* from 2 localities, separated mainly by altitude, from the Biosphere Reserve Barranca de Metztitlán, Hidalgo, Mexico. Both localities have supported populations of *L. spectabilis* for more than 15-20 years and provide an ideal setting for a comparative analysis of the population structure of helminths (Pulido-Flores et al., 2009).

## Materials and methods

The Biosphere Reserve Barranca de Metztitlán is in the east-center part of the state of Hidalgo (20°14'15" N, 98°22'59.99" W). The topography is rugged, consisting of a river (Metztitlán) with steep mountains rising on

each side; elevations in the reserve are between 1,000 and 2,000 m asl (Conanp, 2003; INEGI, 2013). The 2 study localities were: Las Pilas (20°28'17.27" N, 98°40'51.27" W), at an altitude of 1,300 m (a large pool formed by a low-water dam on Metztlán River) with shore vegetation cover consisting mainly of pecan trees, *Carya illinoensis* (Wangenh.) K. Koch, 1869, and secondary vegetation; and Metznoxtla pond (man-made) (20°37'46.43" N, 98°51'27.60" W) at an altitude of 1,600 m (mountain top above Las Pilas), with vegetation predominantly of submontane scrub, with coverage between 80 and 90% and a height up to 2 m (Conanp, 2003). The straight-line distance between the 2 localities is about 25 km and the altitude difference is 300 m.

Frogs (40 from Las Pilas and 37 from Metznoxtla pond) were collected during September, October, and November (2017), and January, February, April, June and August (2018). The animals were captured using a hand net during the first hours of night at the 2 localities. Frogs were collected from the low bank of the river, near water but not in it at Las Pilas, and at Metznoxtla they were found sitting in shallow water near the shore of the pond. Animals were taken to the laboratory where they were sacrificed with an overdose of ether. Frogs were dissected and the body cavity and organs were examined for helminths. All helminths were collected and fixed for morphological study using current techniques for each group (Pritchard & Kruse, 1982). Platyhelminthes and acanthocephalans were stained with Mayer's Carmalum, Delafield's hematoxylin and Gomori's trichromic and were mounted on slides in balsam of Canada. Nematodes were sacrificed and fixed in Glacial Acetic Acid, mounted in temporary mounts in glycerin for morphological study, and then transferred to 70% ethanol for storage. Specimens were examined using a compound optical microscope (Leica CME) and drawings were made with the aid of a drawing tube. Specimens were identified using appropriate scientific literature (Anderson, 2000; Anderson et al., 2009; Bray, 2008; Chabaud, 1978; Gibbons, 2010; Gibson et al., 2002; Petrochenko, 1971; Yamaguti, 1961, 1963, 1971).

#### Data analysis

For this study, the sizes of frogs from each locality were compared in a one-way ANOVA using the statistical program Past V. 4.06b (Hammer et al., 2001).

For characterization of the infection, prevalence, abundance, mean intensity, and range of intensity were quantified according to Bush et al. (1997) and Bautista-Hernández et al. (2015). To evaluate potential correlations between abundance of helminths species and the snout-vent length of the frogs from each sex and locality, a Pearson correlation test was performed, and dispersion diagrams

were plotted in RStudio v. 2022.07.2 (RStudio, 2020). The method of Nested Analysis of Variance (ANOVA) was used with the sex factor of the frogs. Analyses were performed using STATISTICA 10 (StatSoft, 2011).

For the analysis of the data at the infracommunity level, only species richness (using the order of diversity  $q = 0$ ) (Hill, 1973), and the average abundance in samples for each locality and species diversity were calculated using the order of diversity  $q = 1$  (Hill, 1973; Jost, 2006). To compare the diversity at the infracommunity level with that reported for other anurans, the Brillouin Index (HB) also was used because it is considered ideal for fully-censused communities, and it measures the homogeneity of the community in a manner that is sensitive to the presence of rare species and is moderately sensitive to the size of the sample (Magurran, 2004); furthermore, it provides a comparison index for previous studies which did not use Hill numbers. For the component community analysis, the sample coverage ( $C$ ) was calculated for each locality.

Hill numbers measure the proportion represented by the individuals of each species in the sample with respect to the total number of individuals (Chao & Jost, 2012). The species accumulation curve was calculated using the method of rarefaction due to sample coverage (Chao & Jost, 2012) in the statistical program R (R Core Team, 2021) with tools from the iNEXT package (Hsieh et al., 2016). The total number of individuals from each of the localities was extrapolated to double and the analysis was carried out with 100 randomizations (Chao et al., 2014).

For the analysis of the diversity the effective number of species, Hill numbers ( ${}^qD = w$ ), or the true diversity, were used ( $q = 0 =$  species richness;  $q = 1 =$  the exponential of Shannon's entropy index, and  $q = 2 =$  the inverse of Simpson's concentration index) (Chao et al., 2014). Hill numbers are a mathematically unified family of diversity indices which are indicators (standardized values) that quantify the number of species that are considered in the sample being analyzed, depending on the common and rare species (Chao et al., 2014; Hill, 1973; Jost, 2006). These standardized metrics incorporate relative abundance and species richness based on the value of the exponent " $q$ ". The value of  $q = 0$  is insensitive to the differences in the relative abundances of species ( $S$ ), which is equal to the species richness ( ${}^0D$ ). The value of  $q = 1$  includes all species with a weight exactly proportional to their abundance in the community; this is Shannon's diversity index. This can be interpreted as the effective number of common species in the assemblage ( ${}^1D$ ). The value of  $q = 2$  considers the dominant species in the assemblage ( ${}^2D$ ) (Hill, 1973; Jost, 2006; Moreno et al., 2011). These measures express the effective number of species that a virtual community would have in which all the species

were equally common, conserving the average relative abundance of the studied community (Jost, 2006; Moreno et al., 2011). As the  $q$  values increase, more emphasis is placed on the dominant species while conserving the relative abundance of each species. The 3 Hill numbers were calculated according to Hill (1973). The calculation of sample coverage and the Hill numbers were performed in the statistical program R (R Core Team, 2021) with the iNEXT package (Hsieh et al., 2016). To determine patterns in the distribution of the abundance of the species of helminths and to identify the dominant species in the 2 localities, rank-abundance curves were calculated using the Excel program (Avolio et al., 2019).

The difference in the species composition was evaluated at the community level using a similarity analysis (ANOSIM). To represent the general pattern of dissimilarity in the composition of species between the 2 localities, a Non-Metric Multidimensional Scaling was performed (NMDS). Both methods were based on the dissimilarity index of Bray-Curtis (Bray & Curtis, 1957; Jongman et al., 1995) and were performed using the statistical R program (R Core Team, 2021) with tools of the Vegan package (Oksanen et al., 2018).

Beta diversity ( $\beta$ -diversity) is represented as the difference in species composition between different communities, which is determined by species turnover (species replacement) and nestedness (richness difference) (Baselga, 2010; Carvalho et al., 2012). The total dissimilarity of helminths between the 2 localities was divided into the dissimilarity due to species replacement (hypothesized replacement) and dissimilarity due to differences in richness (nestedness) by means of the beta diversity partition method (POD approach) (Podani & Schmera, 2011). This method is based on the Jaccard Index ( $\beta_{jac}$ ) and is represented by decomposition of additive terms that allow the consideration of the relative importance of species replacement components ( $\beta-3$ ) and richness difference components ( $\beta_{rich}$ ) in the configuration of the structure with incidence data based (Podani & Schmera, 2011) as follows:  $\beta_{jac} = \beta-3 + \beta_{rich}$ , where:  $\beta_{jac}$  = total dissimilarity,  $\beta-3$  = dissimilarity due to species replacement components, and  $\beta_{rich}$  = dissimilarity due to richness difference components. The analysis of the data was performed in the statistical program R (R Core Team, 2021) with the BAT package (Biodiversity Assessment Tools; Cardoso et al., 2015) using abundance data (Cardoso et al., 2015; Carvalho et al., 2013).

To determine if there was a significant difference in the values of prevalence and abundance of the shared species (helminths occurring in both localities), the non-parametric Chi-square test ( $\chi^2$ ) was used (McDonald, 2009; Plackett, 1983). This test determines if 2 variables are related or

not; the analysis was performed using the STATISTICA 10 program (StatSoft, 2011).

## Results

The total sample of 77 frogs, *L. spectabilis*, was comprised of 40 individuals from Las Pilas (28 females- SVL = 6.2-13.5 cm, mean = 8.9 cm and 10 males- SVL = 4.8-8.7 cm, mean = 7.3 cm) (data on sex and size of 2 frogs were not recorded), and 37 individuals from Metznoxtla (16 females- SVL = 2.9-9.4 cm, mean = 5.92 cm and 21 males- SVL = 4-8.1 cm, mean = 6.07 cm). A total of 1,346 helminths were recovered, corresponding to 12 species, 6 of which were identified to species level and 6 could be identified only to genus level (Table 1); 7 were adults and 5 were larvae. Of the frogs collected, 92.5% ( $n = 37$ ) from Las Pilas and 97.29% ( $n = 36$ ) of the frogs from Metznoxtla were infected with at least 1 species of helminth.

The abundance of species of helminths, with respect to the snout-vent length of male frogs, was not correlated (Las Pilas-  $t = 1.670$ ,  $df = 7$ ,  $p > 0.05$ ; Metznoxtla-  $t = 1.827$ ,  $df = 21$ ,  $p > 0.05$ ). However, the abundance of helminths in female frogs was positively correlated with snout-vent length in Metznoxtla ( $t = 2.884$ ,  $df = 13$ ,  $p < 0.05$ ), but not in Las Pilas ( $t = -1.073$ ,  $df = 24$ ,  $p > 0.05$ ) (Fig. 1, Table 2).

In the ANOVA to test for nestedness, the sex of the frogs nested within the locality for snout-vent length variable; length was associated with the locality ( $SS = 96.502$ ,  $df = 1$ ,  $p < 0.05$ ) but not to gender ( $SS = 10.831$ ,  $df = 1$ ,  $p > 0.05$ ). However, frogs from Metznoxtla were significantly smaller than those from Las Pilas, regardless of sex ( $SS = 49.833$ ,  $df = 1$ ,  $p < 0.05$ ). In the test for nestedness in relation to differences in the abundance of helminths in each sex of frogs from each locality, the difference was not significant between localities ( $SS = 1.001$ ,  $df = 1$ ,  $p > 0.05$ ), nor between sexes ( $SS = 0.459$ ,  $df = 1$ ,  $p > 0.05$ ). Although the average abundance was higher in Metznoxtla than Las Pilas, the variation was higher, so the difference was not significant (Table 3).

The most prevalent species of helminth in frogs from Las Pilas was *Foleyellides cf. flexicauda* (Schacher and Crans, 1973) Esslinger, 1986, present in 26 of 40 frogs, followed by *Lueheia inscripta* (Westrumb, 1821) Travassos, 1919, present in 21 of 40 frogs, and *Glypthelmins quieta* (Stafford, 1900) Stafford, 1905, present in 10 of 40 frogs. The species with the lowest prevalence were *Falcaustra* sp. and *Oncicola* sp., each present in 1 of 40 frogs. *Glypthelmins quieta* was the most abundant species, followed by *L. inscripta*; the mean intensity followed a similar pattern as the abundance (Table 1).

Table 1

Prevalence, abundance, mean intensity, and range of intensity of helminths in *Lithobates spectabilis* from the 2 localities of the Reserva de la Biosfera Barranca de Metztlán, Hidalgo, Mexico. \* = Undescribed species, † = juvenal/larvae, ■ = adults, only females, without symbol = adult.

Species/ Maturity	Number of helminths		Prevalence (%)		Abundance		Mean intensity		Range of intensity	
	Las Pilas (LP)	Metznoxtla (M)	LP	M	LP	M	LP	M	LP	M
<b>Platyhelminthes</b>										
<i>Glythelmins quieta</i>	183	408	25	51.35	4.57	11.03	18.30	31.11	1-73	1-165
<i>Megalodiscus americanus</i>	–	257	–	75.68	–	6.95	–	9.18	–	1-48
<i>Haematoloechus caballeroi</i>	10	2	17.5	2.70	0.25	0.05	1.43	2	1-3	2
<i>Halipegus</i> sp.*	–	97	–	40.54	–	2.62	–	6.47	–	1-30
<i>Clinostomum</i> sp.†	–	1	–	2.70	–	0.03	–	1	–	1
<b>Nematoda</b>										
<i>Foleyellides</i> cf. <i>flexicauda</i>	79	8	65	10.81	1.97	0.22	3.00	2	1-8	1-5
<i>Rhabdias</i> cf. <i>joaquinensis</i>	15	–	17.5	–	0.37	–	2.14	–	1-4	–
<i>Physaloptera</i> sp.†	70	–	17.5	–	1.75	–	10	–	1-38	–
<i>Falcaustra</i> sp.†	7	–	2.5	–	0.17	–	7	–	7	–
<i>Aplectana</i> sp.■	84	–	15	–	2	–	14	–	2-62	–
<b>Acanthocephala</b>										
<i>Lueheia inscripta</i> †	120	3	52.5	5.41	3	0.08	5.71	0.13	1-12	1-2
<i>Oncicola</i> sp.†	2	–	2.5	–	0.05	–	2	–	2	–

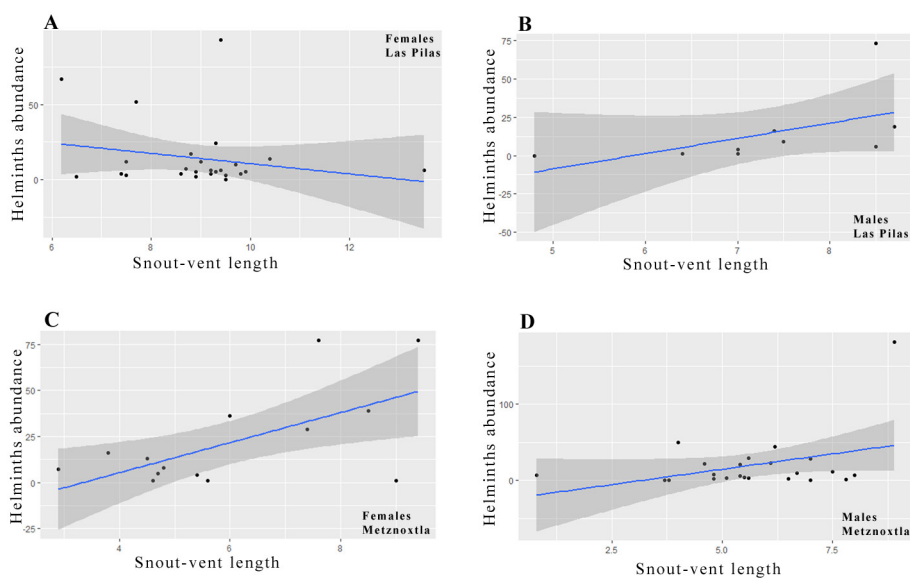


Figure 1. Scatter plots of the abundance of helminths in relation to the snout-vent length of frogs, *Lithobates spectabilis*. Each graph shows the locality and data of sex and Snout-vent length (SVL).

Table 2

Values of Pearson's correlation coefficients to evaluate the relationship between abundance of helminths and Snout-Vent Length of *Lithobates spectabilis*. \* = Significant at  $p < 0.05$ .

Locality	Sex	Pearson's correlation	t	df.	p-value
Las Pilas	Females	-0.214	-1.073	24	0.293
	Males	0.533	1.670	7	0.138
Metznoxtla	Females	0.624	2.884	13	0.012*
	Males	0.370	1.827	21	0.081

Table 3

Results of the nested ANOVA for snout-vent length (SVL) (a) and abundance of helminths (b) data.

Source	Sum of squares	df	Mean square	F-value	p-value
<b>(a) SVL</b>					
Locality	96.502	1	96.502	35.029	0.000
Sex	10.831	1	10.831	3.931	0.051
Residuals	190.091	69	2.755		
<b>(b) Abundance</b>					
Locality	1.001	1	1.001	0.649	0.423
Sex	0.460	1	0.460	0.298	0.587
Residuals	106.366	69	1.542		

Table 4

Ecological parameters of helminth infracommunity reported from the genus *Lithobates* in Mexico. HB = Brillouin diversity index.

References	Present study	García-Altamirano (1993)	Paredes-Calderón et al. (2004)	Yáñez-Arenas (2007)	Adán-Torres et al. (2018)
Host	<i>Lithobates spectabilis</i> Hillis et Frost	<i>L. dumni</i> (Zweifel)	<i>L. vaillanti</i> (Brocchi)	<i>L. brownorum</i> (Sanders)	<i>L. montezumae</i> (Baird)
Locality	Las Pilas      Metznoxtla	Lago de Pátzcuaro	Los Tuxtlas	Celestún; Lagunas de Yalahau and Río Lagartos	San Pedro Tlaltizapán
State	Hidalgo	Michoacán	Veracruz	Yucatán	Estado de México
Richness	2.27 (± 1.22)*	1.91 (± 0.86)*	3.3 (± 1.5)	1.19 (± 0.91)	2.4 (± 1.1)
Diversity (HB)	0.37 (± 0.32)	0.31 (± 0.30)	0.54 (± 0.43)	0.16 (± 0.26)	0.42 (± 0.36)

Index used to calculate the average diversity; \* Hill numbers ( $q = 0$ ).

In Metznoxtla, the most prevalent species was *Megalodiscus americanus* Chandler, 1923, present in 28 of 37 frogs, followed by *G. quieta* in 19 of 37 frogs and *Halipegus* sp., present in 15 of 37 frogs. Species with the lowest prevalence were *L. inscripta*, present in 2 of 37 frogs, followed by *Haematoloechus caballeroi* (Skrjabin and Antipin, 1962) León-Règagnón and Tabon, 2018, and *Clinostomum* sp., each presents in 1 of 37 frogs. *Glythelmins quieta* was the most abundant species, followed by *L. inscripta*. The mean intensity followed a similar pattern as the prevalence (Table 1).

Infracommunity diversity, measured by the first Hill number ( $q = 0 =$  species richness), in frogs from Las Pilas was 2.27 species of helminths per frog, whereas, in Metznoxtla there were 1.91 species of helminths per frog (Table 4). The second Hill number ( $q = 1 =$  the exponential of Shannon's diversity index = effective species diversity), indicated that Las Pilas had 1.8 effective species per frog and Metznoxtla had 1.6 effective species. Nevertheless, Metznoxtla had a greater mean abundance (20.97) than Las Pilas (14.56).

The third Hill number  $q = 2$  does not apply at the infracommunity level, so the Brillouin index (HB) was used (Moreno et al., 2011). The diversity estimated using the Brillouin index in Las Pilas was 0.37 and in Metznoxtla 0.31 (Table 4).

At the level of the component community, in Las Pilas the sample coverage was 100%, and in Metznoxtla the coverage was 99% (Fig. 2); i.e., these numbers indicate that there is little likelihood (0% and 1%, respectively) that more species would have been discovered with an increase in sampling effort. The calculated species diversity ( $q = 0$ ) at Las Pilas was 9 species of helminth, and 7 species

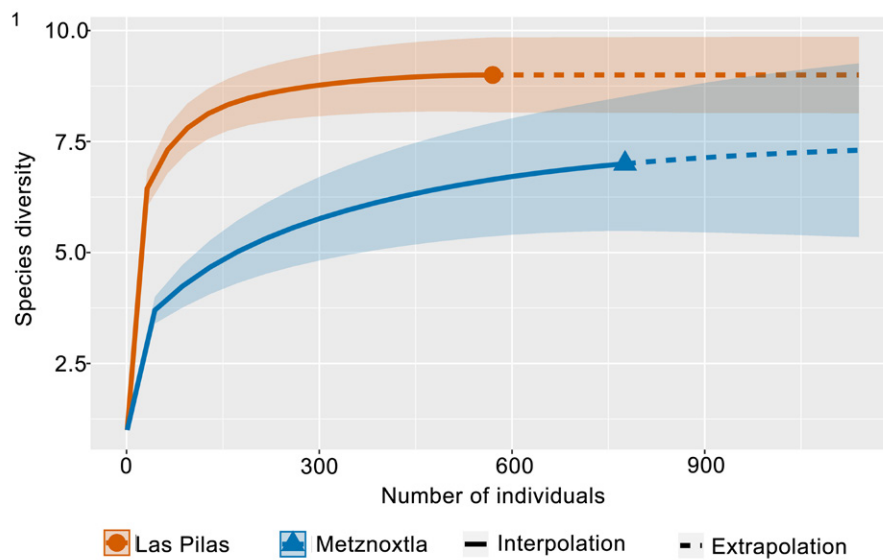


Figure 2. Species accumulation curves of the species of helminth from *Lithobates spectabilis* from the 2 localities in the Biosphere Reserve Barranca de Metztlán. Shaded area indicates 95% confidence intervals; continuous lines are interpolations of the model, and the dashed lines are extrapolated values that would be achieved if additional samples were made.

Table 5

Helminth component community diversity of anurans from Yucatán and Hidalgo, Mexico, calculated using the formulas for Hill numbers.

Host	<i>Rhinella marina</i>	<i>Incilius valliceps</i>	<i>Lithobates spectabilis</i>	
Locality	Yalahau, Yucatán, Mexico		Las Pilas	Metznoxtla
Environment	Terrestrial	Aquatic-terrestrial	Aquatic-terrestrial	Aquatic
Sample coverage (%)	100	100	100	99
$q = 0$ ( ${}^0D$ )	7	4	9	7
$q = 1$ ( ${}^1D$ )	4	2	5.73	2.87
$q = 2$ ( ${}^2D$ )	3	2	4.48	2.48
Reference	Espínola-Novelo et al. (2017)		This study	

at Metznoxtla; however, extrapolating the accumulation curves the confidence intervals for species richness for the 2 localities overlap, so the differences between the 2 curves are not statistically significant at the component community level (Fig. 2). With the order of diversity = 1 ( $q = 1$ ), the number of effective species for Las Pilas was 5.73, almost double that of Metznoxtla (2.87 effective species). With the order of diversity  $q = 2$ , the same pattern was found; Las Pilas had 4.48 effective species and Metznoxtla had about half as many (2.48 effective species) (Table 5). *Glythelmins quieta* was the dominant species in both localities. In Las Pilas, the species with

the second highest dominance value was *L. inscripta*, followed by *Aplectana* sp.; *L. inscripta* was present in both localities but *Aplectana* sp. was present only in Las Pilas. In Metznoxtla, the second most dominant species was *M. americanus*, followed by *Halipegus* sp. (Fig. 3); these 2 species were found only in Metznoxtla.

The difference in the species composition between the 2 localities was significant (Anosim;  $R = 0.54$ ,  $p < 0.05$ ) and the grouping given by the NMDS corroborates the results of the Anosim; overlapping but partially separated groups of each locality were formed with their respective samples with a high level of reliability (stress 0.098) (Fig. 4). The

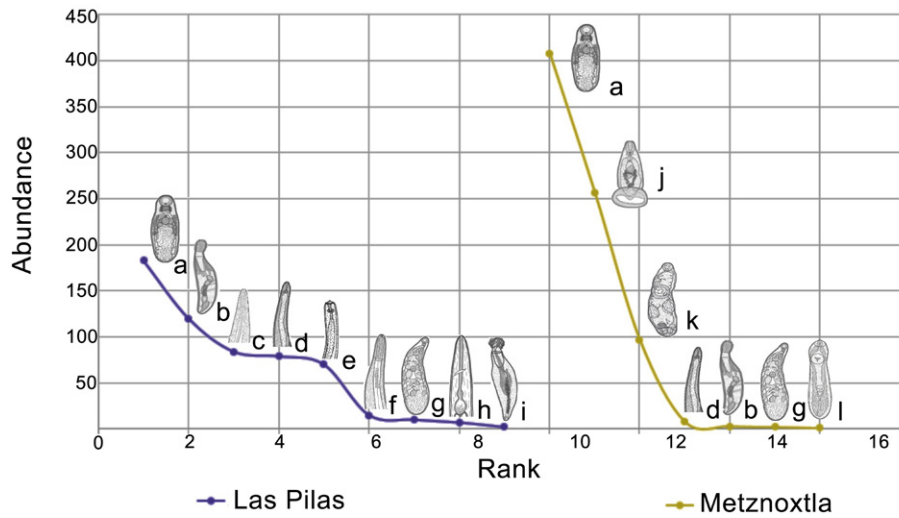


Figure 3. Rank-abundance curves of the species of helminth illustrating the difference in the composition of the component communities of *Lithobates spectabilis* from Las Pilas and Metznoxtla. Letters represent each species in the curves (a) *Glyphelmins quieta*; (b) *Lueheia inscripta*; (c) *Aplectana* sp.; (d) *Foleyellides* cf. *flexicauda*; (e) *Physaloptera* sp.; (f) *Rhabdias* cf. *joaquinensis*; (g) *Haematoloechus caballeroi*; (h) *Falcaustra* sp.; (i) *Oncicola* sp.; (j) *Megalodiscus americanus*; (k) *Halipegus* sp.; and (l) *Clinostomum* sp.

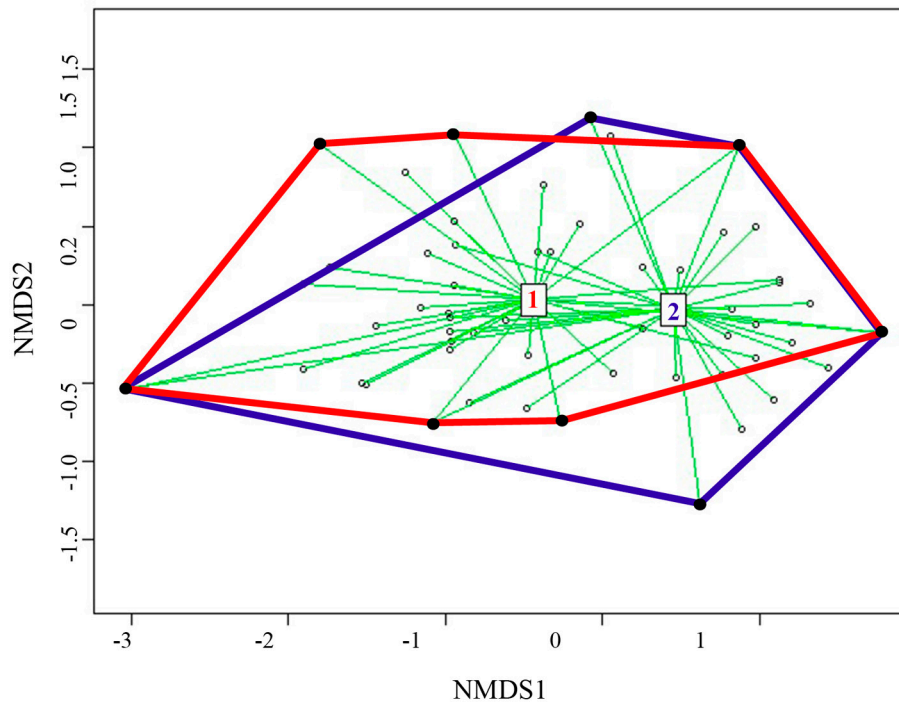


Figure 4. Ordination analysis of the samples from both localities using of the NMDS technique. The enclosed groups correspond to the localities with their respective samples. 1 (red) = Las Pilas; 2 (blue) = Metznoxtla.



total beta diversity ( $\beta_{jac}$ ) between both localities was 66%, and of this percentage, 50% ( $\beta_3$ ) corresponded to the replacement components and 16% ( $\beta_{rich}$ ) corresponded to richness difference components. The result of the  $\chi^2$  test of the abundance values was significant ( $\chi^2 = 257.36$ , gl 3,  $p < 0.05$ ); however, the prevalence values were not significantly different ( $\chi^2 = 48.00$ , gl 49,  $p > 0.5$ ).

## Discussion

Inclusion of helminths in biodiversity studies increases the knowledge of interspecies interactions. Amphibians are opportunistic predators and are prey to a great diversity of organisms; therefore, they function as intermediate, paratenic and final hosts of a great diversity of parasites that have different transmission strategies (Aho, 1990; Campião et al., 2012; Hamann et al., 2010; Imasuen et al., 2012; King et al., 2008). Since most of their lives they are found near the breeding area, amphibians have been considered to be biological markers of local ecological conditions (Aho, 1990). For this reason, they are an excellent model for the study of biological interactions between parasites and hosts (Aho, 1990; Campião et al., 2012). Environmental conditions in which the host develops are of great importance in the transmission dynamics of parasitic species, so changes, or differences, in environmental variable directly affect amphibians. Factors such as the temperature, humidity, salinity, pH and oxygen, as well as the quality of water, local landscape characteristics and the geographical distance between habitat patches are involved in and determine the structure of helminth communities in anurans (Adán-Torres et al., 2018; Bower et al., 2018; de Sena et al., 2018; King et al., 2008; Koprivnikar & Poulin, 2009; Paredes-Calderón et al., 2004; Poulin, 2003).

The Biosphere Reserve Barranca de Metztitlán has extreme altitude gradients that occur between localities only short distances apart and climatic variations throughout the region that corresponds to the protected area. The 2 localities are relatively close together, but in different altitudes, with corresponding differences in microclimate (Conanp, 2003). The distance between Metznoxtla and Las Pilas is about 25 km in a straight line, but the distance between Metznoxtla and Metztitlán River is only about 2.5 km; Las Pilas is in the same river, but about 22 km upstream from that closest point to the river. The difference in altitude between Metznoxtla, on the mountain top, and the river is about 300 m. Consequently, the microclimates are different in each locality.

Las Pilas is in the valley floor, on the banks of Metztitlán River, which functions as a regulator of the local climate and provides the ecological conditions

(humidity, shade, etc.) that allows frogs to spend more time out of the water. These conditions allow helminths with heteroxenous life cycles to complete their life cycles. The pond at Metznoxtla is shallow, less than 1 m depth, and in an open area on the mountaintop in a xeric scrub habitat that is warmer, and the trade winds arrive with little humidity and contribute to its semi-dry habitat (Conanp, 2003). There is no shade around the pond, and these conditions cause frogs to spend most of the time in the shallow waters of the pond (Pulido-Flores et al., 2009). This habitat favors digeneans, dominant in this locality, which use snails and tadpoles as intermediate hosts.

Frogs collected in Metznoxtla were captured within the pond, they probably spend most of their time in the water rather than the shore, where there is no shelter, and rarely were seen in shore/terrestrial environments. Because of this, they probably feed mainly on insects found in or near the water, which are more likely intermediate hosts of the digeneans. This behavior could explain the helminth composition and values in the ecological parameters reported for the digeneans, since some of these species use aquatic insect larvae to reach their definitive host and others use aquatic snails as intermediate hosts (Rankin, 1944; Razo-Mendivil & Pérez-Ponce de León, 2008; Stigge & Bolek, 2016). The results of the present study suggest that the physiographic characteristics of each locality are directly involved in producing the differences in the composition of the helminth infracommunity of *Lithobates spectabilis*.

In Las Pilas, nematodes were the group with the highest species richness (Table 1). Of these, *F. cf. flexicauda* was the most prevalent species, and the digenean *G. quieta* was the most abundant. In Metznoxtla, *M. americanus*, *G. quieta* and *Halipegus* sp. were the helminths with the highest values of ecological parameters (Table 1). This suggests that frogs from both localities are consuming insects (intermediate hosts of digeneans and nematodes). However, at Metznoxtla, snails, intermediate hosts of these digeneans, although the life cycle of *Halipegus* Looss, 1899 also includes dragonflies (Goater et al., 1990). Snails are more obvious at Metznoxtla, and were observed at the shoreline and in shallow waters. As well, *G. quieta* can be transmitted by cannibalism of infected tadpoles and juvenal frogs and ingesting the shed skin containing encysted metacercaria after metamorphosis (Leigh, 1946). Because of the size and shallowness of the pond, frogs were in proximity sitting in water and on the muddy shore, bringing them in in the vicinity of infective stages of digeneans.

At Las Pilas, frogs were captured mainly on the riverbank, a more terrestrial environment than at Metznoxtla. The higher prevalence of *F. cf. flexicauda*

at Las Pilas (65% vs. 10.81% at Metznoxtla), an obligate parasite of amphibians, could be related to the life cycle of this parasite, which uses mosquitoes of the family Culicidae (Anderson, 2000). No report of mosquitos has been made in the reserve, but mosquitoes were present in the more sheltered riverbank while collecting frogs. Abundance of mosquitoes, and the prevalence of *F. cf. flexicauda*, suggests that they are feeding constantly on the frogs.

Cystacanths of *Lueheia inscripta* were found in the mesentery of the frogs; prevalence of 52.5% at Las Pilas and 5.41% at Metznoxtla. Frogs, a paratenic host of this helminth, must eat an infected arthropod intermediate host, thought to be cockroaches (*Periplaneta americana* Linnaeus, 1758) (Acholonu, 1976) and the parasites re-encyst in the frog, which, in turn, would be eaten by a bird; however, it is not known if this insect is present in these localities. *Lueheia inscripta*, as adult, is a parasite of the intestines of birds of the families Ardeidae, Icteridae and Turdidae (Salgado-Maldonado & Caspeta-Mandujano, 2010; Smales, 2013; Werby, 1938); all of which have members present in the reserve (Ortiz-Pulido et al., 2010).

Helminths that had the lowest values of the ecological parameters were juveniles of the nematode, *Falcaustra* sp. and the acanthocephalan, *Oncicola* sp. Kathlaniid nematodes develop to the third stage outside the host and then invade various species of invertebrates (aquatic insects, snails) and fishes (Bartlett & Anderson, 1985; Hasegawa & Nishikawa, 2009; Moravec et al., 1995), which, along with frogs, serve as paratenic hosts of third-stage larvae that do not develop further in those hosts (Anderson, 2000); large reptiles (lizards, turtles, and snakes) that eat frogs are typical definitive hosts. However, although invertebrates are common in frog's diets, the low parameter values indicate that the helminths are most likely sporadic in this locality. Acanthocephala of the genus *Oncicola* Travassos, 1916, involve amphibians and lizards as paratenic hosts (Becker et al., 2019; Nickol et al., 2006), and feline mammals as definitive hosts (Fuller & Nickol, 2011; Santos et al., 2016); although, the specific life cycles have not been thoroughly studied (Nickol et al., 2006; Palmer et al., 2020; Romero-Mayén et al., 2016; Schmidt, 1972). *Lithobates spectabilis* appears to be a paratenic host of the nematode and this acanthocephalan, although future studies would have to be done to confirm this hypothesis.

The abundance and prevalence of *G. quieta* and *M. americanus* in Metznoxtla may be related to the life cycle. Both species use gastropods as the first intermediate host; *G. quieta* uses *Physella gyrina* (Say, 1821) and *M. americanus* uses 1 or several species of *Helisoma*

Swainson, 1840. In both life cycles, the cercaria leave the first intermediate host and swims actively until finding the second intermediate host, tadpoles. They penetrate the epidermis of the tadpoles and form metacercariae in cysts. Adult frogs become infected by ingesting the skin shed during metamorphosis or by feeding on juvenile frogs infected with the metacercaria (Pulido-Flores et al., 2009; Rankin, 1944; Razo-Mendivil & Pérez-Ponce de León, 2008; Schell, 1970). For *Halipegus* sp., found in the buccal cavity of the frogs, molluscs are the first intermediate hosts, copepods, and ostracods are second intermediate hosts, and odonate larvae, as paratenic hosts, are involved in the life cycle (Krull, 1935; Stigge & Bolek, 2016; Zelmer & Esch, 1999). Frogs, the definitive host, are infected with this helminth by feeding on intermediate or paratenic hosts carrying the metacercaria.

The helminths with lower values of ecological parameters in Metznoxtla were *H. caballeroi*, parasites of the lungs, *Clinostomum* sp., found in the cloaca, and *L. inscripta*, encysted in the mesentery. In the case of *H. caballeroi*, the parameter values may be influenced by the local abiotic conditions (Metznoxtla is much arid than Las Pilas) and the absence of some undetermined species of potential intermediate host. Species of *Clinostomum* Leidy, 1856 are not common for amphibians; they normally use fish as intermediate hosts and ictiophagus and piscivorous birds as definitive hosts (Dias et al., 2003). This species was found in the cloaca of a single frog. The acanthocephalan, *L. inscripta*, thought to use insects as intermediate host and known to mature in birds (Turdidae), was not as common in Metznoxtla (but common in Las Pilas), possibly because of the difference in habits of the frogs (setting in water vs. sitting on the shore) or because either intermediate hosts or infected birds are not common in that locality or because the presence of more vegetation in Las Pilas makes it a better habitat for birds.

At the infracommunity level, Las Pilas had a greater species richness and diversity than Metznoxtla (Table 4). The species richness and diversity in this study is consistent with previous reports for species of *Lithobates* Fitzinger (Table 4) in Mexico. Yáñez-Arenas & Guillén-Hernández (2010) reported the species richness and diversity of the helminth infracommunity of *L. brownorum* (Sanders, 1973) in Yucatán, and observed that the parameters were low (Table 4). This condition was attributed to the constant presence of tropical cyclones, which directly or indirectly affect the populations of the definitive and intermediate hosts. The regular perturbation of the habitat by the cyclones was thought to have a considerable influence that would lower the values of richness, diversity, and abundance (Yáñez-Arenas & Guillén-Hernández, 2010). Adán-Torres et al. (2018) suggested that, for the small

number of infracommunities studied so far in Nearctic and Neotropical biogeographic regions, it appears that local ecological conditions of the studied localities are more important factors in the structure of helminth community structure of frogs than the biogeographic region is. Furthermore, they considered the limited information available so far was insufficient for them to draw definite conclusions.

Aho (1990) argued that helminth parasite communities of anurans generally are depauperate than other types of definitive hosts, and that they consist mainly of species of nematodes. However, in previous studies of frogs with semi-aquatic habits, the helminthological fauna has been found to be composed mainly of digeneans. This trend has been reported several species closely associated with water: *L. berlandieri* (Baird, 1859) (León-Règagnon et al., 2005); *L. forreri* (Boulenger, 1883) (Goldberg et al., 2002); *L. cf. forreri* (Cabrera-Guzmán et al., 2007); *L. psilonota* (Webb, 2001) (Romero-Mayén et al., 2016); and *L. vaillanti* (Brocchi, 1877) (Paredes-Calderón et al., 2004). The dominance of digeneans is thought to reflect the close association of these species with aquatic environments. In contrast, the helminth composition reported for species that are more terrestrial (not spending as much time in water), have more species of nematodes than digeneans: such as *L. brownorum* (Velázquez-Urrieta & León-Règagnon, 2018; Yáñez-Arenas & Guillén-Hernández, 2010); *L. tarahumaræ* (Boulenger, 1917) (Burse & Goldberg, 2001); *L. cf. forreri* (Velázquez-Urrieta & León-Règagnon, 2018); and *L. magnaocularis* (Frost and Bagnara, 1974) (Goldberg & Bursey, 2002). This difference is reflected in the results of the present study; the frogs at Las Pilas are more terrestrial (more species of Nematoda) and the frogs at Metznoxtla are more aquatic (more species of Digenea) (Table 4).

Differences in the composition of species of helminths in each locality ( $\beta$ -diversity) is influenced by such factors as feeding habits, characteristics of the habitat, the ecological conditions in which the host develops, and the presence of potential intermediate hosts (Adán-Torres et al., 2018; Bower et al., 2018; Cabrera-Guzmán et al., 2007; Campião et al., 2012, 2014; García-Altamirano et al., 1993; Paredes-Calderón et al., 2004; Poulin, 1997; Yáñez-Arenas & Guillén-Hernández, 2010). Furthermore, these conditions may influence the survival of free-living stages of some species of helminths (Adán-Torres et al., 2018; de Sena et al., 2018; Luque et al., 2005; Muzzall, 1991; Muzzall et al., 2001). The presence or absence of particular species of helminth in each locality can be related to the type of life cycle of the parasite present (Poulin, 1997) and the presence of potential intermediate hosts (Paredes-

Calderón et al., 2004). The behavior of frogs in their respective localities is also thought to affect  $\beta$ -diversity (Bolek & Coggin, 2003; Espínola-Novelo et al., 2017; Hamann et al., 2006a; Kehr, et al., 2006; McAlpine, 1997; Muzzall & Mychek-Londer, 2014; Romero-Mayén et al., 2016; Santos & Amato, 2010; Yáñez-Arenas & Guillén-Hernández, 2010). Local differences in the strength of these factors, and interactions between the factors present in given localities, generates dissimilarity in the structure of the communities of helminths at local levels, which, combined with local environmental factors, generate  $\beta$ -diversity. Thus, local conditions produce higher species richness, abundance, and prevalence of some species in one locality and, in others with different local conditions, lower values of ecological parameters occur. Comparing  $\beta$ -diversity is an important area of basic and applied ecological research; however, few studies have addressed  $\beta$ -diversity in studies of communities of parasitic organisms, especially in anurans. Studies of  $\beta$ -diversity are carried out more commonly with parasites of mammals and fish (Krasnov et al., 2019; Qin et al., 2019; Spickett et al., 2017; Spickett et al., 2019). The present study suggests that increased research in the understanding of the patterns of spatial variation of parasite communities at the level of  $\beta$ -diversity will provide information that will aid in the interpretation of comparative results.

Among the factors listed above that can influence the composition of species in a helminths community in a given species of host, host size is considered to be an important predictor of helminth community structure, and a positive correlation between host size and helminth abundance is somewhat expected (Poulin, 1997; Williams & Jones, 1994). However, in this study correlation between the abundance of helminths and the snout-vent length of frogs was found only in females from Metznoxtla, even though, as mentioned above, on the average they were significantly smaller than those in Las Pilas. A correlation only in Metznoxtla could be because of the probable habitat-related differences in the diet and behavior of the frogs in this locality; both factors are important in the recruitment of helminths (Camião et al., 2014; Hamann et al., 2006b).

To date, there are no published studies of the helminths of frogs at Las Pilas; however, Pulido-Flores et al. (2009) carried out a pilot study of 49 individuals of *L. spectabilis* at Metznoxtla in 2003. They reported 4 species: *G. quieta*, *H. complexus* (Seely, 1906) Krull, 1933, *Gorgoderina attenuata* (Stafford, 1902) Stafford, 1905, and *Ochoterenella digiticauda* Caballero y Caballero, 1944. The specimens reported as *H. complexus* were reexamined for the present study and found to be *H. caballeroi*. The

present study also reported *G. quieta* and *H. caballeroi* but did not report *G. attenuata* or *O. digiticauda*, both of which had low prevalence and abundance in the study of (Pulido-Flores et al., 2009). Despite the greater number of frogs collected in that study compared to the present study (49 vs. 37), the species richness was much lower (4 species vs. 7 species). Two species were reported by Pulido-Flores et al. (2009) that were not reported in the present study and 5 species were reported in the present study that were not reported in the previous one; 2 species were common to both studies. The species with the highest prevalence and abundance was *G. quieta* in both studies, but in the previous study the values (37.9% and 7.39, respectively) were lower than in the present study (51.35% and 11.03, respectively). In contrast, the prevalence and abundance of *H. caballeroi* in the previous study (13.9% and 0.44, respectively) were higher than in the present study (2.70% and 0.05, respectively). However, it is interesting to note that 584 individuals of *G. quieta* and 35 individuals of *H. caballeroi* were collected by Pulido-Flores et al. (2009) and only 408 of *G. quieta* and 2 individuals of *H. caballeroi* were collected in the present study. No data was collected between the dates of the 2 studies, so we have no information on which to base an interpretation of the differences between them.

As discussed above, Hill numbers are based on a sampling theory that proposes to produce indices that can provide a basis of comparison between the ecological parameters of communities with biological and environmental conditions that always are different. The Hill numbers are indices that smoothly link rarefaction (interpolation) and prediction (extrapolation) to standardize samples based on sample size and sample completeness and to facilitate the comparison of biodiversity data. Although the concept of Hill numbers is not new (Hill, 1973), they have not been widely applied in studies of parasite communities, notorious for having unique evolutionary and biological that affect the host-parasite interactions in distinctive environments.

The only study employing Hill numbers in describing communities of helminths in Mexican anurans is that of Espínola-Novelo et al. (2017). In that study, the authors quantified the ecological parameters of the helminth communities of *Rhinella marina* Linnaeus, 1758 and *Incilius valliceps* Wiegmann, 1833 from Lagunas de Yalahau, Yucatán, Mexico. The sample size of the helminths in these amphibians and the results of the richness and diversity estimators (Hill numbers; Table 5) were sufficient to suggest that the richness of species of helminth in that locality was relatively low, and the pattern proposed for amphibians is followed; i. e., nematodes are commonly more dominant, and the richness of other species is lower (Aho, 1990).

One of the important aspects of the Hill numbers is their usefulness for making predictions about the richness and diversity of communities of similar organisms (Jost, 2006, 2007). Based on the study of the helminth community of the 2 species of toads (*I. valliceps* and *Rhinella marina*) by Espínola-Novelo et al. (2017), the anurans in a more terrestrial environment would have  $q$  values lower than those in a combination of aquatic-terrestrial environments; in that case, the toads are in the same general locality, but they have different habitat preferences. In the present study, the frogs in Las Pilas are in an aquatic-terrestrial environment and those in Metznoxtla are in an aquatic one. Thus, it would be predicted that the  $q$  values of the helminth community of frogs in the in the more complex 2 component environment (Las Pilas) would have higher richness and diversity than the frogs in the single-component environment (Metznoxtla); in the present study, the species of host is the same in both localities, but because one is a flowing river and one is a small pond, the habitat usage and behavior is different. As predicted, the 3  $q$  values were higher for Las Pilas than for Metznoxtla (Table 5). Of course, this validity and usefulness is supported by the results of 2 studies. The predictive value of  $q$  values must be evaluated using Hill numbers in future studies.

## Acknowledgements

To the following people for their help during field and laboratory work: Diana Calderon, Cristian R. Olvera-Olvera, José C. Iturbe-Morgado, and Guillermo Sánchez. We also wish to thank the people living near the localities, Las Pilas and Metznoxtla, for giving us access to the collecting localities, especially Sr. Guillermo Sánchez and his family. We are grateful for the support of Claudia Moreno and Pablo Octavio Aguilar for their advice on data analysis. This work forms part of the Master's thesis of the first author, who thanks Consejo Nacional de Ciencia y Tecnología (Conacyt) for a postgraduate scholarship (Number: 857903). The fieldwork was carried out under the scientific permit provided by Secretaría del Medio Ambiente y Recursos Naturales (Semarnat-Mexico).

## References

- Acholonu, A. D. (1976). Helminth fauna of saurians from Puerto Rico with observations on the life cycle of *Lueheia inscripta* (Westrumb, 1821) and description of *Allopharynx puertoricensis* sp. n. *Proceedings of the Helminthological Society of Washington*, 43, 106–116.
- Adán-Torres, B., García-Prieto, L., & Mata-López, R. (2018). Helminth Infracommunities of the Montezuma's Frog

- Lithobates montezumae* (Anura: Ranidae) in the Nearctic–Neotropical Transition Zone of Mexico. *Journal of Parasitology*, 104, 544–549. <https://doi.org/10.1645/17-188>
- Aho, J. M. (1990). Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes. In G. W. Esch, A. O. Bush, & J. M. Aho (Eds.), *Parasite communities: patterns and processes* (pp. 157–195). London: Chapman and Hall. [https://doi.org/10.1007/978-94-009-0837-6\\_7](https://doi.org/10.1007/978-94-009-0837-6_7)
- Anderson, R. C. (2000). *Nematode parasites of vertebrate: their development and transmission (2nd edition)*. Wallingford, UK: CABI Publishing.
- Anderson, R. C., Chabaud, A. G., & Willmott, S. (Eds.). (2009). *Keys to the nematode parasites of vertebrates: archival volume*. Wallingford: CABI. <https://doi.org/10.1079/9781845935726.0000>
- Avolio, M. L., Carroll, I. T., Collins, S. L., Houseman, G. R., Hallett, L. M., Isbell, F. et al. (2019). A comprehensive approach to analyzing community dynamics using rank abundance curves. *Ecosphere*, 10, e02881. <https://doi.org/10.1002/ecs2.2881>
- Bartlett, C. M., & Anderson, R. C. (1985). Larval nematodes (ascaridida and spirurida) in the aquatic snail, *Lymnaea stagnalis*. *Journal of Invertebrate Pathology*, 46, 153–159. [https://doi.org/10.1016/0022-2011\(85\)90143-0](https://doi.org/10.1016/0022-2011(85)90143-0)
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19, 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Bautista-Hernández, C. E., Monks, S., Pulido-Flores, G., & Rodríguez-Ibarra, A. E. (2015). Revisión bibliográfica de algunos términos ecológicos usados en parasitología, y su aplicación en estudios de caso. In G. Pulido-Flores, S. Monks, & M. López-Herrera (Eds.), *Estudios en biodiversidad, Vol. I* (pp. 11–19). Lincoln, Nebraska: Zea Books. <https://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1001&context=biodiversidad>
- Becker, A., Rajeev, S., Freeman, M. A., Beierschmitt, A., Savinon, V., Wulcan, J. M. et al. (2019). Extraintestinal acanthocephalan *Oncicola venezuelensis* (Oligacanthorhynchidae) in small Indian mongooses (*Herpestes auro-punctatus*) and African green monkeys (*Chlorocebus aethiops sabaeus*). *Veterinary Pathology*, 56, 794–798. <https://doi.org/10.1177/0300985819848502>
- Bolek, M., & Coggins, J. (2003). Helminth community structure of sympatric Eastern American toad, *Bufo americanus americanus*, northern leopard frog, *Rana pipiens*, and blue-spotted salamander, *Ambystoma laterale*, from Southeastern Wisconsin. *The Journal of parasitology*, 89, 673–680. <https://doi.org/10.1645/GE-70R>
- Bolek, M. G., Stigge, H. A., & Gustafson, K. D. (2016). The iron wheel of parasite life cycles: then and now! In J. Janovy & G. W. Esch (Eds.), *A century of parasitology: discoveries, ideas and lessons learned by scientists who published in the Journal of Parasitology, 1914–2014* (pp. 131–147). Garsington Road, Oxford: John Wiley & Sons, Ltd. <https://doi.org/10.1002/9781118884799.ch9>
- Bower, D. S., Brannelly, L. A., McDonald, C. A., Webb, R. J., Greenspan, S. E., Vickers, M. et al. (2018). A review of the role of parasites in the ecology of reptiles and amphibians. *Austral Ecology*, 44, 433–448. <https://doi.org/10.1111/aec.12695>
- Bray, J. R., & Curtis, J. T. (1957). An Ordination of the Upland Forest Communities of Southern Wisconsin. *Ecological Monographs*, 27, 325–349. <https://doi.org/10.2307/1942268>
- Bray, R. A. (2008). Introduction and key to superfamilies. In R. A. Bray, D. I. Gibson, & A. Jones (Eds.), *Keys to the Trematoda, Vol. 3* (pp. 1–5). Wallingford, UK: CAB International and Natural History Museum.
- Bursey, C. R., & Goldberg, S. R. (2001). *Falcaustra lowei* n. sp. and other helminths from the Tarahumara frog, *Rana tarahumarae* (Anura: Ranidae), from Sonora, Mexico. *Journal of Parasitology*, 87, 340–344. <https://doi.org/10.2307/3285051>
- Bush, A. O., Lafferty, K. D., Lotz, J. M., & Shostak, A. W. (1997). Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology*, 83, 575–583. <https://doi.org/10.2307/3284227>
- Cabrera-Guzmán, E. (2002). Comunidades de helmintos parásitos de *Rana forreri* Boulenger, 1883 (Amphibia: Ranidae) en dos localidades del Municipio de Acapulco, Guerrero, México. *Boletín de la Sociedad Herpetológica de México*, 10, 63.
- Cabrera-Guzmán, E., Garrido-Olvera, L., & León-Règagnon, V. (2010). Helminth parasites of the leopard frog *Lithobates* sp. Colima (Amphibia: Ranidae) from Colima, Mexico. *Journal of Parasitology*, 96, 736–739. <https://doi.org/10.1645/ge-2335.1>
- Cabrera-Guzmán, E., León-Règagnon, V., & García-Prieto, L. (2007). Helminth parasites of the leopard frog *Rana* cf. *forreri* (Amphibia: Ranidae) in Acapulco, Guerrero, Mexico. *Comparative Parasitology*, 74, 96–107. <https://doi.org/10.1654/4247.1>
- Cabrera-Guzmán, E., Papes, M., & García -Prieto, L. (2021). Research on helminths from Mexican amphibians: gaps, trends, and biases. *Journal of Helminthology*, 95, e67. <https://doi.org/10.1017/S0022149X21000614>
- Campião, K. M., Delatorre, M., Rodrigues, R. B., da Silva, R. J., & Ferreira, V. L. (2012). The effect of local environmental variables on the helminth parasite communities of the pointedbelly frog *Leptodactylus podicipinus* from ponds in the Pantanal Wetlands. *Journal of Parasitology*, 98, 229–235. <https://doi.org/10.1645/GE-2877.1>
- Campião, K. M., Morais, D. H., Dias, O. T., Aguiar, A., Toledo, G. d. M., Tavares, L. E. R. et al. (2014). Checklist of helminth parasites of amphibians from South America. *Zootaxa*, 3843, 1–93. <https://doi.org/10.11646/zootaxa.3843.1.1>
- Canseco-Márquez, L., & Gutiérrez-Mayén, M. G. (2010). *Anfibios y reptiles del Valle de Tehuacán-Cuicatlán*. Ciudad de México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad/ Fundación para la Reserva de la Biosfera

- Cuicatlán, A. C./ Benemerita Universidad Autónoma del Puebla.
- Cardoso, P., Rigal, F., & Carvalho, J. C. (2015). BAT–Biodiversity Assessment Tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods Ecology Evolution*, 6, 232–236. <https://doi.org/10.1111/2041-210X.12310>
- Carvalho, J. C., Cardoso, P., Borges, P. A. V., Schmera, D., & Podani, J. (2013). Measuring fractions of beta diversity and their relationships to nestedness: a theoretical and empirical comparison of novel approaches. *Oikos*, 122, 825–834. <https://doi.org/10.1111/j.1600-0706.2012.20980.x>
- Carvalho, J. C., Cardoso, P., & Gomes, P. (2012). Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. *Global Ecology and Biogeography*, 21, 760–771. <https://doi.org/10.1111/j.1466-8238.2011.00694.x>
- Chabaud, A. G. (1978). Key to the genera of the superfamilies Cosmocercoidea, Seuratoidea, Heterakoidea and Subuluroidea. In R. C. Anderson, A. G. Chabaud, & S. Willmott (Eds.), *CIH Keys to the nematode parasites of vertebrates (No. 6)* (pp. 1–71). Buckinghamshire, England: Commonwealth Agricultural Bureaux.
- Chao, A., Gotelli, N., Hsieh, T. C., Sander, E., Ma, K. H., Colwell, R. K. et al. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84, 45–67. <https://doi.org/10.1890/13-0133.1>
- Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, 93, 2533–2547. <https://doi.org/10.1890/11-1952.1>
- Conanp (Comisión Nacional de Áreas Naturales Protegidas). (2003). *Programa de manejo de la Reserva de la Biosfera Barranca de Metztlán*. México D.F.: Dirección General de Manejo para la Conservación, Conanp.
- de Sena, P. A., Conceição, B. M., Silva, P. F., Silva, W. G. O., Ferreira, W. B., da Silva Júnior, V. A. et al. (2018). Helminth communities of *Pithecopus nordestinus* (Anura: Phyllomedusidae) in forest remnants, Brazil. *Herpetology Notes*, 11, 565–572.
- Dias, M. L. G. G., Eiras, J. C., Machado, M. H., Souza, G. T. R., & Pavanelli, G. C. (2003). The life cycle of *Clinostomum complanatum* Rudolphi, 1814 (Digenea, Clinostomidae) on the floodplain of the high Paraná river, Brazil. *Parasitology Research*, 89, 506–508. <https://doi.org/10.1007/s00436-002-0796-z>
- Espinola-Novelo, J. F., Guillén-Hernández, S., González-Salas, C. F., & Canto, A. (2017). Helminth diversity of two anurans: *Rhinella marina* and *Incilius valliceps* (Anura: Bufonidae) from lagunas de Yalahua, Yucatán, Mexico. *Revista Mexicana de Biodiversidad*, 88, 365–371. <https://doi.org/10.1016/j.rmb.2017.03.023>
- Falcón-Ordaz, J., Monks, S., Pulido-Flores, G., García-Prieto, L., & Lira-Guerrero, G. (2015). Riqueza de helmintos parásitos de vertebrados silvestres del Estado de Hidalgo, México. In G. Pulido-Flores, S. Monks, & M. López-Herrera (Eds.), *Estudios en biodiversidad, Vol. I* (pp. 20–37). Lincoln, Nebraska: Zea Books. <https://digitalcommons.unl.edu/cgi/viewcontent.cgi?article=1002&context=biodiversidad>
- Falcón-Ordaz, J., Monks, S., Pulido-Flores, G., & Rodríguez-Amador, R. (2014). A new species of *Aplectana* (Nematoda: Cosmocercoidea) in *Ambystoma velasci* (Amphibia: Ambystomatidae) from Mexico. *Comparative Parasitology*, 81, 220–224. <https://doi.org/10.1654/4684.1>
- Frosts, D. R. (2018). *Amphibian species of the World: an online reference*. New York: American Museum of Natural History. <https://amphibiansoftheworld.amnh.org>
- Fuller, C. A., & Nickol, B. B. (2011). A description of mature *Oncicola venezuelensis* (Acanthocephala: Oligacanthorhynchidae) from a feral house cat in the U. S. Virgin Islands. *Journal of Parasitology*, 97, 1099–1100. <https://doi.org/10.1645/GE-2849.1>
- Galicia-Guerrero, S., Bursey, C. R., Goldberg, S. R., & Salgado-Maldonado, G. (2000). Helminths of two sympatric toad species *Bufo marinus* (Linnaeus) and *Bufo marmoratus* Weigmann, 1833 (Anura: Bufonidae) from Chamela, Jalisco, Mexico. *Comparative Parasitology*, 67, 129–132.
- García-Altamirano, I., Pérez-Ponce de León, G., & García-Prieto, L. (1993). Contribución al conocimiento de la comunidad de helmintos de dos especies de anfibios endémicos del Lago de Pátzcuaro, Michoacán: *Rana dunni* y *Ambystoma dumerilii*. *Cuadernos Mexicanos de Zoología*, 1, 73–80.
- Gibbons, L. M. (2010). *Keys to the nematode parasites of vertebrates: supplementary volume*. Wallingford, UK: CAB International.
- Gibson, D. I., Jones, A., & Bray, R. A. (2002). *Keys to the Trematoda (Vol. 1)*. Wallingford, UK: CABI Publishing/ The Natural History Museum.
- Goater, T. M., Browne, C. L., & Esch, G. W. (1990). On the life history and functional morphology of *Haliipegus occidialis* (Trematoda: Hemiuridae), with emphasis on the cystophorous cercaria stage. *International Journal for Parasitology*, 20, 923–934. [https://doi.org/10.1016/0020-7519\(90\)90031-H](https://doi.org/10.1016/0020-7519(90)90031-H)
- Goldberg, S. R., & Bursey, C. R. (2002). Helminth parasites of seven anuran species from Northwestern Mexico. *Western North American Naturalist*, 62, 160–169. <http://www.jstor.org/stable/41717188>
- Goldberg, S. R., Bursey, C. R., & Gergus, E. W. A. (2001). Helminth communities of subpopulations of the Pacific treefrog, *Hyla regilla* (Hylidae), from Baja California, México. *Southwestern Naturalist*, 46, 223–230. <https://doi.org/10.2307/3672535>
- Goldberg, S. R., Bursey, C. R., Salgado-Maldonado, G., Baez, R., & Cañeda, C. (2002). Helminth parasites of 6 species of anurans from Los Tuxtlas and Catemaco lake, Veracruz, Mexico. *Southwestern Naturalist*, 47, 293–329. <https://doi.org/10.2307/3672917>
- Hamann, M. I., González, C. E., & Kehr, A. I. (2006). Helminth community structure of the oven frog *Leptodactylus latinasus*

- (Anura, Leptodactylidae) from Corrientes, Argentina. *Acta Parasitologica*, 51, 294–299. <https://doi.org/10.2478/s11686-006-0045-1>
- Hamann, M. I., Kehr, A. I., & González, C. E. (2006). Species affinity and infracommunity ordination of helminths of *Leptodactylus chaquensis* (Anura: Leptodactylidae) in two contrasting environments from Northeastern Argentina. *Journal of Parasitology*, 92, 1171–1179. <https://doi.org/10.1645/GE-862R1.1>
- Hamann, M. I., Kehr, A. I., & González, C. E. (2010). Helminth community structure of *Scinax nasicus* (Anura: Hylidae) from a South American subtropical area. *Diseases of Aquatic Organisms*, 93, 71–82. <https://doi.org/10.3354/dao02276>
- Hammer, Ø., Harper, D. A. T., & Ryan, P. D. (2001). PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia electronica*, 4, 9. [http://palaeo-electronica.org/2001\\_1/past/issue1\\_01.htm](http://palaeo-electronica.org/2001_1/past/issue1_01.htm)
- Hasegawa, H., & Nishikawa, K. (2009). New species of kathlaniid (Nematoda: Cosmocercoidea) collected from hynobiid salamanders in Japan. *Journal of Parasitology*, 95, 186–190. <https://doi.org/10.1645/GE-1635.1>
- Hill, M. O. (1973). Diversity and evenness: a unifying notation and its consequences. *Ecology*, 54, 427–432. <https://doi.org/10.2307/1934352>
- Hillis, D. M., & Frost, J. S. (1985). Three new species of leopard frogs (*Rana pipiens* complex) from the Mexican plateau. *Occasional Papers of the Museum of Natural History*, 117, 1–14.
- Horwitz, P., & Wilcox, B. A. (2005). Parasites, ecosystems and sustainability: an ecological and complex systems perspective. *International Journal for Parasitology*, 35, 725–732. <https://doi.org/10.1016/j.ijpara.2005.03.002>
- Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods Ecology Evolution*, 7, 1451–1456. <https://doi.org/10.1111/2041-210X.12613>
- Imasuen, A. A., Ozemoka, H. J., & Aisien, M. S. O. (2012). Anurans as intermediate and paratenic hosts of helminth infections in the rainforest and derived savanna biotopes of Southern Nigeria. *International Journal of Zoology*, 2012, 823970. <https://doi.org/10.1155/2012/823970>
- INEGI (Instituto Nacional de Estadística y Geografía). (2013). Perspectiva estadística: Hidalgo. Diciembre 2013. [https://books.google.com.mx/books?id=FdbSDwAAQBAJ&pg=PT83&lpg=PT83&dq=INEGI.++Perspectiva+estadística+del+estado+de+Hidalgo.++Septiembre+2013.&source=bl&ots=Tuli0gYAcu&sig=ACfU3U03YxrB5xr11JxA11rDsKq6\\_\\_NiRQ&hl=en&sa=X&ved=2ahUKEwiP7KTbw4H0AhWWtJ4KHdyfBiIQ6AEwBH0ECAoQAQ#v=onepage&q=INEGI.%20%20Perspectiva%20estadística%20del%20estado%20de%20Hidalgo.%20%20Septiembre%3B%202013.&f=false](https://books.google.com.mx/books?id=FdbSDwAAQBAJ&pg=PT83&lpg=PT83&dq=INEGI.++Perspectiva+estadística+del+estado+de+Hidalgo.++Septiembre+2013.&source=bl&ots=Tuli0gYAcu&sig=ACfU3U03YxrB5xr11JxA11rDsKq6__NiRQ&hl=en&sa=X&ved=2ahUKEwiP7KTbw4H0AhWWtJ4KHdyfBiIQ6AEwBH0ECAoQAQ#v=onepage&q=INEGI.%20%20Perspectiva%20estadística%20del%20estado%20de%20Hidalgo.%20%20Septiembre%3B%202013.&f=false)
- Jongman, R. H. G., Ter Braak, C. J. F., & Van Tongeren, O. F. R. (1995). *Data analysis in community and landscape ecology, 2nd Edition*. Cambridge: Cambridge University Press. <https://doi.org/10.1017/CBO9780511525575>
- Jost, L. (2006). Entropy and diversity. *Oikos*, 113, 363–375. <https://doi.org/10.1111/j.2006.0030-1299.14714.x>
- Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, 88, 2427–2439. <https://doi.org/10.1890/06-1736.1>
- King, K. C., Gendron, A. D., McLaughlin, J. D., Giroux, I., Brousseau, P., Cyr, D. et al. (2008). Short-term seasonal changes in parasite community structure in northern leopard froglets (*Rana pipiens*) inhabiting agricultural wetlands. *Journal Parasitology*, 94, 13–22. <https://doi.org/10.1645/GE-1233.1>
- Koprivnikar, J., & Poulin, R. (2009). Effects of temperature, salinity, and water level on the emergence of marine cercariae. *Parasitology Research*, 105, 957–965. <https://doi.org/10.1007/s00436-009-1477-y>
- Krasnov, B. R., Shenbrot, G. I., Warburton, E. M., van der Mescht, L., Surkova, E. N., Medvedev, S. G. et al. (2019). Species and site contributions to  $\beta$ -diversity in fleas parasitic on the Palearctic small mammals: ecology, geography and host species composition matter the most *Parasitology*, 146, 653–661. <https://doi.org/10.1017/S0031182018001944>
- Krull, W. H. (1935). Studies on the life history of *Halipegus occidialis* Stafford, 1905. *The American Midland Naturalist*, 16, 129–142.
- Leigh, W. H. (1946). Experimental studies on the life cycle of *Glythelminis quieta* (Stafford, 1900), a trematode of frogs. *American Midland Naturalist*, 35, 460–483. <https://doi.org/10.2307/2421672>
- León-Règagnon, V., Martínez-Salazar, E. A., Lazcano-Villareal, D., & Rosas-Valdez, R. (2005). Helminth parasites of 4 species of anurans from Nuevo Leon, Mexico. *Southwestern Naturalist*, 50, 251–258. [https://doi.org/10.1894/0038-4909\(2005\)050\[0251:HPOFSO\]2.0.CO;2](https://doi.org/10.1894/0038-4909(2005)050[0251:HPOFSO]2.0.CO;2)
- Luque, J. L., Martins, A. N., & Tavares, L. E. R. (2005). Community structure of metazoan parasites of the yellow cururu toad, *Bufo ictericus* (Anura, Bufonidae) from Rio de Janeiro, Brazil. *Acta Parasitologica*, 50, 215–220. <https://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.484.19&rep=rep1&type=pdf>
- Magurran, A. E. (2004). *Measuring biological diversity*. Malden, Massachusetts: Blackwell Publishing Company.
- Mata-López, R., León-Règagnon, V., & García-Prieto, L. (2013). Helminth infracommunity structure of *Leptodactylus melanotus* (Anura) in Tres Palos, Guerrero, and other records for this host species in Mexico. *Journal of Parasitology*, 99, 564–569. <https://doi.org/10.1645/GE-3026.1>
- McAlpine, D. F. (1997). Helminth communities in bullfrogs (*Rana catesbeiana*), green frogs (*Rana clamitans*), and leopard frogs (*Rana pipiens*) from New Brunswick, Canada. *Canadian Journal of Zoology*, 75, 1883–1890. <https://doi.org/10.1139/z97-818>
- McDonald, J. H. (2009). *Handbook of biological statistics*. Baltimore, Maryland: Sparky House Publishing.
- Mejía-Madrid, H. H. (2013). Parascript, parasites and historical biogeography. In M. Silva-Opps (Ed.), *Current progress in biological research* (pp. 125–148). Rijeka, Croatia: IntechOpen. <https://doi.org/10.5772/55459>

- Moravec, F., Huffman, D. G., & Swim, D. J. (1995). The first record of fish as paratenic hosts of *Falcaustra* spp. (Nematoda: Kathlianiidae). *Journal of Parasitology*, *81*, 809–812. <https://doi.org/10.2307/3283986>
- Moreno, C. E., Barragán, F., Pineda, E. N., & Pavón, N. P. (2011). Reanálisis de la diversidad alfa: alternativas para interpretar y comparar información sobre comunidades ecológicas. *Revista Mexicana de Biodiversidad*, *82*, 1249–1261. <https://doi.org/10.22201/ib.20078706e.2011.4.745>
- Muzzall, P. M. (1991). Helminth infracommunities of the frogs *Rana catesbeiana* and *Rana clamitans* from Turkey Marsh, Michigan. *Journal of Parasitology*, *77*, 366–371. <https://doi.org/10.2307/3283121>
- Muzzall, P. M., Gilliland III, M. G., Summer, C. S., & Mehne, C. J. (2001). Helminth communities of green frogs, *Rana clamitans* Latreille, from southwestern Michigan. *Journal of Parasitology*, *87*, 962–968. [https://doi.org/10.1645/0022-3395\(2001\)087\[0962:HCOGFR\]2.0.CO;2](https://doi.org/10.1645/0022-3395(2001)087[0962:HCOGFR]2.0.CO;2)
- Muzzall, P. M., & Mychek-Londer, J. G. (2014). *Echinorhynchus salmonis* (Acanthocephala: Echinorhynchidae) in the Spoonhead Sculpin, *Cottus ricei*, from Lake Superior, Wisconsin, U.S.A. and a Summary of Acanthocephalans Infecting Sculpins from the Great Lakes. *Comparative Parasitology*, *81*, 179–184. <https://doi.org/10.1654/4671.1>
- Nickol, B. B., Fuller, C. A., & Rock, P. (2006). Cystacanths of *Oncicola venezuelensis* (Acanthocephala: Oligacanthorhynchidae) in caribbean termites and various paratenic hosts in the U.S. Virgin Islands. *Journal of Parasitology*, *92*, 539–542. <https://doi.org/10.1645/GE-3557.1>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D. et al. (2018). *Vegan: Community Ecology Package*. R package version 2.5-2. <https://CRAN.R-project.org/package=vegan>
- Ortiz-Pulido, R., Bravo-Cadena, J., Martínez-García, V., Reyes, D., Mendiola-González, M. E., Sánchez, G. et al. (2010). Avifauna de la Reserva de la Biosfera Barranca de Metztitlán, Hidalgo, México. *Revista Mexicana de Biodiversidad*, *81*, 373–391. <https://doi.org/10.22201/ib.20078706e.2010.002.260>
- Palmer, J. O. P. S., Dib, L. S. V., Lobão, L. F., Pinheiro, J. L., Ramos, R. C. F., Uchoa, C. M. A. et al. (2020). *Oncicola venezuelensis* (Marteau, 1977) (Acanthocephala: Oligacanthorhynchidae) in *Puma concolor* in Rio de Janeiro, Brazil. *Revista Brasileira de Parasitologia Veterinária*, *29*, e009620. <https://doi.org/10.1590/S1984-29612020046>
- Paredes-Calderón, E. L., León-Régagnon, V., & García-Prieto, L. (2004). Helminth infracommunities of *Rana vaillanti* Brocchi (Anura: Ranidae) in Los Tuxtlas, Veracruz, Mexico. *Journal of Parasitology*, *90*, 692–696. <https://doi.org/10.1645/GE-226R>
- Parra-Olea, G., Flores-Villela, O., & Mendoza-Almeralla, C. (2014). Biodiversidad de anfibios de México. *Revista Mexicana de Biodiversidad*, *85* (Suppl.), S460–S466. <https://doi.org/10.7550/rmb.32027>
- Pérez-Ponce de León, G., García-Prieto, L., & Mendoza-Garfias, B. (2011). Describing parasite biodiversity: the case of the helminth fauna of wildlife vertebrates in Mexico. In O. Grillo (Ed.), *Changing diversity in changing environment*. Rijeka, Croatia: InTech. <https://doi.org/10.5772/25011>
- Petrochenko, V. (1971). *Acanthocephala of domestic and wild animals, Vol. 1-2*. Moscow: Publishing House of the Academy of Sciences of the USSR.
- Plackett, R. L. (1983). Karl Pearson and the Chi-Squared Test. *International Statistical Review / Revue Internationale de Statistique*, *51*, 59–72. <https://doi.org/10.2307/1402731>
- Podani, J., & Schmera, D. (2011). A new conceptual methodological framework for exploring and explaining pattern in presence absence data. *Oikos*, *120*, 1625–1638. <https://doi.org/10.1111/j.1600-0706.2011.19451.x>
- Poulin, R. (1997). Species richness of parasite assemblages: evolution and patterns. *Annual Review of Ecology and Systematics*, *28*, 341–358. <https://doi.org/10.1146/annurev.ecolsys.28.1.341>
- Poulin, R. (2003). The decay of similarity with geographical distance in parasite communities of vertebrate hosts. *Journal of Biogeography*, *30*, 1609–1615. <https://doi.org/10.1046/j.1365-2699.2003.00949.x>
- Pritchard, M. H., & Kruse, G. O. W. (1982). *The collection and preservation of animal parasites*. Technical Bulletin No. 1, The Harold W. Manter Laboratory. Lincoln, Nebraska: University of Nebraska Press.
- Pulido-Flores, G., Monks, S., & Pérez-Romero, G. (2009). Helmintos parásitos de *Lithobates spectabilis* Hillis y Frost, 1985, de la Reserva de la Biosfera Barranca de Metztitlán, Hidalgo, México. In S. Monks, G. Pulido-Flores, & M. López-Herrera (Eds.), *Estudios científicos en el estado de Hidalgo, y zonas aledañas, Vol. I*. (pp. 23–33). Pachuca, Hidalgo: Universidad Autónoma del Estado de Hidalgo.
- Qin, J., Liu, X., Xu, Y., Wu, X., & Ouyang, S. (2019). Beta diversity patterns of fish and conservation implications in the Luoxiao Mountains, China. *Zookeys*, *817*, 73–93. <https://doi.org/10.3897/zookeys.817.29337>
- R Core Team. (2021). *R: a language and environment for statistical computing*. In R Foundation for Statistical Computing. <https://www.R-project.org/>
- Ramírez-Bautista, A., Hernández-Salinas, U., Cruz-Elizalde, R., Berriozabal-Islas, C., Lara-Tuñiño, D., Goyenechea Mayer-Goyenechea, I. et al. (2014). *Los anfibios y reptiles de Hidalgo, México: diversidad, biogeografía y conservación*. Pachuca, Hidalgo: Sociedad Herpetológica Mexicana.
- Rankin, J., & John, S. (1944). A review of the Trematode genus *Glyphelminis* Stafford, 1905, with an account of the life cycle of *G. quieta* (Stafford, 1900) Stafford, 1905. *Transactions of The American Microscopical Society*, *63*, 30–43.
- Razo-Mendivil, U., & Pérez-Ponce de León, G. (2008). Taxonomic revision of the genus *Glyphelminis* Stafford, 1905 (Platyhelminthes: Digenea: Plagiorchiida), parasites of anurans in the Americas. *Zootaxa*, *1882*, 1–45. <https://doi.org/10.11646/ZOOTAXA.1882.1.1>



- Rodríguez-Amador, R., Monks, S., & Pulido-Flores, G. (2013). Primer reporte helmintológico de *Ambystoma velasci* Dugés, 1888 de Lago de Tecocomulco, Hidalgo, México. In G. Pulido-Flores & S. Monks (Eds.), *Estudios científicos en el estado de Hidalgo y zonas aledañas, Volumen II* (pp. 133–120). Lincoln, Nebraska: Zea Books. <http://dx.doi.org/10.13140/2.1.1153.1844>
- Romero-Mayén, Á. R., García-Prieto, L., & León-Règagnon, V. (2016). Helminth parasites of the smooth-backed frog, *Lithobates psilonota* (Amphibia: Ranidae), from Western Mexico. *Comparative Parasitology*, 83, 178–191. <https://doi.org/10.1654/4791RR.1>
- RStudio, T. (2020). *RStudio: integrated development for R. RStudio, PBC*. Boston, MA. <http://www.rstudio.com/>
- Ruiz-Torres, N., García-Prieto, L., Lagunas-Calvo, O., Violante-González, J., & Osorio-Sarabia, D. (2017). Helminth infracommunity of the cane toad *Rhinella marina* (Anura: Bufonidae) within its native distribution range. *Parasitology International*, 66, 567–572. <https://doi.org/10.1016/j.parint.2017.05.002>
- Salgado-Maldonado, G., & Caspeta-Mandujano, J. M. (2010). *Lueheia inscripta* (Westrumb, 1821) (Acanthocephala: Plagiorhynchidae) in anurans (Leptodactylidae: Bufonidae) from Mexico. *Parasite*, 17, 161–165. <https://doi.org/10.1051/parasite/2010172161>
- Santos, E. G. N., Chame, M., Chagas-Moutinho, V. A., & Santos, C. P. (2016). Morphology and molecular analysis of *Oncicola venezuelensis* (Acanthocephala: Oligacanthorhynchidae) from the ocelot *Leopardus pardalis* in Brazil. *Journal of Helminthology*, 91, 605–612. <https://doi.org/10.1017/s0022149x16000651>
- Santos, V. G. T., & Amato, S. B. (2010). Helminth fauna of *Rhinella fernandezae* (Anura: Bufonidae) from the Rio Grande do Sul coastland, Brazil: analysis of the parasite community. *Journal Parasitology*, 96, 823–826. <https://doi.org/10.1645/GE-2388.1>
- Schell, S. C. (1970). *How to know the trematodes*. Dubuque, Iowa: WM. C. Brown Company Publishers.
- Schmidt, G. D. (1972). Revision of the class Archiacanthocephala Meyer, 1931 (Phylum Acanthocephala), with emphasis on Oligacanthorhynchidae Southwell et MacFie, 1925. *Journal of Parasitology*, 58, 290–297. <https://doi.org/10.2307/3278091>
- Smales, L. R. (2013). Acanthocephala including the descriptions of new species of *Centrorhynchus* (Centrorhynchidae) and the redescription of *Lueheia inscripta* (Westrumb, 1821) (Plagiorhynchidae) from birds from Paraguay South America. *Revue Suisse de Zoologie*, 120, 175–202. [http://institutions.ville-geneve.ch/fileadmin/user\\_upload/mhn/documents/Museum/rsz120\\_2.pdf](http://institutions.ville-geneve.ch/fileadmin/user_upload/mhn/documents/Museum/rsz120_2.pdf)
- Spickett, A., Junker, J., Krasnov, B. R., Haukisalmi, V., & Matthee, S. I. (2017). Intra- and interspecific similarity in species composition of helminth communities in two closely related rodents from South Africa. *Parasitology*, 144, 1211–1220. <https://doi.org/10.1017/S003118201700049X>
- Spickett, A., van der Mescht, L., Junker, K., Krasnov, B. R., Haukisalmi, V., & Matthee, S. (2019). Beta diversity of gastrointestinal helminths in two closely related South African rodents: species and site contributions. *Parasitology Research*, 118, 2863–2875. <https://doi.org/10.1007/s00436-019-06411-w>
- StatSoft, I. (2011). STATISTICA (data analysis software system), version 10. In Inc. <http://www.statsoft.com>
- Stigge, H. A., & Bolek, M. G. (2016). Evaluating the biological and ecological factors influencing transmission of larval digenetic trematodes: a test of second intermediate host specificity of two North American *Halipegus* species. *Journal Parasitology*, 102, 613–621. <https://doi.org/10.1645/15-891>
- Velazquez-Urrieta, M. Y., & León-Règagnon, V. (2018). Helminths of two species of leopard frogs (Amphibia: Ranidae) from Chiapas, Mexico. *Comparative Parasitology*, 85, 141–152. <https://doi.org/10.1654/1525-2647-85.2.141>
- Werby, H. J. (1938). A new genus of Acanthocephala with forked lemnisci. *Transactions of the American Microscopical Society*, 57, 204–212.
- Williams, H. H., & Jones, A. (1994). *Parasitic worms of fish*. London, Bristol: Taylor & Francis.
- Yamaguti, S. (1961). *Systema Helminthum: nematodes of vertebrates (Vol. III)*. New York: Interscience Publishers Inc.
- Yamaguti, S. (1963). *Systema Helminthum: Acanthocephala (Vol. V)*. New York, London: Intel-Science Publishers (John Wiley & Sons Ltd).
- Yamaguti, S. (1971). *Synopsis of digenetic trematodes of vertebrates*. Tokyo, Japan: Keigaku Publishing Co.
- Yáñez-Arenas, C. (2007). *Descripción de las comunidades de helmintos de la rana leopardo Rana brownorum Sanders, 1973 (Anura: Ranidae) en tres localidades del Estado de Yucatán (Tesis)*. Universidad Autónoma de Yucatán. Mérida, Yucatán.
- Yáñez-Arenas, C. A., & Guillén-Hernández, S. (2010). Helminth fauna of *Lithobates brownorum* (Anura: Ranidae) en tres localidades del estado de Yucatán, México. *Revista Mexicana de Biodiversidad*, 81, 191–195. <https://doi.org/10.22201/ib.20078706e.2010.001.198>
- Zelmer, D., Paredes-Calderón, E. L., León-Règagnon, V., & García-Prieto, L. (2004). Nestedness in colonization-dominated systems: helminth infracommunities of *Rana vaillanti* brocchi (Anura: Ranidae) in Los Tuxtlas, Veracruz, Mexico. *Journal of Parasitology*, 90, 705–710. <https://doi.org/10.1645/GE-3316>
- Zelmer, D. A., & Esch, G. W. (1999). Reevaluation of the taxonomy status of *Halipegus occidualis* Stafford, 1905 (Digenea: Hemiuridae). *Journal of Parasitology*, 85, 157–160. <https://doi.org/10.2307/3285726>