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Seasonal and biological drivers of gastrointestinal parasites in wild rodents from two areas with different anthropogenic pressures in a semi-arid region

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Abstract

Background Environmental and biological factors can regulate host-parasite interactions. However, in the context of habitat alteration due to human-induced activities, little is known about its effects on parasite infections in wildlife populations. This study focused on the study of 363 wild rodents (*Phyllotis darwini* Waterhouse 1837) inhabiting two areas with different anthropogenic pressures (i.e., non-altered [protected] and altered [rural] area) in the Coquimbo Region, in Chile, during five consecutive seasons (2021–2022). Coprological examinations were carried out using the Mini-FLOTAC method, and factors associated with parasite infections (i.e., seasons, site types, sex, and body mass) were evaluated.

Results The overall prevalence of gastrointestinal parasitism was 74.9% (272/363), and 16 parasite taxa were found, some of which were reported for the first time in *P. darwini*, such as Archiacanthocephala, Ascaridina, Trichosomoididae, *Schistosoma* sp., *Iso spora* spp., *Giardia* sp., and Entamoebidae. The best predictors of parasitism included type of site, seasonality, and body condition. The infection probability and density (as eggs/oocysts per gram of feces) of some parasite taxa were lower in rodents inhabiting the rural area compared to those in the protected area, but no difference was observed in the gastrointestinal parasite richness according to the type of site. Seasonal effects were also observed, with a higher likelihood of parasite infection and greater parasite richness in winter and spring of 2022 in both protected and rural areas. Rodents with higher scaled body mass index showed higher likelihood of parasite infection and higher parasite richness in both kinds of areas. Sex-biased parasitism was not detected in adults.

Conclusions The results presented in this one-year study indicate that gastrointestinal parasites in *Phyllotis darwini* in north-central Chile are influenced by habitat alteration, seasonality, and body mass. Reduction of host populations due to anthropogenic effects may limit parasite transmission in altered sites. Non-native hosts may still introduce new

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species to the parasite fauna of *P. darwini* in the altered area. Seasonal patterns may be explained by favorable biotic and abiotic conditions during wetter winter, for both hosts and developmental parasitic stages, including time-lagged effects extended into spring. Finally, larger rodents may show higher exposure to parasite transmission.

Keywords Parasitism, Wildlife, Metazoan, Protozoa, Land-use change, Mammals, Chile, Parasite, Mini-FLOTAC, One health

Background

The dynamics of endoparasite infections involve a complex interplay of host and parasite factors that tend to be specific to the environmental setting [1]. In a context of accelerated environmental changes due to anthropogenic activities (e.g., agriculture, logging, urbanization); however, key ecological functions on ecosystems can be disrupted with subsequent effects on biodiversity across scales, including changes in host-parasite interactions [2].

Wildlife inhabiting these human-altered habitats is likely to exhibit variations in infection rates (e.g., prevalence, intensity, and richness) of gastrointestinal parasites, such as helminths and protozoa, as a consequence of various effects on hosts and the environment [3, 4]. For example, higher infection rates of directly (e.g., some nematodes, and protozoa) and indirectly (e.g., cestodes, trematodes) transmitted parasites in hosts inhabiting altered habitats are often associated with higher host densities and microhabitat alterations that support parasite development [5, 6]. Conversely, lower infection rates of some helminths and protozoa in animals living in degraded areas are commonly attributed to the reduction of density of host populations (i.e., definitive or intermediate) and unfavorable abiotic conditions for the viability of parasitic eggs/oocysts and larvae [7, 8].

In addition to environmental changes due to anthropogenic activities, seasonal variations in parasitic infection rates of are well known in wildlife [9, 10]. Specific temporal changes in infection patterns are related to fluctuations of biotic (e.g., food sources) and abiotic (e.g., temperature, rainfall) conditions that can affect both host physiology (e.g., immunity) and parasite development [11, 12]. Also, biological host traits such as sex and body condition are recognized as drivers of parasitic infections [5]. Males can exhibit higher parasite infection rates because of the effects of testosterone on behavior and immune responses, causing increased parasite exposure and susceptibility [13]. Likewise, individuals with larger body sizes can be more parasitized presumably because of the increased intra-habitat available for parasites to colonize [11, 14]. However, females and individuals with a low body condition can also show higher levels of parasitic infections, which are ascribed to the immunosuppressive effects of hormones and poor nutritional condition, respectively [11, 15].

Wild rodents are commonly used models for the study of host-parasite interactions and the impact of habitat

alteration [7, 8]. This is because rodents exhibit the ability to adapt to different kinds of environments, with short generation times and high population densities [16]. In addition, wild rodents are reservoirs and carriers of several infectious agents, some of which of public health significance, including helminths and protozoa [17–19].

The Mediterranean semi-arid region in north-central Chile is considered a global biodiversity hotspot because it has high floristic species richness and high levels of endemism [20–22]. However, over the last few decades, landscapes in the Chilean Mediterranean ecosystem have encountered pressures due to human-induced activities (e.g., agriculture, forestry, urbanization) and global climate change, which have compromised the ecological integrity of some areas, and affected their flora and fauna [23–25]. The Darwin's leaf-eared mouse (*Phyllotis darwini* Waterhouse 1837) (Family: Cricetidae) is a small rodent (adults: ~ 50 g) that inhabits semi-arid and Mediterranean-type ecosystems in north-central Chile [26]. It is a nocturnal, short-lived multiparous species with short gestations and a marked breeding season usually after the rainfall and flowering periods (i.e., July to December or January) [26–28]. It is a diet generalist that consists mainly of plants, seeds and insects [29]. Although a range of information on parasites of wild rodents (including *P. darwini*) is available in Chile [30], little is known about the seasonal and biological drivers of gastrointestinal parasites and the influence of habitat alteration on parasitic infections [31–33].

This study aimed to evaluate the effects of seasonal and biological factors on helminth and protozoa infections in the wild rodent model *P. darwini* inhabiting two areas with different anthropogenic pressures in the Mediterranean ecosystem in north-central Chile: (a) non-altered (protected) and (b) altered (rural) areas. It was expected to find a lower likelihood of infection of gastrointestinal parasites with direct and indirect life cycles and a lower parasite richness in rodents living in anthropogenically altered areas given the potential negative impacts on host populations (including both definitive and intermediate hosts), whereas individuals living in altered areas would show a higher parasite loads related to poor host conditions. Also, it was expected to find a higher likelihood of parasite infection and higher parasite richness in adult males as well as in individuals with larger body mass. Lastly, it was expected a higher likelihood of parasite infection and higher parasite richness during the winter

and spring seasons. Understanding the changes and patterns of the parasite infections in wild rodents inhabiting anthropogenically altered and natural landscapes will allow to determine potential impacts on wildlife conservation and public health.

Methods

Study sites

Two sites with different degrees of anthropogenic pressure (i.e., protected and rural areas) were studied in the Coquimbo Region, north-central Chile, during five consecutive seasons between spring 2021 and spring 2022 (Fig. 1a). The Coquimbo Region is characterized by a semiarid Mediterranean climate with an average annual temperature of 14.7 °C and a daily mean variation of 6 °C [34]. Autumn (March – June) and winter (June – September) are the coolest seasons, in which precipitation occurs sporadically (Fig. 1b2), whereas drought is usually observed during spring (September – November) and summer (December – March) [22, 34].

The protected (non-altered) area corresponds to semi-arid lowland within the Bosque Fray Jorge National Park (BFJNP: 9 959 ha; since 1941) which is characterized by xerophytic shrub vegetation (e.g., *Porlieria chilensis* Johnston 1938, *Adesmia bedwellii* Skottsb 1946) and represents a natural habitat for various wild small mammals [35–37] (Fig. 1b). The rural (altered) area corresponds to private farmland (El Tangué Farm/ETF: 45000 ha), in which several economic activities have historically altered the landscape, including sheep and goat production, agriculture, tourism, and more recently, real estate [38]. Plant communities in ETF consist of a mixture of agricultural plantations (e.g., winter wheat *Triticum aestivum* Linneo 1753) and native and exotic shrubs (e.g. *Atriplex nummularia* Linneo 1753) [37] (Fig. 1c). In the two types of sites (i.e., protected and rural areas) fluctuating population densities of *P. darwini* were previously reported over several years and seasons [27, 39, 40].

Four rectangular grids (150 × 135 m; 2 ha) were mounted and evaluated per site and season. In each grid, 200 capture points were spatially arranged according to the established methods [41–43]. The grids were formed using 10 parallel rows (150 m in length) with a separation distance of 15 m. In the rows, 110 capture points were evenly distributed at 15 m along each other. In addition, another capture point was placed at the center of each of the four capture points (i.e., 90 capture points). Grids were set up with a separation distance of >1 km in accordance with the home range of *P. darwini* (i.e., up to 1154 m²) to prevent individual recaptures between grids [44] (Fig. 1a).

Host capture and sampling

Rodents were captured using 200 Sherman-like traps (dimensions = 300 × 100 × 110 mm) placed at the capture points in each grid for 3–4 nights during the sampling seasons. The traps were left activated with bait (oat flakes and vanilla essence) from 19:00 to 7:00 (i.e., 12 h) and subsequently inspected in next morning (7:10–9:00). The captured rodents were processed under sedation (Ketamine 0,044 mg/g bodyweight + Xylazine 0,006 mg/g bodyweight; IM) with immediate induction and handling time of up to 10 min [45]. Once individuals were recovered with complete signs of consciousness (~20 min after sedation), they were released at the specific capture point. All captured individuals were identified using an ear tag (National Band & Tag Company®, New Port, RI, US), weighed (Pesamatic Newton Series®, Model EJ1500, A&D Weighing, San Jose, CA, USA; ±0.1 gr SD), and measured (e.g., body length, anogenital distance) using a digital caliper (Uberman®, precision 0.01 mm). Fresh fecal samples (between 0.01 and 1.2 g.) were collected by spontaneous defecation and/or from the material available in the previously disinfected trap base. Fecal pellets were stored in clean plastic vials with 1.5 ml ethanol (96%) at room temperature until further analysis, which was performed in a time no longer than two months after collection to minimize the effects of ethanol on parasite morphology.

Parasitological examination

Parasitic elements (e.g., helminth eggs and protozoan oocysts) in preserved feces (0.01–0.7 g.) were identified and counted by the Mini-FLOTAC method (Mini-FLOTAC®, University of Naples Federico II) using a saturated zinc sulfate solution (ZnSO₄·7H₂O; FS7; specific gravity = 1.35) [46]. Each sample was inspected for helminth eggs and protozoan oocysts in both chambers using a compound microscope (Carl Zeiss 183858 Axio-star, Fisher Scientific, Schwerte DE 58239 Germany) with a digital camera (Axiocam ERc 5s, Carl Zeiss Microscopy, Göttingen 37081, Germany). A drop of Lugol's iodine solution was added to assist in parasite identification when needed. Helminth eggs and protozoan cysts/oocysts were identified to the lowest possible taxonomic level using morphological keys (Electronic Supplemental Material ESM 1: Table S1). Subsequently, between 1 and 10 representative parasitic elements related to each morphotype in all positive samples were digitally measured (length and width; µm) and photographed (Zen 3.2 Blue Edition, ZEISS Group, München 81379, Germany). Finally, parasite morphotypes were counted in the positive samples, and egg per gram (EPG) and oocyst per gram of feces (OPG) were determined by calculating the dilution and multiplication factor, as described [47]. In this sense, the dilution factor was calculated by dividing

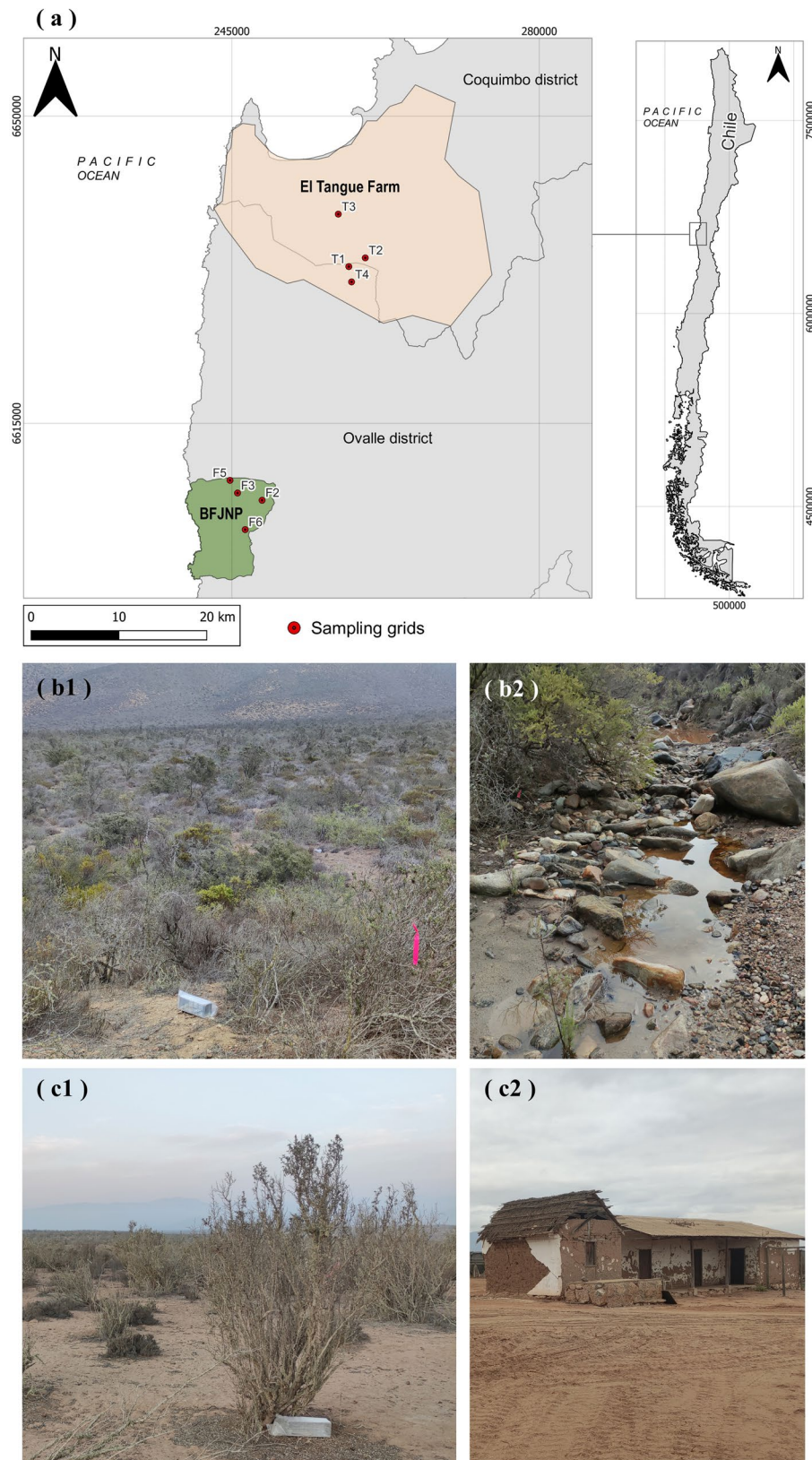


Fig. 1 Study location in north-central Chile. **(a)** Map of the Coquimbo region in Chile indicating the two areas with different anthropogenic pressures (i.e., Bosque Fray Jorge National Park - BFPNP [in green]; El Tangué Farm [in orange]) where Darwin's leaf-eared mice (*Phyllotis darwini*) were studied. Four grids were established in each area, and 200 capture points were allocated per grid. (UTM projection. Datum WGS84, Zone 19 J). **(b 1–2)** A grid at the BFPNP during the winter season is shown. **(c 1–2)** A grid at the El Tangué Farm during autumn is shown.

the final volume of the solution (15 ml) by the amount of faeces analyzed (i.e., 0.1–0.7 g), and the multiplication factor was calculated by dividing the corresponding dilution factor by the analyzed volume of 2 ml in both Mini-FLOTAC® chambers [47]. The taxonomic classification and terminology of helminths and protozoa followed the current guidelines: Nematoda [48], Acanthocephala [49, 50], Platyhelminthes, and Protozoa [51].

Determination of biological factors

Sexes (males, and females) and age groups (adults and juveniles) of the rodents were classified based on their weight and body measurements. Males corresponded to individuals with longer anogenital distance, while adult individuals were considered to have higher body weight (males ≥ 40 g; females ≥ 35 g) than juveniles [44, 52]. To obtain an individual approximation of body condition, data on body length and weight, separated by age group (adults and juveniles), were used to calculate the scaled mass index (SMI) [53].

Recording of environmental data

Temperature (C°) and relative humidity (RH; %) were recorded in each grid during the four-day seasonal sampling using a HOBO data logger (MX2300 Series, Onset Corporation, Bourne, Massachusetts) installed in the center of each grid to record data every hour. In addition, the Normalized Difference Vegetation Index (NDVI) data were extracted using the grids coordinates (buffer = 2 km) on the third day of each seasonal sampling using the Sentinel-2 satellite image data and Google Earth Engine [54, 55]. As NDVI measures the reflectance difference between red and infrared light in a given area using satellite sensors and is often correlated with patterns of plant growth and arthropod biomass, NDVI measurements (i.e., -1 to $+1$) can be used as a proxy for the availability of intermediate hosts [56, 57]. In addition, the relative host density (RHD) was estimated in each grid using the total number of captured *P. darwini* individuals in each seasonal sampling (without intra-seasonal recaptures), as previously described [5].

Data analyses

Parasitological Parameters

Parasite prevalence, density, abundance, and richness infection parameters [58] were calculated for each parasite taxon. Prevalence was defined as the number of individuals with a given parasite type (eggs and oocysts) divided by the total number of individuals examined, and 95% confidence intervals (CI) were estimated using the Clopper-Pearson method [59]. Parasite density (PD) was defined as the number of parasitic morphotypes (EPG, OPG) in each sample. As the diagnostic method was obtained from a noninvasive coprological test, this

parameter was used as a proxy for adult parasite intensity [60]. The mean parasite density (i.e., the sum of each parasite morphotype per gram in feces divided by the number of hosts infected with that parasite), mean parasite abundance (i.e., the total number of each isolated parasitic morphotypes divided by the number of total analyzed hosts), and their corresponding 95% CI were estimated using the bootstrapping method (2000 replications) in the Quantitative Parasitology web [61]. The mean gastrointestinal parasite richness (GPR) was calculated as the average number of simultaneously present parasite morphotypes in the feces of individuals.

Drivers of infection

The association between gastrointestinal parasitism and environmental and biological factors was assessed by building a series of models with different types of predictor and dependent variables using software R [62] and RStudio (2024.04.2) [63].

Generalized linear mixed (GLMM) and generalized linear (GLM) models with binomial error and logit links were built to assess the best model for the presence or absence of the most prevalent parasite taxa or groups ($>5\%$) (that is overall parasitism, helminths, nematodes, *Spirurina* fam. gen. sp., *Strongyloidea* gen. sp., *Schistosoma* sp., coccidia, and protozoa) as response variables. The four predictor variables included seasons, sex of adults [male vs. female], body condition [SMI], and site [protected area vs. rural area]. In the case of *Schistosoma* sp. seasonality was not included as a predictor because eggs were only found in winter and spring in 2022. Rodent ID was included as a random factor in the GLMMs models to account for the recapture of individuals during inter-seasonal sampling. No interactions between predictors were included. To avoid collinearity, age class was not included as a predictor in the statistical analyses. GLMM and GLM models fit were evaluated by comparing the Akaike Information Criterion (AIC) and deviances estimates [64], and GLM models were selected for further analyses because they exhibited a better fit with lower AIC values (ESM 1: Table S3) than GLMM models. Subsequently, GLM models for all possible combinations, including the four predictor variables and each parasite taxon, were built (ESM 1: Tables S4–S7). The selection of the best-fitting models was based on the AIC corrected for small samples (AICc) retaining models with $\Delta AICc \leq 2$ [65]. The quality of fit was estimated using Nagelkerke's pseudo R^2 [66] and the Hosmer-Lemeshow test [67]. Odds ratios and 95% confidence intervals (CI) were calculated for the significant variables in the best model with the highest statistical support.

Second, the distribution of gastrointestinal parasite richness (GPR) and parasite density (PD) data were inspected by frequency histograms (ESM 1: Fig. S1). To

test the relationship between GPR and the four ecological predictor variables, GLM models were built using log-link and Poisson distribution. No interactions between predictors were included. Subsequently, GLM models with all possible combinations were built, including the four predictor variables and GPR as response variable (ESM 1: Table S8). The best-fitting model was selected using the AICc criterion, and the quality of fit was estimated by the Nagelkerke's pseudo R^2 . The incidence rate ratio and 95% CI values were calculated for significant variables in the best model.

In addition, GLMM and GLM models were built to test the association between the PD of each parasite taxa and the two types of sites (i.e., protected area vs. rural area) as predictors, using log-link and Negative Binomial distribution (ESM 1: Fig. S1). Rodent ID was included as a random factor in the GLMM model. After evaluation of the fit of both kinds of models by the lowest AIC and deviance values, GLM models were selected for analyses of overall gastrointestinal parasitism, nematodes, Strongyloidea gen. sp., *Schistosoma* sp., and coccidia; and GLMM models were chosen for overall helminths, Spirurina fam. gen. sp. and overall protozoa (ESM 1: Fig. S2). The quality of fit of each model was estimated using the Nagelkerke's pseudo R^2 for the GLMs, and marginal and conditional R^2 for the GLMMs [68]. Incidence rates and 95% CI values were calculated for significant variables in each parasite taxa (ESM 1: Table S9).

All models were built using the R packages: *lme4* [69], *randomforest* [70], and *MASS* [71]. Combinations of predictor variables from the global models were computed using the model selection function *dredge()* included in the R-library *MuMIn* [72] and ranked according to their AICc values. Nagelkerke's R^2 and marginal and conditional R^2 were estimated using *fmsb* [73] and *lme4* R libraries. Odds, incidence rate ratios, and their corresponding 95% CI were estimated using the *broom.mixed* library [74]. Regression plots were built using *Sjplot* [75] and *ggplot2* [76].

Environmental data

The distribution of max T° , max RH (%), escalated NDVI (i.e., NDVI $\times$ 100), and relative host density data in each grid in all seasonal samplings were inspected using frequency histograms in R (ESM 1: Fig. S2). Univariate analyses were performed to evaluate the influence of seasonality and the site type on the recorded environmental data. Linear (LM) models with a normal distribution were chosen for the analyses of max T° and escalated NDVI. A GLM model with Poisson distribution was chosen for the relative host density data. The maximum RH data were not adequate for further analysis.

Results

Sample size

A total of 363 faecal samples from 299 *P. darwini* individuals were examined for parasitic helminths and protozoans during the five-season sampling period between 2021 and 2022. Of the examined rodents, 246 were captured only once during the entire study period, and 53 were captured multiple times during different seasons.

Parasite identification and infection parameters

Of 363 fecal samples of *P. darwini*, 272 (74.9%; 95% CI = 70.1–79.3%) were positive for at least one parasite taxon. Overall, 131 (36.1%; 31.1–41.3%) samples were positive for helminths, 226 (62.2%; 57.1–67.3%) were positive for protozoa, and 91 (25.1%; 20.7–29.8%) showed multi-parasitism. The mean parasite density, parasite abundance, and prevalence for the different parasite taxa identified among all five sampling seasons and sampled animals are presented in Fig. 2.

Several types of helminths were identified in *P. darwini* samples from north-central Chile (Fig. 3): Archiacanthocephala (Meyer 1931) fam. gen. sp. (Fig. 3a), *Rodentolepis* sp. (Weinland 1858) (Fig. 3b), Ascaridina (Inglis 1983) fam. gen. sp. (Fig. 3c), *Syphacia* sp. (Seurat 1916) (Fig. 3d), Oxyuroidea (Cobbold 1864) gen. sp. (Fig. 3e), Spirurina (Railliet & Henry 1915) fam. gen. sp. (Fig. 3f), Strongyloidea (Baird 1853) gen. sp. (Fig. 3g), Trichosomoididae (York & Maplestone 1926) gen. sp. (Fig. 2h), *Trichuris* sp. (Roederer 1761) (Fig. 3i), nematode larvae (Fig. 3j), and *Schistosoma* sp. (Weinland 1858) (Fig. 3k–l). Protozoan oocysts/cysts found in *P. darwini* are shown in Fig. 4, and included unsporulated coccidia–Eucoccidiorida (Léger & Duboscq 1910) fam. gen. sp. (Fig. 4a–b), *Eimeria* sp. (Schneider 1875) (Fig. 4c), *Isospora* spp. (Schneider 1881) (Fig. 4d–e), *Giardia* sp. (Künstler 1882) (Fig. 4f), and Entamoebidae (Cavalier-Smith 1993) gen. sp. cysts (Fig. 4g–h) and a trophozoite (Fig. 4i).

The characteristics and measurements of the helminths and protozoa found in the present study and their references are described in ESM 1: Table S1. The most prevalent parasite taxa (i.e., >5%) were Spirurina fam. gen. sp., Strongyloidea gen. sp., *Schistosoma* sp., and coccidia (Fig. 2). The highest mean PD rate was observed in *Schistosoma* sp. (4390 EPG; 95% CI: 948–12400 EPG), Strongyloidea gen. sp. (4320 EPG; 1700–11600 EPG), *Trichuris* sp. (2670 EPG; 552–6990 EPG), and coccidia (2570 OPG; 1840–3700 OPG). The overall mean GPR among all the individuals was 1. Data on the overall parasite prevalence, mean parasite density, mean abundance, and their 95% CI according to each parasite taxon, and seasonal, habitat, and biological factors are shown in ESM 1: Table S2.

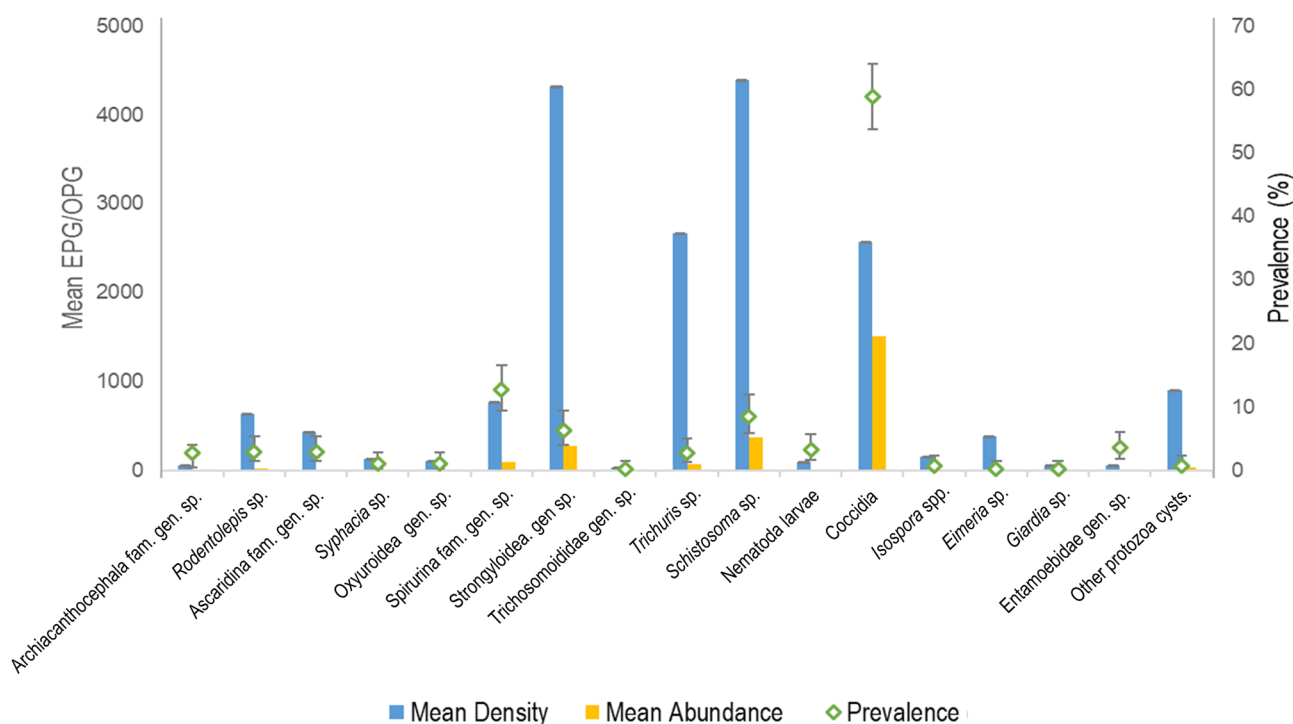


Fig. 2 Parasitological parameters of gastrointestinal parasites found in *P. darwini* in north-central Chile, in the five consecutive seasons between spring 2021 and spring 2022 and among all sampled animals ($n=363$). Mean parasite density (in eggs per gram [EPG] or oocysts per gram [OPG]), mean abundance, and prevalence (± 95 CI), represented by blue bars, yellow bars and green squares, respectively

Factors influencing overall gastrointestinal parasites

(prevalence > 5%)

Overall Gastrointestinal parasitism

The fittest model for gastrointestinal parasite infection status (i.e., presence-absence of helminth eggs and protozoa cysts) included season as a predictor (ESM 1: Table S4). A greater likelihood of infection with gastrointestinal parasites in *P. darwini* was observed in the spring 2022 ($\beta=2.34$, OR=2.09–189, $p=0.02$). In addition, the incidence rate of density of parasite eggs in the altered rural area was lower than that in the non-altered protected area (Rural transition $\beta= -1.38$, IRR=0.14–0.42, $p<0.01$) (ESM 1: Table S9).

Overall helminths

The best model of helminth infection status (presence/absence of helminth eggs) included season and sex as predictors (ESM 1: Table S5). The probability of helminth infection was greater in the winter of 2022 ($\beta=1.51$, OR=2.37–8.98, $p<0.01$) and spring of 2022 ($\beta=1.43$, OR=1.79–10.4, $p=0.00$) than in the other evaluated seasons. No association was observed between the density of helminth eggs (EPG) and site type ($p>0.05$).

Overall nematodes

The best model of nematode infection status (presence or absence) included the type of site as a predictor, with greater infection in the rural area than in the

protected area (ESM 1: Table S5). No associations were observed between the presence of nematodes and the density of nematode eggs (i.e., egg counts; EPG) with site type ($p>0.05$).

Overall protozoa

The best model of protozoan infection status as a response included the type of site and SMI as predictors (ESM 1: Table S7). The likelihood of protozoan infection in *P. darwini* was positively associated with SMI ($\beta=0.01$, OR=1.00–1.04, $p=0.03$), and there was a lower likelihood of protozoan infection in the rural area ($\beta= -0.58$, OR=0.36–0.85, $p<0.01$). Moreover, the incidence rate of the density of protozoa oocysts/cysts in the rural area was lower than that in the protected areas (rural area: $\beta= -1.22$, IRR=0.14–0.59, $p<0.01$) (ESM 1: Table S9).

Factors influencing infection of parasites with indirect life cycle (prevalence > 5%)

Spirurina fam. gen. sp

The best model of spirurid infection status as a response included the site type as a predictor (ESM 1: Table S6). No statistically significant association was observed between the presence of spirurids and the density of spirurid eggs with the site type ($p>0.05$).

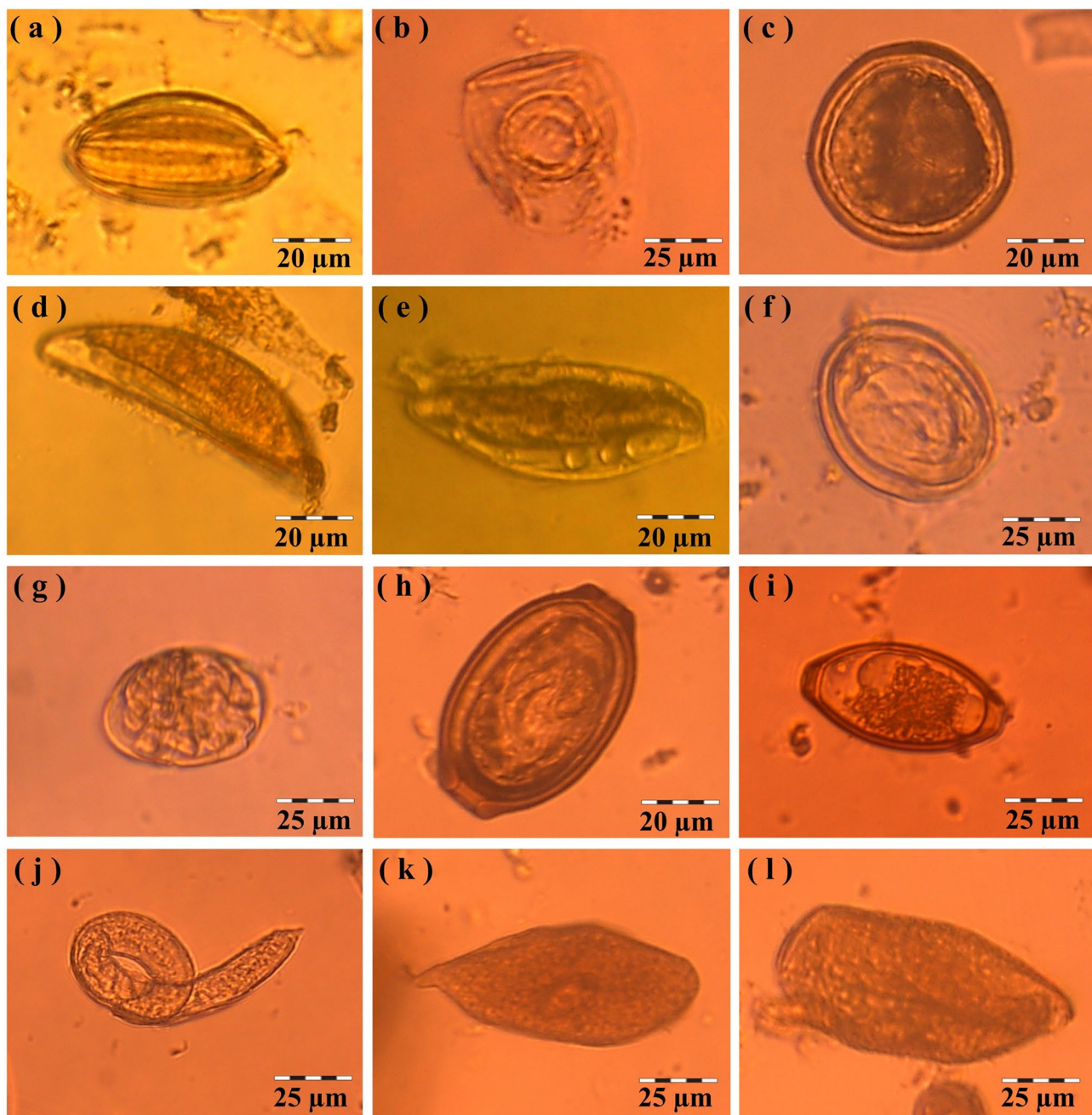


Fig. 3 Helminths in *Phyllotis darwini* in north-central, Chile (400x): (a) Archiacanthocephala fam. gen. sp., (b) *Rodentolepis* sp., (c) Ascaridina fam. gen. sp., (d) *Syphacia* sp., (e) Oxyuroidea gen. sp., (f) Spirurina fam. gen. sp., (g) Strongyloidea gen. sp., (h) Trichosomoididae gen. sp., (i) *Trichuris* sp., (j) nematode larvae, (k-l) *Schistosoma* sp.

Schistosoma sp

The best model of *Schistosoma* sp. infection status as a response included SMI and type of site as predictors (ESM 1: Table S6). The likelihood of *Schistosoma* sp. infection was positively associated with SMI ($\beta = 0.06$, OR = 1.03–1.13, $p < 0.01$), and there was a lower likelihood of *Schistosoma* sp. infection in rodents living in

the rural transition ($\beta = -2.49$, OR = 0.01–0.29, $p < 0.01$) (Fig. 5a). No *Schistosoma* infection was observed during spring 2021, summer and autumn 2022. Additionally, the incidence rate of density of *Schistosoma* eggs in the rural area was lower than that in protected areas (Rural transition $\beta = -3.71$, IRR = 0.00–0.25, $p < 0.01$) (ESM 1: Table S9).

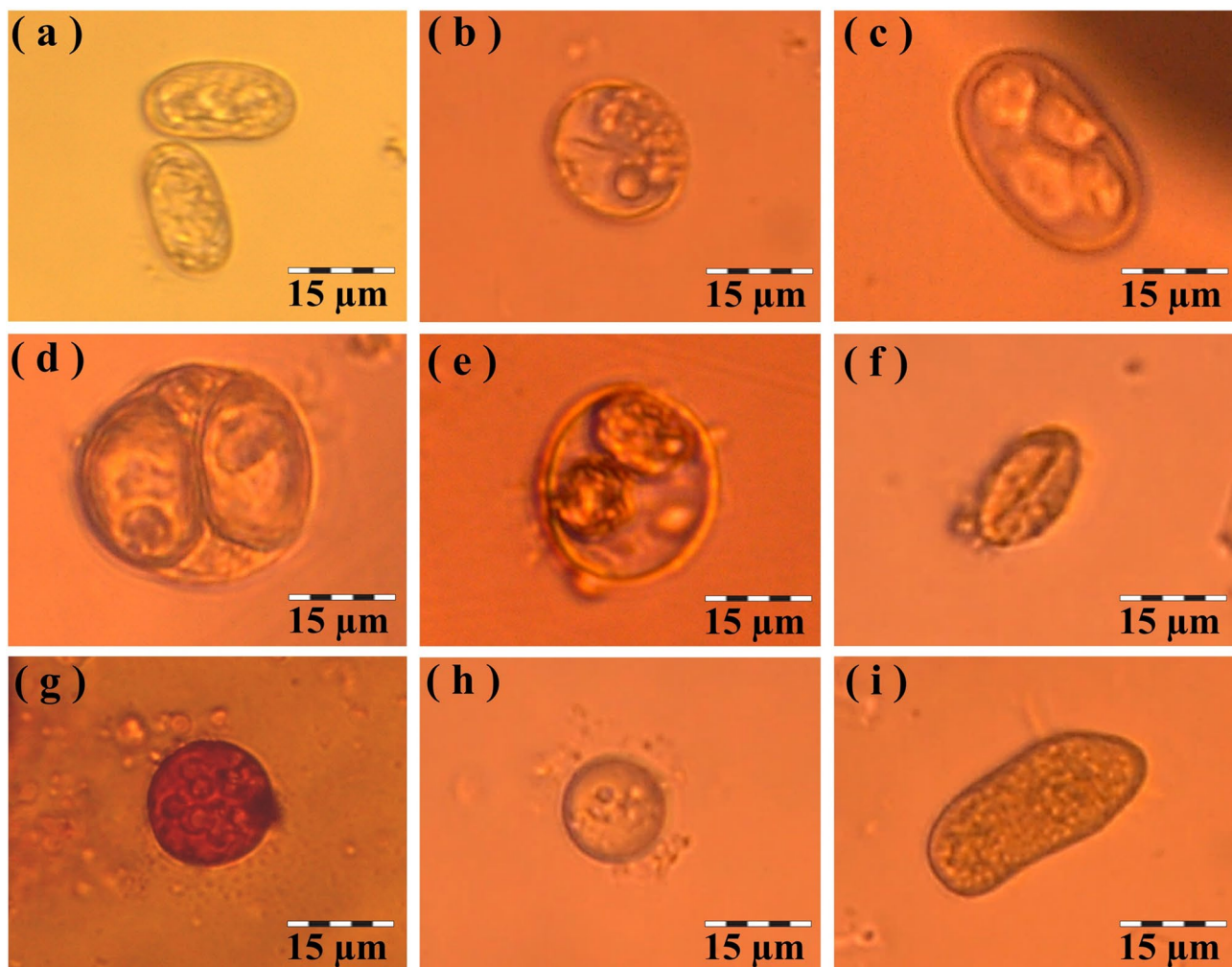


Fig. 4 Protozoa in *Phyllotis darwini* in north-central, Chile (400x): (a-b) unsporulated coccidia–Eucoccidiorida fam. gen. sp., (c) *Eimeria* sp., (d-e) *Isospora* spp., (f) *Giardia* sp., (g-i) Entamoebidae gen. sp.

Factors influencing infection of parasites with direct life cycle (prevalence > 5%)

Strongyloidea gen. sp.

The best model of strongylid infection status as a response involved the type of site as a predictor (ESM 1: Table S7). A lower likelihood of strongylid infection in *P. darwini* was observed at the rural site than at the protected area ($\beta = -0.99$, OR = 0.13–0.91, $p = 0.04$). No association was observed between the density of strongylid eggs (EPG) and the site type ($p > 0.05$).

Coccidia

The best model of coccidia infection status as a response included the site type and SMI as predictors (ESM 1: Table S7). The likelihood of coccidia infection in *P. darwini* was positively associated with SMI ($\beta = 0.02$, OR = 1.01–1.04, $p < 0.01$), and there was a lower likelihood of coccidia infection in the rural transition ($\beta = -0.81$, OR = 0.28–0.67, $p = 0.00$) (Fig. 5b). Additionally,

the incidence rate of coccidia oocyst density in the rural site was lower than that in the protected areas (rural area: $\beta = -1.12$, IRR = 0.17–0.62, $p < 0.01$) (ESM 1: Table S9).

Factors influencing the gastrointestinal parasite richness (GPR)

The best model of the GPR as a response included season and SMI as predictor variables (ESM 1: Table S8). The incidence rate of gastrointestinal parasite richness in *P. darwini* was higher in winter 2022 ($\beta = 0.42$, IRR = 1.15–2.01, $p < 0.01$) and spring 2022 ($\beta = 0.40$, OR = 1.03–2.13, $p = 0.02$). GPR was positively associated with SMI ($\beta = 0.42$, IRR = 1.15–2.01, $p < 0.01$) (Fig. 5c).

Environmental data

The incidence rate of NDVI was lower in summer 2022 ($\beta = -6.69$, IRR = 0.00–0.2, $p = 0.01$), autumn 2022 ($\beta = -8.55$, IRR = 0.00–0.002, $p < 0.01$) and winter 2022 ($\beta =$

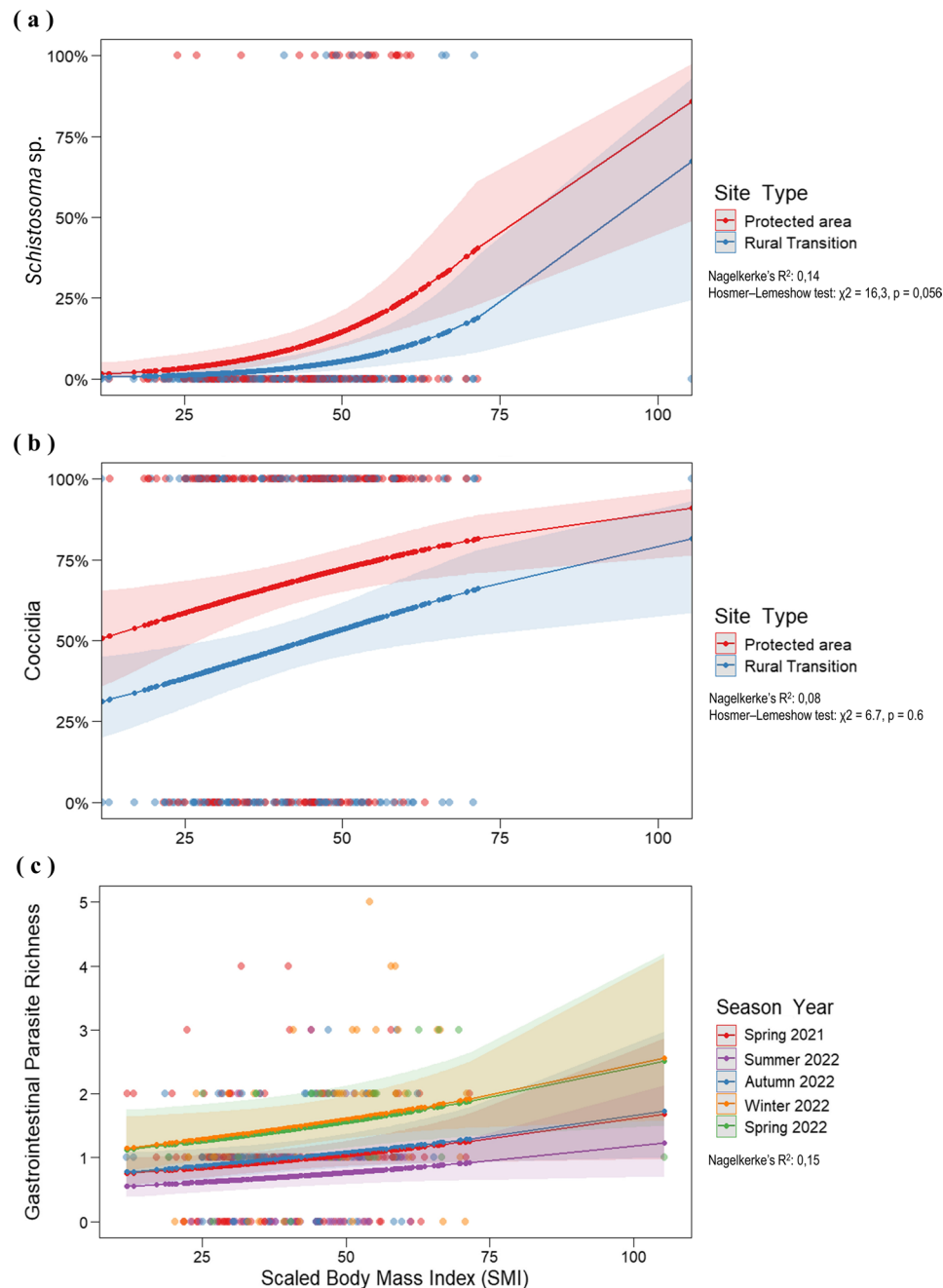


Fig. 5 Best predictors of gastrointestinal parasitism in *P. darwini* in north-central Chile. **(a)** Relationship between the presence of *Schistosoma* sp. eggs, type of site, and SMI, **(b)** Relationship between the presence of coccidia, type of site, and SMI, **(c)** Relationship between Gastrointestinal Parasite Richness, seasons and SMI. Shading indicates the 95% CI around the regression line

−6.92, IRR = 0.00–0.16, $p < 0.01$) than in spring 2021 (ESM 1: Table S10). In contrast, no statistically significant association was observed between NDVI and the site type ($p > 0.05$). Also, the incident rate of relative host density was lower in summer 2022 ($\beta = -0.46$, IRR = 0.47–0.83, $p = 0.01$), autumn 2022 ($\beta = -0.67$, IRR = 0.37–0.67, $p < 0.01$), winter 2022 ($\beta = -0.73$, IRR = 0.34–0.64, $p < 0.01$), and spring 2022 ($\beta = -1.65$,

IRR = 0.12–0.28, $p = 0.00$) compared to that in spring 2021. In addition, the incident rate of relative host density was lower in rural sites than in protected areas (Rural area: $\beta = -0.21$, IRR = 0.65–0.99, $p = 0.04$). Lastly, no statistically significant associations were observed between max T° and the predictors such as seasons or site type ($p > 0.05$) (ESM 1: Table S10).

Discussion

In this one-year study, the infection dynamics of gastrointestinal parasites of wild rodents (*Phyllotis darwini*) in non-altered (protected) and anthropogenically altered (rural) areas in north-central Chile were investigated, and the effects of ecological and biological factors on gastrointestinal parasite prevalence, parasite richness, and parasite density were assessed.

The overall prevalence of gastrointestinal parasites (74.9%) in *P. darwini* in north-central Chile was similar to that reported (89.65%) in a rodent community in Chiloé-Chile employing the Mini-FLOTAC [77], but it was higher than a previous study of parasite prevalence in wild rodents using a modified Telemann test in central Chile (16.95%) [31]. The copro-parasitological technique chosen for this research was Mini-FLOTAC, which is known to be more sensitive (e.g., 90%) than other coprological tests (e.g., formol-ether sedimentation) [78]. Overall, 16 of gastrointestinal parasite taxa were discriminated, some of which were reported for the first time in *P. darwini*, such as Archiacanthocephala, Ascaridina, Trichosomoididae, *Schistosoma* sp., *Isospora* spp., *Giardia* sp., and Entamoebidae [30, 32, 77, 79]. Importantly, some parasite taxa found in *P. darwini* in north-central Chile such as *Rodentolepis* sp., *Schistosoma* sp., *Giardia* sp., and *Amoeba* sp. have the potential to infect humans [19]. Further molecular studies are needed to determine parasite species and public health risks.

Effect of anthropogenic pressure on gastrointestinal parasites

As expected, the likelihood of infection of some parasite taxa, such as Strongyloidea gen. sp., *Schistosoma* sp., coccidia, and overall protozoa, was lower in rodents in the site with the anthropogenic impact (i.e., rural transition) than those in the protected area. These results differ from previous studies in central Chile, in which the prevalence of *Giardia* sp. was higher in rodents living in altered areas (i.e., young pine plantations) [32]; however, they agreed with the lower likelihood of infection with *Hymenolepis* sp. and *Strongyloides* sp. in small mammals living in altered areas of Madagascar [5]. Negative impacts on hosts (e.g., abundance of definitive and intermediate hosts) and adverse microhabitat conditions associated with anthropogenic pressures could reduce persistence of fecal parasitic elements and lower transmission rates in the altered area (i.e., transmission reduction) [80, 81]. Indeed, in this study, the relative host density of *P. darwini* was lower at the rural area than at the protected site, and this finding was consistent with previous work in the same location [39].

Interestingly, and contrary to the initial hypotheses, no difference was observed in the gastrointestinal parasite richness between sampling sites, whereas the density

rates of some parasite taxa (i.e., gastrointestinal parasitism, *Schistosoma* sp., coccidia, and protozoa) were lower in the rural area. The similar parasite richness of *P. darwini* in the rural transition compared to the protected area could have been the result of the transmission and addition of parasites from non-native hosts such as domestic animals to the rodents inhabiting the altered area [80, 82]. For example, Trichosomoididae and *Giardia* sp. are common parasites of synanthropic rats [83, 84] and were found only in rural areas. In addition, the fact that rodents in the protected site shed a higher number of parasite eggs and oocysts may suggest that such individuals are potentially more tolerant to parasitic infections mediated by an increased immunity due to better life conditions (e.g., greater availability of food resources) in comparison with the rural area, or it may be related to higher parasite exposure and higher densities of host populations in the protected area [85]. In this study, the NDVI values were similar in the protected and rural areas. More studies with small-scale spatial characterization of ecological features might be useful to test the trade-offs between parasites, immunity, and habitat quality.

Effect of seasonality on gastrointestinal parasites

The likelihood of infection was higher in winter 2022 and spring 2022 for the overall gastrointestinal parasitism, helminths, and parasite richness than in the other evaluated seasons. Seasonal variations in helminths and protozoa have been widely reported in rodents, and colder and wetter conditions (including time-lagged effects) are often associated with higher prevalence rates [31, 32, 86]. This could be related to favorable biotic and abiotic conditions in the winter season for both hosts (i.e., definitive and intermediate) and parasite development (i.e., viability of parasitic stages) [19]. In fact, in north-central Chile, a higher density of *P. darwini* was previously reported during spring, which is related to the breeding season [26–28]. In addition, NDVI values recorded in the present study were higher during spring, which could indicate a higher presence of invertebrates and thus potential intermediate hosts (e.g., cockroach for Acanthocephala) [56, 57]. Interestingly, no associations were observed between seasonality and the infection probability of certain parasites with direct (i.e., Strongyloidea gen. sp. and coccidia) and indirect (i.e., Spirurina fam. gen. sp.) life cycles. For such parasite taxa, the survival of developmental parasitic stages and their intermediate hosts may not be influenced by seasonality.

A higher rate of parasitism was observed in the spring of 2022 than in the spring of 2021. This finding may be related to the higher rainfall and relative humidity (%) in 2022 which could have intensified the parasite transmission patterns (see ESM 1: Table S11). Indeed, *Schistosoma*

sp. eggs in *P. darwini* were only detected in winter and spring in 2022. A higher abundance of potential intermediate hosts of *Schistosoma* sp., including endemic mollusks such as *Chiloborus rosaceus* (King & Broderip 1831) in winter and spring in 2022 could have favored temporal parasite development and transmission [87].

Nevertheless, the present study evaluated only five seasons within one year. Thus, long-term studies are needed to confirm seasonal patterns of parasite infections.

Effect of biological features of hosts on gastrointestinal parasites

In this study, the likelihood of infection with *Schistosoma* sp., coccidia and protozoa, as well as gastrointestinal parasite richness increased while increasing the scaled body mass index (SMI). Similar findings were reported in other small mammals, in which body condition was positively correlated with infection of certain Nematoda and Acanthocephala [5, 7]. Transmission of parasites with direct and indirect life cycles is likely to be facilitated in hosts with larger body sizes because larger individuals show more physical space in contact with the environment for parasite infection (e.g., skin penetration for furcocercariae in *Schistosoma* sp.) and often show higher levels of food consumption that can be contaminated with infective parasitic stages (e.g., coccidian oocysts) and infected intermediate hosts (e.g., Spirurina) [14].

Sex-biased parasitism of adult individuals was not observed in the present study. This non-specific effect of sex on parasite infections has also been reported in other wild rodents in natural and disturbed locations [8, 10] and in previous research on *Cryptosporidium* infection in *P. darwini* [33]. Thus, *P. darwini* individuals of both sexes may show physiological and behavioral strategies that make them equally exposed to gastrointestinal parasites in altered and rural areas of north-central Chile.

Limitations and future research

In this study, gastrointestinal parasitism in *P. darwini* was determined by a non-invasive parasitological examination of fecal samples that included morphometric analyses of parasitic elements. This approach allowed the discrimination of a high number of parasitic morphotypes; however, parasite richness data might be inaccurately estimated as it was not possible to identify parasites at species level based on morpho-metric features, and the use of ethanol may have altered parasite morphology. To address these issues in the present study, fecal samples were examined in a time no longer than two months after collection, and representatives of each parasite morphotypes in fecal samples were photographically recorded and measured to enhance the discrimination and identification. Also, the coprological examination was carried out after a pilot study [77], which enabled to refine the

technique and develop skill in the identification of gastrointestinal parasites of rodents. Molecular characterization of parasite species from fecal samples was beyond the scope of the present study.

Additionally, considering that a non-invasive coprological test was employed as a diagnostic method in this research, the count of parasitic eggs and oocysts (EGG, OPG) (i.e., parasite density) in feces was used as a proxy for adult parasite intensity in the gastrointestinal tract using microscopy [60]. To accurately determine the actual parasite load, the gold standard is to conduct necropsies to count adult parasites in the gastrointestinal tract; however, this is not feasible in long-term studies. Future research may benefit from using Multiplex Quantitative PCR in fecal samples and metabarcoding focused on a specific parasite species for more accurate diagnostic approaches [88, 89]. Also, future endeavours on the assessment and validation of the relationship between the number of eggs in feces and adult parasites in the digestive tract as well as the evaluation of the interaction between different types of parasites may be useful for understanding parasite dynamics in the long-term.

In addition, it was not possible to characterize the microhabitats of the protected and rural areas. This limitation prevents further ecological associations with parasite infections. Thus, a follow-up study of gastrointestinal parasitism in *P. darwini* should include recording environmental data, such as the abundance of arthropods and mollusks (i.e., potential intermediate hosts), vegetation types, and assessing a greater number of grids in different ecological settings. Besides, the potential interaction between sex and body condition was not included in the statistical analyses in this research. Future studies may evaluate interactions between biological features to better understand parasite infection dynamics.

Conclusions

The results presented in this one-year study indicate that gastrointestinal parasites in *Phyllotis darwini* in north-central Chile are influenced by habitat alteration, seasonality, and body mass. While the likelihood of infection and copro-parasitic density of certain parasite taxa were lower in rodents inhabiting the rural transition compared to those in the protected area, no difference was observed in the gastrointestinal parasite richness according to the type of site. Reduction of host populations (including the intermediate hosts for parasites with indirect life cycle) due to anthropogenic effects may limit parasite transmission, but non-native hosts may introduce new parasites to the parasite fauna of *P. darwini* in the rural area. In addition, a higher likelihood of infection of certain parasite taxa and parasite richness was found in the winter and spring seasons of 2022. Favorable biotic and abiotic conditions for both host populations

(definitive and intermediate) and developmental parasitic elements under wetter conditions can explain the higher rates of parasitism in winter, including their time-lagged effects in spring. Also, rodents with a higher scaled body mass showed a higher likelihood of parasite infection and parasite richness, which could be related to higher exposure to parasite transmission. Finally, sex-biased parasitism in adult individuals was not detected in *P. darwini*. Further longitudinal studies with a molecular diagnostic approach and in different ecological settings are required to better understand how human-induced activities influence parasitic infections in *P. darwini* in Chile and their implications for public health and conservation.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s12917-025-05129-5>.

Supplementary Material 1

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Authors' contributions

GAJ and PDCJ conceived the ideas and designed the methodology. PDCJ conducted fieldwork, carried out coproparasitological examinations, performed statistical analyses, and wrote the draft of the manuscript as part of a doctoral dissertation. GAJ carried out supervision, funding acquisition, and project administration. GAJ, CV, CLA, and MPE validated the methodology, wrote and review the manuscript, and provided editorial advice.

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Data availability

The online version contains supplementary material available. The dataset generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Animal capture and sampling were carried out under the approval and supervision of the Scientific Ethics Committee Resolution for the Use of Animals in Research of the Universidad Austral de Chile (N° 430/2021), the Agricultural and Livestock Service of Chile, SAG, Chile (Exempt Resolution N° 3245/2021), and the National Forest Corporation, CONAF, Chile (Letter N° 26/2021).

Consent for publication

Not applicable.

Competing interests

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