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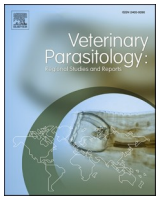

Original Article

Exploring gastrointestinal helminth infections in Amazonian non-human primates

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ABSTRACT

Although gastrointestinal helminths have a high prevalence in non-human primates (NHPs), there is still a large lack of knowledge about their interactions with climate-driven seasonal patterns, particularly in tropical rainforests. Using gastrointestinal dissections from 11 free-ranging NHP species ($N = 190$ individuals) donated by indigenous subsistence hunters, we investigated gastrointestinal helminth infections in two areas in the northeastern Peruvian Amazon. Helminth richness included seven nematodes, two cestodes, and one acanthocephala. Parasites were detected in 85.3% of NHPs, with the most common helminth taxa identified being *Physaloptera dilatata*, *Trypanoxyuris* sp., *Strongyloides cebus*, *Molineus torulosus* and *Prosthenorchis elegans*. We obtained data on helminth occurrence, diversity, and location within the gastrointestinal tract and parasite-induced histopathological lesions. Significant differences in parasitic indicators in relation to seasonal variations in climate, particularly temperature and water levels. These findings provide valuable insights into the helminth infection dynamics of free-ranging primates in the Amazon, highlighting key parasite-host relationships and their pathological impacts. This study contributes to our understanding of primate health and parasite ecology in a highly biodiverse region and provides valuable information for understanding the potential consequences of global warming on the transmission of parasitic infections.

1. Introduction

Helminth parasites are common in non-human primates (NHP) inhabiting tropical environments, where natural and anthropogenic factors affect host-parasite dynamics in free-ranging populations (Gillespie et al., 2005; Gillespie and Chapman, 2006; Obanda et al., 2019). Among these, nematodes, cestodes, trematodes, and acanthocephalans, often have complex life cycles and diverse transmission routes that are intricately linked to ecosystem characteristics and climate (Corrêa et al., 2016; Moravec et al., 2009).

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The impact of helminths on primate health can vary widely, depending on the intensity of infection and the parasite species involved. Heavy parasite loads can lead to gastrointestinal disorders, malnutrition, anemia, and impaired growth, particularly in young or immunocompromised individuals (Stoner et al., 2005). Infected NHPs may also exhibit behavioral changes, such as reduced activity levels or altered foraging patterns, which can have cascading effects on their fitness and reproductive success (Rodríguez Diego et al., 2014).

Parasites impose continuous costs on the host, resulting in ongoing adaptations and counter-adaptations between host and parasite at physiological and ecological levels (Dybdahl and Srofer, 2003; Ebert and Fields, 2020; Gandon et al., 2008). Humidity, rainfall and temperature may affect parasite survival, development, transmission, and the abundance of intermediate hosts (Paaijmans et al., 2013; Wagner et al., 2023). Thus, changes in the ecosystem and climate may affect this host-parasite relationship. These factors also affect host behavior and immune function, altering infection susceptibility (Rodríguez Diego et al., 2014), and other ecological covariates such as fruit availability (Conga et al., 2022; Klein, 2004; Medeiros and Py-Daniel, 2004). For example, increased fruit production during wetter periods may lead to aggregation of primates around key feeding sites, facilitating parasite transmission, while drier seasons might reduce environmental parasite stages. Or, periods of fruit scarcity, driven by climate variables, may lead primates to lose condition (Dew, 2005; Stevenson et al., 2000) and to increase parasite loads (Muehlenbein, 2006; Webster-Marketon and Glaser, 2008).

Understanding how seasonal climate patterns interact with ecological factors is key to interpreting parasitism patterns in wild populations. However, research on helminth parasites in wild primates and their interactions with climate-driven seasonal patterns, particularly in tropical rainforests, remains limited. In the Amazon, a region of unparalleled biodiversity, there is a significant gap in our understanding of the complex interactions between primates, their parasites, and the environment. Addressing this knowledge deficit is essential for identifying the factors driving helminth infections and their broader impacts. Expanding research efforts in this area would fill important gaps in NHP health and ecological studies and support conservation initiatives to ensure the long-term sustainability of these iconic species and their fragile ecosystems.

In this paper, we describe: 1) infection metrics (prevalence, intensity, and species richness) of helminths within the gastrointestinal tracts in 190 individuals belonging to 11 free-ranging Amazonian NHP species, 2) patterns of helminth distribution across digestive organs, 3) associated parasite-induced lesions and host tissue responses, as well as 4) the relationship between seasonality and infection prevalence. This study provides unprecedented insights into the ecology of helminth parasites in Amazonian NHPs, addressing a critical gap in our understanding of host-parasite interactions.

2. Material and methods

2.1. Study area

The study was conducted in two ecologically distinct locations ~510 km apart, within the Loreto region in the northeastern Peruvian Amazon:

A. Yavari-Mirin River Basin (YMR): This remote area, located on the border between Peru and Brazil, is characterized by well-conserved upland *terra firme* forests interspersed by permanently waterlogged *aguaje* (*Mauritia flexuosa*) palm tree swamps. The site has minimal human disturbance. The rivers are flanked by floodplains dominated by white-water *várzea* forests, which are flooded with silt-laden waters during the rainy season between December and April each year, extending inland up to 2 km. Fruit availability varies seasonally, with periods of relative scarcity during the dry months between July and August, when many primate species depend on a few abundant palm species, principally *Mauritia flexuosa* (Conga et al., 2022).
B. Interfluvial area between the Pastaza and Corrientes River Basins (PCRB): This site has been subjected to oil extraction since the early 1970s, following allocation of Oil Block 192 (formerly Block 1AB), which spans 512,347 ha across the Tigre, Corrientes, and Pastaza River basins. Over four decades, up to one million barrels per day of *produced water*—a toxic mix of formation water, chemicals, hydrocarbons, heavy metals, and potentially radioactive materials—have been discharged into land and surface waters (Orta-Martínez et al., 2018). This extensive pollution has severely impacted soils, water quality, and wildlife (Mayor et al., 2024; Rosell-Melé et al., 2018; Yusta-García et al., 2017). In response, the Peruvian government declared an environmental and health emergency in the area in 2013 and 2014 (Ministerio del Ambiente, 2013a, 2013b; Ministerio de Salud, 2014). In the PCRB, river levels rise during the rainy season between April and August, and reach their lowest levels during the dry season between December and January.

The study sites encompass the ancestral territories of the Achuar, Kichwa and Yagua Indigenous Peoples. Resident communities traditionally engage in small-scale farming, fishing, logging, and subsistence hunting (Mayor et al., 2015). Travelling beyond their villages is rare, reflecting these communities' remote, self-sustaining nature. The region's climate is typically equatorial, with annual temperatures ranging from 22 to 36 °C, relative humidity levels of 80–100%, and annual rainfall of 1500–3000 mm.

2.2. Data collection

From 2009 to 2015, local subsistence hunters collected the entire gastrointestinal tracts of 190 individuals across 11 species of wild NHPs for analysis as part of a community-based wildlife management program. We sampled a total of 190 NHPs of 11 species. Local hunters were previously trained to collect and preserve organs in 4% buffered formaldehyde solution (*v*/v), and to document the species, sex, date, and location of each animal. Sampling occurred year-round, with only organs unaffected by lead-based ammunition analyzed. Hunters donated an average of 3.7 ± 2.7 NHP individuals per month. The hunters and their families consumed all animals.

2.3. Sample analysis

Gastrointestinal organs were dissected under a stereoscopic microscope to search for helminth parasites. Distilled water was used to wash the helminths found in the esophagus, stomach, small intestine and large intestine (colon and cecum), and they were subsequently preserved in 70% ethanol. The nematodes were clarified with 20% Amman's lactophenol, while acanthocephalans and cestodes were stained with alcoholic hydrochloric acid-carmine for taxonomic identification following Amato and Amato (2010). Selected helminths were prepared for scanning electron microscopy. For coproparasitological examinations, spontaneous sedimentation technique (Conga et al., 2013) was employed from feces collected directly from the rectum of the dead primate during dissection. We identified the parasites based on established morphological criteria (Anderson et al., 2009; Corrêa et al., 2016). Due to the possibility of co-infections by multiple species of the genus *Trypanoxyuris* in neotropical primates, individual species were not determined and, instead, we used the genus for practical analyses.

2.4. Parasite infection metrics

To assess helminth infections in NHPs we used the following two main metrics:

Prevalence: The proportion of hosts infected with one or more

individuals of a particular parasite species, expressed as a percentage. It is calculated as: (Number of infected hosts / Total number of hosts examined) × 100.

Parasitic Load: The total number of individuals of a specific parasite species in a single host.

Parasitic Mean Abundance (PMA): The total number of individuals of a specific parasite species in a host sample divided by the total number of hosts examined (including both infected and uninfected individuals).

Parasitic Mean Intensity (PMI): The total number of parasites of a specific species found in a sample divided by the number of infected hosts with that parasite.

Total Parasites (TNP): The total number of parasites identified per host species.

2.5. Climatic variables

Climatic variables were available only for YMR. River water level (m. a.s.l.), month-year average temperature (°C), rainfall (mm), and number of annual rainy days were obtained from daily records taken at the Yavari River Hydrological Station (~50 km from YMR) of the Brazilian National Water Agency (HidroWeb, Estirão do Repouso Station, http://www.snirh.gov.br/hidroweb/). The hydrological station calculates the monthly average of the climatic variables included in the study. All epidemiological outcomes in the sampled NHPs were associated with climatic variables by month and year of hunting.

The climate in YMR exhibits distinct seasonal variations throughout the year. Rainfall peaks during the wet season, from December to April, with monthly averages exceeding 250 mm, while the dry season, from June to August, experiences significantly lower rainfall, often below 200 mm. Temperature remains relatively stable, with monthly averages ranging from 25.7 °C to 26.7 °C, though minor seasonal fluctuations are observed. Water levels in YMR closely mirror rainfall patterns, rising sharply during the wet season and reaching their lowest levels during the dry months.

2.6. Statistical methods

We used Generalized Linear Mixed Models (GLMMs) to evaluate the differences among hosts and the effects of climatic predictors on parasite prevalence and load (number of parasites) in NHPs from YMR. The analysis was confined to the YMR because climatic variables were available only for this region.

We developed a model framework to account for variation across host species, incorporating climatic predictors as fixed effects. To control host-specific variability not addressed in this study, we included 'host species' as a random effect, accounting for unexplained variation within each species. The presence or absence of parasites (binary outcome) was modeled using binomial GLMMs with the lme4 package. Parasite load was analyzed using zero-inflated Poisson GLMMs to account for an excess of zero values in parasite load data, using the glmmTMB package.

Variance Inflation Factor (VIF) analysis was performed to identify and exclude highly collinear predictors. Among the variables analyzed ('rainfall,' 'number of annual rainy days,' and 'water elevation'), only 'water elevation' was retained for the final models, as it served as a proxy for rainfall and the extent of inundated foraging areas. Model optimization involved testing combinations of two environmental predictors, with interaction terms included. The models were optimized using the bobyqa algorithm with extended iterations (maxfun = 100,000) to ensure convergence and stability.

An Information-Theoretic approach was employed for model selection and inference, using Akaike's Information Criterion corrected for small sample sizes (AICc). Models with ΔAICc <2 were selected for averaging, which was performed using the MuMIn package to incorporate model uncertainty into parameter estimates. However, due to this criterion, only one model was selected per parasite species for the parasite load analysis. Predictor importance was determined by summing the Akaike weights (w_i) of the models in which each predictor appeared and normalizing these values so that the total importance across all predictors summed to 1. Odds ratios (ORs) for binomial models (prevalence) and incidence rate ratios (IRRs) for Poisson models (parasite load) were calculated by exponentiating the model-averaged coefficients.

Continuous predictors such as temperature and water elevation were scaled to a 0–1 range to enhance comparability. Water elevation was further divided by 100 to reflect its relationship to rainfall and inundated foraging areas, allowing for more straightforward interpretation of ORs and IRRs. Descriptive statistics included parasite prevalence, defined as the mean proportion of infected hosts, and parasite load, represented as the mean and standard deviation of parasite counts in infected hosts.

All statistical analyses were conducted in R Studio (R Studio Team, 2021). Generalized Linear Mixed Models (GLMMs) were built using the lme4 and glmmTMB packages. Model selection and averaging were performed using the MuMIn package. Overdispersion was addressed by incorporating appropriate distribution families (e.g., binomial, Poisson with zero-inflation). The PCRB site was used only to describe parasite metrics and was not included in any statistical analyses.

3. Results

We collected the gastrointestinal tract of 190 individuals from 11 species NHPs: Poeppig's woolly monkey (*Lagothrix lagothricha poeppigii,* $N = 88$), large-headed capuchin (*Sapajus macrocephalus,* $N = 42$), monk saki (*Pithecia monachus,* in YMR, $N = 13$, and *P. napensis* in PCRB, $N = 4$), Ucayali bald uakari (*Cacajao ucayalii,* $N = 11$), red howler monkey (*Alouatta seniculus,* $N = 10$), white-fronted capuchin (*Cebus unicolor,* $N = 10$), Peruvian black spider monkey (*Ateles chamek,* $N = 3$), coppery titi monkey (*Plecturocebus cupreus,* $N = 3$), common squirrel monkey (*Saimiri macrodon,* $N = 5$), and brown-mantled tamarin (*Leontocebus nigrifrons,* $N = 1$).

3.1. Morphological characterization of helminths

Detailed morphological descriptions of the helminths provided taxonomic clarity and highlighted species-specific adaptations. *Physaloptera dilatata* were distinguished by a head collar, triangular teeth, and cephalic papillae (Fig. 1). They also showed two pairs of cephalic papillae, two amphids, and a pair of deirids located posterior to the nerve ring. The esophagus displayed a muscular anterior portion and a glandular posterior portion. Females exhibited pointed tails, while males had caudal wings and cloacal papillae.

Molineus torulosus displayed distinct features, including a discrete cephalic vesicle, a simple mouth, a claviform esophagus, an equatorial vulva, synlophe present with numerous cuticular lateral ridges, and a copulatory pouch and winged spicules in males (Fig. 2). *Prosthenorchis elegans* were identified by six oblique rows with six hooks each at the anterior end, and a collarette between the proboscis and body (Fig. 3).

Trypanoxyuris sp. were identified as fine and whitish nematodes (Fig. 4), presenting a simple mouth with lips, cephalic vesicles, esophagus with pre-bulbar dilation and bulb. Males showed a caudal wing, cloacal papillae, and caudal spine, and females presented a vulvar opening in the anterior third with a densely gravid uterus.

Graphidioides berlai was a medium sized nematode characterized by a simple mouth with lips cephalic vesicles, a claviform esophagus with pre-bulbar dilation and bulb, synlophe present, spiniform deirids. Males had a caudal wing, cloacal papillae, a spicule long without a gubernaculum, and females exhibited a muscular ovejector and a vulvar opening in the anterior third with a densely gravid uterus (Fig. 5).

Spirura delicata exhibited transverse cuticular striae, an oral opening with two bifid pointed projections, two amphids, four cephalic papillae, a muscular and glandular esophagus, a ventral protuberance in the

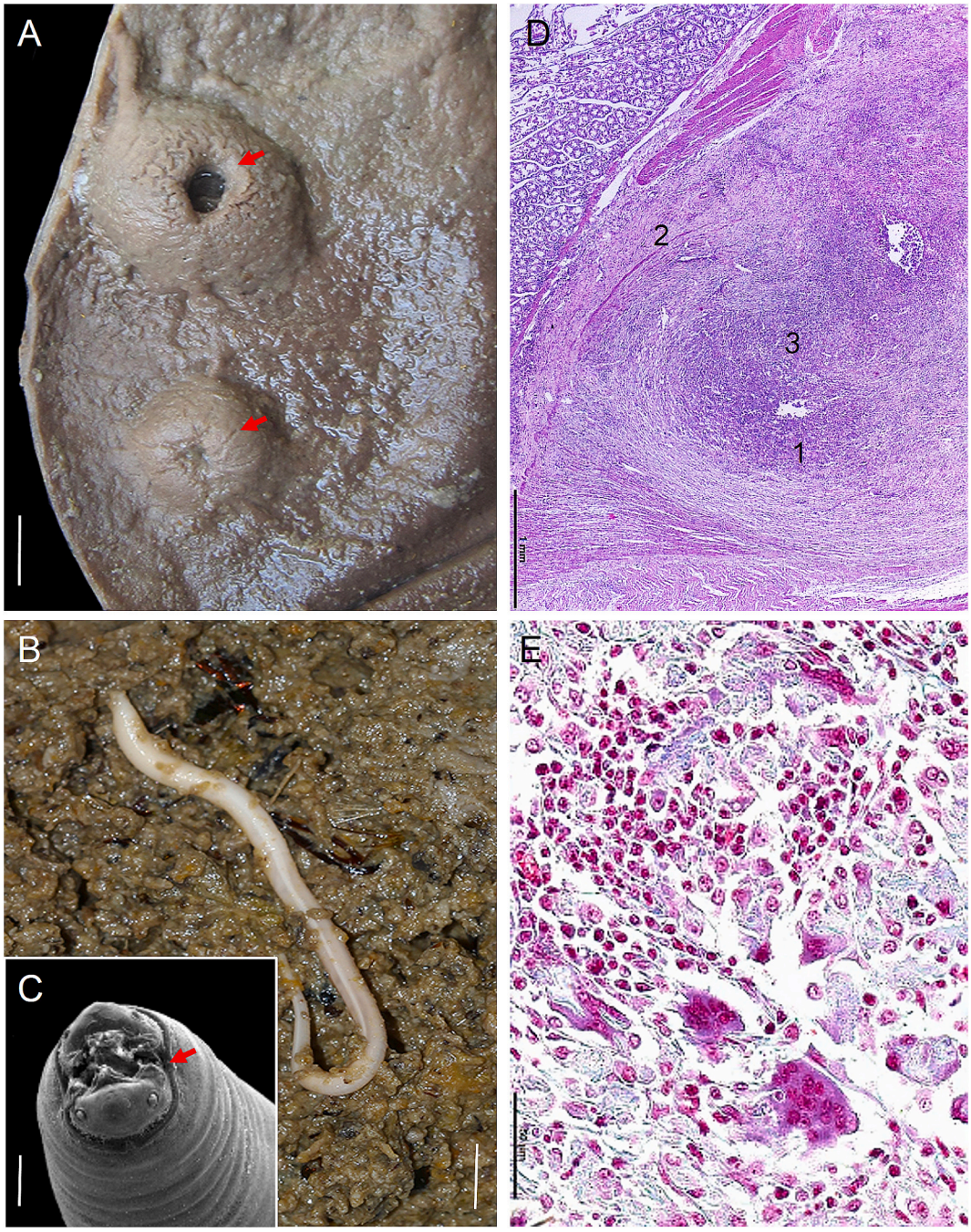

Fig. 1. Macroscopic and microscopic lesions caused by *Physaloptera dilatata* in the stomach of *Lagothrix* l. *poeppigii.* A) Formation of nodules with a crateriform lesion and an umbilicated appearance (arrows) in the gastric wall, bar = 0.5 cm. B) Adult specimen within the stomach contents, bar = 0.5 cm. C) Anterior end of an adult specimen, showing lips and teeth (arrow), scanning electron microscopy, bar = 200 μm. D) Nodular lesion with (1) fibrotic reparative reaction in Gomori Trichrome, (2) erosion of muscle segments, and (3) presence of collections of polymorphonuclear cells, including neutrophils and eosinophils, and chronic-active pattern in central areas. Hematoxylin and Eosin, bar = 1 mm. E) Granulomatous reaction and presence of giant cells. Hematoxylin and Eosin, bar = 50 μm.

anterior third, a vulvar opening in the posterior third in females, and caudal wings with papillae in males. *Strongyloides cebus* had a thin cuticle, a simple oral opening, and a vulvar opening in the posterior third of the uterus containing thin-shelled larvated eggs (Fig. 5).

Cestodes, such as *Bertiella mucronata*, were identified by their broad proglottids, irregular genital pores, a genital atrium located in the middle of the lateral proglottid margin, and a single set of reproductive organs in each proglottid and a pyriform apparatus in their eggs. The small, thick-walled cirrus sac contained an internal seminal vesicle, and the cirrus was unarmed. The testes formed a broad band in the dorsal anterior portion of the proglottid, with a single uterus filled with eggs characterized by a pyriform apparatus (Fig. 6). We could not associate the presence of cestodes with any tissue damage.

In *Mathevotaenia megastoma*, fragments of proglottids from a small tapeworm were observed, featuring an unarmed scolex with oval suckers, a long neck, and mature proglottids that were wider than long. The genital pores were alternately arranged, and the testes were visible in a single intervascular field located posterior and lateral to the vitelline gland. The ovary, positioned in the medial portion of the proglottid, was bilobed, with the vitelline gland also medial, and the seminal receptacle was absent.

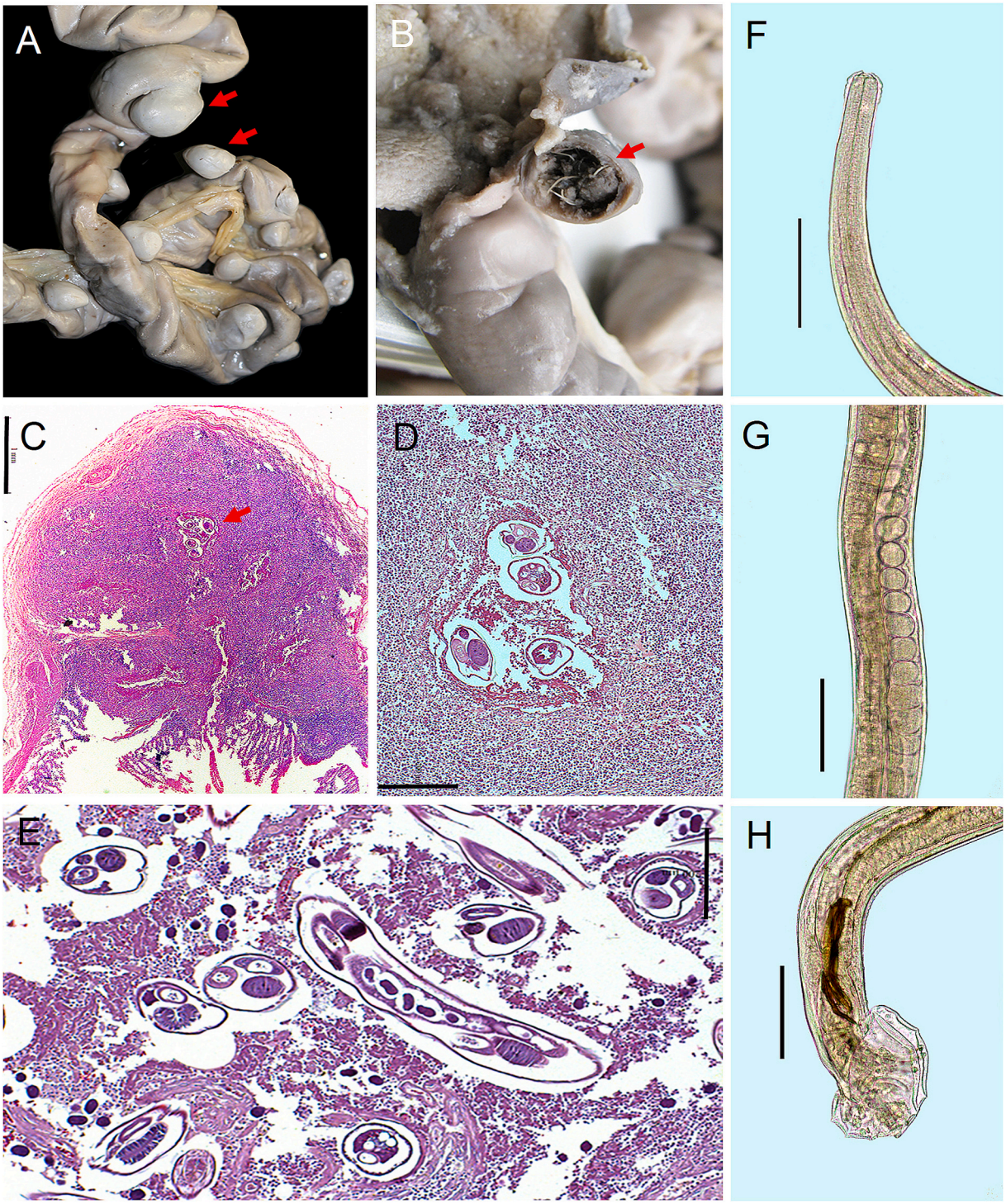

Fig. 2. Macroscopic and microscopic lesions caused by *Molineus torulosus* in the small intestine of *Sapajus macrocephalus.* A) The wall of the small intestine shows numerous nodules of different sizes (arrows). B) Transverse segment of a nodule with nematodes inside (arrow). C) Photomicrograph of nodulation with nematodes (arrow) surrounded by pyogenic exudate. Hematoxylin and Eosin, bar = 1 mm. D-E) Detail view of nematodes surrounded by pyogenic exudate in the small intestine. Hematoxylin and Eosin, bar = 200 μm. F) Anterior end of an adult specimen, bar = 100 μm. G) Uterus with eggs of a female specimen, bar = 100 μm. H) Posterior end of a male specimen, bar = 100 μm.

3.2. Distribution of helminths across digestive organs

The small intestine harbored most adult helminths, including *M. torulosus*, *G. berlai, S. cebus*, *Prosthenorchis elegans*, *Bertiella mucronata*, and *M. megastoma* (Figs. 1 and 4). This concentration highlights the small intestine as a critical site for helminth establishment and host-parasite interactions. Other helminths were found in other specific digestive organs, including *P. dilatata* in the stomach (Fig. 1), *S. delicata* in the esophagus (Fig. 5), and *Trypanoxyuris* in the large intestine (Fig. 4).

The observation of helminth eggs in fecal samples coincided with the presence of the respective adult specimens, including those of *Capillaria* sp. (60 μm long), *P. elegans* (59 μm long), *Trypanoxyuris* sp. (47 μm long), *P. dilatata* (45 μm long), *S. cebus* (41 μm long), and *B. mucronata* (38 μm

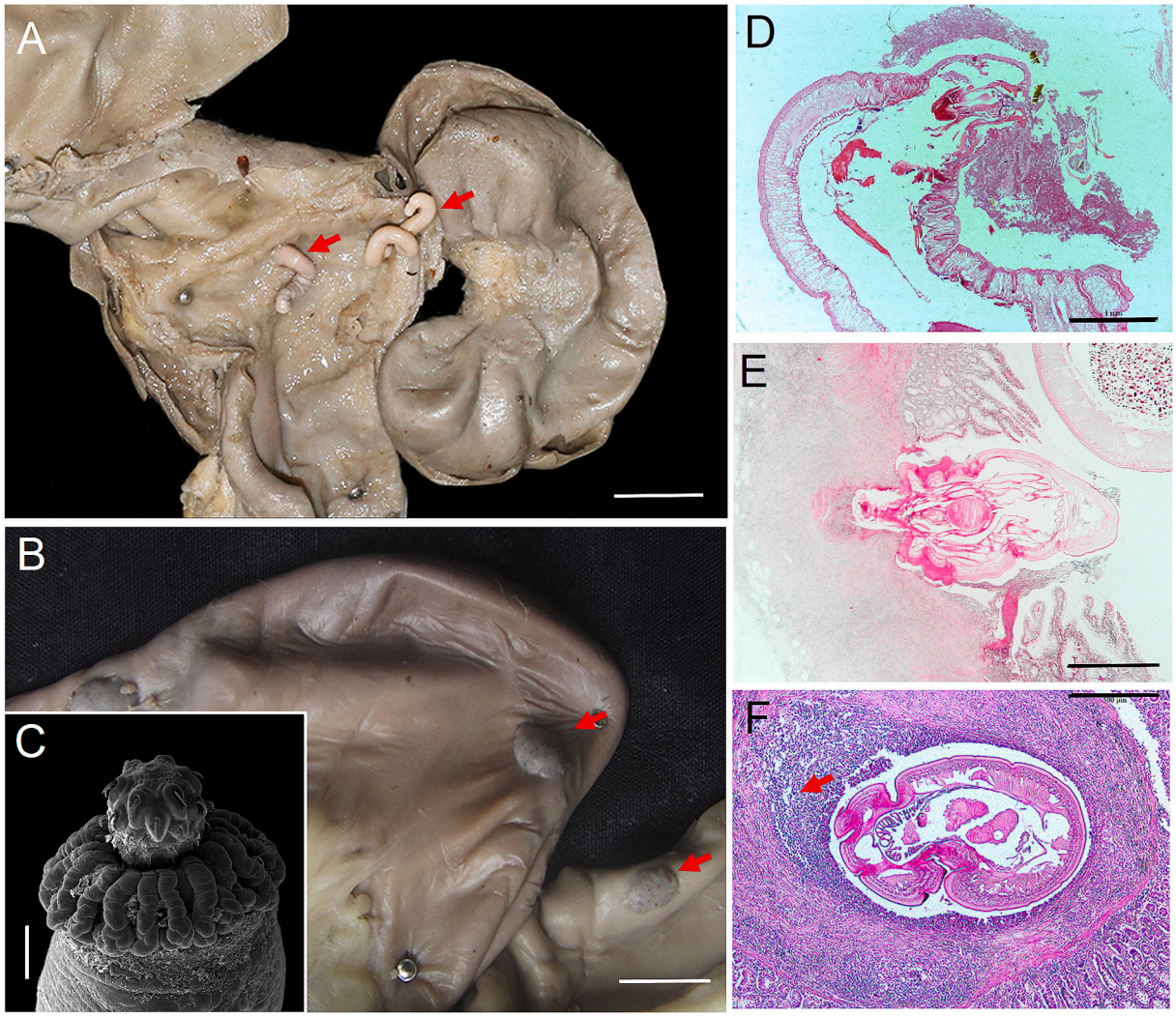

Fig. 3. Macroscopic and microscopic lesions caused by *Prosthenorchis elegans* in the small intestine of *Cebus unicolor*. A) Intestinal aperture showing several parasite specimens attached to the mucosa (arrows), bar = 1 cm. B) Nodules of different sizes (arrows) in the small intestine, bar = 1 cm. C) Anterior end of an adult specimen, showing hooks and proboscis. Scanning electron microscopy, bar = 200 μm. D-E) Detail of nodulation with adult specimens attached to the intestinal mucosa in pyogenic exudate. Hematoxylin and Eosin, bar = 1 mm. F) Detailed view of the parasite surrounded by pyogenic exudate (arrow). Hematoxylin and Eosin, bar = 100 μm.

long) (Fig. 6). The eggs of *Molineus* and *Graphidioides* were not observed. This reflects the broad diversity of helminths infecting NHPs and emphasizes the role of fecal examination in understanding parasitic burdens and transmission dynamics.

3.3. Macroscopic and microscopic lesions

Lesions were observed in all hosts infected with *P. dilatata, M. torulosus,* and/or *P. elegans.* We found no evidence of tissue alterations with the other helminth species observed.

Gastric lesions attributed to *P. dilatata* consisted of ulcerative mucosal damage ranging from 0.3 to 1 cm in diameter, with worms attached to the stomach lining (Fig. 1). Histologically, these lesions were characterized by chronic inflammation, including infiltration of polymorphonuclear cells such as neutrophils and eosinophils. Ulcerated areas, accompanied by oedema and inflammatory reactions, extended into the submucosa and superficial muscular layer. In addition, marked mechanical damage and associated inflammatory responses were consistent with the physical attachment of *P. dilatata*.

In the small intestine, nodules (0.2–0.6 cm in diameter) containing *M. torulosus* were distributed along its length, with the highest concentration in the duodenum and jejunum (Fig. 2). These nodules formed pseudocystic cavities connected to the intestinal lumen via thin channels. Microscopically, there were multiple foci of nodular lesions with a reaction involving the mucosa, submucosa, muscle, and adventitia. Fibroplasia and infiltration of lymphocytes and neutrophils were noted, along with a marked presence of macrophages associated with helminths, and signs of a focal, chronic-active reparative enteritis.

Prosthenorchis elegans caused nodulations measuring approximately 0.1–0.5 cm in the ileum near the ileocecal valve (Fig. 3). Microscopically, these nodulations were associated with chronic ulcerative enteritis, macrophage-rich infiltration with the presence of lymphocytes and plasma cells and, to a lesser extent, neutrophils, and fibroblastic activity in the lamina propria. Lesions and local immune activation are observed, with mechanical fixation of numerous *P. elegans*, with their six rows of hooks. In the mucosa and the lumen of the large intestine, including both the colon and the cecum, abundant *Trypanoxyuris* specimens were observed, but no inflammatory cells or tissue alterations were observed associated with the nematodes (Fig. 4A-D).

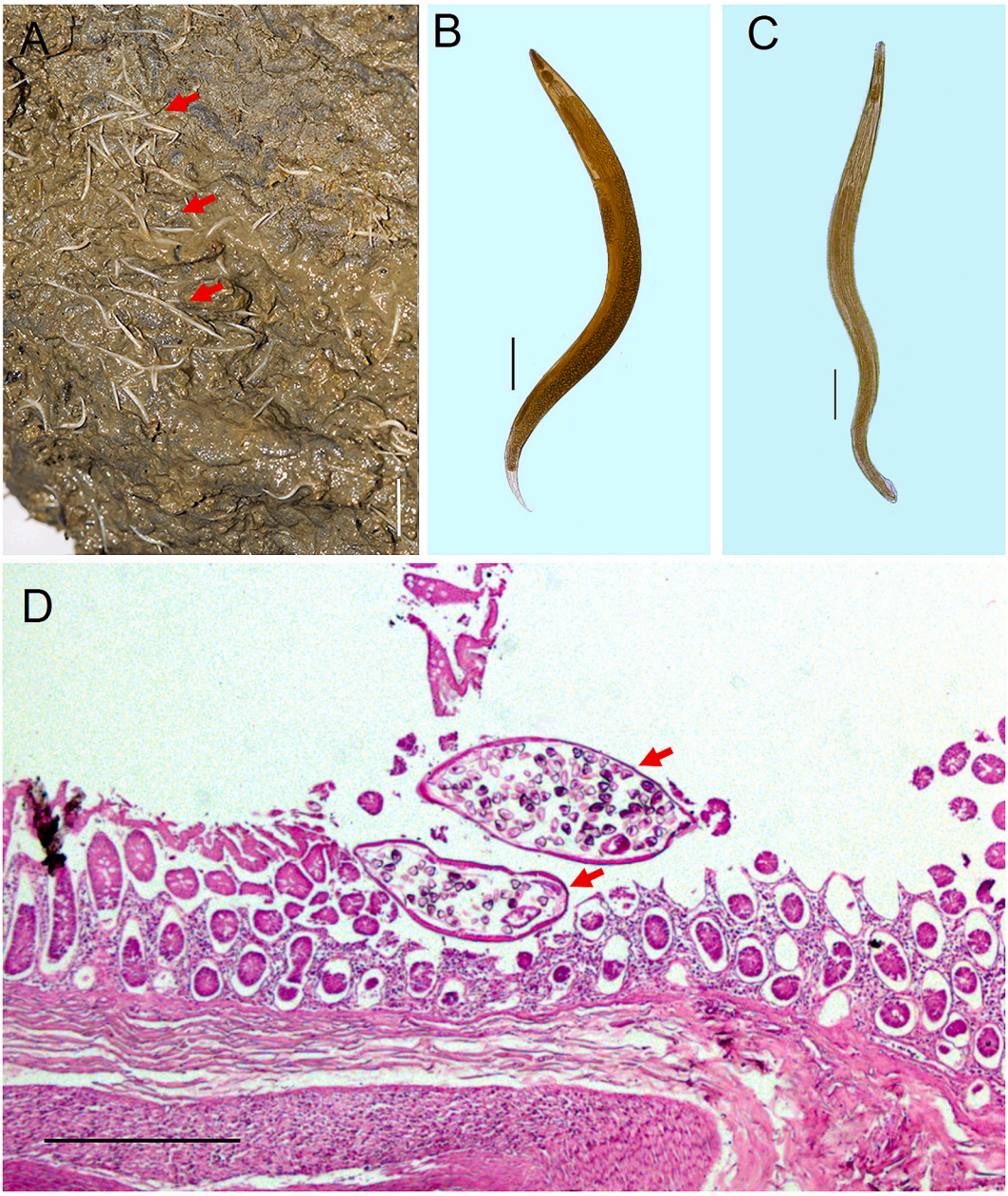

Fig. 4. Macroscopic and microscopic images of *Trypanoxyuris* sp. in the large intestine (colon and caecum) in the *Alouatta seniculus.* A) Numerous adult nematode specimens (arrows), bar = 0.5 cm. B) Female specimen, bar = 500 µm. C) Male specimen, bar = 200 µm. D) Female specimens (arrows) in the large intestinal lumen. Hematoxylin and Eosin, bar = 200 µm.

3.4. Parasite infection dynamics

A total of 10 helminth genera were recorded, including seven nematodes (*Trypanoxyuris* sp., *P. dilatata*, *M. torulosus*, *S. cebus*, *Capillaria* sp., *G. berlai*, *S. delicata*), two cestodes (*M. megastoma*, *B. mucronata*), and one acanthocephalan (*P. elegans*).

Considering both studied sites, 85% (162/190) of the NHPs were parasitized, with variations in the occurrence and distribution of helminth genera among host species and infection sites (Table 1, Suppl. Table 1 and Suppl. Table 2). General prevalence was 50% ($N = 16$) in the PCRB (Tables 2 and 3), and 88.5% ($N = 174$) in YMR (Tables 4 and 5). Overall, the most frequently encountered helminths were *Trypanoxyuris* sp. (59%), *P. dilatata* (58%), *M. torulosus* (44%), *S. cebus* (27%), and *P. elegans* (25%).

Among the host species in the YMR, *L. l. poeppigii* exhibited 96% of parasitized individuals and a wide diversity of helminth genera ($N = 9$), with notable infections by *Trypanoxyuris* sp. (91%) and *P. dilatata* (86%) (Table 4). Similarly, *C. ucayalii* showed a 100% prevalence with a diverse range of helminths (N = 8), including *Trypanoxyuris* sp. (82%) and *P. dilatata* (36%). In contrast, *P. cupreus* and *P. monachus* had a lower percentage of infected hosts (67% and 61.5%, respectively). Primates harbored a median of two helminth taxa, ranging from 0 to six helminth taxa per individual host. *Strongyloides cebus* infections were observed across multiple host species ($N = 8$), with the highest prevalence in *S. macrocephalus* (76%). *Capillaria* sp. and *M. megastomus* were infections that affected fewer hosts (four and one host species, respectively).

Tables 3 and 5 present PMI, PMA and TNP across the ten NHP species in both study sites. Due to the small sample size in the PCRB, we focused on parasitic indicators in YMR. Significant variation in parasite infection metrics was detected among host species and parasite genera in YMR. *Trypanoxyuris* sp. exhibited the highest PMI and PMA values across most primate species, with average PMI of 37.5 ± 88.3 parasites per infected

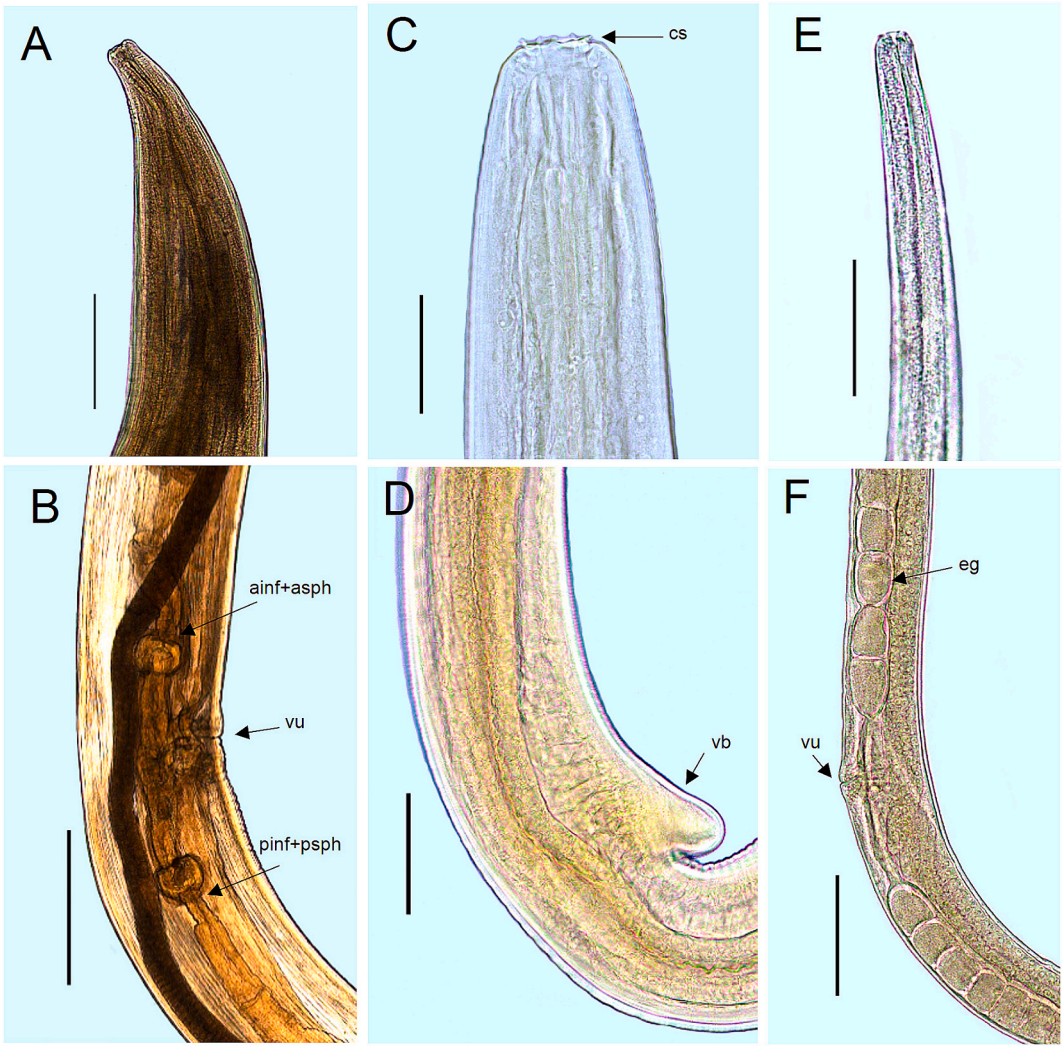

Fig. 5. Microscopic photographs of different helminths identified in NHPs in the northern Peruvian Amazon. A-B) Anterior end and ovejector (right lateral view) in the *Graphidioides berlai*, showing relationships for the vulva (vu), vestibules, and combined anterior infundibulum and sphincter (ainf + asph), and posterior infundibulum and sphincter (pinf + psph), bar = 500 μm. C-D) Anterior end showing cephalic structures (cs) and ventral boss (vb) of *Spirura delicata,* bar = 200 μm. *E*-F) Anterior end and vulvar region with uterine eggs in the *Strongyloides cebus,* bar = 100 μm.

host and a TNP of 6490 individuals.

Other helminth species, including *M. torulosus*, *P. elegans*, and *B. mucronata*, were less prevalent but contributed significantly to parasitism. Finally, rare helminths, such as *Capillaria* sp. and *M. megastoma*, had low prevalence and low parasite load, often in specific host species.

3.5. Influence of annual climatics

In the parasite prevalence models, water elevation showed marginal associations across taxa, although none of the effects reached statistical significance (Suppl. Table 3). Odds ratios were consistently close to 1.0, with confidence intervals narrowly including the null value. For instance, in *Capillaria* sp. and *B. mucronata*, water elevation yielded odds ratios of 1.01 (95% CIs: 0.96–1.06 and 0.98–1.04, respectively), suggesting a weak but possibly consistent association with elevated water levels. However, the wide uncertainty in all estimates and moderate relative importance values indicate that these associations should be interpreted cautiously. Temperature also showed no notable or borderline effects. Interaction terms between temperature and water elevation (T:WE) showed uniformly low relative importance (RI < 0.2) across models.

In the parasite load models, significant relationships were observed with climatic variables (Suppl. Table 4). Temperature was negatively (IRR < 1) associated with the abundance of *Trypanoxyuris* sp. (IRR $= 0.052$, $P < 0.001$) and *G. berlai* (IRR $= 0.003$, $P < 0.001$), suggesting lower infection intensity at higher temperatures. A minor effect of temperature was observed on *M. torulosus* and *Capillaria* sp.

Variations in water levels played a more variable role in affecting parasite load. Water elevation was positively associated with load of *P. elegans* (IRR $= 8.91$, $P = 0.012$) and *S. cebus* (IRR $= 4.23$, $P = 0.051$); contrary, the water level was negatively associated with *Trypanoxyuris* parasitic load (IRR $= 0.08$, $P < 0.001$). Finally, the interaction between temperature and water elevation (T:WE) revealed complex relationships that significantly increased the *Trypanoxyuris* parasitic load (IRR $= 415.43$, $P < 0.001$).

4. Discussion

A high diversity and frequency of helminths were observed in both study areas in the northern Peruvian Amazon, in the well-conserved forests of the YMR and in the forests of the PCBR, affected by decades by oil-extractive industry. While the greater diversity and prevalence of helminth species observed in the well-preserved YMR than in the oil-polluted interfluvial area suggest different biotic and abiotic

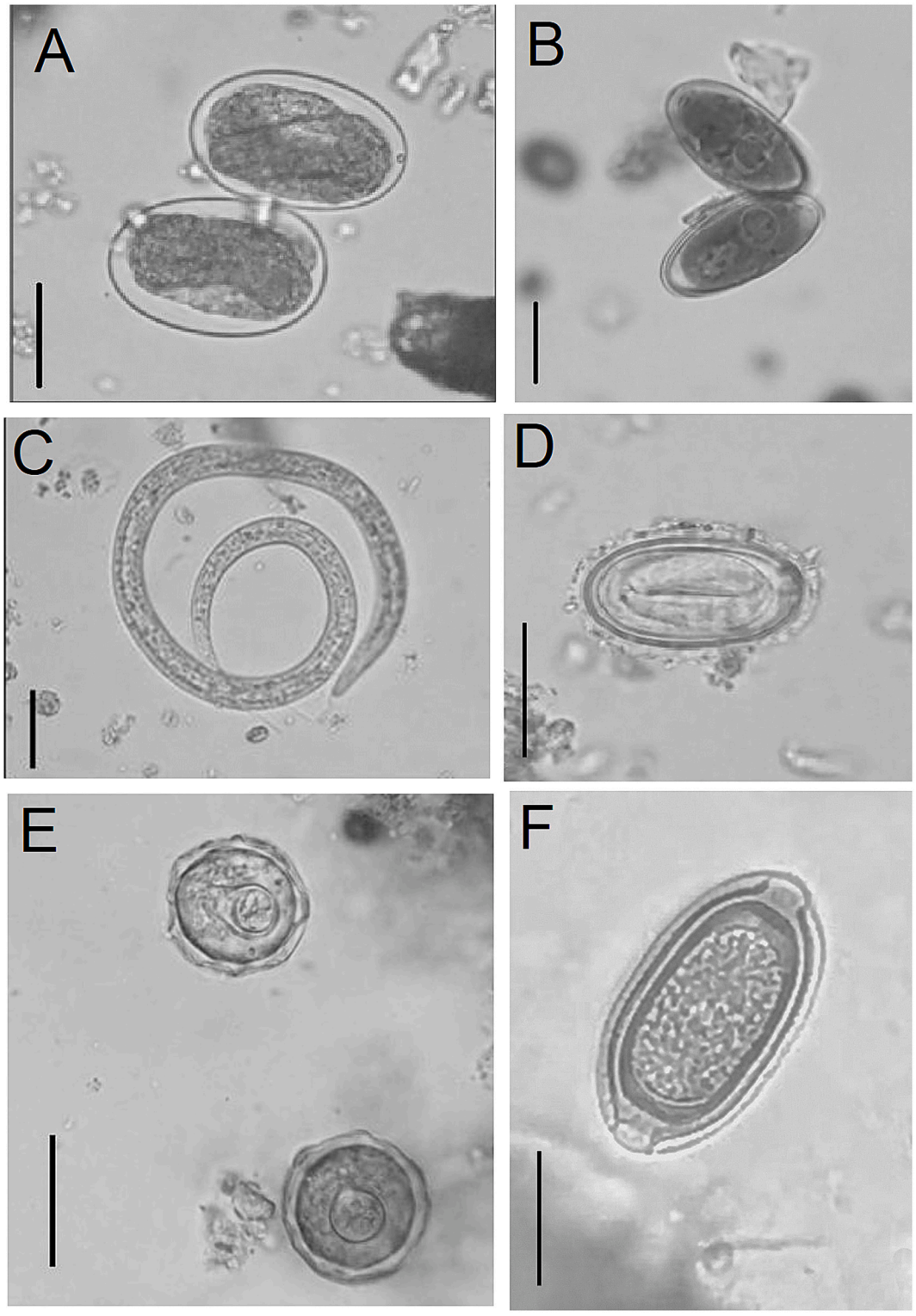

Fig. 6. Eggs of different helminth species identified in non-human primates from the Yavari-Mirin River basin in the northern Peruvian Amazon. A) *Strongyloides cebus*, bar = 20 µm. B) *Trypnoxyuris* sp., bar = 20 µm. C) *Strongyloides cebus* larva, bar = 20 µm. D) *Physaloptera dilatata*, bar = 20 µm. E) *Bertiella mucronata*, bar = 20 µm. F) *Capillaria* sp., bar = 20 µm.

conditions for parasitic organisms; the small sample size, especially in the oil-contaminated area, prevented a more comprehensive statistical analysis. As yet, comparable measures of parasite prevalence, intensity, and abundance across large samples of wild NHP species, have not been made at sufficient sites to allow us to examine spatial relationships or the effects of anthropogenic activity, but we were able to examine the seasonal dynamics of parasitic infections in divergent sites in western lowland Amazon.

4.1. Helminths and lesions

Mechanisms of NHP hosts injury caused by helminths examined here

Table 1
Adult helminth prevalence (%) in 190 free-living NHPs in the two study areas, in the interfluvial area between the Pastaza and the Corrientes River basins (PCRB) and in the Yavarí-Mirín River basin (YMR), in the northern Peruvian Amazon.

Prevalence	PCRB	YMR	Total
Species	N = 16	N = 174	N = 190
Nematoda			
Trypanoxyuris sp.	37.5	61	59
Physaloptera dilatata	15	61.5	58
Molineus torulosus	15	46	44
Strongyloides cebus	0	29	27
Capillaria sp.*	0	5	5
Graphidioides berlai	0	4	4
Spirura delicata	20	0	1
Cestoda			
Bertiella mucronata	0	8	7.5
Mathevotaenia megastoma	0	1	0.5
Acantocephala			
Prosthenorchis elegans	8	26	25
Total Helminths	50	88.5	85

* Only eggs in the coproparasitological examination.

include damage to mucosal surfaces and ulcers. We observed mucosal erosion and multifocal ulceration in the gastric wall. Histological sections of the stomach and intestine infected by *P. dilatata* and *P. elegans* revealed intense inflammatory infiltrates in gastric and intestinal mucosa. This suggests that these parasites promote deep chronic lesions, like those observed in *Callithrix geoffroyi*, *Leontopithecus chrysomelas*, *Callithrix kuhlii* and *Plecturocebus oenanthe* by *P. elegans* (Catenacci et al., 2016; López et al., 2021; de Oliveira et al., 2017).

Parasite infections are usually subclinical, and pathology, including lesions, is mainly observed in cases of high-intensity infections or hyperinfections with helminths in captive NHPs, where diarrhea, loss of appetite, enteritis, intestinal perforations, and peritonitis are observed (Pérez et al., 2008; Pissinatti et al., 2007). However, in natural infection conditions, parasitized NHPs are observed in apparently good health (Rondón et al., 2021). Therefore, the pathogenic potential of these helminths seems to be associated with captivity facilities and the environmental stress induced in these conditions (Zarate-Ramos et al., 2018).

4.2. Zoonotic helminths and primate conservation

The study highlights the presence of helminths with zoonotic potential such as *P. dilatata*, and *B. mucronata* that could represent health risks to humans. In Amazonian communities, the proximity between humans and primates increases the likelihood of transmission of parasites, as infective larvae in soil contaminated by *Strongyloides* or accidental ingestion of the arthropod vectors in the case of *Bertiella* and *Physaloptera*, previously reported (Errea et al., 2019; Furtado et al., 2012; Kishi et al., 2024; Lopes et al., 2015; Passamani-Ambrósio et al., 2022). These findings point out the urgent need for integrated approaches addressing wildlife conservation and public health. Monitoring parasitic infections in primates provides a dual opportunity for researchers: identifying potential zoonotic risks and utilizing parasites as bioindicators to evaluate ecosystem health.

4.3. Influence of climate

Helminths exhibit diverse responses to climatic variations, reflecting their distinct ecological strategies. Understanding these adaptations requires detailed knowledge of the life history of parasites and their definitive and intermediate hosts. Parasites with a direct life cycle require only one host to complete their development. Their transmission and survival depend primarily on environmental factors and population density, which facilitate contact between an infected and a healthy host. In contrast, Parasites with an indirect life cycle, which is much more complex, depend on the abundance of host species (intermediate and

Table 2
Prevalence (%) and number of infected individuals (in parentheses) in non-human primates (N = 16) in the interfluvial area between the Pastaza and Corrientes River Basins in the northern Peruvian Amazon.

Host species	n	Total	*Physaloptera dilatata*	*Trypanoxyuris* sp.	*Prosthenorchis elegans*	*Spirura delicata*
A. seniculus	1	100 (1)	0 (0)	100 (1)	0 (0)	0 (0)
L. l. poeppigii	7	57 (4)	27 (2)	57 (4)	14 (1)	0 (0)
P. napensis	4	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
S. macrocephalus	1	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
S. macrodon	3	100 (3)	0 (0)	33 (1)	0 (0)	68 (2)
Total	16	50 (8)	12.5 (2)	37.5 (6)	6 (1)	12.5 (2)

Table 3
Quantitative indicators (PMI: parasite mean intensity, PMA: parasite mean abundance, TNP: total number of parasites identified per host species) in non-human primates (N = 16) in the Interfluvial area between the Pastaza and Corrientes River Basins in the northern Peruvian Amazon.

Host species	N		*Physaloptera dilatata*	*Trypanoxyuris* sp.	*Prosthenorchis elegans*	*Spirura delicata*
A. seniculus	1	PMI		136		
		PMA		136		
		TNP		136		
L. l. poeppigii	7	PMI	9.00 ± 8.48	49.50 ± 25.01	11	
		PMA	3.60 ± 6.50	28.29 ± 31.83	2.20 ± 4.92	
		TNP	18	198	11	
P. napensis	4	PMI				
		PMA				
		TNP				
S. macrocephalus	1	PMI				
		PMA				
		TNP				
S. macrodon	3	PMI		73		2.50 ± 0.71
		PMA		18.2 ± 36.5		2.50 ± 0.71
		TNP		73		2
Total	16	PMI	9.00 ± 8.48	67.83 ± 39.73	11	2.50 ± 0.71
		PMA	1.13 ± 3.78	25.44 ± 40.95	0.69 ± 2.75	0.13 ± 0.34
		TNP	18	407	11	2

Table 4
Prevalence (%), and number of infected individuals (in parentheses) in non-human primates (N = 174) in the Yavari-Mirin River basin in the northern Peruvian Amazon.

Host species	N	Total	*Physaloptera dilatata*	*Trypanoxyuris* sp.	*Molineus torulosus*	*Strongyloides cebus*	*Prostenorchis elegans*	*Bertiella mucronata*	*Capillaria* sp.*	*Graphidioides berlai*	*Mathevotaenia megastoma*
A. chamek	3	100 (3)	33 (1)	100 (3)	100 (3)	33 (1)	0 (0)	33 (1)	33 (1)	100 (3)	0 (0)
A. seniculus	9	67 (6)	0 (0)	56 (5)	11 (1)	33 (3)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
C. unicolor	10	90 (9)	30 (3)	30 (3)	50 (5)	10 (1)	50 (5)	10 (1)	0 (0)	0 (0)	0 (0)
C. ucayalii	11	100 (11)	36 (4)	82 (9)	18 (2)	27 (3)	67 (7)	27 (3)	36 (4)	9 (1)	0 (0)
P. cupreus	3	67 (2)	0 (0)	67 (2)	0 (0)	0 (0)	33 (1)	0 (0)	0 (0)	0 (0)	0 (0)
L. l. poeppigii	81	96 (78)	86 (70)	91 (73)	46 (37)	42.5 (34)	22.5 (18)	5 (4)	4 (3)	1 (1)	1 (1)
P. monachus	13	61.5 (8)	38.5 (5)	23 (3)	8 (1)	8 (1)	8 (1)	8 (1)	8 (1)	8 (1)	0 (0)
S. macrocephalus	41	83 (34)	58.5 (24)	17 (7)	76 (31)	15 (6)	24 (10)	10 (4)	0 (0)	2 (1)	0 (0)
S. macrodon	2	100 (2)	0 (0)	0 (0)	0 (0)	50 (1)	100 (2)	0 (0)	0 (0)	0 (0)	0 (0)
L. nigrifrons	1	100 (1)	0 (0)	0 (0)	0 (0)	0 (0)	100 (1)	0 (0)	0 (0)	0 (0)	0 (0)
Total	174	88.5 (154)	61.5 (107)	60 (105)	41 (72)	29 (50)	26 (45)	8 (14)	5 (9)	4 (7)	1 (1)

* Only eggs in coproparasitological examination.

definitive), the food chain, and multiple environmental factors to survive, and these are more likely to be disrupted in a changing environment (Benesh et al., 2021, 2022). Nevertheless, intermediate hosts provide an adaptive advantage, enabling parasites to persist in otherwise unsuitable environments (Hoberg, 2010). The interplay among climate variability, food availability, and helminth transmission dynamics highlights the relationship between parasite ecology and environmental variability (Aleuy and Kutz, 2020; Short et al., 2017). These dynamics demand careful interpretation and consideration to avoid oversimplifying their broader ecological impacts.

Recent studies in wild NHPs indicated that climatic factors may have greater effects on parasitism than even host physiology (Conga et al., 2022; Martínez-Mota et al., 2017). Our study reports significant differences in the parasitic parameters of certain parasite species associated with seasonal climatic variations, in particular, an association was observed between the parasitic load and temperature and water levels, experienced by tropical forests throughout the year (Haugaasen and Peres, 2005). These observations have implications for the potential consequences of climate change on the transmission of parasitic infections. For the western Amazon basin, recent models predict warmer temperatures and an intensification of hydrological cycles, including increased intensity and duration of flooding during the rainy season, as well as lower water levels and less precipitation during the dry season (Boisier et al., 2015; Espinoza et al., 2011; Gloor et al., 2015). Under this scenario, most research suggests that increased temperatures and altered precipitation could favor or harm some helminth species or their intermediate hosts, to the detriment of others (Blum and Hotez, 2018). A moderate increase in temperature could temporarily lead to an initial increase in development rates and, consequently, in prevalence and parasitic load (Mangal et al., 2008; Okulewicz, 2017) and could also favor vector-borne transmission of helminths by expanding their distribution (Blum and Hotez, 2018). In its turn, heavy rainfall and increased river levels can exacerbate the spread of geohelminth infections by dispersing contaminated soil and potentially contaminating water sources (Brooker and Michael, 2000). However, the results obtained to date have been divergent, demonstrating the need for further studies to improve the understanding of the effect of climatic variables on parasitic diseases.

In general, the wide confidence intervals observed in the relationship between parasite indicators and climatic variables may be attributed to the multifactorial nature that affects parasitic cycles. This wide variability in the effects of the factors suggests that other factors not studied here may have a significant impact on prevalence and parasitic burden. However, these data provide a baseline for evaluating future changes in the ecosystem and offer valuable insights to guide conservation efforts and mitigate the impacts of environmental stressors.

The YMR site provides a critical benchmark for understanding how undisturbed ecosystems sustain primate health and regulate parasite-host dynamics. In the absence of significant human disturbance, ecological processes operate in a relatively stable manner, allowing natural patterns of infection, immunity, and parasite transmission to persist. This makes the site particularly valuable for distinguishing baseline conditions from those altered by anthropogenic pressures.

These insights are highly relevant for conservation. As deforestation, habitat fragmentation, and other human activities continue to disrupt ecological integrity, the balance between hosts and parasites is likely to shift, with potential consequences for primate health and disease emergence. Findings from YMR therefore offer an essential reference against which such changes can be measured and interpreted.

Building on this foundation, future research should prioritise the establishment of longitudinal studies to monitor parasite–host interactions over time, particularly in landscapes undergoing environmental change. In parallel, comparative analyses between undisturbed and disturbed sites would help clarify the mechanisms driving variation in parasite dynamics and health outcomes. Together, these approaches would strengthen our ability to predict and manage the impacts of

Table 5
Quantitative indicators (PMA: parasite mean abundance, PMI: parasite mean intensity, TNP: total number of parasites identified per species host) in non-human primates ($N = 174$) in the Yavari-Mirin River basin in the northern Peruvian Amazon.

Host species	N		*Physaloptera dilatata*	*Trypanoxyuris* sp.	*Molineus torulosus*	*Strongyloides cebus*	*Prostenorchis elegans*	*Bertiella mucronata*	*Capillaria* sp.	*Graphidioides berlai*	*Spirura delicata*	*Mathevotaenia megastoma*
A. chamek	3	PMA	0.3 ± 0.6	133.3 ± 77.0	2.3 ± 2.3	0.3 ± 0.6		1.7 ± 2.9	0.3 ± 0.6	18.3 ± 30.0		
		PMI	1.0	133.3 ± 77.0	2.3 ± 2.3	1.0		5.0	1.0	18.3 ± 30.0		
		TNP	1	400	7	1		5	1	55		
A. seniculus	9	PMA		118.9 ± 288.5	0.1 ± 0.3	0.6 ± 1.0						
		PMI		214.0 ± 375.5	1.00	1.7 ± 1.15						
		TNP		1070	1	5						
Cebus unicolor	10	PMA	0.4 ± 0.7	6.4 ± 17.2	3.8 ± 6.3	0.1 ± 0.3	1.7 ± 2.7	0.1 ± 0.3				
		PMI	1.3 ± 0.6	21.3 ± 29.2	7.6 ± 7.3	1.0	3.4 ± 3.05	1.0				
		TNP	4	64	38	1	17	1				
C. ucayalii	11	PMA	0.6 ± 1.2	71.6 ± 107.7	0.45 ± 1.2	0.9 ± 1.7	4.2 ± 9.6	0.3 ± 0.5	0.4 ± 0.5	0.45 ± 1.5		
		PMI	1.75 ± 1.5	87.6 ± 113.8	2.5 ± 2.1	3.3 ± 1.5	6.6 ± 11.7	1.0 ± 0.0	1.0 ± 0.0	5.00		
		TNP	7	788	5	10	46	3	4	5		
P. cupreus	3	PMA		13.0 ± 11.4			3.7 ± 6.35					
		PMI		19.5 ± 2.1			11.0					
		TNP		39			11					
L. l. poeppigii	81	PMA	2.4 ± 2.4	46.2 ± 63.8	1.9 ± 4.5	1.6 ± 4.6	0.4 ± 1.3	0.1 ± 0.8	0.0 ± 0.2	0.7 ± 6.4		0.0 ± 0.1
		PMI	2.8 ± 2.35	50.6 ± 65.1	4.1 ± 5.9	3.8 ± 6.5	1.7 ± 2.35	2.5 ± 3.0	1.0 ± 0.0	57.00		1.0
		TNP	195	3695	153	130	31	10	3	57		1
P. monachus	13	PMA	0.4 ± 0.5	11.85 ± 33.1	0.1 ± 0.3	0.1 ± 0.3	0.15 ± 0.55	0.1 ± 0.3		0.8 ± 2.8		
		PMI	1.0 ± 0.0	51.3 ± 59.5	1.0	1.0	2.0	1.0		10.00		
		TNP	5	154	1	1	2	1		10		
S. macrocephalus	41	PMA	2.7 ± 4.1	6.8 ± 31.7	5.0 ± 6.2	0.7 ± 3.2	0.4 ± 0.8	0.2 ± 0.6		0.0 ± 0.2		
		PMI	4.5 ± 4.5	40.0 ± 71.8	6.6 ± 6.4	4.8 ± 7.5	1.6 ± 1.0	1.75 ± 1.0		1.00		
		TNP	109	280	205	29	16	7		1		
S. macrodon	2	PMA				1.5 ± 2.1	2.5 ± 0.7					
		PMI				3.0	2.5 ± 0.7					
		TNP				3	5					
L. nigrifrons	1	PMA					7.0					
		PMI					7.0					
		TNP					7					
Total	174	PMI	1.8 ± 2.8	37.5 ± 88.3	2.4 ± 4.8	1.0 ± 3.6	0.8 ± 2.9	0.2 ± 0.7	0.05 ± 0.2	0.7 ± 5.95		0.0 ± 0.1
		PMA	3.0 ± 3.0	61.8 ± 106.6	5.1 ± 6.1	3.6 ± 5.9	3.0 ± 5.2	1.9 ± 1.9	1.0 ± 0.0	18.3 ± 25.3		1.0
		TNP	321	6490	410	180	135	27	8	128		1

increasing anthropogenic pressure on primate populations and the ecosystems they inhabit.

Continuing to work with hunter communities in tropical forests offers unparalleled insights into local ecosystems, wildlife behavior, and environmental changes (Mayor et al., 2024; Menajovsky et al., 2024). Their generational knowledge provides a detailed understanding of species distribution and health, complementing scientific methods. Collaborating with these communities also facilitates the collection of biological materials, such as tissue samples and parasites, essential for studying wildlife health and parasite-host dynamics; it could even be more complete if information on the health status of hunted animals were included. This partnership integrates traditional knowledge with science, enhancing ecological research and empowering communities to actively preserve their natural heritage, fostering sustainable and inclusive conservation strategies.

5. Conclusion

The presence, diversity, and prevalence of parasitic species reflect broader ecological dynamics, offering valuable insights into environmental stability, biodiversity, and habitat quality. By studying parasitic infections, researchers can assess how habitat degradation, climate change, and human encroachment influence host-parasite relationships and overall ecosystem resilience. This integrated approach highlights the dual role of helminth infections as indicators of ecosystem health and potential zoonotic threats. Monitoring parasitic infections in NHPs deepens our understanding of tropical ecosystems and aids in developing integrated strategies that safeguard biodiversity while addressing public health concerns. Strengthening research in such biodiverse regions is critical for mitigating the impacts of environmental changes and ensuring these ecosystems' long-term sustainability.

CRediT authorship contribution statement

David F. Conga: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Luis A. Gomez-Puerta:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation. **Julia E. Fa:** Writing – review & editing, Writing – original draft, Methodology. **Mark Bowler:** Writing – review & editing, Methodology. **Eva Casas Astos:** Writing – review & editing, Methodology, Investigation. **Carlos González-Crespo:** Writing – review & editing, Formal analysis. **Elane G. Giese:** Writing – review & editing, Methodology, Investigation. **Washington A. Pereira:** Writing – review & editing, Methodology, Investigation. **Richard E. Bodmer:** Writing – review & editing, Methodology. **Pedro Mayor:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Informed consent statement

Not applicable.

Ethics approval

The study was approved by the Peruvian Forest and Wildlife Service (Servicio Forestal y de Fauna Silvestre; Committee for Ethical Wildlife Research, protocol no. 108–2008-INRENA-IFFS-DCB, 0127-2010-AG-DGFFS-DGEFFS, 0229-2011-DGFFS-DGEFFS, 0350-2012-AG-DGFFS-DGEFFS, 0249-2013-MINAGRI-DGFFS/DGEFFS). No animals were killed specifically for our research, and hunters were not compensated for the sample collection. The biological samples were obtained as part of regular subsistence hunting activities conducted by the local communities.

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Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Pedro Mayor reports financial support was provided by Fundació Autònoma Solidària at the Universitat Autònoma de Barcelona, the Earthwatch Institute, Wildlife Conservation Society. David F. Conga reports financial support was provided by Programa de Pós-graduação em Saúde e Produção Animal na Amazônia (PPGSPAA-UFRA) and PNPD-CAPES, Brazil. J.E. Fa reports financial support was provided by USAID.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.vprsr.2026.101548.

Data availability

The data used to support the findings of this study are available in the CORA Repositori de Dades de Recerca Support (https://dataverse.csuc.cat/dataset.xhtml?persistentId=doi:10.34810/data2575).

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