



Review

Nematodes of Amphibians from the South American Chaco: Distribution, Host Specificity and Ecological Aspects

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Abstract: This is the first review of the nematode parasites of amphibians from Dry Chaco (DC) and Humid Chaco (HC) ecoregions of South America, covering aspects related to their systematics, distribution, host range and ecology, including their life cycles. Of approximately 100 species of amphibians that inhabit these ecoregions, the nematode parasites of 32 species are known. The parasite species consisted of 51 taxa: 27 in HC and 18 in DC. The family Cosmocercidae alone included 18 species. *Aplectana hylambatis* and *Cosmocerca podicipinus* showed the widest geographical and host distribution. *Leptodactylus bufonius* and *Rhinella major* presented a high number of nematode parasites. The species richness of nematodes was related to the host body sizes and to the strategy to obtain prey. The mean species richness was higher in terrestrial amphibians with intermediate characteristics in the generalist–specialist spectrum in terms of diet, and in amphibians with intermediate characteristics between actively foraging and the “sit-and-wait” approach in terms of searching for prey. The patterns of similarity among amphibian species showed groups linking with their habitats. Nematodes usually have direct life cycles with the infectious form entering the host passively or actively. However, many amphibians are also involved in heteroxenous cycles that develop in the aquatic environment.

Keywords: nematode parasites; amphibians; Dry Chaco; Humid Chaco; distribution; specificity; ecological aspects; life cycles



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Citation: González, C.E.; Hamann, M.I.; Duré, M.I. Nematodes of Amphibians from the South American Chaco: Distribution, Host Specificity and Ecological Aspects. *Diversity* **2021**, *13*, 321. <https://doi.org/10.3390/d13070321>

Academic Editors: Ulrich Sinsch and Patrick Leander Scheid

Received: 15 June 2021
Accepted: 12 July 2021
Published: 15 July 2021

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1. Introduction

With the knowledge of the diversity, life cycle and distribution of helminth parasites, ecological and historical assessments of biota can be carried out [1]. Reliable data on the spatial distribution of parasites are needed to estimate global parasite diversity and thus, to establish robust conservation and global public health management. In addition, knowledge on the geographic distributions of parasites and host species are the empirical basis for future research using amphibians as models of parasite–host interaction patterns [2–4]. In this sense, there are investigations that contribute to the knowledge of the distribution and diversity of helminths in amphibians of different biogeographic regions such as Afrotropical [5–7], Australasian [8–10], Indomalayan [11–13], Nearctic [14–16] and Palearctic [17–21].

In the Neotropical region, reviews on the parasites of amphibians from specific ecoregions or biomes have been compiled during the last decade [4,22–25]. These include, for example, studies on the digeneans of the Humid Chaco (HC), the helminths of the Pantanal, the nematodes of the Atlantic Forest, the helminths of the Pampas and the endoparasites in a transition area between the Cerrado and the Atlantic Forest.

Studies on parasitic nematodes of amphibians in the HC and Dry Chaco (DC) have been carried out exclusively in Argentina and Paraguay, while there are no records from the Brazilian and Bolivian Chaco. Research on the nematodes of the Paraguayan Chaco refer mainly to descriptions of new species or to reports of new hosts or localities for a specific taxon. Most were occasional reports widely separated in time [26–28]. However, they had

a great boost in a series of works published in the 1980s [29–33]. In the Argentinean Chaco, studies on amphibian parasites began towards the end of the 1990s [34–38]. They focused on the systematics of the different groups of helminths, dynamics of parasite population and the ecological relationships between trematode parasites and amphibian hosts from the province of Corrientes, located in the HC. Recently, studies in the HC focused on the biodiversity, population dynamics and community structure of helminth parasites in natural and anthropic environments, e.g., rice fields [22,39–46]. Then, the studies were extended to hosts collected in different points of the DC, specifically in the Chaco and Formosa provinces. Similar to the investigations carried out in the HC, DC studies treated systematic as well as ecological aspects [47–51]. A single study compared the helminth community in four localities of the DC and HC [52]. Review studies refer specifically to the biodiversity of trematodes in amphibians with diverse habitats in a specific locality of the HC ecoregion of Argentina [22].

This study will provide, for the first time, an overview of nematode species in amphibians of the South American Gran Chaco, covering aspects related to their systematics, distribution, host range and ecology, including their life cycles. This review will include all previously published studies on parasitic nematodes of amphibians in both the HC and DC in Argentina and Paraguay. The aims of this study are: (i) to present a systematic compilation of nematode parasites of amphibians from DC and HC ecoregions in South America, (ii) to indicate the geographical distribution and nematode parasite–host associations in both ecoregions, (iii) to analyze the nematofauna with respect to body size, habitat preference, diet type and foraging mode of the amphibian host, (iv) to examine the similarity of the nematofauna of both ecoregions and (v) to analyze the nematode cycles of transmission.

2. Study Area

The Gran Chaco or Chaco *sensu lato* is a large region located in south-central South America that is characterized by extensive wooded areas. It is the second largest forest area in South America after the Amazon. The region extends from 16°55' South latitude, in the tropical region, to 33°52' South latitude, in the temperate region, and from 67°50' West longitude at the foot of the Andes up to 57°52' West longitude in the province of Corrientes, Argentina. It occupies approximately 1,141,000 km², where 59% is in Argentina, 23% in Paraguay, 13% in Bolivia and 5% in Brazil [53].

Within the Gran Chaco, two ecoregions are geographically defined in which certain characteristics of relief, geology, soil groups, types of vegetation and fauna complexes dominate. The main characteristic is that temperature and rainfall present an aridity gradient that increases from East to West, which determines the distinction between HC and DC [54–56].

The DC is a vast plain that presents a gentle slope towards the East modeled by the action of the rivers that cross it in a Northwest–Southeast direction, which transport a large amount of sediments from their high basins that form ridges or fluvial fans. The climate is subtropical warm continental and hosts the South American heat pole, with absolute maximums that exceed 47 °C; there is also a great daily temperature range associated with great seasonal variation. Rainfall ranges from 700 to 400 mm and 80% of the rains are concentrated between October and March, with droughts being very frequent [56].

Depending on the area, mountain forests, savannas and grasslands are abundant. The characteristic vegetation type is the xerophilous forest, whose trees become shorter and sparser towards the southwest of the ecoregion. The highest areas, within the flat relief, have xerophilous forests of the genera *Schinopsis*, *Aspidosperma*, *Bulnesia*, *Mimosa* and *Celtis* with various cacti, peaches and shrubs of the genera *Acacia* and *Capparis*. In some low-lying areas, salinity and drainage restrictions condition the floristic composition, giving rise to communities of genus *Prosopis* and *Geoffroea*. The forests alternate with grasslands of genus *Elionurus* [54]. There is a great diversity of fauna, including the jaguar, *Panthera onca*, the giant armadillo *Priodontes maximus*, peccaries or wild pigs, *Tayassu pecari* and *T. tajacu*,

and the anteater, *Myrmecophaga tridactyla*, among mammals; the Chaco martineta, *Eudromia formosa* and the black-footed chuña *Chunga burmeisteri*, among birds; and the lampalagua, *Boa constrictor* and different species of yararás, *Bothrops* spp. among reptiles [56].

The HC is a flat plain, with gentle slopes in the West–East direction. Fluvial and fluvio-lacustrine landscape predominates, whose drainage network drains into the Paraná and Paraguay rivers. The hydrological regime, together with the geomorphological, climatic and edaphic characteristics, determine the existence of the largest surface area and percentage of wetlands. Temperatures follow a North–South gradient and the rains are organized in an East–West gradient with more than 1300 mm in the area of the fluvial collectors and about 750 mm in the border with the DC. In some years, when the El Niño phenomenon occurs, intense rainfall occurs that causes extraordinary floods in large areas of this region [56].

The vegetation presents greater diversity than that of the DC. The forests are mainly made up of *Enterolobium contortisiliquum*, *Ruprechtia laxiflora*, *Gleditsia amorphoides* and *Handroanthus impetiginosus*. In the interfluvia, various mosaic vegetal features appear: low, dense or open forests that border estuaries or ravines, grasslands composed of herbaceous and arboreal elements, ravines made up of grasslands or palm trees and estuaries with a free water bottom without vegetation cover [54]. The vertebrate fauna includes two species of alligator, *Caiman yacare* and *C. latirostris*, the iguana, *Salvator merianae*, the Chaco side-necked turtle, *Acanthochelys pallidipectoris*, the yellow anaconda, *Eunectes notaeus*, and the yarará grande, *Bothrops alternatus*, among the reptiles; the tuyuyú, *Mycteria americana*, the yellow-headed vulture, *Cathartes burrovianus*, and the crowned eagle, *Harpyhaliaetus coronatus*, among birds; the black howler monkey, *Alouatta caraya*, the nine-banded armadillo, *Dasyus novemcinctus*, the white-eared opossum, *Didelphis albiventris*, the maned wolf, *Chrysocyon brachyurus*, and the capybara, *Hydrochaeris hydrochaeris*, among mammals [56].

Some 100 species of amphibians have been recorded in Gran Chaco [53,57]. Some of them are endemic to the Gran Chaco, such as the three species of the genus *Lepidobatrachus* and *Chacophrys pierottii* (Ceratophryidae), and the recent leptodactylid species described, *Leptodactylus apepyta* [58,59]. Others, such as *Leptodactylus laticeps*, inhabit the DC ecoregion almost exclusively [60]. Despite all these advances, the information available on the biodiversity of the Chaco remains fragmented and limited [61].

The Gran Chaco has suffered the loss of large areas of natural ecosystems during the past decades. For example, in the first decades of the 20th century, the forests of *Schinopsis* spp. were razed for the production of tannins and sleepers. In the last decades of the last century and until now, deforestation continued and the lands were used for livestock activities, mainly in Paraguay, and for the cultivation of pastures and soybeans, mainly in Argentina [62–64].

3. Materials and Methods

3.1. Systematic of Parasitic Nematodes

To compile this review, we took into account all nematode species published by our research group from 1997 to date, together with papers of other authors that published on nematode species in amphibians from the Argentine Chaco and from different points of the Paraguayan Chaco (see details Supplementary Materials, Table S1 [65–93]). Some studies were not included because the collection locations were not specified or it was not specified in which host (of a group of hosts) a particular nematode species was collected [27,32]. From the data on nematodes published in a more recent paper, references to departments with more than one ecoregion were not taken into account, due to the impossibility of knowing to which ecoregion the reference belongs; however, the references of the Boquerón department were considered because this department is located entirely in the DC [28].

3.2. Richness of Nematode Parasites and Geographical Distribution

We analyzed, for each of the amphibian species, the total nematode species richness (S) for both ecoregions and for each one separately. Geographically, a total of twelve localities

were defined throughout the two ecoregions; five are points within the DC and seven within the HC (Figure 1). The maps were created using the program QGIS 2.18 [94].

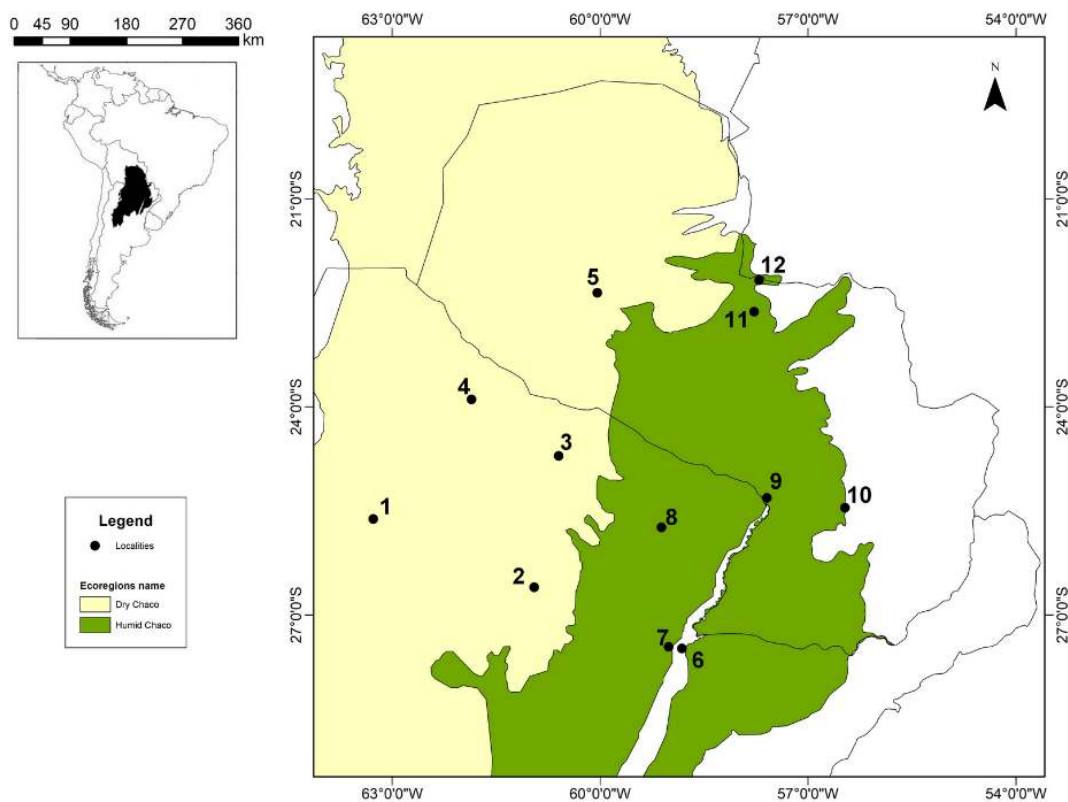


Figure 1. Geographic location of localities where studies on amphibian parasitic nematodes have been carried out in the Dry Chaco ecoregion (Argentina: 1. Taco Pozo, Chaco Province, 2. Concepción del Bermejo, Chaco Province, 3. Las Lomitas, Formosa Province, 4. Ingeniero Juárez, Formosa Province; Paraguay: 5. Boquerón, Boquerón Department) and in the Humid Chaco ecoregion (Argentina: 6. Corrientes, Corrientes Province, 7. Resistencia, Chaco Province, 8. Pirané, Formosa Province; Paraguay: 9. Asunción, Capital District, 10. Coronel Oviedo, Caaguazú Department, 11. Puerto Max, Concepción Department, 12. Estancia Estrellas, Concepción Department).

So far, 32 species of amphibians, belonging to 7 families (Bufonidae, Ceratophryidae, Hylidae, Microhylidae, Leptodactylidae, Odontophrynidae and Phyllomedusidae) have been listed. Five species of amphibians (15.6%) were studied exclusively in the DC (*Ceratophrys cranwelli* (Barrio, 1980), *Chacophrys pierottii* (Vellard, 1948), *Lepidobatrachus laevis* (Budgett, 1899), *Dermatonotus muelleri* (Boettger, 1885) and *Odontophrynus lavillai* (Ceï, 1985)), 23 species (71.8%) were exclusively studied in the HC (*Rhinella bergi* (Céspedes, 2000), *Rhinella dorbignyi* (Duméril and Bibron, 1841) (= *R. fernandezae*), *Melanophryniscus klappenbachi* (Prigioni and Langone, 2000), *Boana raniceps* (Cope, 1862), *Dendropsophus nanus* (Boulenger, 1889), *D. sanborni* (Schmidt, 1944), *Lysapsus limellum* (Cope, 1862), *Pseudis platensis* (Gallardo, 1961), *Scinax acuminatus* (Cope, 1862), *Trachycephalus typhonius* (Linnaeus, 1758), *Leptodactylus elenae* (Heyer, 1978), *L. fuscus* (Schneider, 1799), *L. latinasus* (Jiménez de la Espada, 1875), *L. luctator* (Hudson, 1892), *L. macrosternum* (Miranda-Ribeiro, 1926) (= *L. chaquensis*), *L. mystacinus* (Burmeister, 1861), *L. podicipinus* (Cope, 1862), *Physalaemus albonotatus* (Steindachner, 1864), *P. santafecinus* (Barrio, 1965), *Pseudopaludicola boliviana* (Parker, 1927), *P. falcipes* (Hensel, 1867), *O. americanus* (Duméril and Bibron, 1841) and *Pithecopus azureus* (Cope, 1862)); finally, four species of amphibian (12.5%), *R. diptycha* (Cope, 1862), *R. major* (Müller and Hellmich, 1936), *S. nasicus* (Cope, 1862) and *L. bufonius* (Boulenger, 1894), were studied in both ecoregions. Figure 2 shows the localities of both ecoregions and the list of hosts analyzed in each of them.

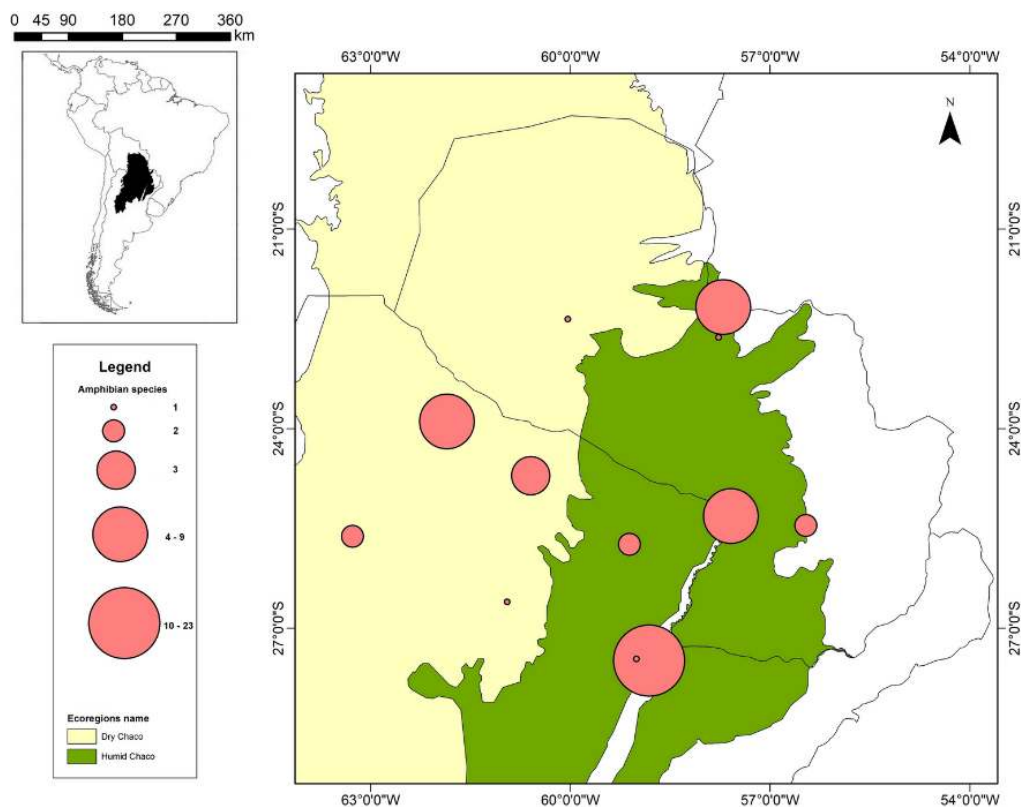


Figure 2. Number of amphibian species analyzed for nematode parasites in twelve localities in Dry and Humid Chaco ecoregions. *Corrientes*: *Rhinella bergi*, *R. diptycha*, *R. dorbignyi*, *R. major*, *Boana raniceps*, *Dendropsophus nanus*, *D. sanborni*, *Lysapsus limellum*, *Pseudis platensis*, *Scinax acuminatus*, *S. nasicus*, *Leptodactylus bufonius*, *L. elenae*, *L. latinasus*, *L. luctator*, *L. macrosternum*, *L. podicipinus*, *Physalaemus albonotatus*, *P. santafecinus*, *Pseudopaludicola falcipes*, *P. boliviana*, *Odontophrynus americanus*, *Pithecopus azureus*; *Resistencia*: *Melanophryniscus klappenbachii*; *Pirané*: *Trachycephalus typhonius*, *P. azureus*; *Asunción*: *R. diptycha*, *L. bufonius*, *L. luctator*, *L. elenae*, *L. mystacinus*, *P. azureus*; *Coronel Oviedo*: *L. elenae*, *L. fuscus*; *Puerto Max*: *L. macrosternum*; *Estancia Estrellas*: *R. diptycha*, *R. major*, *L. bufonius*, *L. elenae*, *L. podicipinus*; *Boquerón*: *R. major*; *Taco Pozo*: *R. major*, *L. bufonius*; *Concepción del Bermejo*: *R. major*; *Las Lomitas*: *R. major*, *D. muelleri*, *L. bufonius*; *Ingeniero Juárez*: *R. diptycha*, *R. major*, *C. cranwelli*, *C. pierottii*, *L. laevis*, *S. nasicus*, *D. muelleri*, *L. bufonius*, *O. lavillai*.

3.3. Nematode Parasites vs. Host Life History

Total species richness and mean species richness of nematode parasites have been related to different life-history traits of the host: body size, habitat preference, diet type and foraging mode. We defined five categories of habitat preference: terrestrial, arboreal (includes bushes), fossorial, semi-aquatic and aquatic. Three categories were defined for the diet type: generalists (those that consume a wide range of prey without a preference for some of them), intermediate (those that feed on different types of prey but show a preference for some prey) and specialists (those that consume few specific categories of prey and the rest can be considered accidental ingestion). Three categories were defined for the foraging mode: active, sit-and-wait and intermediate (Supplementary Material, Table S2 [95–115]).

The mean species richness was calculated by adding the total nematode species for each amphibian species and dividing it by the total number of amphibians in each category (habitat preference, diet type and foraging mode). These analyses were carried out taking into account the two ecoregions jointly.

Generalized linear models (GLM), with logarithm link function and Poisson distributed error, were used to calculate the influence of the biotic predictor variables (host body size, habitat preference, foraging mode, diet type) on the pattern of variation in the nematode species richness. We ran models with all possible combinations of sets of

variables and we ranked them according to plausibility based on the Corrected Akaike information criterion, with the better model having the lower AIC score [116]. We also calculated the relative importance of each predictor variable as the sum of the Akaike weights over all models in which each variable appears. For the model selection, we consider those models whose delta AICc were less than 4 [117]. The GLMs were conducted using the glm function of the R statistical language and environment [118].

3.4. Similarity in Nematode Fauna in HC and DC

To determine the qualitative similarity between component communities, Jaccard's coefficient similarity index was used and a cluster analysis was then performed using the UPGMA (Unweighted Pair Group Method Average) method. Analyses were performed using the software packages PAST [119].

3.5. Life Cycles

For the analysis of the life cycles of the different species of nematodes, we consider classic works on this topic [120,121] and other specific studies of different groups (for details see Tables 1 and 2).

Table 1. Summary of nematode taxa in adult stage found in amphibian hosts from Dry and Humid Chaco ecoregions. Life cycle: M: monoxenous, H: heteroxenous.

Nematode Taxa	Life Cycle	Summary of Transmission	References
<i>Rhabdias</i> spp.	M	Heterogonic life cycle with two generations; one of free-living males and females in the soil, and a parasitic generation in the lungs of amphibians. Males and females of the gonochoristic generation mate and breed in the soil and the resulting larvae reach L3 stage and penetrate amphibians through the skin, or through the mucosa or eye cavity.	[122]
<i>Strongyloides</i> sp.	M	No information is available from amphibian hosts. Homogonic and heterogonic. Hosts become infected when free-living L3 penetrate the skin; then, larvae migrate through the host body, going through the lungs, and they molt via an L4 stage so that there is an adult parasitic female in the gut. Eggs in feces hatch to release L1; larvae are either male or female; both develop via L2–L4 into rhabditiform. The free-living adults mate and the females lay eggs that hatch to release L1 that reach L3 stage. All the progeny of the free-living adult generation are female.	[123]
<i>Oswaldocruzia</i> spp.	M	The eggs of these nematodes, in stages of 8 to 16 cells, are shed with the host's feces and develop to L3 in the environment. Amphibians become infected by L3 penetration. The larvae migrate in the body of the host to the lumen of the intestine, where they reach adulthood. There, the males and females mate and the females' egg-laying begins	[120]
<i>Schulzia travassosi</i>		No information is available.	
<i>Gyrinicola</i> spp.	M	Nematodes present in tadpoles exclusively. Dependent on the development time to metamorphosis of anuran tadpole hosts, this taxon presents distinct reproductive strategies. Female nematodes reproduce parthenogenetically and only produce thick-shelled eggs for parasite transmission from host to host in tadpoles with short development periods. In tadpoles with longer developmental periods, this nematode reproduces by haplodiploidy, and females produce thick-shelled as well as autoinfective thin-shelled eggs.	[120]
<i>Parapharyngodon</i> sp.	M	No information is available in amphibian hosts. Like other oxyurids has a direct life cycle. The infection occurs by ingestion of eggs in the environment (soil), as well as via geophagy (in lizards).	[124]
<i>Cosmocerca</i> spp.	M	Amphibians become infected when the L3 that occurs in the environment (soil) penetrates through the skin of the hosts and, after pulmonary migration, are located in the large intestine; in there they reach the adult stage, copulate and the females begin to lay eggs.	[120]
<i>Aplectana</i> spp.	M	Similar to <i>Cosmocerca</i> but the hosts are infected orally (passive infection).	[120]
<i>Cosmocercella minor</i>	M (?)	No information is available.	
<i>Neocosmocercella paraguayensis</i>	M (?)	No information is available.	
<i>Oxyascaris</i> spp.	M (?)	No information is available.	
<i>Falcaustra mascula</i>	H (?)	No information is available in amphibian hosts. L3 was found in freshwater snails; ten of these larvae were given to laboratory-reared turtle. Then, a single adult male was found in the intestine of a reptile. Snail could be serving as paratenic host.	[120]
<i>Schrankiana</i> spp.	M (?)	No information is available in amphibian hosts. In atractids, eggs develop to L3 in utero and autoinfect the host. Their transmission from host to host is not understood for most species; suspected to occur during mating in turtles.	[120]
<i>Physaloptera venancioi</i>	H	There is no information available for this species. For the genus, invertebrates act as intermediate hosts for L3 and vertebrates as the definitive host, where L3 develops to adults. In the intestine, adult parasites mate and the eggs are eliminated with the feces.	[120]
<i>Ochoterenella digiticauda</i>	H	Adults of this species are found in the peritoneal cavities, and the microfilariae are sheathed and found in the blood and coelomic fluid of host. Presumably, the transmission occurs by a vector where the nematode reaches the infective stage.	[125]

Table 2. Summary of heteroxenous life cycles of nematode parasites from amphibians in Dry and Humid Chaco. Nematode taxa (in alphabetical order), site of infection, free, encysted or encapsulated larva, environment (Env., A: aquatic; T: terrestrial) and type of hosts in the life cycle (DH: definitive hosts; IH: intermediate hosts; PH: paratenic hosts; TH: transport hosts).

Nematode Taxa/ Site of Infection	Free/Encysted/ Encapsulated Larva	Env.	IH/PH/TH	DH	References
<i>Brevimulticaecum</i> sp. M, AC, SE; WSI	Inside thin-walled, almost spherical capsule.	A	IH-PH: fishes, amphibians	Alligators	[126]
<i>Camallanus</i> sp. SI	Free	A	IH: copepods PH: planktivorous fishes TH: amphibians	Fishes, amphibians, reptiles (especially turtles)	[120,127]
<i>Contracaecum</i> sp. M	Encapsulated	A	1st. IH: commonly copepods 2nd. IH-PH: fishes PH: amphibians	Piscivorous birds	[120,128]
<i>Ortleppascaris</i> sp. L	Within elongated, thick-walled cysts	A	IH: amphibians PH: amphibians	Crocodiles	[129,130]
<i>Physaloptera</i> sp. GM	Attached by the cephalic collaret	T	IH: insects (beetles, crickets, cockroaches) PH: lizards, snakes, amphibians, rodents	Amphibians, reptiles, birds, mammals	[120,131]
<i>Porrocaecum</i> sp. L	Within elongated, thick-walled cysts	T	IH: annelids (earthworms) PH: shrews and other small mammals, amphibians	Birds	[120]
Rhabdochoniidae gen. sp. SE	Inside almost spherical cysts	A/T	IH: crustaceans (amphipods, crabs), insects (ephemeropterans, trichopteran, blatids) PH: amphibians	Cold-blooded vertebrates (rare in mammals)	[120]
<i>Serpinema</i> cf. <i>trispinosum</i> SI	Free	A	IH: copepods PH: damselflies, aquatic snails, fishes, amphibians	Freshwater turtles	[121,132,133]
Seuratoidea gen. sp. * SE	Inside almost spherical, brownish, thin-walled cysts	A/T	IH: insects, polychaetes, chironomids, vertebrates (fish) PH: insects (crickets, simuliids)	All vertebrate groups	[120,134]
<i>Spiroxys</i> sp. SE	Inside almost spherical cysts	A	IH: copepods PH: snails, aquatic insects, tadpoles and adults frogs and, larval and adult of newts, fishes	Freshwater turtles	[121]

* The data for the intermediate and paratenic hosts include those relating to families Seuratidae, Schmeidernematidae, Chitwoodchabaudiidae and Quimperidae. M: mesentery; GA: gastric mucosa; AC: abdominal cavity; SE: serous of stomach; WSI: wall of small intestine; SI: small intestine; L: liver.

4. Results

4.1. Systematics of Parasitic Nematodes

The compiled database includes a total of 51 taxa of nematodes from 22 genera and 15 families recorded from 7 families of amphibians from DC and HC ecoregions (Supplementary Material, Table S1). Of these, five taxa were not identified to the species or genus level (*Ascarididae* gen. sp., *Rhabdochoniidae* gen. sp., *Cosmocercidae* gen. sp., *Seuratoidea* gen. sp. and *Rhabditida* larva).

The order *Rhabditida* included 15.7% of the nematodes found ($S = 8$), *Strongylida* 9.8% ($S = 5$), *Oxyurida* 5.9% ($S = 3$), *Ascaridida* 54.9% ($S = 28$) and *Strongylida* 13.7% ($S = 7$). In the order *Ascaridida*, the richest in terms of number of species, most of these species belonged to the family *Cosmocercidae* (18 species), followed by the family *Rhabdiasidae* of the order *Rhabditida* (7 species). Figure 3 shows the composition by family and superfamily of nematodes (%) in each family of amphibians analyzed; the *Cosmocercidae* was present in all amphibian families and with the highest proportion of number of species. The leptodactylid amphibians were parasitized by the largest number of nematode families (10) and superfamily (1).

4.2. Richness of Nematode Parasites and Geographical Distribution

Leptodactylus bufonius was the amphibian parasitized by the highest number of nematode species ($S = 16$), followed by *Rhinella diptycha* ($S = 14$). In five species of amphibians (*L. laevis*, *B. raniceps*, *D. sanborni*, *P. falcipes* and *O. lavillai*) a single species of nematode was found. Likewise, when considering the species richness in the ecoregions separately, in the HC *L. bufonius* was the most parasitized, whereas in the DC it was *R. major*.

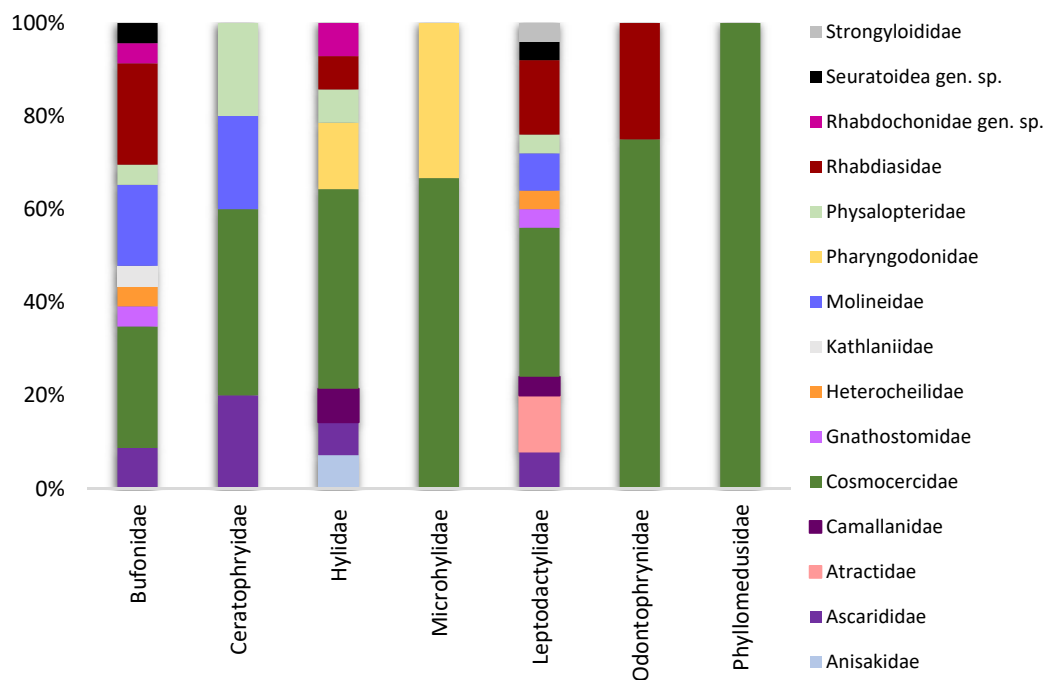


Figure 3. Composition of nematode family in percentage, in each amphibian family analyzed from Dry and Humid Chaco.

Some nematode species were specific for a host species or genus, e.g., the cosmocercids *N. paraguayensis*, *C. minor* and *C. phyllomedusae* were only found in *Pithecopus azureus*, and the atractids of genus *Schrankiana* only in *Leptodactylus* spp.

Fourteen (27.4%) of the 51 species of nematodes (*A. hylambatis*, *Brevimulticaecum* sp., *C. podicipinus*, *Falcaustra mascula*, *O. caudacutus*, *Oswaldocruzia mazzai*, *O. subauricularis*, *Oswaldocruzia* sp., *Physaloptera* sp., *Porrocaecum* sp., *Rhabdias elegans*, *Rhabdias* sp., *Schrankiana formosula* and *Schulzia travassosi*) were found in both ecoregions.

Cosmocerca podicipinus was the nematode species that parasitized the largest number of host species (20 species), being present in 6 of the 12 sampled locations (Figure 4). Likewise, *A. hylambatis* was found in 7 of the 12 localities sampled.

In the HC ecoregion, the total number of parasitic nematode species was 48 (Figure 4). Twenty-seven species of amphibians were analyzed in this ecoregion. The amphibian with the highest species richness of nematodes was *L. bufonius* (13 species), followed by *R. diptycha* (11 species). The nematode species that parasitized the largest number of hosts was *C. podicipinus* (17 species) followed by *C. parva* (16 species). These two species were the most widely distributed, found in four of the seven localities sampled in the HC.

In the DC ecoregion, the total number of nematode parasites was 18 species (Figure 4). Nine species of amphibians were analyzed in this ecoregion. *Rhinella major* presented the highest species richness ($S = 9$), followed by *L. bufonius* ($S = 7$). The nematode species that parasitized the largest number of hosts was *A. hylambatis* (seven species), and it was found in all the sampled localities in the DC.

In general, there was a relationship between the amphibian species analyzed and the nematode species found (See Figures 2 and 4); localities such as Corrientes in the HC with 23 species of amphibians analyzed so far present a total of 35 species of nematodes, and Ingeniero Juárez in the DC with nine species of amphibians analyzed presents a total of 11 species of nematodes.

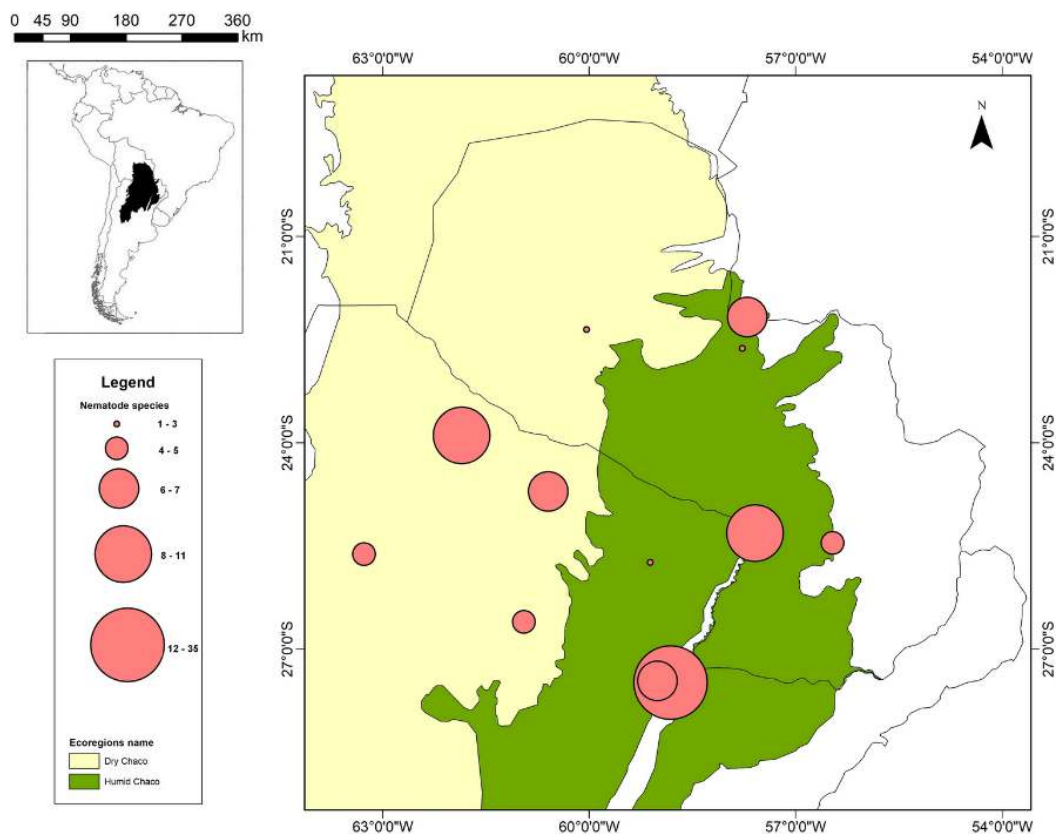


Figure 4. Number of nematode species found in each locality in Dry and Humid Chaco. Corrientes: *Aplectana delirae*, *A. hylambatis*, *Aplectana* sp., *Brevimulticaecum* sp., *Camallanus* sp., *Contraecacum* sp., *Cosmocerca cruzi*, *C. parva*, *C. podicipinus*, *C. rara*, *Cosmocerca* sp., *Cosmocercella minor*, *Cosmocercoides* gen. sp., *Falcaustra mascula*, *Gyrinicola chabaudi*, *Gyrinicola* sp., *Ortleppascaris* sp., *Oswaldocruzia proencai*, *O. subauricularis*, *Oswaldocruzia* sp., *Oxyascaris caudacutus*, *Physaloptera* sp., *Porrocaecum* sp., *Rhabdias elegans*, *R. fuelleborni*, *R. mucronata*, *R. aff. sphaerocephala*, *Rhabdias* sp., *Rhabditida*, *Rhabdochonidae* gen. sp., *Schrankiana schranki*, *Serpinema* cf. *trispinosum*, *Seuratoidea* gen. sp., *Spiroxys* sp., *Strongyloides* sp.; Resistencia: *Cosmocerca* sp. 1, *Cosmocerca* sp. 2, *Physaloptera* sp., *Rhabdochonidae* gen. sp., *Seuratoidea* gen. sp., *Spiroxys* sp.; Pirané: *A. hylambatis*, *Neocosmocercella paraguayensis*, *R. cf. elegans*; Asunción: *Aplectana macintoshii*, *Cosmocercella minor*, *C. phyllomedusae*, *Cosmocerca parva*, *C. paraguayensis*, *F. mascula*, *N. paraguayensis*, *Oswaldocruzia mazzai*, *Ochoterenella digiticauda*, *Physalopteroides venancioi*; Coronel Oviedo: *Aplectana elenae*, *A. paraelenae*, *Cosmocerca parva*, *C. podicipinus*, *Schrankiana formosula*; Puerto Max: *C. podicipinus*; Estancia Estrellas: *Aplectana macintoshii*, *A. elenae*, *Cosmocerca paraguayensis*, *C. parva*, *C. podicipinus*, *Oxyascaris oxyascaris*, *Schulzia travassosi*; Boquerón: *Aplectana hylambatis*, *Falcaustra mascula*; Taco Pozo: *Aplectana hylambatis*, *Oswaldocruzia mazzai*, *R. elegans*, *Schrankiana chacoensis*, *Schulzia travassosi*; Concepción del Bermejo: *A. hylambatis*, *Physaloptera* sp., *R. elegans*, *Schulzia travassosi*; Las Lomitas: *A. hylambatis*, *Ascarididae* gen. sp., *C. podicipinus*, *Physaloptera* sp., *Porrocaecum* sp., *Rhabdias pseudosphaerocephala*, *Schulzia travassosi*; Ingeniero Juárez: *A. hylambatis*, *Brevimulticaecum* sp., *C. podicipinus*, *Oswaldocruzia subauricularis*, *Oswaldocruzia* sp., *Oxyascaris caudacutus*, *Parapharyngodon* sp., *Physaloptera* sp., *Rhabdias* sp., *Schrankiana formosula*, *Schulzia travassosi*.

4.3. Nematode Parasites vs. Host Life History

The GLM model that explained most of the variation in nematode species richness included host body size and foraging mode as predictor variables, with a weight of 0.762. Considering all the models with an AICc delta less than 4 [117], another model was also relevant, which additionally included the diet type, with a weight of 0.231. In contrast, the model including habitat preference, with a delta AICc > 10 and a weight < 0.005, was considered as highly implausible. The relative importance of each variable was: foraging mode = 0.999, host body size = 0.997, diet type = 0.232 and habitat preference = 0.004.

Considering the habitat preference of the host, the mean species richness of nematodes for both ecoregions was higher for terrestrial (6.33 ± 1.43) and fossorial am-

phibians (5.33 ± 2.23), whereas the lowest mean species richness was found in aquatic amphibians (2.33 ± 0.66) (Figure 5a). Regarding the foraging mode, the mean species richness was higher in the species considered intermediate between active foraging and the “sit-and-wait” strategy (6.25 ± 1.52), and the lowest for those with a passive strategy (2.11 ± 0.3) (Figure 5b). Finally, amphibians that had an intermediate diet between generalist and specialist had the highest mean species richness (7 ± 1.73) (Figure 5c).

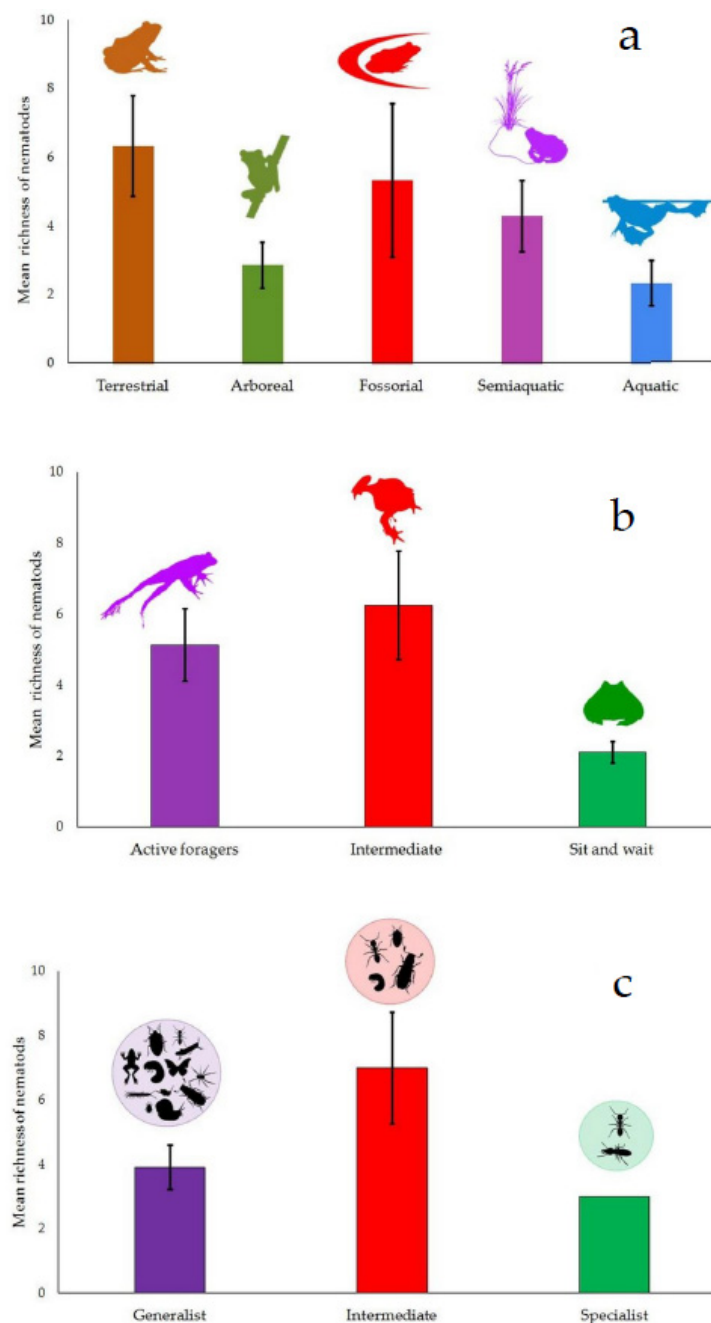


Figure 5. Comparison of host habitat preferences (a), foraging mode (b) and diet type (c) with the mean species richness (± 1 SE) of nematode parasites.

4.4. Similarity in Nematode Fauna in Humid and Dry Chaco

In HC, a cluster analysis based on the Jaccard's coefficient grouped *B. raniceps* and *D. sanborni* with highest similarity (1.0), followed by *R. bergi* and *L. podicipinus* (0.75) and by *S. acuminatus* and *S. nasicus* (0.66; Figure 6a). *P. azureus* formed an outgroup because

they did not share any nematode species with other amphibians (0.0) (Figure 6a). In DC, a cluster analysis grouped *C. pierottii*, *C. cranwelli* and *D. muelleri* with highest similarity (0.5), and *S. nasicus* and *L. laevis* formed an outgroup because they did not share any nematode species with other amphibian hosts (0.0) (Figure 6b).

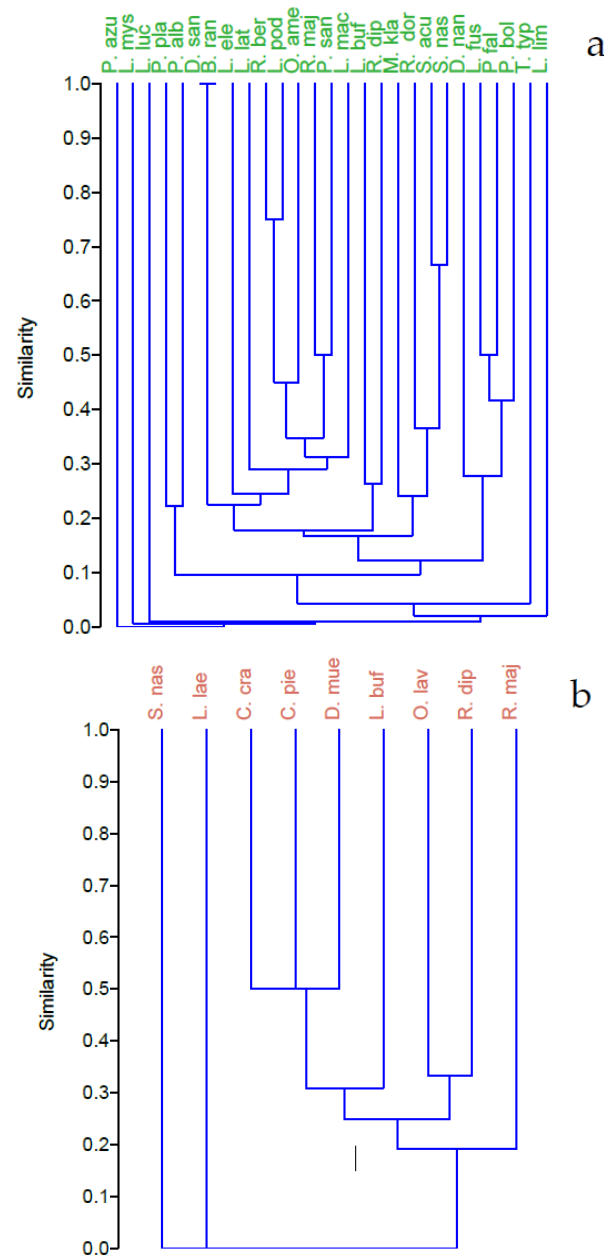


Figure 6. Dendrogram for cluster analysis (UPGMA) using the Jaccard's Similarity Index between species of amphibians with respect to the presence of nematode parasites in Humid Chaco (a) and Dry Chaco (b). *Rhinella bergi*, R. ber; *R. diptycha*, R. dip; *R. dorbignyi*, R. dor; *R. fernandezae*, R. fer; *R. major*, R. maj; *Melonophryniscus klappenbachi*, M. kla; *Ceratophrys cranwelli*, C. cra; *Chacophrys pierottii*, C. pie; *Lepidobatrachus laevis*, L. lae; *Boana raniceps*, B. ran; *Dendropsophus nanus*, D. nan; *D. sanborni*, D. san; *Lysapsus limellum*, L. lim; *Pseudis platensis*, P. pla; *Scinax acuminatus*, S. acu; *S. nasicus*, S. nas; *Trachycephalus typhonius*, T. typ; *Dermantonotus muelleri*, D. mue; *Leptodactylus bufonius*, L. buf; *L. elenae*, L. ele; *L. fuscus*, L. fus; *L. latinasus*, L. lat; *L. luctator*, L. luc; *L. macrosternum*, L. mac; *L. podicipinus*, L. pod; *Physalaemus albonotatus*, P. alb; *P. santafecinus*, P. san; *Pseudopaludicola falcipes*, P. fal; *P. boliviana*, P. bol; *Odontophrynus americanus*, O. ame; *O. lavillai*, O. lav; *Pithecopus azureus*, P. azu.

4.5. Life Cycles

Most of the nematode taxa identified in these ecoregions were found in the adult stage (74.5%; $n = 38$), and 13 in the larval stage (25.5%). The forms of transmission and hosts involved in their life cycles are not yet elucidated for many species. In these taxa, the life cycles of congeneric species for which information on their biological cycle is available were considered.

Amphibians are the definitive hosts for nematode species found in the adult stage. These nematodes had a heteroxenous life cycle in two taxa (*Physaloptera venancioi*, *Ochoterenella digiticauda*) and a monoxenous life cycle in the rest of the taxa [120,121]. Table 1 summarizes the transmission mode of adult nematodes found in amphibians of both ecoregions analyzed.

If infected by nematode larvae, amphibians act as paratenic, intermediate or transport hosts in the life cycle (except those identified as Cosmocercidae). These larvae have heteroxenous life cycles in which the intermediate host can be found in the aquatic or in the terrestrial environment and, likewise, the definitive hosts can be more closely related to one or the other environment. Table 2 summarizes the hosts, intermediate, paratenic, transport and definitive, involved in the life cycles of nematodes found in the larval stage and that developed both in the aquatic and terrestrial environments in the area studied. Two taxa not included in this table were Rhabditida and *R. mucronata*. In the first case, this finding is considered an accidental infection. The adults of this larva, identified specifically as of gonochoristic generation of *Serpentirhabdias*, parasitize the lung of snakes [86]. In the second case, the finding of *R. mucronata* in *L. luctator* corresponded to “juvenile” and there are no subsequent records of this species [83].

5. Discussion

5.1. Systematics of Parasitic Nematodes

In this study, we found that 48 taxa of nematode parasites are currently known from amphibians in HC, and 18 from amphibians in DC. They sum up to a total of 51 taxa of nematode parasites in both ecoregions. This is one third of the 150 nematode taxa listed for amphibians throughout South America [135]. The species richness of parasitic nematodes occurring in the Neotropical region varies among ecoregions: 21 taxa are known from the transition area between the Atlantic Forest and the Cerrado [4], 28 taxa from the Pantanal [23], 6 taxa from the Pampean region [24] and 20 taxa from the Atlantic Forest [25].

We demonstrate that the dominant nematode group in the amphibians of the HC and DC is the Cosmocercidae family. A similar result was shown in South American amphibians [136], as well as in a checklist of amphibian nematodes of Argentina [137] where these cosmocercids present the highest species richness (13 species identified).

In the present study, we identified 18 cosmocercid species, most belonging to the genera *Cosmocerca* and *Aplectana* (six species each). Similarly, in the Pantanal, cosmocercids (e.g., *A. hylambatis* and *C. podicipinus*) were the most prevalent and abundant nematodes [23]. The same applies to amphibians of the Pampean ecoregion, in which four of six nematode species found were cosmocercids [24]. Another family with high species richness was Rhabdiasidae. These pulmonary nematodes are among the most reported in South American amphibians [136]. Only in the Atlantic Forest, more rhabdisids than cosmocercids were found in amphibian hosts (eight vs. six taxa) [25]. The rest of the families included fewer species, which agrees with the studies in other areas. In contrast, common taxa of the Neotropical region, such as *Physocephalus* larvae in the Pantanal, adults of *Raillietnema* spp. in the Atlantic Forest, in the transition area between Cerrado and Atlantic Forest and in the Pantanal [4,23,25], have not been found in the DC or in the HC.

The nematofauna may be even more diverse if two additional factors are considered: the collection and identification of the nematode parasites. We believe that the larval forms are undersampled. Many of the cysts that contain these stages are found within the wall of organs such as the stomach and can be missed in the specimen count [138]. Only the most recent studies have included these stages in community analyses. Concerning the identification of species, we insist on the need to include in the studies an identification as

exact as possible of the taxa. It is understandable that, for the larval stages, identified taxa are presented at the level of genus or family (or superfamily), since it is the adult stages that provide the morphological characteristics for their identification. However, as other authors emphasize [139,140], at the adult stages it is necessary to be as precise as possible since the identification of species is crucial in diversity studies.

5.2. Richness of Nematode Parasites and Geographical Distribution

A little more than a quarter of the nematode species found (27.4%) were common to both ecoregions. The exclusive species of each ecoregion are nematodes found in other locations in the Neotropical Region. *Aplectana hylambatis* was the species with the widest geographic distribution considering both ecoregions. Moreover, *A. hylambatis*, *C. parva* and *C. podicipinus* have the widest distribution range in South America, occurring in five countries [135].

Looking at the ecoregions separately, the most widely distributed species were the cosmocerids *C. parva* and *C. podicipinus* in the HC, and *A. hylambatis* in the DC. The reason why *C. parva* was found exclusively in the HC is not clear, since it infested the second highest number of hosts after *C. podicipinus*.

A geographic bias might be introduced by the fact that, historically, the greatest sampling effort for amphibian nematodes was centered in the HC. In the Argentine DC there are more recent studies, but in fewer numbers [30,31,35,58,70], while for the Paraguayan DC there is one [28]. This is an important impediment to completing the world inventory of parasite species. The limited search for parasite species in tropical hotspots of amphibian diversity is due to the fact that most researchers work in temperate regions and direct their efforts mainly towards the study of the biota near their home institution [2].

This is, on a smaller scale, what happens in the Chaco. Our research group in Corrientes, Argentina, is the only one contributing to the knowledge of the parasitic nematode fauna of the HC. In Paraguay, the research focus is on the biology of amphibians, but host–parasite associations have been neglected [141–145].

In the compilation referring to helminths from South America [135], the amphibian species that were associated with the highest number of nematode species were *L. latrans* and *R. marina*. Yet, this is probably an artifact because the two species in *sensu strictu* were historically mixed up with several cryptic species. Specifically, the leptodactylids *L. fuscus* and *L. macrosternum* (= *L. chaquensis*) were associated with 14 nematode species each in the Pantanal [23] and, in the transition area between the Atlantic Forest and Cerrado, *L. podicipinus*, a hylid, *S. fuscovarius*, and a bufonid, *R. diptycha* were infested with eight nematode species each [4]. In the Pampean region, *L. luctator* was associated with six nematode species [24]. This is in agreement with the host–parasite associations in Gran Chaco where leptodactylids (*L. bufonius*) and bufonids (*R. major*) are the amphibians with the highest species richness of nematodes in HC and DC, respectively.

Leptodactylus bufonius, together with *R. major*, was the best-studied species in both ecoregions [26,30–32,42,48,49,52,67,70,71,79,81]. Therefore, we emphasize that estimates on parasite species richness are strongly influenced by sampling effort [136]. Some taxa, such as *B. raniceps*, *D. nanus*, *O. lavillai* and *L. luctator*, having numerous and stable populations and presenting a wide distribution, have been scarcely studied and, in the case of *L. luctator*, these studies were carried out more than five decades ago [26,27,83].

Other amphibians that have been scarcely studied are those of the Ceratophryidae family. The species of this family, endemic to the Chaco, are detected almost exclusively during the rainy season. *L. laevis*, *C. pierottii* and *C. cranwelli* are species that can be found in late spring and summer, in temporary rain pools, on clay soils, where they reproduce [104]. Consequently, studies on these species are limited to a few months in the year, in turn limiting the knowledge on their nematode fauna.

Two genera of nematodes, *Cosmocercella* and *Neocosmocercella*, were specific to one family of amphibians, Phyllomedusidae, and, so far, have been reported in the HC, the Pantanal and the Amazon [23,146,147]. For a long time, the genus *Schrankiana* was only

reported in leptodactylid amphibians [33,148], but recent studies found species of this genus parasitizing phyllomedusine frogs in the Pantanal [23]. In the HC and DC, *Cosmocercella* and *Neocosmocercella* were exclusively reported in Phyllomedusidae, and *Schrankiana* in Leptodactylidae, as expected. On the other hand, nematode species such as *P. venancioi*, *O. digiticauda* and *A. macinthoshii* that present a wide geographic and host distribution in other ecoregions [26,149] have been scarcely reported so far in the HC and DC.

A case to highlight is that of the amphibians of the genus *Pseudopaludicola*. The helminth fauna of *P. falcipes* and *P. boliviana* has been analyzed in the HC [29,79–81], and as a general rule, these amphibians were parasitized by a single nematode species; this contrasts with the seven species identified in *P. pocoto* from Caatinga [150].

5.3. Nematode Parasites vs. Host Life History

The most significant predictor variables that explained the variation in nematode species richness were host body size and foraging strategy. In general, a correlation exists between parasite species richness and host body size [136,151,152], holding true for the amphibians of the HC and DC [39,41–43,52]. The hosts with a larger body size have a larger surface area for infection with the parasitic forms.

It has been often documented that the composition of the helminth community in herps is closely related to the foraging mode [153,154]. Specifically, sit-and-wait ambush predators capture generally few large prey individuals, and wide-ranging searching predators capture small, sedentary and locally abundant prey. Hence, amphibians with greater agility are expected to have greater numbers of parasite species, higher prevalence and infection intensity, since active foraging increases the probability of contact with the infecting forms.

In terrestrial amphibians, the mean species richness of nematodes is greater than in aquatic, arboreal and semi-aquatic species [25,153–156]. For example, *A. hylambatis* was the dominant species in the helminth community of the terrestrial *L. bufonius*, *R. major* and *D. muelleri* [42,52,80], and *C. podicipinus* was the dominant species in the terrestrial host *R. dorbignyi* (= *R. fernandezae*) [43].

On the other hand, amphibians with intermediate strategies in terms of prey capture mode present the highest mean nematode species richness. It is not clear what is the reason why the DC and HC amphibians with active foraging strategies presented lower mean species richness than those presenting an intermediate strategy, but perhaps it is because those that use intermediate strategies are more related to the terrestrial and fossorial habits (e.g., *D. muelleri*, *L. mystacinus*, *M. klappenbachi*, *L. bufonius*, *L. elenae*).

Generalist host groups that consume a greater variety of prey have richer and more diverse helminth communities [153,154]. However, the amphibians with an intermediate diet had the highest mean species richness. This result can be explained by the fact that this work refers to parasitic nematodes and not to the entire helminth community. Most species have a monoxenous life cycle, and they do not require the presence of an intermediate host (item prey).

5.4. Similarity in Nematode Fauna in Humid and Dry Chaco

In the HC, the host species that showed the greatest similarity in terms of the composition of their parasitic nematodes, *B. raniceps* and *D. sanborni*, were parasitized by a single species (*C. parva*), and *L. podicipinus* and *R. bergi* that shared three species (*C. parva*, *C. podicipinus* and *Rhabdias* sp.). Three amphibian species, *P. azureus*, *P. mystacinus* and *L. luctator*, were the most different in terms of parasitic nematode composition (see Supplementary Materials, Table S1).

In the DC, two ceratophryids and a microhylid showed the greatest similarity, having in common *A. hylambatis* and *C. podicipinus*. The amphibians that presented the least similarity were *S. nasicus* and *L. laevis*. Each of them was parasitized by a single nematode species that was not found in any other species of amphibian, *O. caudacutus* and *Brevimulticaecum* sp., respectively.

The composition of nematofauna depends strongly on the habitat of amphibians. This is clearly observed in the DC, where the amphibians *L. laevis* and *S. nasicus* differ from the rest. They are aquatic and arboreal amphibians, respectively, whereas all other species are fossorial or terrestrial.

In the HC, without considering the outgroup formed by *P. azureus*, *P. mystacinus* and *L. luctator*, the rest of the amphibians were grouped in two clusters, one formed by *L. limellum* only, a clearly aquatic amphibian, and the other, formed by the rest of the species with semi-aquatic, fossorial, terrestrial and arboreal habitats. In this last group, pairs or groups of species with the same habitat or related habitats were observed (e.g., *B. raniceps*/*D. sanborni* and *S. acuminatus*/*S. nasicus* with arboreal habitat; *L. bufonius*/*R. diptycha* with fossorial and terrestrial habitat).

5.5. Life Cycles

Amphibians are definitive hosts for a wide range of parasites that exhibit direct life cycles. These parasites can infect them both actively, by penetration of the infesting larvae through the skin, mucous membranes or eyes, or by consuming contaminated prey or by geophagy [120] (see Table 1). These cycles are simple and do not require intermediate hosts. The high percentage of amphibians parasitized by the genera *Cosmocerca* and *Aplectana* and their wide distribution in both Chaco ecoregions suggests that they are well-established nematode species in the area and that their cycles are carried out without any inconvenience.

Clearly, monoxenous life cycles are those that predominate among adult amphibian nematodes of the Gran Chaco. However, when analyzing the larval forms, interesting conclusions can be drawn about the role of amphibians in their life cycle and, indirectly, in the trophic chains that are established in the different environments of these ecoregions. For these larval stages, amphibians act as transport and intermediate hosts, but above all, as paratenic hosts (see Table 2) [120,126,130]. In these cycles, amphibians become infected with larvae when they ingest other organisms that contain them. It is interesting to highlight the wide range of organisms that act as intermediate hosts in the life cycles of these nematodes and on which amphibians feed by entering the cycle as paratenic hosts.

In the aquatic environment, larvae of insects such as Ephemeroptera and Trichoptera, and crustaceans such as amphipods, but especially copepods, are consumed by amphibians, which in this way become infested. Aquatic amphibians such as *L. limellum* and *P. platensis* carry nematodes with this life cycle. Aquatic invertebrates do not usually form part of the diet of these anurans, but spending most of their lives in this environment, they are more likely to ingest, even accidentally, these organisms. Non-aquatic amphibians such as *P. albonotatus* and *M. klappenbachi* were also infected by several of these larvae. In the reproductive period, male and female *P. albonotatus* spend a lot of time in the water to build foam nests [103] and may acquire the infection by consumption of invertebrates. In the second case, *M. klappenbachi*, which is an explosive breeder forming large congregations of individuals in temporary pools, could also acquire the infection of larvae at the time of reproduction [44].

In the case of *Ortleppascaris*, amphibians may be intermediate hosts for these nematodes, although they are not a significant component of the definitive hosts' diet [129]. However, *R. marina* was considered the intermediate host of these larvae because, despite a strong immunological reaction of the host, viable larvae were found in different stages and with a considerable prevalence of infection [130].

Further larvae related to the aquatic environment were *Contracaecum* and *Camallanus*; these taxa were rarely recorded in HC and DC and always with a very low prevalence of infection. For this reason, amphibians cannot be considered suitable paratenic hosts for these larvae.

All these larvae are found in amphibians in variable quantities. They parasitize various organs both as free larvae, cysts or encapsulated in the wall of hollow organs or parenchymal organs (see Table 2). In any case, they may reach the definitive host preying

on the amphibian, and then, they can continue their life cycles. The definitive hosts of these larvae can be vertebrates of various groups, but especially crocodiles, turtles and piscivorous birds that consume amphibians as part of their diet. There are numerous records of predation by birds of different species of amphibians [157,158]. Turtles usually feed on tadpoles [159,160], but occasionally may consume adult amphibians [161,162]. Crocodiles can also ingest amphibians in larval and adult stages [163,164].

Nematodes with cycles related to a terrestrial environment are represented by the genera *Physaloptera* and *Porrocaecum* [120]. It should be noted that *Physaloptera* is the only genus for which amphibians can act as definitive (*P. venancioi*) or paratenic hosts (*Physaloptera* larvae).

The diet of the amphibians of the American Chaco has been studied mainly for the HC anurans [89,95–97,99,102,106–108,112]. They have mostly a generalist diet, consuming different groups of invertebrates, including those related to the cycles described above. At the same time, reptiles, birds and mammals, both domestic and wild, have been recorded in numerous studies as predators of amphibians [159,165–167].

Nematodes of the family Rhabdochoniidae and the superfamily Seuratoidea can develop their cycle in both environments (see Table 2). Seuratoidea taxa show two distinct types of cycles. Seuratidae of terrestrial mammals produce eggs that are eliminated with the feces and are infectious for the intermediate insect host. In contrast, Quimperidae, Chitwoodchabaudiidae and Cucullanidae, parasites of aquatic vertebrates, produce eggs that hatch in the environment and reach the infectious stage free ranging in the environment [134]. Amphibians ingesting both aquatic and terrestrial intermediate hosts become subsequently infested. The heteroxenous life cycles of parasitic nematodes found in amphibians of the HC and DC are shown schematically in Figure 7.

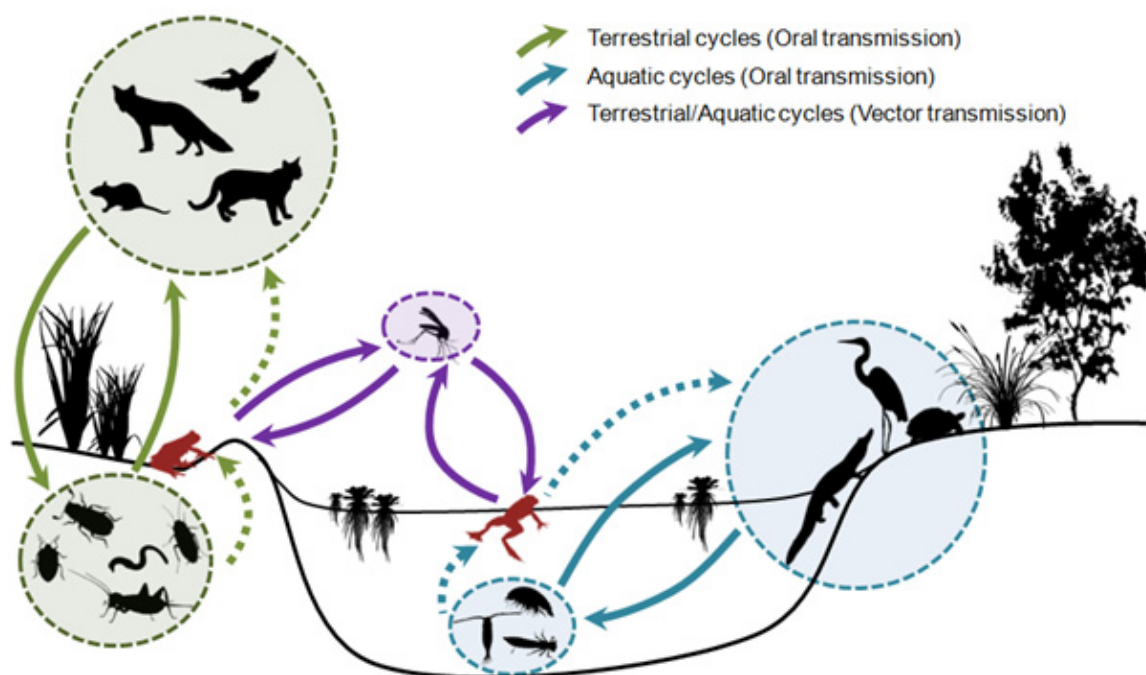


Figure 7. Schematic compilation of heteroxenous life cycles of parasitic nematodes found in amphibians of the Dry and Humid Chaco, in aquatic and terrestrial environments. Solid lines represent life cycles with “typical hosts”; the dotted lines represent the role of amphibians as paratenic hosts in these cycles.

6. Conclusions

Considering that the amphibian fauna of the Gran Chaco includes about 100 species [53,57] and that the nematode parasites of only a third of them (32 species) are known to date, it is obvious that the nematode diversity in the HC and DC is far from being fully known.

Moreover, parasitological studies concentrate often on few species, with *L. bufonius* being the most studied species in these ecoregions. There is also a geographical bias, suggesting that future investigations should be directed mainly to areas located to the north of DC. In the Paraguayan DC, there is only one record, in a locality and in a single host species [28].

Amphibians and reptiles are assumed to have the highest proportion of undescribed endoparasite species [168]. The parasite species richness of amphibians from South America is clearly underestimated [136]. This applies to a lesser extent also to DC and HC. Evidently, the species richness of plathelminthes, nematodes and acanthocephalan covariates positively in the different groups of vertebrate hosts, e.g., trematode diversity is a predictor of the diversity in other parasite groups [152].

In the amphibians of the Chaco, features of life history are reflected in their fauna of nematodes. In general, infections by nematodes with a direct cycle are lower in amphibians that obtain their prey as sit-and-wait predators and are not closely associated with the terrestrial environment. At the other extreme of this continuum, there are terrestrial and fossorial amphibians that present an intermediate feeding strategy in which contact with the soil and active search for prey are the factors favoring the infection with nematodes.

Monoxenous life cycles of nematodes dominate in amphibians of the two ecoregions, and 74.5% of the taxa present this type of life cycle. Cosmocercidae is the family with the highest species richness; also, all amphibian families were parasitized by at least one cosmocercid species. *Cosmocerca podicipinus* was the species with the widest host distribution and *Aplectana hylambatis* was found in 7 of the 12 sampled localities. Considering that soil moisture is essential for the development of nematodes because they require a film of water to move through the soil [120], it could be expected that in the DC, with high temperatures during the summer and rains confined to a few months, monoxenous nematodes would not be found in such a high proportion. However, in Ingeniero Juárez and Taco Pozo, two of the most arid localities of all those sampled, the presence of these nematodes was the one that prevailed.

In addition, there is a considerable proportion of taxa whose life cycles employ more than one host, connected with each other by trophic relationships. Although amphibians are not obligatory hosts in these life cycles, their importance is not minor. They favor dispersal and can preserve parasites from unfavorable conditions, contributing to their temporal and spatial distribution [120]. Due to their life-history, amphibians link aquatic and terrestrial food webs, acting as predators and prey. They are an important prey for many vertebrates and some invertebrates because they lack hard tissues difficult to digest, such as beaks, hair or feathers [169,170]. They are predators of a wide range of typically small organisms [170]. The incorporation of parasites in the study of food webs will increase our appreciation of their role in ecosystems, promoting a better understanding, evaluation and mitigation of human impacts on ecosystems, including biodiversity loss [171–173]. Yet, in both ecoregions, the studies of parasites in amphibians were scarce in disturbed ecosystems [39,45,46]. Such studies will contribute to understand the role of landscape disturbance in the mode of transmission of parasites, which may increase or decrease parasitism [156,174,175].

For more than a century, the Gran Chaco has been subject to the degradation and loss of its natural heritage due to the unplanned extraction of its natural resources [57]. As a host group, amphibians have been the subject of numerous studies to determine priority areas for conservation to deal the loss of their diversity due to the development of different human activities [60,61,176]. If the amphibian and reptile hosts are threatened, their parasites are co-threatened as well [177]. The specificity of the parasites and the vulnerability of the hosts combined may even pose a significant risk of coextinction of helminths in anurans [178]. Knowing the geographic distributions and the species they parasitize is the empirical basis that can help to inform future investigations, aiding in completing the inventory of world parasitic diversity [3].

Supplementary Materials: The following are available online at <https://www.mdpi.com/article/10.3390/d13070321/s1>, Table S1: Nematode parasites found in amphibians of DC and HC; Table S2: Biological variables of amphibian hosts from DC and HC.

Author Contributions: Conceptualization, C.E.G. and M.I.H.; methodology, C.E.G., M.I.H. and M.I.D.; software, M.I.D. and C.E.G.; formal analysis, C.E.G. and M.I.H.; investigation, C.E.G., M.I.H. and M.I.D.; resources, C.E.G. and M.I.H.; data curation, C.E.G.; writing—original draft preparation, C.E.G.; writing—review and editing, C.E.G., M.I.H. and M.I.D.; visualization, C.E.G. and M.I.H. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: Data sharing not applicable to this article.

Acknowledgments: The authors would like to thank to Félix Ignacio Contreras for his help in elaboration of the maps. Special thanks to Ulrich Sinsch and anonymous reviewers for their invaluable comments and suggestions that improved the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

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