REVIEW

Influence of habitat alteration on the structure of helminth communities in small mammals: a systematic review and critical appraisal of theory and current evidence

Patricio D. Carrera-Játiva[1] · Gerardo Acosta-Jamett[2]

Abstract

Despite the extensive information on the effects of habitat alteration on the structure of helminth communities in small mammals, the evidence is still inconclusive. A systematic review was carried out using the PRISMA (Preferred Reporting Items for Systematic Review and Meta-Analysis) guideline to compile and synthesize available literature on the influence of habitat alteration on the structure of helminth communities in small mammals. The aim of this review was to describe the variation in infection rates of helminth species associated with habitat alteration and to discuss the theoretical framework that may explain such changes in relation to parasite, host, and environmental features. Twenty-three scientific articles published between 2005 and 2022 were reviewed, 22 of which investigated parasite prevalence, 10 parasite burden, and 14 parasite richness in both altered and natural habitats. Information in assessed articles suggests that the structure of helminth communities in small mammals can be impacted by anthropogenic habitat alteration in various ways. Infection rates of monoxenous and heteroxenous helminths may increase or decrease in small mammals depending on whether their hosts (definitive and intermediate) are available, and environmental and host conditions modify the survival and transmission of parasitic forms. Also, given that habitat alteration may favor inter-species contacts, transmission rates of low host-specific helminths could be increased due to exposure to new reservoir hosts. In a continually changing world, it is essential to assess the spatio-temporal variations of helminth communities in wildlife inhabiting altered and natural habitats to determine potential impacts on wildlife conservation and public health.

Introduction

Human-induced alteration on natural environments is transforming landscapes across the earth and modifying balancing ecological processes, which can subsequently result in variation of host-parasite interactions (Patz et al. 2004). Globally, rapid land use changes due to expanding agriculture, natural resource extraction, and urbanization are leading to modifications of natural habitats which have impacts on biodiversity (Jones et al. 2008; Suzán et al. 2012; Haddad et al. 2015). From this perspective, two processes can be regarded as human-created habitat alteration such as fragmentation and degradation. Fragmentation is defined as the discontinuity in the spatial distribution of resources available in a given area (Franklin et al. 2002). Degradation, in counterpart, is the gradual deterioration of the habitat quality (Mortelliti et al. 2010) that could lead to habitat loss (i.e., non-habitat) for a given animal species (Lindenmayer and Fischer 2006). Fragmentation and degradation can act independently or simultaneously in landscapes negatively affecting free-living species (Lindenmayer and Fischer 2006; Mortelliti et al. 2010; Irwin 2016). In particular, it has been proven that species density and richness are often modified in human-induced altered habitats causing significant disruptions in trophic relationships within ecosystems

✉ Patricio D. Carrera-Játiva
patricio.carrera.j@gmail.com

1 Escuela de Graduados, Facultad de Ciencias Veterinarias, Universidad Austral de Chile, Valdivia, Chile

2 Instituto de Medicina Preventiva Veterinaria and Center for Surveillance and Evolution of Infectious Diseases, Facultad de Ciencias Veterinarias, Universidad Austral de Chile, Valdivia, Chile

(Patz et al. 2000; Haddad et al. 2015). Also, the creation and expansion of habitat edges can facilitate wildlife to be in contact with both domestic animals and humans, thus increasing cross-species transmission risks of parasites (Holmes 1996; Cleaveland et al. 2007). These changes in host-parasite interactions in altered environments can subsequently result in variations of parasite assemblages and host ranges, higher pathogenicity, and the emergence of previously unrecognized infectious agents (Holmes 1996; Daszak et al. 2000; Patz et al. 2004; Suzán et al. 2012).

Parasitic helminths, including Platyhelminthes (class Cestoda and Trematoda), Nematoda, and Acanthocephala, are manifold in nature with approximately 75,000 to 300,000 extant species that use vertebrates as hosts (Dobson et al. 2008). Helminths display distinct mechanisms of development and transmission that make them of interest in the context of human-induced habitat alteration. Unlike microparasites (e.g., bacteria and viruses), helminths exhibit long generation times with persistent infections, in which hosts can continually be re-infected (Anderson and May 1991). Transmission of monoxenous helminths such as some nematodes (i.e., ageohelminths, pseudohelminths, and geohelminths) (see Table 1) is host density-dependent, involving life cycles in a single host species (Bush et al. 1997; Taylor et al. 2016; Sáez-Durán et al. 2021). The developmental stages of monoxenous helminths require suitable abiotic conditions to remain viable with exception of ageohelminths which can be directly infective to hosts since their eggs embryonate in a short time (< 4 h) (e.g., Oxyurida) (Taylor et al. 2016; Sáez-Durán et al. 2021). In contrast, transmission of heteroxenous helminths with complex life cycles (e.g., Cestoda, Trematoda, Acanthocephala, and some Nematoda) is conditioned to the availability of compatible intermediate and definitive hosts, and their free-living

Table 1 Classification of helminths described in 23 reviewed articles following the Sáez-Durán et al. (2021) criteria.

Monoxenous			Heteroxenous			
Nematoda			Trematoda	Cestoda	Nematoda	Acanthocephala
Ageohelminth[a]	*Pseudogeohelminth*[b]	*Geohelminth*[c]				
Aspiculuris tetraptera	*Ascaris* sp.	*Heligmonina spira*	*Brachylaima* spp.	*Catenotaenia* sp.	*Capillaria* sp.	*Moniliformis* sp.
Callistoura sp.	*Heterakis* spp.	*Heligmonoides speciosus*	*Brachylaima asakawai*	Catenotaeniidae Gen. spp.	*Eucoleus bacillatus*	
Colobenterobius sp.	*Heterakis spumosa*	*Heligmosomoides kurilensis*	*Controrchis biliophilus*	*Gallegoides arfaai*	*Labiobulura* spp.	
Enterobius sp.	*Toxascaris* spp.	*Heligmosomoides polygyrus*	*Dicrocoelium* spp.	*Hymenolepis* sp.	*Linstowinema* spp.	
Heteromoxyuris sp.	*Toxocara* spp.	*Neoheligmonella capensis*	*Metagonimus* sp.	*Hymenolepis straminea*	*Mastophorus dipodomis*	
Lemuricola sp.	*Trichuris* sp.	*Oesophagostomum* sp.	*Opisthorchis* sp.	*Mesocestoides* spp. larvae	*Mastophorus muris*	
Opisthorchis sp.	*Trichuris muris*	Strongylida		*Microsomacanthus* sp.	*Parabronema* sp.	
Oxyuridae		*Strongyloides* sp.		*Potorolepis* spp.	*Physaloptera* sp.	
Syphacia sp.		*Strongyloides fulleboni*		*Pseudocatenotaenia matovi*	*Pterygodermatites dipodomis*	
Syphacia agraria		*Strongyloides stercoralis*		*Skrjabinotaenia lobata*	Spirurida	
Syphacia emileromani		Rhabditida		*Taenia martis* larvae	*Streptopharagus* sp.	
Syphacia frederici		*Trichostrongylus* sp.		*Taenia parva* larvae	*Subulura* sp.	
Syphacia stroma		*Trichostrongylus probulurus*				
Trypanoxyuris sp.						

[a]Release embryonated and directly infected eggs or that embryonate in a short period of less than 4 h

[b]Release non-embryonated eggs that require development period in the environment (≈ 2–3 weeks depending on the climate) to embryonate and become infective

[c]Display a free-living larval stage in the environment

developmental stages depend on appropriate environmental conditions (Anderson and May 1991; Taylor et al. 2016).

The helminth component community involves the assemblage of parasite individuals of all species within a host population (Holmes 1987; Bush et al. 1997; Poulin 2001). In this regard, patterns of the structure of the helminth communities in wildlife populations are the result of complex processes of adaptation and coevolution, and transmission dynamics can be shaped by several determinants such as host (e.g., behavior, body condition, genetics, diet), parasite (e.g., life cycle, transmission routes, parasite genetics), and environmental conditions (e.g., habitat quality and abiotic conditions) (Poulin and Morand 2000; Tompkins et al. 2002; Wilson et al. 2002; Nunn et al. 2003). At population level, helminths have been proven to regulate host populations in a cyclical manner by producing mortality and reproduction decline (Hudson et al. 1998; Tompkins et al. 2002; Wilson et al. 2002). This is the reason why adapted and coevolved helminths are considered to provide essential ecological services related to the stability of populations (Dobson et al. 2008; Gómez and Nichols 2013). However, the variation of helminth communities in wildlife populations due to anthropogenic habitat alteration has been identified as an important driver for species extinctions when combined with other pathogens (e.g., bacteria and viruses) or with environmental stressors (Pedersen et al. 2007). Indeed, parasites showing host frequency-dependent transmission (e.g., parasite with complex life cycles) are of concern to endangered species since individuals can continually be re-infected even as populations decrease (Pedersen et al. 2007). As isolated wildlife populations tend to harbor helminth communities dominated by coevolved parasite species that are highly host-specific (Holmes 1987; Poulin 2001), the establishment of exotic low host-specific helminths on native populations due to cross-species transmission may have adverse implications on the health of living organisms since parasites may become more virulent and pathogenic given their increased range size (Gillespie and Chapman 2008; Loiseau et al. 2012).

The understanding of the effect of anthropogenic habitat alteration on the structure of helminth communities in wildlife is still unclear. In a recent meta-analysis on the variation of infection rates of helminths and microparasites in wildlife in urban and natural habitats, it was stated that only carnivores and primates living in urban settings exhibited reduced transmission rates for parasites with complex life cycles, and no effect was found in rodents and marsupial hosts, or for monoxenous parasites (Werner and Nunn 2020). Considering that helminths show diverse host and environmental requirements for their development and transmission in animal populations, human-induced habitat alteration may have either promoting or deleterious effects on infection rates (e.g., prevalence, abundance, and richness) in accordance with their specific life cycle including monoxenous

(i.e., ageohelminths, pseudohelminths, and geohelminths) and heteroxenous (i.e., complex) species. Therefore, this systematic review aimed at compiling and summarizing the available peer-reviewed literature on the effects of habitat alteration on the structure of helminth communities in small mammals and discuss the evidence and theoretical framework on the development and transmission of monoxenous and heteroxenous helminths in human-induced altered habitats. In this systematic review, the following question were addressed: (i) what are the effects of habitat alteration on the infection rates (e.g., prevalence, abundance, richness) of monoxenous and heteroxenous helminths in small-mammals? (ii) What are the environmental and host conditions that influence variations in infections rates of helminths in small mammal populations in altered habitats? (iii) Are low host-specific helminth species more frequent and abundant than those highly host-specific in small mammal populations in altered habitats?

Methodology

Search strategy

Systematic search was carried out following the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) declaration guidelines (http://www.prisma-statement.org/) (Dea et al. 2021). Relevant scientific documents were initially collected by using the online databases Web of Science Core Collection (https://www.webofscience.com; 14 November 2021), Google Scholar Database (https://scholar.google.cl/; 21 November 2021), and PubMed Central (PMC) (https://www.ncbi.nlm.nih.gov/pmc/advanced; 21 November 2021). The literature was searched using the following search query: "parasite" OR "helminths" AND "habitat" AND "degraded" AND "natural" AND "fragmented" AND "mammals." In addition, a second search was carried out to collect any other studies using the PubMed Central and PubMed databases (https://pubmed.ncbi.nlm.nih.gov/; 11 February 2022), in which the search terms included "parasite" AND "helminth" AND "rodents" AND "habitat" AND "fragmentation" AND "natural." The reference lists of peer-reviewed studies were also checked, and relevant papers were included into the database. Also, certain benchmark studies that were not retrieved by the systematic searches were included for further assessment. Information of all retrieved literature was included into a database (Electronic Supplementary Material ESM1: Database 1).

Study selection

Titles, abstracts, and/or full text were evaluated to determine whether the studies collected by the systematic search were

relevant to the review questions. Studies were selected using the following inclusion criteria: (a) studies published before 11 February 2022; (b) studies that investigate helminths; (c) reports of parasites in small mammals as definitive hosts, including only those which overall weight was less than 5 kg, as indicated by Merritt (2010); (d) studies that compare parasite infection rates in both natural and altered habitats. In this regard, altered type habitats were considered those anthropogenically disturbed and fragmented areas, while natural habitats consisted of those areas with larger, continuous, native, and/or protected habitats. Such categories were explicitly identified from descriptions in each paper. (e) Studies only in peer-reviewed journals; (f) studies were restricted to English language.

Pertinent studies from references ($n = 60$) and other sources ($n = 9$) were also selected for revision if they comply with the inclusion criteria. When necessary, appendices and supplementary materials were also inspected.

Data extraction and synthesis

For each identified study, data were extracted and compiled into a summary table (ESM2: Table 1). Extracted data included (a) information about year of publication; (b) reference (i.e., authors, year, title of journal, volume, issue, pages); (c) location of the study; (d) host species in the Latin binomial (i.e., scientific name); (e) host order; (f) helminth species in the Latin binomial (i.e., scientific name); (g) sample size; (h) risk factors (e.g., habitat type, host body condition, among others); (i) infection rates as response variables to address the risk factors (i.e., prevalence, parasite burden (mean intensity and mean abundance), mean parasite richness, and diversity indexes), which were interpreted according to Bush et al. (1997). In this context, prevalence is the number of individuals of a host species infected with a specific parasite type divided by the number of hosts examined. The mean intensity corresponds to the sum of parasitic forms of each parasite type divided by the number of hosts infected with such parasites. The mean abundance is the total number of each parasite divided by the number of total analyzed hosts. The mean parasite richness is the average number of simultaneously present helminth type in individual hosts. Diversity indexes are estimates of the diversity of species within a community (e.g., Shannon's diversity index); (j) methods used to evaluate helminth infections; and (k) brief explanation of findings of each study.

Also, when information was available in studies, data about the number of individuals infected with a parasite species and the total sample size in each habitat type (i.e., altered and natural) were extracted in an additional database (ESM3: Database N. 3). In this regard, in reports of multiple altered habitats and/or along a gradient of alteration, extracted data consisted of those sites with the highest degree of environmental alteration (i.e., fragmentation or degradation) explicitly detailed in each paper. Zero (0) was included as a result whether a parasite species was searched but it was not found in a population. Additionally, the life cycle of each parasite species was added into the database following the classification proposed by Sáez-Durán et al. (2021) for monoxenous (i.e., nematodes: ageohelminths, pseudogeohelminths, geohelminths) and heteroxenous species (see Table 1) and based on available literature (Taylor et al. 2016).

Numbers of selected studies per country were displayed in a map by using the Microsoft Excel® software with the Geographic Heat Map add-in tool. For data visualization regarding parasite prevalence, forest plots were used to display the odds ratio of parasite species infecting small mammals in altered and natural habitats according to the type of parasite life cycles. In each forest plot, the 95% confidence interval (CI) and the expected heterogeneity (i.e., I^2 and Cochrane's Q test (significance level of $p < 0.1$)) were included, in which the size of squares showed the weight of every study finding and the crossed lines indicated the CI. The "meta" package (Schwarzer 2007) was used for forest plot elaboration in the software R (R Foundation for Statistical Computing, Vienna, Austria) (R Development CoreTeam 2011) and RStudio (Integrated Development for RStudio, Inc.) (RStudio Team 2022).

Results

PRISMA-guided study selection

A total of 1658 papers were recovered from the final search (ESM1: Database 1), 23 of which were retained following the PRISMA-guided study selection (Fig. 1). Briefly, 36 duplicate papers and 86 non-peer-reviewed articles (i.e., poster abstracts, conference abstracts, book chapters) and reviews were omitted. After reading the abstracts of the remaining papers, 1430 were removed because they did not directly involve either helminths, mammals, or habitat alteration. Subsequently, full-text revision was performed in 106 articles, of which 83 were removed because they did not investigate habitat fragmentation/degradation (43), natural habitat comparison (23), helminths (11), or small mammals (6).

Information on quantitative data of prevalence of helminth species in small mammals in altered and natural areas was available in 14 studies (ESM 3: Quantitative extracted data).

Fig. 1 PRISMA flow diagram of the study selection process
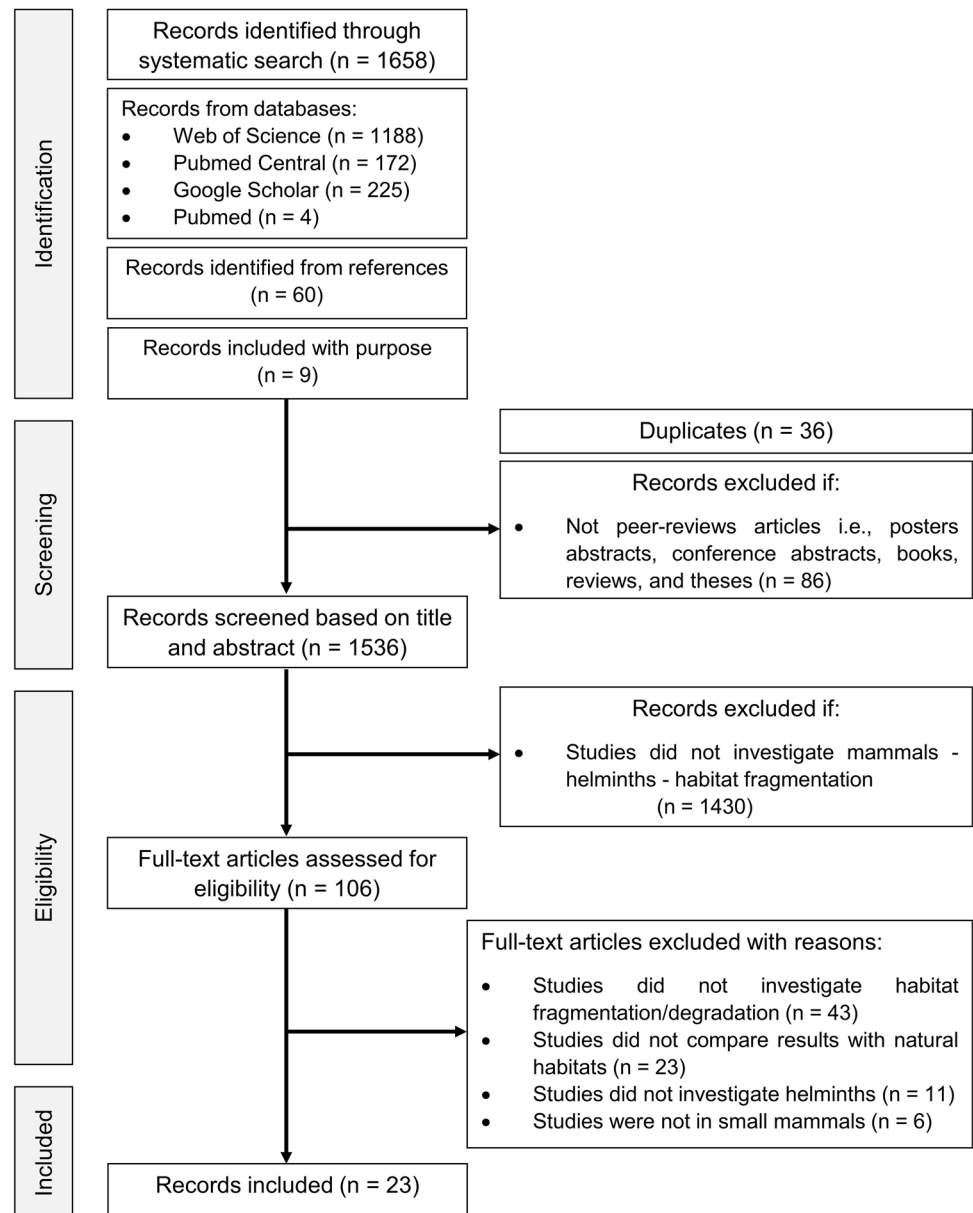
General trend in literature

Trends in the literature were inspected in 23 papers which evaluated helminth infections in small mammals under altered and natural environmental conditions. Studies were carried out between the years 2005 and 2022, with most of them ($n = 5$, 22%) published in 2021. Studies were conducted in 16 different countries and were geographically biased with 43% ($n = 10$) of the reports describing the effects of habitat alteration in small mammals in Africa (Fig. 2). The orders of small mammals examined in selected studies belonged to Primata Linnaeus 1758 (57%; $n = 13$), Rodentia Bowdich 1821 (43%; $n = 10$), Peramelemorphia Kirsch 1968 (4%; $n = 1$), and Didelphimorphia Gill 1872 (4%; $n = 1$). In

this regard, two studies examined two mammalian orders simultaneously. Twenty-one studies (91%) aimed at investigating the structure of helminth communities, identifying at least 4 different helminth taxa, and in counterpart, two studies (9%) examined specific helminth species. The median sample size (i.e., number of mammalian host species) in altered and natural habitats was 158 (min = 1, max = 1167) in 20 studies that evaluated individual host. Parasitism in pooled fecal samples of groups of individuals was assessed in three studies (Gillespie and Chapman 2006, 2008; Trejo-Macías et al. 2007).

In identified manuscripts, several metrics were considered to evaluate the influence of habitat alteration on the structure of helminth communities in small mammals.
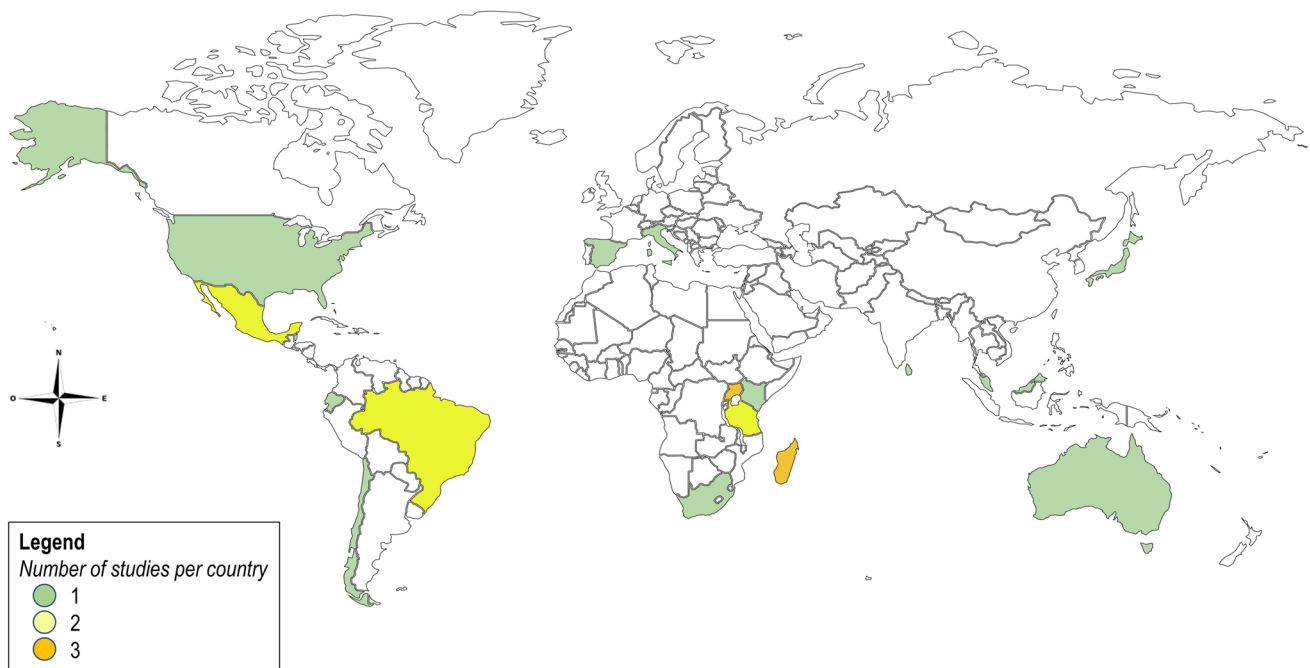
Fig. 2 Geographic distribution of the 23 reviewed publications

Prevalence of helminth infection was assessed in 22 studies (96%). Helminth parasite burden (i.e., abundance or intensity) was estimated in 10 studies (43%), and helminth species richness was evaluated in 13 studies (59%). Diversity indexes (i.e., Shannon's diversity index (H′) ($n=3$; Trejo-Macías et al. 2007, Anders et al. 2019, Sáez-Durán et al. 2021); Simpson index (D), Berger–Parker index (d), Shannon evenness (E) ($n=1$; Sáez-Durán et al. 2021); and Whittaker index ($n=1$; Costa et al. 2019)) were assessed only in four studies (17%). Additional metrics included multiple infection estimates ($n=1$) (Rakotoniaina et al. 2016) and infection risk assessment (i.e., availability of parasitic infective stages from the environment) ($n=2$) (Gillespie et al. 2005; Gillespie and Chapman 2008).

Explanatory variables of identified studies comprised habitat features (e.g., habitat type, distance to forest edge, stump density), host characteristics (e.g., sex, body condition, host species, host density), and temporary variation such as seasonality (see ESM2: Table 1).

Methods of recovering and identification of helminths species in reviewed studies consisted of mainly coprological examination by microscopy such as conventional and modified flotation and sedimentation methods (77%; $n=17$), or purpose or opportunistic necropsies (26%; $n=6$). Four studies (17%) validated their coprological findings by opportunistic necropsies and fecal cultures (Gillespie et al. 2005; Gillespie and Chapman 2006, 2008), or with molecular methods in targeted helminth species (Kiene et al. 2021).

Research questions

Variations in infection rates in helminth communities in small mammals living in altered and natural habitats

Parasite prevalence Of 22 articles that assessed prevalence, nine studies (39%) concluded that the presence of a given helminth infection significantly increased in small mammals living in altered (degraded or fragmented) habitats compared to that in more natural areas (Gillespie et al. 2005; Gillespie and Chapman 2006, 2008; Trejo-Macías et al. 2007; Mbora et al. 2009; Hillman et al. 2017; Costa et al. 2019; de Winter et al. 2020; Fernando et al. 2022). In such studies, helminths with significant increase in prevalence involved monoxenous nematodes such as *Strongyloides fuelleborni* Blackie 1932, *Stilestrongylus freitasi* Durette-Desset 1968, *Trichuris* sp., *Oesophagostomum* sp., *Lemuricola* sp., *Tripanoxyuris* sp., Strongylida, and Rhabditida and certain heteroxenous species, including *Physaloptera* sp., *Linstowinema* sp., and Trematoda. On the other hand, one study (4%) reported a significant decrease in prevalence for some helminth taxa in small mammals inhabiting more altered settings, and helminth species comprised monoxenous nematodes (i.e., *Trichuris* sp., *Strongyloides* sp.) (Barelli et al. 2020). In addition, seven studies (30%) displayed varied results of helminth infections in small mammals inhabiting altered habitats, in which prevalence rates of some species increased while others decreased, showing no patterns regarding parasite

species life cycles and the effect of habitat alteration (Wells et al. 2007; Froeschke and Matthee 2014; Rakotoniaina et al. 2016; Helenbrook et al. 2017; Anders et al. 2019; Kiene et al. 2021; Sáez-Durán et al. 2021). Five reports (22%) did not found any correlation between infection prevalence and habitat quality (Martínez-Mota et al. 2018; Cardoso et al. 2019; Barelli et al. 2021; Hurtado et al. 2021; Riquelme et al. 2021). Odds ratios of the infection risk per helminth species in small mammals in altered and non-altered are shown in Figs. 3, 4, 5, and 6, in accordance with types of life cycles, based on data retrieved from identified studies. In these plots, it can be observed that there are no explicit patterns in prevalence rates of helminths species regarding the type of life cycle and the habitat quality in small mammals. Substantial heterogeneity among studies was observed in studies in all plots, in which the I^2 ranged from 51 to 77%, chi^2 test ($p < 0.001$).

Parasite burden Of 10 studies that assessed parasite burden, five studies ($n = 50\%$) reported a significant increase in burden of helminths in small mammals living in most altered habitats compared with those in natural habitats (Froeschke and Matthee 2014; Santicchia et al. 2015; Cardoso et al. 2016; Barelli et al. 2020; Fernando et al. 2022). From these studies, an increase in parasite burden was observed in the monoxenous nematode *Strongyloides* spp. (Barelli et al. 2020; Fernando et al. 2022) and in overall helminth burden

(Froeschke and Matthee 2014; Santicchia et al. 2015; Cardoso et al. 2019). In two studies (20%), the parasite burden exhibited contrasting results in accordance with parasite species, in which, for example, some monoxenous nematodes (e.g., *Heligmosomoides kurilensis* Nadtochi, 1966, *Heterakis spumosa* Schneider, 1866, and *S. freitasi*) and certain heteroxenous species (e.g., Cestoda) increased in abundance in altered habitats, but other species decreased in burden such as *Syphacia agraria* Sharpilo 1973, *Heligmonoides speciosus* Konno 1958, and *Rodentolepis akodontis* Rêgo 1967 (Anders et al. 2019; Costa et al. 2019). On the other hand, in one study (10%), it was reported a decrease in burden for both monoxenous (i.e., strongylids) and heteroxenous (i.e., spirurids and cestodes) helminths in small mammals living in more altered habitats than in natural non-disturbed areas (Wells et al. 2007). There was no correlation between parasite burden and habitat quality in two studies (Mbora et al. 2009; de Winter et al. 2020).

Parasite richness Of 14 studies that evaluated parasite species richness, five studies (36%) found an increased parasite richness in small mammals living in more altered habitats (Gillespie et al. 2005; Wells et al. 2007; Gillespie and Chapman 2008; Sáez-Durán et al. 2021; Fernando et al. 2022). Conversely, three studies (21%) reported a decrease in parasite richness indexes in small mammals inhabiting more altered and smaller areas (Cardoso et al. 2016; Anders et al.

Study	Helminth	Host	OR	Odds Ratio	95%–CI	Weight (random)
Sáez–Durán et al. (2021)	*Aspiculuris tetraptera*	*Apodemus sylvaticus*	0.66		[0.18; 2.45]	6.7%
de Winter et al. (2020)	*Callistoura sp.*	*Eulemur spp.*	0.20		[0.08; 0.51]	8.1%
Barelli et al. (2019)	*Colobenterobius sp.*	*Procolobus gordonorum*	0.59		[0.05; 6.72]	3.7%
Gillespie et al. (2008)	*Colobenterobius sp.*	*Procolobus rufomitratus*	0.90		[0.24; 3.43]	6.6%
Fernando et al. (2022)	*Enterobius sp.*	*Macaca sinica sinica*	0.32		[0.01; 8.26]	2.4%
Hurtado et al. (2021)	*Heteromoxyuris sp.*	*Dipodomys merriami*	1.00		[0.06; 16.26]	3.1%
Rakotoniaina et al. (2016)	*Lemuricola sp.*	*Cheirogaleus medius*	9.91		[0.57; 173.11]	3.0%
Rakotoniaina et al. (2016)	*Lemuricola sp.*	*Microcebus murinus*	1.19		[0.06; 22.22]	2.9%
de Winter et al. (2020)	*Lemuricola sp.*	*Eulemur spp.*	28.93		[2.77; 302.53]	3.8%
Rakotoniaina et al. (2016)	*Opisthorchis sp.*	*Microcebus murinus*	1.39		[0.05; 35.64]	2.5%
Rakotoniaina et al. (2016)	*Oxyuridae*	*Cheirogaleus medius*	1.77		[0.19; 16.20]	4.1%
Rakotoniaina et al. (2016)	*Oxyuridae*	*Microcebus murinus*	0.12		[0.02; 0.91]	4.6%
Anders et al. (2019)	*Syphacia agraria*	*Apodemus speciosus*	0.02		[0.00; 0.45]	2.9%
Anders et al. (2019)	*Syphacia emileromani*	*Apodemus speciosus*	0.28		[0.01; 6.89]	2.5%
Sáez–Durán et al. (2021)	*Syphacia frederici*	*Apodemus sylvaticus*	0.64		[0.39; 1.05]	9.5%
Riquelme et al. (2021)	*Syphacia sp.*	*Abrothrix longipilis*	0.36		[0.03; 4.11]	3.7%
Riquelme et al. (2021)	*Syphacia sp.*	*Abrothrix olivacea*	1.53		[0.05; 47.40]	2.2%
Riquelme et al. (2021)	*Syphacia sp.*	*Oligoryzomys longicaudatus*	1.05		[0.03; 34.57]	2.2%
Froeschke et al. (2014)	*Syphacia sp.*	*Rhabdomys pumilio*	1.00		[0.63; 1.59]	9.5%
Sáez–Durán et al. (2021)	*Syphacia stroma*	*Apodemus sylvaticus*	4.16		[2.44; 7.09]	9.4%
Trejo–Macías et al. (2007)	*Trypanoxyuris sp.*	*Alouatta palliata mexicana*	1.17		[0.32; 4.22]	6.8%
Common effect model			1.07		[0.86; 1.33]	––
Random effects model			0.87		[0.49; 1.56]	100.0%

Heterogeneity: $I^2 = 69\%$, $\chi^2_{20} = 65.55$ ($p < 0.01$)

0.01 0.1 1 10 100

Fig. 3 Forest plot indicating the effects of habitat alteration for monoxenous ageohelminths in small mammals living in altered and natural habitats from reviewed publications

Study	Helminth	Host	OR	Odds Ratio	95%–CI	Weight (random)
Rakotoniaina et al. (2016)	*Ascaris sp.*	*Cheirogaleus medius*	2.28		[0.43; 12.03]	3.1%
Rakotoniaina et al. (2016)	*Ascaris sp.*	*Microcebus murinus*	2.72		[1.02; 7.24]	5.1%
Fernando et al. (2022)	*Ascaris sp.*	*Macaca sinica sinica*	8.20		[0.40; 169.90]	1.3%
Fernando et al. (2022)	*Ascaris sp.*	*Macaca sinica opisthomelas*	5.54		[0.25; 123.08]	1.3%
Gillespie et al. (2008)	*Ascaris sp.*	*Procolobus rufomitratus*	11.64		[0.61; 220.64]	1.4%
Gillespie et al. (2008)	*Ascaris sp.*	*Colobus guereza*	14.72		[0.81; 266.46]	1.4%
Mbora et al. (2009)	*Heterakis spp.*	*Cercocebus galeritus*	0.53		[0.28; 1.02]	6.2%
Anders et al. (2019)	*Heterakis spumosa*	*Apodemus speciosus*	0.75		[0.23; 2.42]	4.5%
Mbora et al. (2009)	*Toxascaris spp.*	*Cercocebus galeritus*	1.51		[0.09; 25.64]	1.5%
Mbora et al. (2009)	*Toxocara spp.*	*Cercocebus galeritus*	1.20		[0.03; 55.48]	0.9%
Sáez–Durán et al. (2021)	*Trichuris muris*	*Apodemus sylvaticus*	3.53		[1.55; 8.03]	5.6%
Barelli et al. (2019)	*Trichuris sp.*	*Procolobus gordonorum*	0.42		[0.22; 0.83]	6.2%
Rakotoniaina et al. (2016)	*Trichuris sp.*	*Cheirogaleus medius*	0.27		[0.02; 4.88]	1.4%
Rakotoniaina et al. (2016)	*Trichuris sp.*	*Microcebus murinus*	0.54		[0.16; 1.85]	4.2%
Fernando et al. (2022)	*Trichuris sp.*	*Macaca sinica aurifrons*	1.59		[0.24; 10.70]	2.6%
Fernando et al. (2022)	*Trichuris sp.*	*Macaca sinica sinica*	1.89		[0.38; 9.27]	3.3%
Fernando et al. (2022)	*Trichuris sp.*	*Macaca sinica opisthomelas*	3.15		[0.12; 82.16]	1.2%
Gillespie et al. (2005)	*Trichuris sp.*	*Cercopithecus ascanius*	6.41		[2.90; 14.15]	5.7%
Gillespie et al. (2005)	*Trichuris sp.*	*Piliocolobus tephrosceles*	1.19		[0.80; 1.76]	7.0%
Gillespie et al. (2005)	*Trichuris sp.*	*Colobus guereza*	0.72		[0.44; 1.16]	6.8%
Gillespie et al. (2008)	*Trichuris sp.*	*Procolobus rufomitratus*	1.78		[1.37; 2.31]	7.3%
Gillespie et al. (2008)	*Trichuris sp.*	*Colobus guereza*	1.71		[0.73; 4.01]	5.5%
Froeschke et al. (2014)	*Trichuris sp.*	*Rhabdomys pumilio*	0.43		[0.04; 4.56]	1.9%
Mbora et al. (2009)	*Trichuris spp.*	*Cercocebus galeritus*	4.50		[0.49; 41.55]	2.1%
Hillman et al. (2017)	*Trichuris spp.*	*Isoodon obesulus*	2.06		[1.27; 3.32]	6.8%
Barelli et al. (2020)	*Trichuris sp.*	*Procolobus gordonorum*	0.39		[0.17; 0.90]	5.6%
Common effect model			**1.40**		**[1.21; 1.61]**	**––**
Random effects model			**1.42**		**[0.97; 2.09]**	**100.0%**

Heterogeneity: $I^2 = 68\%$, $\chi^2_{25} = 78.24$ ($p < 0.01$)
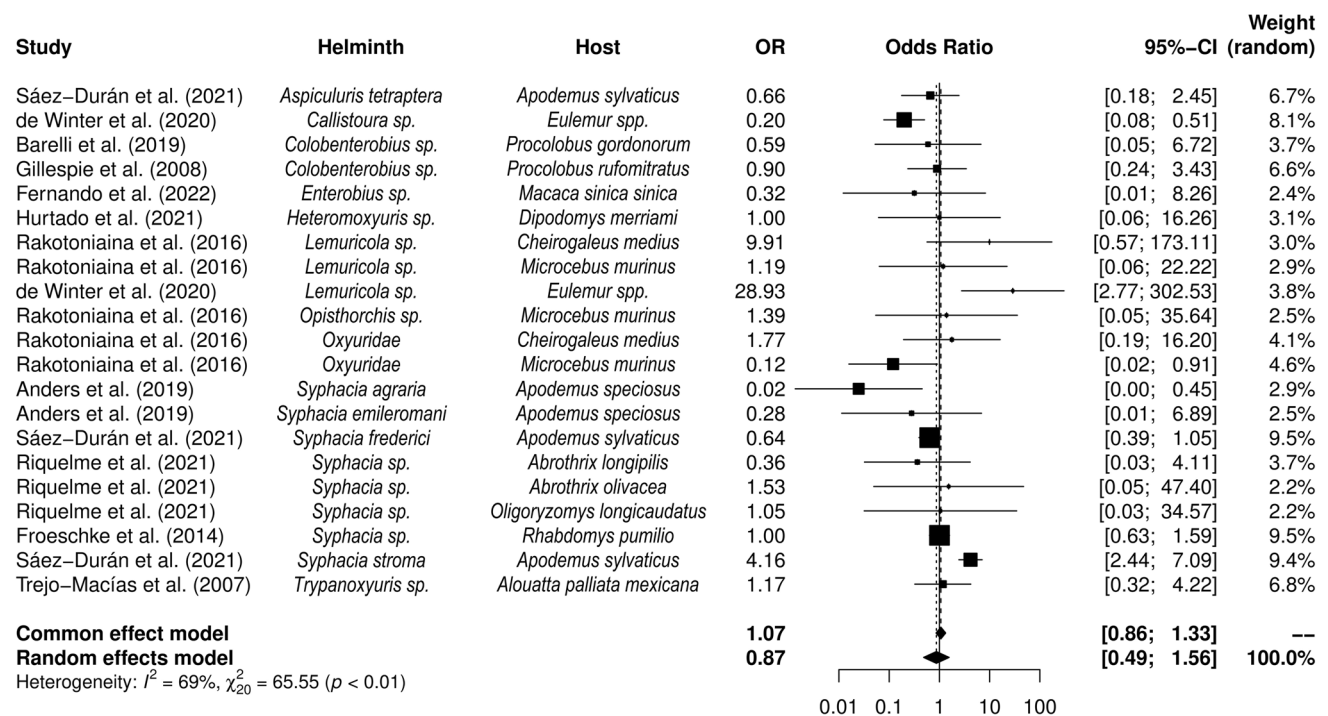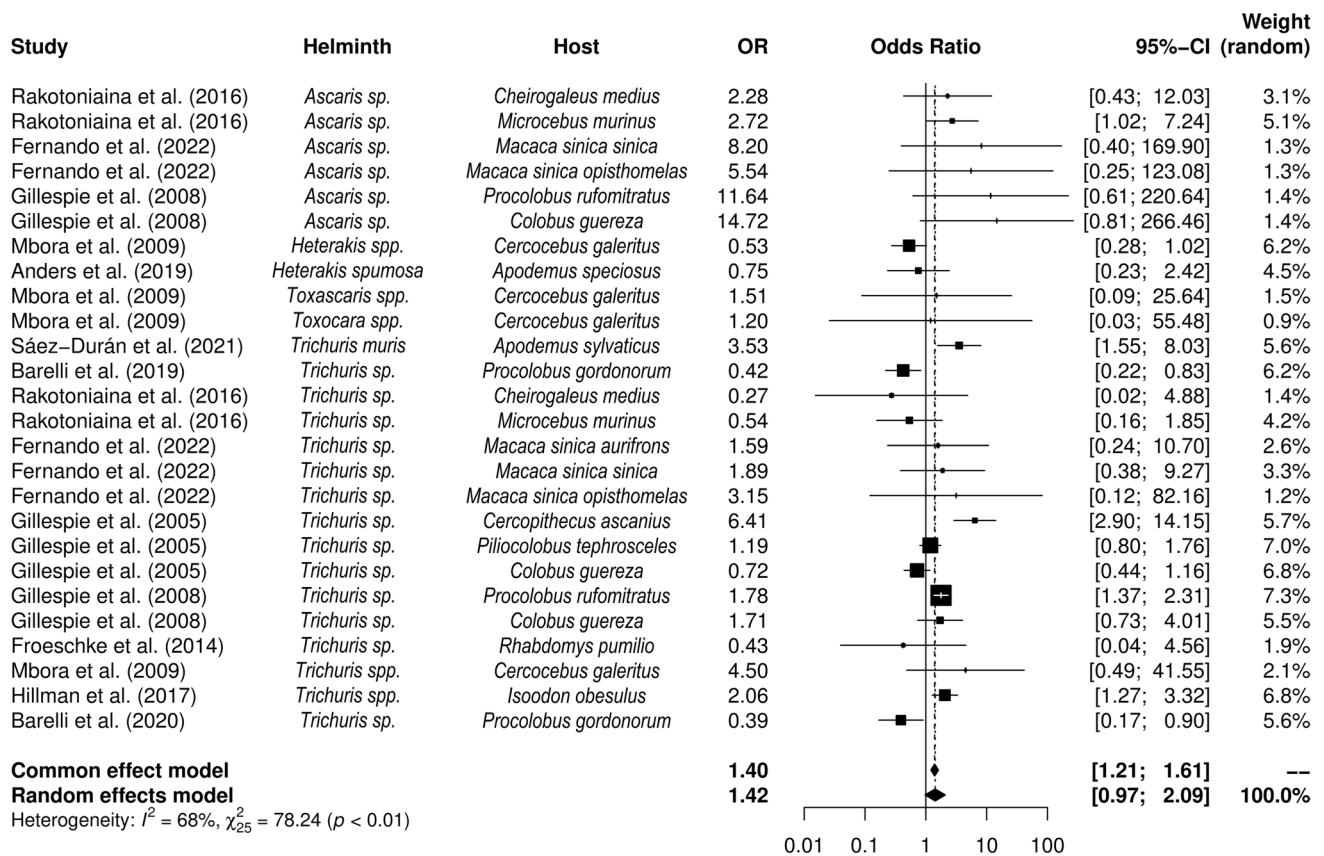
0.01 0.1 1 10 100

Fig. 4 Forest plot indicating the effects of habitat alteration for monoxenous pseudohelminths in small mammals living in altered and natural habitats from reviewed publications

2019; Barelli et al. 2020). In one study, the helminth richness was higher in only crop fragments compared to natural forest, but it was lower than that in livestock and urban fragments (Froeschke and Matthee 2014). Five studies ($n = 36\%$) did not found any statistical relationship between the habitat type and parasite species richness (Trejo-Macías et al. 2007; Rakotoniaina et al. 2016; Helenbrook et al. 2017; Martínez-Mota et al. 2018; Barelli et al. 2021).

Parasite diversity Indexes of helminth diversity showed no consistent pattern in reviewed articles. In a single study, Shannon's diversity index was higher in rural disturbed areas than in natural habitats (Anders et al. 2019). Conversely, in other reports, diversity indexes (e.g., Shannon's diversity and Whittaker indexes) were higher in continuous natural forests (Trejo-Macías et al. 2007), or they did not show correlation (Costa et al. 2019; Sáez-Durán et al. 2021).

Changes in environmental and host factors that influence variations in the community of helminth in small mammals in altered habitats

Vegetation condition Four papers (17%) investigated the vegetation characteristics in relation to habitat alteration and helminth infection rates in small mammals. Helenbrook et al. (2017) concluded that *Controrchis* sp. that parasitizes *Alouatta palliata aequatorialis* Festa 1903 was more likely to be found in forests showing lower levels of alteration (i.e., higher percentage of trees greater than 40-cm DBH and/ or basal area) in Ecuador. In Madagascar, the vegetation clearance (e.g., low tree density, seedlings, and saplings) was negatively associated with *Strongyloides* sp., Subuluroidea, and Spiruromorpha, as well as the forest maturation index (i.e., measured by the number of cut trees, seedlings, saplings, and lianas) was negatively correlated with
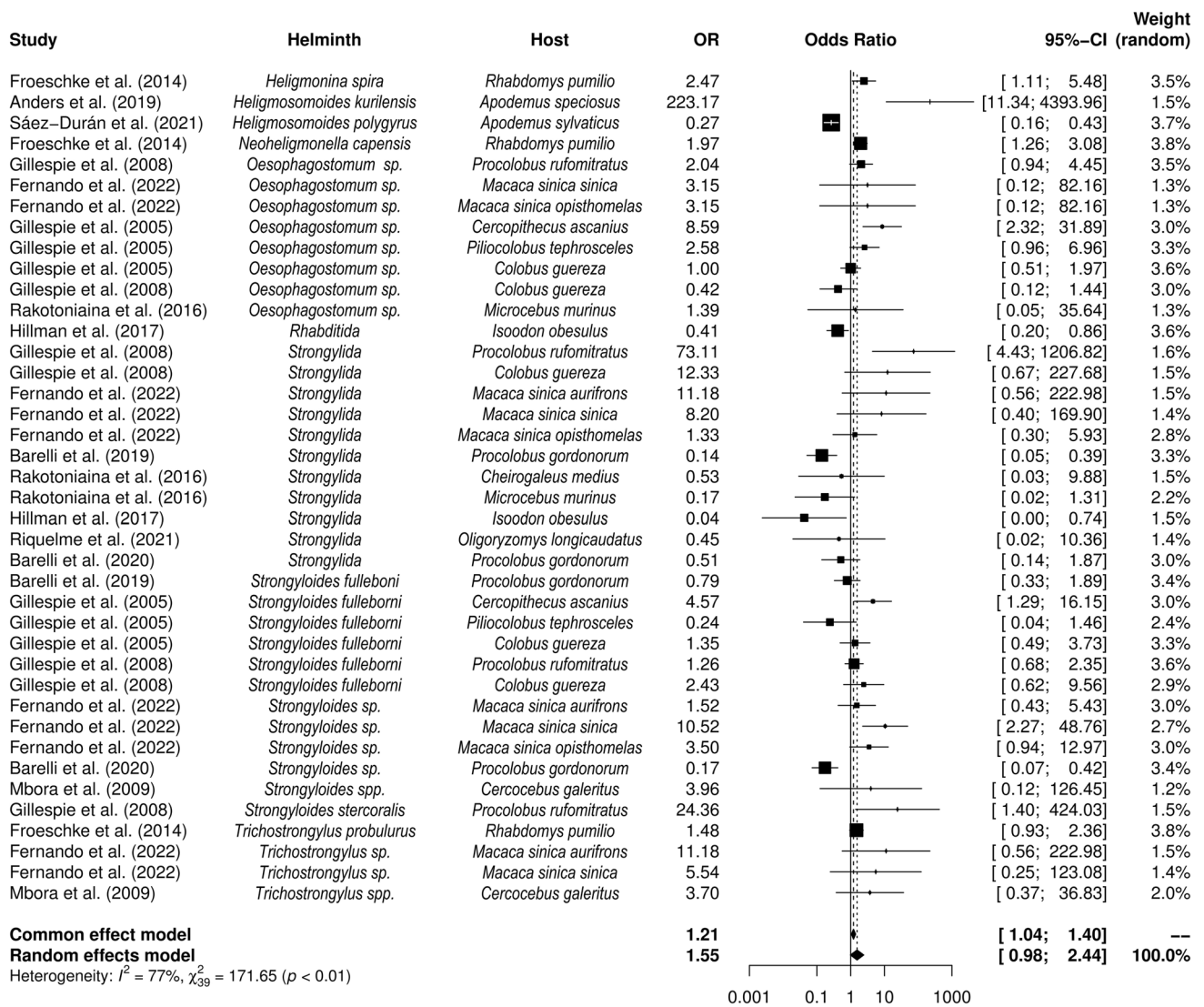
Study	Helminth	Host	OR	Odds Ratio	95%–CI	Weight (random)
Froeschke et al. (2014)	*Heligmonina spira*	*Rhabdomys pumilio*	2.47		[1.11; 5.48]	3.5%
Anders et al. (2019)	*Heligmosomoides kurilensis*	*Apodemus speciosus*	223.17		[11.34; 4393.96]	1.5%
Sáez–Durán et al. (2021)	*Heligmosomoides polygyrus*	*Apodemus sylvaticus*	0.27		[0.16; 0.43]	3.7%
Froeschke et al. (2014)	*Neoheligmonella capensis*	*Rhabdomys pumilio*	1.97		[1.26; 3.08]	3.8%
Gillespie et al. (2008)	*Oesophagostomum* sp.	*Procolobus rufomitratus*	2.04		[0.94; 4.45]	3.5%
Fernando et al. (2022)	*Oesophagostomum* sp.	*Macaca sinica sinica*	3.15		[0.12; 82.16]	1.3%
Fernando et al. (2022)	*Oesophagostomum* sp.	*Macaca sinica opisthomelas*	3.15		[0.12; 82.16]	1.3%
Gillespie et al. (2005)	*Oesophagostomum* sp.	*Cercopithecus ascanius*	8.59		[2.32; 31.89]	3.0%
Gillespie et al. (2005)	*Oesophagostomum* sp.	*Piliocolobus tephrosceles*	2.58		[0.96; 6.96]	3.3%
Gillespie et al. (2005)	*Oesophagostomum* sp.	*Colobus guereza*	1.00		[0.51; 1.97]	3.6%
Gillespie et al. (2008)	*Oesophagostomum* sp.	*Colobus guereza*	0.42		[0.12; 1.44]	3.0%
Rakotoniaina et al. (2016)	*Oesophagostomum* sp.	*Microcebus murinus*	1.39		[0.05; 35.64]	1.3%
Hillman et al. (2017)	*Rhabditida*	*Isoodon obesulus*	0.41		[0.20; 0.86]	3.6%
Gillespie et al. (2008)	*Strongylida*	*Procolobus rufomitratus*	73.11		[4.43; 1206.82]	1.6%
Gillespie et al. (2008)	*Strongylida*	*Colobus guereza*	12.33		[0.67; 227.68]	1.5%
Fernando et al. (2022)	*Strongylida*	*Macaca sinica aurifrons*	11.18		[0.56; 222.98]	1.5%
Fernando et al. (2022)	*Strongylida*	*Macaca sinica sinica*	8.20		[0.40; 169.90]	1.4%
Fernando et al. (2022)	*Strongylida*	*Macaca sinica opisthomelas*	1.33		[0.30; 5.93]	2.8%
Barelli et al. (2019)	*Strongylida*	*Procolobus gordonorum*	0.14		[0.05; 0.39]	3.3%
Rakotoniaina et al. (2016)	*Strongylida*	*Cheirogaleus medius*	0.53		[0.03; 9.88]	1.5%
Rakotoniaina et al. (2016)	*Strongylida*	*Microcebus murinus*	0.17		[0.02; 1.31]	2.2%
Hillman et al. (2017)	*Strongylida*	*Isoodon obesulus*	0.04		[0.00; 0.74]	1.5%
Riquelme et al. (2021)	*Strongylida*	*Oligoryzomys longicaudatus*	0.45		[0.02; 10.36]	1.4%
Barelli et al. (2020)	*Strongylida*	*Procolobus gordonorum*	0.51		[0.14; 1.87]	3.0%
Barelli et al. (2019)	*Strongyloides fulleboni*	*Procolobus gordonorum*	0.79		[0.33; 1.89]	3.4%
Gillespie et al. (2005)	*Strongyloides fulleborni*	*Cercopithecus ascanius*	4.57		[1.29; 16.15]	3.0%
Gillespie et al. (2005)	*Strongyloides fulleborni*	*Piliocolobus tephrosceles*	0.24		[0.04; 1.46]	2.4%
Gillespie et al. (2005)	*Strongyloides fulleborni*	*Colobus guereza*	1.35		[0.49; 3.73]	3.3%
Gillespie et al. (2008)	*Strongyloides fulleborni*	*Procolobus rufomitratus*	1.26		[0.68; 2.35]	3.6%
Gillespie et al. (2008)	*Strongyloides fulleborni*	*Colobus guereza*	2.43		[0.62; 9.56]	2.9%
Fernando et al. (2022)	*Strongyloides* sp.	*Macaca sinica aurifrons*	1.52		[0.43; 5.43]	3.0%
Fernando et al. (2022)	*Strongyloides* sp.	*Macaca sinica sinica*	10.52		[2.27; 48.76]	2.7%
Fernando et al. (2022)	*Strongyloides* sp.	*Macaca sinica opisthomelas*	3.50		[0.94; 12.97]	3.0%
Barelli et al. (2020)	*Strongyloides* sp.	*Procolobus gordonorum*	0.17		[0.07; 0.42]	3.4%
Mbora et al. (2009)	*Strongyloides* spp.	*Cercocebus galeritus*	3.96		[0.12; 126.45]	1.2%
Gillespie et al. (2008)	*Strongyloides stercoralis*	*Procolobus rufomitratus*	24.36		[1.40; 424.03]	1.5%
Froeschke et al. (2014)	*Trichostrongylus probulurus*	*Rhabdomys pumilio*	1.48		[0.93; 2.36]	3.8%
Fernando et al. (2022)	*Trichostrongylus* sp.	*Macaca sinica aurifrons*	11.18		[0.56; 222.98]	1.5%
Fernando et al. (2022)	*Trichostrongylus* sp.	*Macaca sinica sinica*	5.54		[0.25; 123.08]	1.4%
Mbora et al. (2009)	*Trichostrongylus* spp.	*Cercocebus galeritus*	3.70		[0.37; 36.83]	2.0%
Common effect model			1.21		[1.04; 1.40]	––
Random effects model			1.55		[0.98; 2.44]	100.0%

Heterogeneity: $I^2 = 77\%$, $\chi^2_{39} = 171.65$ ($p < 0.01$)

0.001 0.1 1 10 1000

Fig. 5 Forest plot indicating the effects of habitat alteration for monoxenous geohelminths in small mammals living in altered and natural habitats from reviewed publications

the presence of Enterobiinae gen. sp. (Kiene et al. 2021). Also, the canopy cover was negatively associated with the prevalence of *Stilestrongylus aculeata* Travassos 1918 and *Canaania obesa* Travassos 1944 in a rodent community in Brazil (Cardoso et al. 2016). Moreover, Gillespie and Chapman (2006) found that stump density was significantly associated with Strongylida and Rhabditida prevalence.

Degree of alteration The relationship between levels of habitat alteration (i.e., disturbance and/or fragmentation) and helminth infection rates in small mammals was assessed in 6 papers (26%). In this context, the size of study areas (e.g., fragments or forests) was positively associated with the presence of *Strongyloides* sp. and Subuluroidea in primate and rodent communities in Madagascar

(Kiene et al. 2021), but it was negatively correlated with Strongylida, Rhabditida (Gillespie and Chapman 2006), and *Trichuris* sp. (Gillespie and Chapman 2008) in primates in Uganda. No correlations were reported in the other two papers (Cardoso et al. 2016; Martínez-Mota et al. 2018). Also, the proximity of studied areas to any nearest anthropogenic element (e.g., road, agricultural field, village) was evaluated in three publications. Martínez-Mota et al. (2018) and Kiene et al. (2021) found positive correlation between the distance from fragments to forest edge/villages and the prevalence of *Strongyloides* sp., Subuluroidea, and overall parasitism. In counterpart, one study did not report any association between anthropogenic proximity and parasitism in helminths in small mammals (Helenbrook et al. 2017).
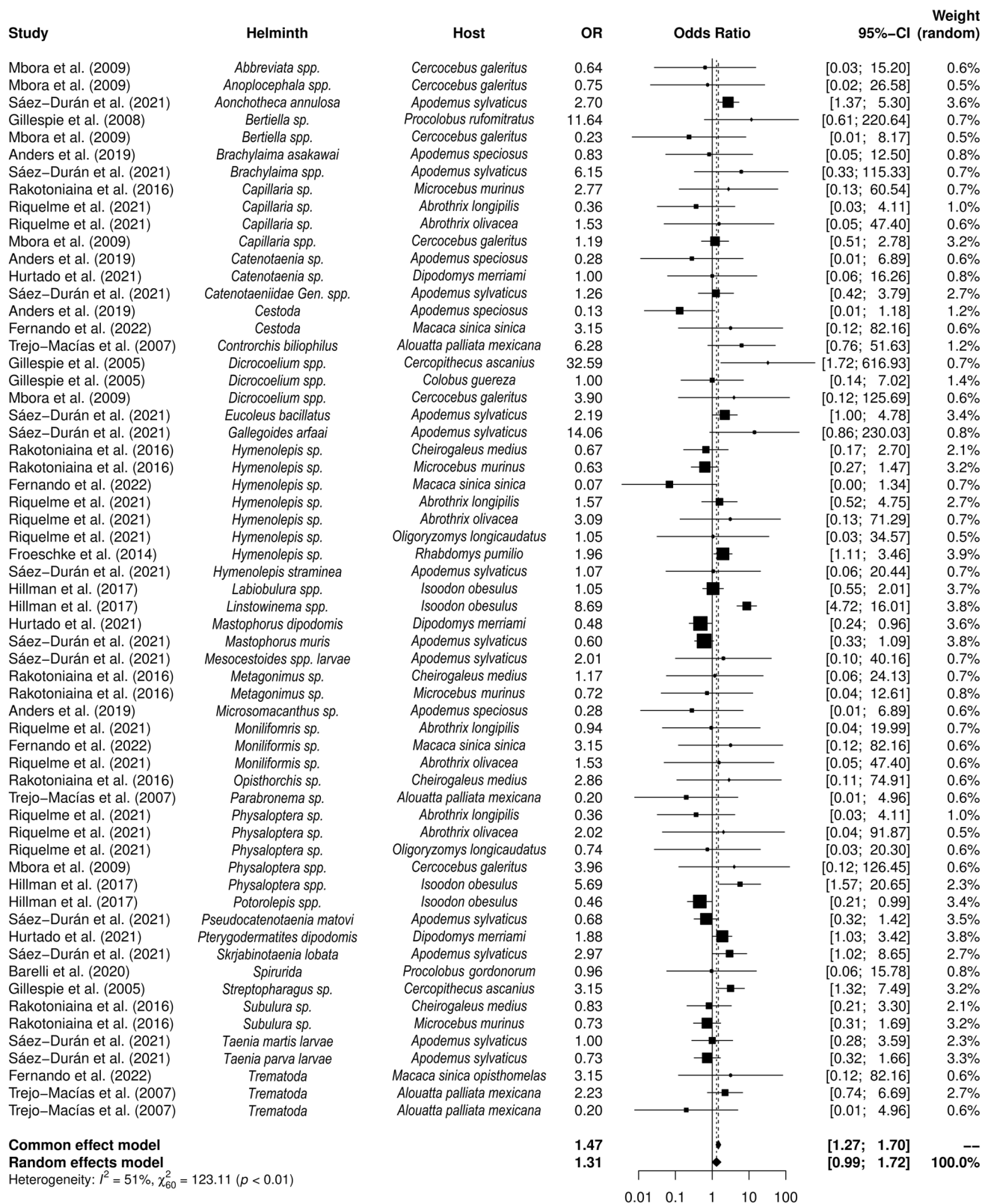
Study	Helminth	Host	OR	Odds Ratio	95%–CI	Weight (random)
Mbora et al. (2009)	*Abbreviata spp.*	*Cercocebus galeritus*	0.64		[0.03; 15.20]	0.6%
Mbora et al. (2009)	*Anoplocephala spp.*	*Cercocebus galeritus*	0.75		[0.02; 26.58]	0.5%
Sáez–Durán et al. (2021)	*Aonchotheca annulosa*	*Apodemus sylvaticus*	2.70		[1.37; 5.30]	3.6%
Gillespie et al. (2008)	*Bertiella sp.*	*Procolobus rufomitratus*	11.64		[0.61; 220.64]	0.7%
Mbora et al. (2009)	*Bertiella spp.*	*Cercocebus galeritus*	0.23		[0.01; 8.17]	0.5%
Anders et al. (2019)	*Brachylaima asakawai*	*Apodemus speciosus*	0.83		[0.05; 12.50]	0.8%
Sáez–Durán et al. (2021)	*Brachylaima spp.*	*Apodemus sylvaticus*	6.15		[0.33; 115.33]	0.7%
Rakotoniaina et al. (2016)	*Capillaria sp.*	*Microcebus murinus*	2.77		[0.13; 60.54]	0.7%
Riquelme et al. (2021)	*Capillaria sp.*	*Abrothrix longipilis*	0.36		[0.03; 4.11]	1.0%
Riquelme et al. (2021)	*Capillaria sp.*	*Abrothrix olivacea*	1.53		[0.05; 47.40]	0.6%
Mbora et al. (2009)	*Capillaria spp.*	*Cercocebus galeritus*	1.19		[0.51; 2.78]	3.2%
Anders et al. (2019)	*Catenotaenia sp.*	*Apodemus speciosus*	0.28		[0.01; 6.89]	0.6%
Hurtado et al. (2021)	*Catenotaenia sp.*	*Dipodomys merriami*	1.00		[0.06; 16.26]	0.8%
Sáez–Durán et al. (2021)	*Catenotaeniidae Gen. spp.*	*Apodemus sylvaticus*	1.26		[0.42; 3.79]	2.7%
Anders et al. (2019)	*Cestoda*	*Apodemus speciosus*	0.13		[0.01; 1.18]	1.2%
Fernando et al. (2022)	*Cestoda*	*Macaca sinica sinica*	3.15		[0.12; 82.16]	0.6%
Trejo–Macías et al. (2007)	*Controrchis biliophilus*	*Alouatta palliata mexicana*	6.28		[0.76; 51.63]	1.2%
Gillespie et al. (2005)	*Dicrocoelium spp.*	*Cercopithecus ascanius*	32.59		[1.72; 616.93]	0.7%
Gillespie et al. (2005)	*Dicrocoelium spp.*	*Colobus guereza*	1.00		[0.14; 7.02]	1.4%
Mbora et al. (2009)	*Dicrocoelium spp.*	*Cercocebus galeritus*	3.90		[0.12; 125.69]	0.6%
Sáez–Durán et al. (2021)	*Eucoleus bacillatus*	*Apodemus sylvaticus*	2.19		[1.00; 4.78]	3.4%
Sáez–Durán et al. (2021)	*Gallegoides arfaai*	*Apodemus sylvaticus*	14.06		[0.86; 230.03]	0.8%
Rakotoniaina et al. (2016)	*Hymenolepis sp.*	*Cheirogaleus medius*	0.67		[0.17; 2.70]	2.1%
Rakotoniaina et al. (2016)	*Hymenolepis sp.*	*Microcebus murinus*	0.63		[0.27; 1.47]	3.2%
Fernando et al. (2022)	*Hymenolepis sp.*	*Macaca sinica sinica*	0.07		[0.00; 1.34]	0.7%
Riquelme et al. (2021)	*Hymenolepis sp.*	*Abrothrix longipilis*	1.57		[0.52; 4.75]	2.7%
Riquelme et al. (2021)	*Hymenolepis sp.*	*Abrothrix olivacea*	3.09		[0.13; 71.29]	0.7%
Riquelme et al. (2021)	*Hymenolepis sp.*	*Oligoryzomys longicaudatus*	1.05		[0.03; 34.57]	0.5%
Froeschke et al. (2014)	*Hymenolepis sp.*	*Rhabdomys pumilio*	1.96		[1.11; 3.46]	3.9%
Sáez–Durán et al. (2021)	*Hymenolepis straminea*	*Apodemus sylvaticus*	1.07		[0.06; 20.44]	0.7%
Hillman et al. (2017)	*Labiobulura sp.*	*Isoodon obesulus*	1.05		[0.55; 2.01]	3.7%
Hillman et al. (2017)	*Linstowinema spp.*	*Isoodon obesulus*	8.69		[4.72; 16.01]	3.8%
Hurtado et al. (2021)	*Mastophorus dipodomis*	*Dipodomys merriami*	0.48		[0.24; 0.96]	3.6%
Sáez–Durán et al. (2021)	*Mastophorus muris*	*Apodemus sylvaticus*	0.60		[0.33; 1.09]	3.8%
Sáez–Durán et al. (2021)	*Mesocestoides spp. larvae*	*Apodemus sylvaticus*	2.01		[0.10; 40.16]	0.7%
Rakotoniaina et al. (2016)	*Metagonimus sp.*	*Cheirogaleus medius*	1.17		[0.06; 24.13]	0.7%
Rakotoniaina et al. (2016)	*Metagonimus sp.*	*Microcebus murinus*	0.72		[0.04; 12.61]	0.8%
Anders et al. (2019)	*Microsomacanthus sp.*	*Apodemus speciosus*	0.28		[0.01; 6.89]	0.6%
Riquelme et al. (2021)	*Moniliformis sp.*	*Abrothrix longipilis*	0.94		[0.04; 19.99]	0.7%
Fernando et al. (2022)	*Moniliformis sp.*	*Macaca sinica sinica*	3.15		[0.12; 82.16]	0.6%
Riquelme et al. (2021)	*Moniliformis sp.*	*Abrothrix olivacea*	1.53		[0.05; 47.40]	0.6%
Rakotoniaina et al. (2016)	*Opisthorchis sp.*	*Cheirogaleus medius*	2.86		[0.11; 74.91]	0.6%
Trejo–Macías et al. (2007)	*Parabronema sp.*	*Alouatta palliata mexicana*	0.20		[0.01; 4.96]	0.6%
Riquelme et al. (2021)	*Physaloptera sp.*	*Abrothrix longipilis*	0.36		[0.03; 4.11]	1.0%
Riquelme et al. (2021)	*Physaloptera sp.*	*Abrothrix olivacea*	2.02		[0.04; 91.87]	0.5%
Riquelme et al. (2021)	*Physaloptera sp.*	*Oligoryzomys longicaudatus*	0.74		[0.03; 20.30]	0.6%
Mbora et al. (2009)	*Physaloptera spp.*	*Cercocebus galeritus*	3.96		[0.12; 126.45]	0.6%
Hillman et al. (2017)	*Physaloptera spp.*	*Isoodon obesulus*	5.69		[1.57; 20.65]	2.3%
Hillman et al. (2017)	*Potorolepis spp.*	*Isoodon obesulus*	0.46		[0.21; 0.99]	3.4%
Sáez–Durán et al. (2021)	*Pseudocatenotaenia matovi*	*Apodemus sylvaticus*	0.68		[0.32; 1.42]	3.5%
Hurtado et al. (2021)	*Pterygodermatites dipodomis*	*Dipodomys merriami*	1.88		[1.03; 3.42]	3.8%
Sáez–Durán et al. (2021)	*Skrjabinotaenia lobata*	*Apodemus sylvaticus*	2.97		[1.02; 8.65]	2.7%
Barelli et al. (2020)	*Spirurida*	*Procolobus gordonorum*	0.96		[0.06; 15.78]	0.8%
Gillespie et al. (2005)	*Streptopharagus sp.*	*Cercopithecus ascanius*	3.15		[1.32; 7.49]	3.2%
Rakotoniaina et al. (2016)	*Subulura sp.*	*Cheirogaleus medius*	0.83		[0.21; 3.30]	2.1%
Rakotoniaina et al. (2016)	*Subulura sp.*	*Microcebus murinus*	0.73		[0.31; 1.69]	3.2%
Sáez–Durán et al. (2021)	*Taenia martis larvae*	*Apodemus sylvaticus*	1.00		[0.28; 3.59]	2.3%
Sáez–Durán et al. (2021)	*Taenia parva larvae*	*Apodemus sylvaticus*	0.73		[0.32; 1.66]	3.3%
Fernando et al. (2022)	*Trematoda*	*Macaca sinica opisthomelas*	3.15		[0.12; 82.16]	0.6%
Trejo–Macías et al. (2007)	*Trematoda*	*Alouatta palliata mexicana*	2.23		[0.74; 6.69]	2.7%
Trejo–Macías et al. (2007)	*Trematoda*	*Alouatta palliata mexicana*	0.20		[0.01; 4.96]	0.6%
Common effect model			**1.47**		**[1.27; 1.70]**	**––**
Random effects model			**1.31**		**[0.99; 1.72]**	**100.0%**

Heterogeneity: $I^2 = 51\%$, $\chi^2_{60} = 123.11$ ($p < 0.01$)

0.01 0.1 1 10 100

Fig. 6 Forest plot indicating the effects of habitat alteration for heteroxenous helminths (i.e., with complex life cycles) in small mammals living in altered and natural habitats from reviewed publications

Abiotic factors Of the evaluated research, abiotic features were assessed in only two studies (9%), which included rainy days, mean temperature, and presence of roots, logs, and rocks. Sáez-Durán et al. (2021) stated that the number of rainy days negatively correlated with the prevalence of heteroxenous helminths infecting *Apodemus sylvaticus* Linnaeus, 1758 only in altered areas and positively correlated with that of monoxenous species in both altered and natural habitats. Also, the mean temperature was positively associated with infections with monoxenous helminths (i.e., geohelminths) in altered areas (Sáez-Durán et al. 2021). Moreover, the presence of roots and logs was positively correlated with infections with *Guerrerostrongylus zetta* Travassos 1937 in a community of rodents in altered and natural areas in Brazil (Cardoso et al. 2016).

Host factors Nine (39%) studies investigated any host condition in relation to helminth infections and habitat alteration. In this sense, body condition was evaluated with different metrics, which included volumetric measurements of body and weight (Wells et al. 2007; Froeschke and Matthee 2014; Anders et al. 2019), the regression of body mass on foot length (Santicchia et al. 2015; Hurtado et al. 2021), and the scaled mass index (SMI) (Kiene et al. 2021). In the USA, a rodent species *Dipodomys merriami* exhibited a lower body condition in parasitized individuals living in natural settings (Hurtado et al. 2021). In addition, four studies reported a positive relationship between body condition (e.g., weight, length, or SMI) and the prevalence or abundance of certain helminth species regardless the type of habitat in which hosts live (Wells et al. 2007; Froeschke and Matthee 2014; Anders et al. 2019; Kiene et al. 2021). No effect between parasitism, body condition, and habitat alteration was observed in one study (Santicchia et al. 2015).

Moreover, host density was evaluated in six studies. It was positively correlated with *Strongyloides stercoralis* Bavay, 1876 in the primate *Piliocolobus tephrosceles* Elliot 1907 in Uganda (Gillespie and Chapman 2006). However, population density was negatively correlated with prevalence of heteroxenous parasites in burned (i.e., altered) areas in the rodent *Apodemus sylvaticus* Linnaeus 1758 in Spain (Sáez-Durán et al. 2021). Also, host density showed no effect regarding helminth infection and habitat alteration in four papers (Trejo-Macías et al. 2007; Gillespie and Chapman 2008; Froeschke and Matthee 2014; Kiene et al. 2021). In addition, the relationship between levels of fecal cortisone and helminth infection rates in altered and natural habitats was evaluated only in one study, in which no correlation was found regarding parasite prevalence and richness (Barelli et al. 2021).

Low host-specific helminths in small mammals inhabiting anthropogenically altered habitats

In five articles (23%), it was addressed the issue on the relationship between anthropogenic habitat alteration and the presence of low host-specific helminths. Higher rates of low host-specific helminth species (e.g., *Strongyloides* sp., *Ascaris* sp., Strongylida) were found in primate host species living in altered environments compared to those in natural areas (Gillespie et al. 2005; Trejo-Macías et al. 2007; Gillespie and Chapman 2008; Helenbrook et al. 2017; Fernando et al. 2022). Such results were attributed to the contamination from domestic animals and human populations that may be acting as reservoirs.

Discussion

In this review, 23 scientific articles were evaluated to compile and summarize the effects of habitat alteration on the structure of helminth communities in small mammals. Evidence on identified articles suggests that variations (i.e., increase or decrease) in rates of helminth infections (e.g., prevalence, abundance, and richness) are context dependent, and generalizations cannot be made by considering only the type of life cycles of helminth species. In Fig. 7, a summary of causal hypotheses proposed in the reviewed articles is shown, in which variations in infection rates of monoxenous and heteroxenous helminths can occur in accordance with both extrinsic and intrinsic host impacts and environmental conditions in such altered habitats.

Changes in infection rates of monoxenous helminths

Increase in infections rates

Human-induced habitat alteration may have an impact in both demography and community composition (Patz et al. 2000; Haddad et al. 2015). Because of habitat incompatibility, animals at higher trophic levels are likely to reduce their population sizes and become locally extinct, while generalist species (i.e., those able to inhabit different types of environments and have a varied diet) are more likely to thrive (i.e., ecological release) (Martinson and Fagan 2014; Keinath et al. 2017). Also, animal populations tend to be more clumped in altered habitats due to lack of dispersal opportunities, which may increase contact with conspecifics (i.e., encounter augmentation) (Hess et al. 2002; Keesing et al. 2006; Rimbach et al. 2015). Moreover, agricultural activities can induce migration or introduction of non-native hosts and their parasites, hence increasing host diversity and the likelihood of transmission of parasites in native populations. Given the density-dependent transmission of monoxenous helminths in the epidemiological modelling sense (Bush et al. 1997), there may be more probability that propagules (i.e., infective parasite eggs or larvae) of monoxenous helminths are available in the
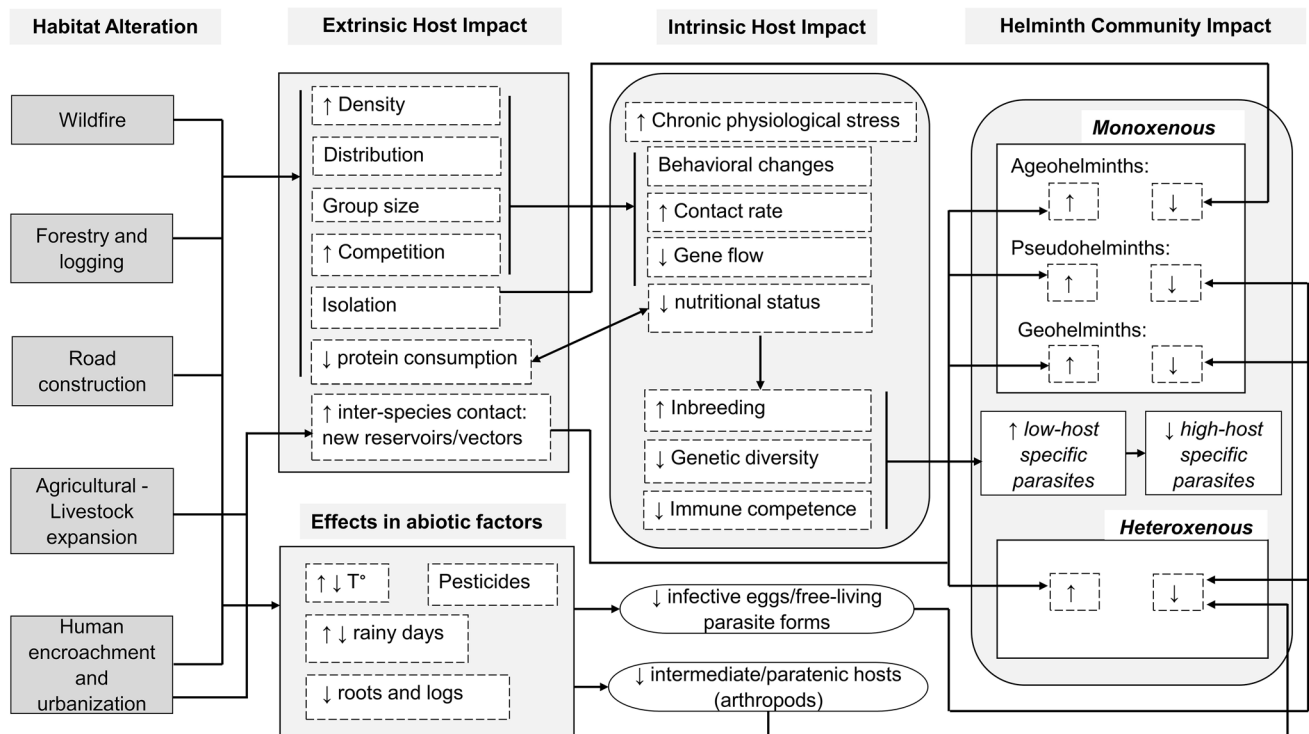
Fig. 7 Hypothesized causal diagram of the impact of habitat alteration on the helminth community structure in small mammals. Arrows indicate likely causal relationship which in some cases may be bi-directional

environment for susceptible hosts that show high population densities in altered habitats, thus increasing parasite transmission rates (Anderson and May 1991; Lafferty and Kuris 1999; Wilson et al. 2002). To illustrate, infection with *S. stercoralis* was positively correlated with the population density of *P. tephrosceles* in Uganda (Gillespie and Chapman 2006). Still, suitable environmental conditions are needed in altered habitats for immature free-living ova/stages of monoxenous helminths to survive and develop, which may include temperature, moisture, humidity, and presence of organic matter (Cardoso et al. 2016; Taylor et al. 2016; Sáez-Durán et al. 2021). For example, Sáez-Durán et al. (2021) concluded that an increase in prevalence and richness of monoxenous helminths in *A. sylvaticus* in burned forest in Spain was related to abiotic changes (e.g., temperature and rain) that may have fostered the survival and development of free-living ova and larvae. In addition, habitat alteration may not only promote population density but also diversity in hosts (Suzán et al. 2012). Consequently, higher infection rates of monoxenous helminths are expected in high-density populations living in altered habitats with appropriate abiotic conditions for parasitic survival and development (Arneberg 2002).

In addition, small mammals inhabiting altered low-quality habitats with high population densities are more prone to show reduced immune response due to long-term distress

(Lafferty and Kuris 1999; Hawley and Altizer 2011). As social competition for food and reproduction costs may be higher in altered habitats, animals could display chronically elevated cortisol levels that induce immune depression (Holmes 1996; Lafferty and Kuris 1999; Saino et al. 2002). Moreover, isolated populations with small sizes may show reduced genetic diversity as a long-term outcome, which can decrease the capacity to mount an efficient immune response and subsequently increase helminth infection susceptibility in populations (Lyles and Dobson 1993; Amos and Harwood 1998; Vandergast et al. 2007). In the reviewed articles, Santicchia et al. (2015) speculated that the finding of a higher abundance of *Trypanoxyuris* (*Rodentoxyuris*) *sciuri* Cameron, 1932 in *Sciurus vulgaris* Linnaeus, 1758 living in fragmented forest compared with those in continuous forests was related to changes in host susceptibility induced by higher stress levels and/or poorer nutritional status and reduced genetic diversity. Moreover, in a study that evaluated the relationship between the diversity of the major histocompatibility complex (MHC) class II and gastrointestinal helminth infection rates in mouse opossums (*Gracilinanus microtarsus* Wagner 1842 and *Marmosops incanus* Lund, 1840) in Brazil, it was found that *M. incanus* exhibited a low diversity of MHC-DAB alleles and a high parasite load, while *G. microtarsus* showed a higher population diversity of MHC-DAB and lower parasite burden (Meyer-Lucht et al. 2010).

Meyer-Lucht et al. (2010) stated that a low MHC polymorphism in *M. incanus* populations may have been related to a recent loss in MHC diversity which may have subsequently led to a lack of resistance alleles and an increased parasite burden. Therefore, poor host body condition and inefficient immune response can also influence higher rates of helminth infections in individuals inhabiting altered habitats in comparison to those living in natural settings (Gulland 1992).

Decrease in infection rates

Alternatively, habitat alteration can promote a variation of the helminth community structure in small mammal populations, in which infection rates of monoxenous helminth species may decrease due to changes in species abundance and environmental conditions (McCallum and Dobson 2002; Keesing et al. 2006; Lafferty 2012; Viana et al. 2014). Theory suggests that modifications on environmental conditions should negatively impact populations dynamics, in which population of specialist wildlife may become isolated in low-quality patches within the landscape (Hess et al. 2002). For directly transmitted helminths to persist, a minimal number of susceptible individuals are needed within their host populations (maintenance population) (Lafferty 2012; Viana et al. 2014). Given the density-dependent transmission for monoxenous helminths, in populations that show reduced sizes, it is likely that infection rates of helminth species are reduced due to encounter reduction (i.e., less availability of infective stages in the environment) (Hess et al. 2002). In case the number of susceptible individuals is below the "critical community size" (i.e., the minimal number of susceptible hosts available for an infection to persist), helminth species could become extinct locally in such population (Anderson and May 1982; Bush and Kennedy 1994; Lafferty and Kuris 1999; Lafferty 2012; Viana et al. 2014). From reviewed studies, Gillespie and Chapman (2006) found that the prevalence of *Strongyloides stercoralis* was positively related to the density of *Piliocolobus tephrosceles* living in fragmented habitats in Uganda. Nevertheless, Bush and Kennedy (1994) argued that extinction of helminth species is somewhat unlikely and would be restricted to highly endangered species because even highly host-specific helminths could show some plasticity to be maintained in less competent hosts until they are re-introduced in their previous populations through migration (Bush and Kennedy 1994).

In addition, unsuitable environmental conditions promoted by anthropogenic intervention are likely to cause a reduction in infection rates of monoxenous helminths (Lafferty and Kuris 1999). In this review, some studies reported a decrease in prevalence for monoxenous nematodes in small mammals living in altered habitats (i.e., *Syphacia agraria*, strongyles, *Strongyloides* spp., *Trichuris*) (Anders et al. 2019; Barelli et al. 2020; Kiene et al. 2021). In such

research, it was stated that lower rates of directly transmitted nematodes may have been related to changes in abiotic conditions and due to the use of pesticides, fertilizers, and anti-helminthics in altered areas. In this context, as free-living developmental stages of monoxenous require favorable environmental conditions to remain viable until they find a suitable host, changes in physical and biochemical features in microhabitats due to anthropogenic alteration may have an impact in their development and transmission (Altizer et al. 2013; Taylor et al. 2016). In particular, lower humidity, higher light exposure, high levels of UV radiation, and elevated temperature in fragmented habitats and edges could preclude the survival of stages of directly and soil-transmitted helminths (Marcogliese and Pietrock 2011; de Winter et al. 2020; Kiene et al. 2021). Other abiotic changes that may influence the helminth community structure could be surface texture, moisture content, biomass, topography, precipitation, and acidification (Loiseau et al. 2012; Marcogliese 2016; Simões et al. 2016). For instance, in a study on lemur and rodent communities in Madagascar, *Strongyloides* sp. infection showed a reduced prevalence in altered forests compared with those living in more continuous forests (Kiene et al. 2021). Kiene et al. (2021) argued that habitat alteration could have affected free-living larvae of *Strongyloides* sp. due to its heterogenic development for which abiotic factors are critical. Likewise, in Brazil, a study on helminth community structure in wild rodents reported that the prevalence of *Stilestrongylus lanfrediae* Souza et al. 2009 was associated with dense understory, *Canaania obesa* Travassos 1944 with open canopy and dense understory, and *Guerrerostrongylus zetta* Travassos 1937 with the presence of roots and logs (Cardoso et al. 2016). Hence, biotic and abiotic conditions could be changed in altered low-quality habitats due to anthropogenic intervention, which could directly impact the survival of free-living ova and larvae of helminths (Altizer et al. 2013; Taylor et al. 2016).

Changes in infection rates of heteroxenous helminths

Increase in infection rates

Anthropogenically modified habitats may also promote the development and availability of certain arthropods (e.g. crickets, cockroaches, beetles) and mollusks (e.g., snails) that act as intermediate hosts for heteroxenous helminths (Lafferty and Kuris 1999). For instance, the prevalence of *Controrchis biliophilus* Price 1929 was higher in subpopulations of *Alouatta palliata mexicana* Merriam, 1902 inhabiting fragmented forests in Mexico (Trejo-Macías et al. 2007). Trejo-Macías et al. (2007) discussed that environmental contamination due to anthropogenic activities such

as agriculture and introduction of domestic animals may foster the presence of intermediate hosts for heteroxenous helminths including invertebrate species. Consequently, an increase in infection rate of certain heteroxenous helminths is likely to occur in small mammal populations living in altered habitats due to increase in host density (i.e., definitive and intermediate), decrease in host susceptibility, and the interplay of environmental conditions for the development of parasitic stages.

Decrease in infection rates

Alternatively, a scenario of parasite diminution is expected for helminths that show indirect life cycles (i.e., heteroxenous) which require specific intermediate hosts to complete their sexual development (Lafferty and Kuris 1999; Lafferty 2012). The disruption of ecological processes in altered habitats may have deleterious effects in species diversity including those that are part of the life cycle of helminths. This could cause a reduction in the prevalence, abundance, and richness of heteroxenous helminth species (Poulin and Morand 2000; Werner and Nunn 2020). For example, Kiene et al. (2021) found that a higher percentage of edge habitat and vegetation clearance was associated with a reduction of the prevalence and richness of Subuluroidea-like eggs (usually heteroxenous) in small mammals in Madagascar. Moreover, this may be particularly true for cestodes, since most studies in this review reported that *Hymenolepis* spp. infection in rodents and primates exhibited a negative correlation between habitat alteration and prevalence rates (Wells et al. 2007; Rakotoniaina et al. 2016; Anders et al. 2019) (see Fig. 6). In this context, in an experimental study in Australia, it was demonstrated that habitat alteration reduced the abundance of an intermediate host (i.e., amphipod *Arcitalitrus sylvaticus* Haswell 1879), which subsequently decreased the transmission of the heteroxenous nematode *Hedruris wogwogensis* Jones & Resasco 2016 in the pale-flecked garden sunskink (*Lampropholis guichenoti* Duméril and Bibron 1839) (Resasco et al. 2019).

Promotion of low host-specific helminths

Human-created habitat alteration may decrease the occurrence of highly host-specific helminths, while increasing the infection rates of low host-specific parasites (Bush and Kennedy 1994; Dharmarajan et al. 2021). As explained above, highly adapted and coevolved specialist helminth may decrease their infection rates in their communities because habitat alteration could reduce their host population densities beyond threshold for their optimal maintenance (Anderson and May 1982; Bush and Kennedy 1994; Viana et al. 2014). Conversely, low host-specific helminths that are present in a variety of host species may be transmitted to the target native

population, such as small mammals, through contact within the shared habitat or through migration between patches (i.e., metapopulations) (Hess et al. 2002; Viana et al. 2014). The critical community size for low host-specific helminths should be guaranteed within an altered habitat, in which a permanent influx of infected host species may be in contact with the target population or contaminating the shared habitat with infective stages (Lafferty and Kuris 1999). Furthermore, forest edges in altered habitats may favor the interaction of native small mammals with exotic species harboring low host-specific helminths (e.g., wildlife, livestock, free-ranging pets, and humans), thus increasing the probability that the wild target population become infected (Cleaveland et al. 2007; Walker and Morgan 2014; Landaeta-Aqueveque et al. 2018). Moreover, the dilution effect can occur for highly host-specific helminths since they may not replicate in introduced exotic species (Johnson and Thieltges 2010). Based on the trophic niche theory, as the community of helminths is altered due to the reduction or absence of highly host-specific parasites, low host-specific helminths may occupy their niche in the target native host population (Warren et al. 2010). Therefore, habitat alteration could lead to homogenization in the parasite community, in which low host-specific species may prevail (Dharmarajan et al. 2021). For example, in Uganda, the presence of four helminth species including *S. stercoralis*, *Ascaris* sp., *Bertiella* sp., and strongyles were found only in the endangered red colobus (*Procolobus rufomitratus* Peters 1879) living in fragmented habitats (Gillespie and Chapman 2008). Since such parasite genera are usually low host-specific and have not been found in natural habitats (i.e., Kibale National Park), Gillespie and Chapman (2008) suggested that humans and livestock may act as reservoir for those parasite species. However, in any of the reviewed papers that discussed parasite sharing between native small mammals and exotic species, authors confirmed cross-transmission either by molecular or experimental tests. The diagnostic methods of the helminths in such studies were based only on coprological examination by microscopy. In this context, Helenbrook et al. (2015, 2017) attempted to demonstrate inter-species transmission of the protozoan *Blastocystis* sp. in primates and humans by using PCR of SSU rDNA sequence with no evidence of parasite subtypes sharing between human and animal species (Helenbrook et al. 2015, 2017).

The establishment of low host-specific helminth species in native populations may have severe implications on the health of the target native population since low host-specific parasites and those able to survive in a wider range of environmental conditions may be more virulent and pathogenic given their increased range size, which could deteriorate the decaying conditions of small mammal populations in altered habitats (Gillespie and Chapman 2008; Loiseau et al. 2012). Moreover, homogenization of helminth structure in wildlife

populations would enhance the reservoir capacity for the maintenance and spread of low host-specific helminth species (Viana et al. 2014). Thus, human-induced habitat alteration can favor helminth communities to be dominated by low host-specific species, which could increase their risk of transmission and emergence of parasitic infections in a variety of host species, including humans (Patz et al. 2000) in spite of the fact that there is still limited empirical evidence.

Concluding remarks and future directions of research

Information in assessed articles suggests that the structure of helminth communities in small mammals can be impacted by anthropogenic habitat alteration in various ways. Infection rates of monoxenous and heteroxenous helminths may increase or decrease in small mammals depending on whether the availability of their hosts (definitive and intermediate), and environmental and host conditions modify the survival and transmission of parasitic forms. Also, given that habitat alteration may favor inter-species contacts, transmission rates of low host-specific helminths could be increased due to exposure to new reservoir hosts.

Specific changes in helminth infection rates may occur in accordance with the inherent temporal and spatial variability of the attributes of altered habitats. Depending on the extent of habitat alteration (e.g., fragment size, shape, level of connectance between remaining fragments, and type of disturbance), the variation of the structure of helminth communities in small mammals could be a long-term process, in which an increase in infection rates of certain helminth species may be expected in the first instance, followed by a gradual decline until the helminth community stabilizes toward a new equilibrium (Wilcox and Gubler 2005). Therefore, long-term surveillance should be undertaken to determine temporal changes in infection rates of helminths in small mammals inhabiting natural and anthropogenically altered habitats as well as evaluation of biotic and abiotic conditions in such altered habitats. In most of the reviewed papers, the microscopic examination of fecal samples was used as the diagnosis method to determine parasite prevalence and burden (i.e., fecal eggs count). Although microscopic examination of feces is a commonly used noninvasive diagnosis test to assess parasite infections in live individuals, one of its major shortcomings is its low accuracy in determining the parasite burden in comparison to other methods (e.g., necropsy), given that parasite egg shedding can significantly vary due to several factors including different ratio of males to females in dioic helminths, diurnal variation, and different maturation state of parasites (Filipiak et al. 2009; Taylor et al. 2016). To determine the actual parasite burden, it may be essential to carry out long-term studies that allow to assess adult helminths in eventual mortality in accordance with conservation laws and animal welfare standards. In addition, more molecular phylogenetic analysis and/or experimental assays with controlled host and environmental conditions (e.g., see Resasco et al. (2019)) should be applied to detect actual changes in infection rates related to habitat alteration and helminth species cross-transmission between native and introduced fauna. Finally, substantial heterogeneity of studies was observed in the forest plots (Figs. 3, 4, 5, and 6), which may be accounted for the differences in samples sizes in reviewed studies. Future endeavors should therefore assess larger sample sizes to minimize selection and information bias.

In a continually changing world, it is essential to assess the spatio-temporal variations of helminth communities in wildlife inhabiting natural and altered habitats to determine potential impacts on wildlife conservation and public health.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interest.

References

Altizer S, Ostfeld RS, Johnson PTJ et al (2013) Climate change and infectious diseases : from evidence to a predictive framework. Science (80-) 341:514–519

Amos W, Harwood J (1998) Factors affecting levels of genetic diversity in natural populations. Philos Trans R Soc B Biol Sci 33:177–186

Anders JL, Nakao M, Uchida K et al (2019) Comparison of the intestinal helminth community of the large Japanese field mouse (*Apodemus speciosus*) between urban, rural, and natural sites in Hokkaido, Japan. Parasitol Int 70:51–57. https://doi.org/10.1016/j.parint.2019.02.001

Anderson RM, May R (1982) Directly transmitted infectious diseases: control by vaccination. Science (80-) 215:1053–1060

Anderson RM, May RM (1991) Infectious diseases of humans: dynamics and control. Oxford University Press Inc, Oxford

Arneberg P (2002) Host population density and body mass as determinants of species richness in parasite communities: comparative analyses of directly transmitted nematodes of mammals. Ecography (cop) 25:88–94. https://doi.org/10.1034/j.1600-0587.2002.250110.x

Barelli C, Pafčo B, Manica M et al (2020) Loss of protozoan and metazoan intestinal symbiont biodiversity in wild primates living in unprotected forests. Sci Rep 10:1–12. https://doi.org/10.1038/s41598-020-67959-7

Barelli C, Gonzalez-astudillo V, Mundry R et al (2021) Correction: Altitude and human disturbance are associated with helminth diversity in an endangered primate Procolobus gordonorum. PLoS One 16:e0251617. https://doi.org/10.1371/journal.pone.0225142

Bush AO, Kennedy CR (1994) Host fragmentation and helminth parasites: hedging your bets against extinction. Int J Parasitol 24:1333–1343

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. J Parasitol 83:575–583

Cardoso TS, Simões RO, Luque JLF et al (2016) The influence of habitat fragmentation on helminth communities in rodent populations from a Brazilian Mountain Atlantic Forest. J Helminthol 90:460–468. https://doi.org/10.1017/S0022149X15000589

Cardoso TDS, Macabu CE, Simões RDO et al (2019) Helminth community structure of two sigmodontine rodents in Serra Dos Órgãos National Park, State of Rio de Janeiro, brazil. Oecologia Aust 23:301–314. https://doi.org/10.4257/oeco.2019.2302.09

Cleaveland S, Mlengeya T, Kaare M et al (2007) The conservation relevance of epidemiological research into carnivore viral diseases in the serengeti. Conserv Biol 21:612–622. https://doi.org/10.1111/j.1523-1739.2007.00701.x

Costa NA, dos Santos CT, da Costa Neto SF et al (2019) Metacommunity structure of helminths of Necromys lasiurus (Rodentia: Sigmodontinae) in different land use areas in the Brazilian Cerrado. J Parasitol 105:271–282. https://doi.org/10.1645/17-199

Daszak P, Cunningham AA, Hyatt AD (2000) Emerging infectious diseases of wildlife - threats to biodiversity and human health. Science (80-) 287:443–449. https://doi.org/10.1126/science.287.5452.443

de Winter II, Umanets A, Gort G et al (2020) Effects of seasonality and previous logging on faecal helminth-microbiota associations in wild lemurs. Sci Rep 10:1–16. https://doi.org/10.1038/s41598-020-73827-1

Dea REO, Lagisz M, Jennions MD et al (2021) Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology : a PRISMA extension. Biol Rev 96:1695–1722. https://doi.org/10.1111/brv.12721

Dharmarajan G, Gupta P, Vishnudas CK, Robin VV. (2021) Anthropogenic disturbance favours generalist over specialist parasites in bird communities: implications for risk of disease emergence. Ecol Lett 1–10. https://doi.org/10.1111/ele.13818

Dobson A, Lafferty KD, Kuris AM et al (2008) Homage to Linnaeus: how many parasites? How many hosts? Proc Natl Acad Sci 105:11482–11489. https://doi.org/10.1073/pnas.0803232105

Fernando SU, Udagama PV, Fernando SP (2022) Effect of urbanization on zoonotic gastrointestinal parasite prevalence in endemic toque macaque (Macaca sinica) from different climatic zones in Sri Lanka. Int J Parasitol Parasites Wildl 17:100–109. https://doi.org/10.1016/j.ijppaw.2021.12.007

Filipiak L, Mathieu F, Moreau J (2009) Caution on the assessment of intestinal parasitic load in studying parasite-mediated sexual selection: the case of Blackbirds coccidiosis. Int J Parasitol 39:741–746. https://doi.org/10.1016/j.ijpara.2008.11.005

Franklin AB, Noon BR, George TL (2002) What is habitat fragmentation? Stud Avian Biol 25:20–29

Froeschke G, Matthee S (2014) Landscape characteristics influence helminth infestations in a peri-domestic rodent - implications for possible zoonotic disease. Parasit Vectors 7:1–13. https://doi.org/10.1186/1756-3305-7-393

Gillespie TR, Chapman CA (2006) Prediction of parasite infection dynamics in primate metapopulations based on attributes of forest fragmentation. Conserv Biol 20:441–448. https://doi.org/10.1111/j.1523-1739.2006.00290.x

Gillespie TR, Chapman CA (2008) Forest fragmentation, the decline of an endangered primate, and changes in host – parasite interactions relative to an unfragmented forest. Am J Primatol 70:222–230. https://doi.org/10.1002/ajp.20475

Gillespie TR, Chapman CA, Greiner EC (2005) Effects of logging on gastrointestinal parasite infections and infection risk in African primates. J Appl Ecol 42:699–707. https://doi.org/10.1111/j.1365-2664.2005.01049.x

Gómez A, Nichols E (2013) Neglected wild life: parasitic biodiversity as a conservation target. Int J Parasitol Parasites Wildl 2:222–227. https://doi.org/10.1016/j.ijppaw.2013.07.002

Gulland FMD (1992) The role of nematode parasites in Soay sheep (Ovis aries L.) mortality during a population crash. Parasitology 105:493–503. https://doi.org/10.1017/S0031182000074679

Haddad NM, Brudvig LA, Clobert J et al (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:1–10. https://doi.org/10.1126/sciadv.1500052

Hawley DM, Altizer SM (2011) Disease ecology meets ecological immunology: understanding the links between organismal immunity and infection dynamics in natural populations. Funct Ecol 25:48–60. https://doi.org/10.1111/j.1365-2435.2010.01753.x

Helenbrook WD, Shields WM, Whipps CM (2015) Characterization of Blastocystis species infection in humans and mantled howler monkeys, Alouatta palliata aequatorialis, living in close proximity to one another. Parasitol Res 114:2517–2525. https://doi.org/10.1007/s00436-015-4451-x

Helenbrook WD, Stehman SV, Shields WM, Whipps CM (2017) Association of anthropogenic disturbances and intestinal parasitism in Ecuadorian mantled howler monkeys, Alouatta palliata aequatorialis. Folia Primatol 88:307–322. https://doi.org/10.1159/000479687

Hess GR, Randolph SE, Arneberg P, Chemini C, Furlanello C, Harwood J et al (2004) Spatial aspects of disease dynamics. In: Hudson PJ, Rizzoli A, Grenfell B, Heesterbeek JAP, Dobson A (eds) The Ecology of Wildlife Diseases. Oxford University Press, Oxford, pp 102–118

Hillman AE, Lymbery AJ, Elliot AD, Andrew Thompson RC (2017) Urban environments alter parasite fauna, weight and reproductive activity in the quenda (Isoodon obesulus). Sci Total Environ 607–608:1466–1478. https://doi.org/10.1016/j.scitotenv.2017.07.086

Holmes JC (1987) The structure of helminth communities. Int J Parasitol 17:203–208

Holmes JC (1996) Parasites as threats to biodiversity in shrinking ecosystems. Biodivers Conserv 5:975–983. https://doi.org/10.1007/BF00054415

Hudson PJ, Dobson AP, Newborn D (1998) Prevention of population cycles by parasite removal. Sci 80(282):2256–2258

Hurtado G, Mayer G, Mabry KE (2021) Does urbanization ameliorate the effect of endoparasite infection in kangaroo rats? Ecol Evol 11:13390–13400. https://doi.org/10.1002/ece3.8062

Irwin M (2016) Habitat change and degradation. In: Witch SA, Marshall AJ (eds) An introduction to primate conservation. Oxford University Press, pp 111–126

Johnson PTJ, Thieltges DW (2010) Diversity, decoys and the dilution effect: how ecological communities affect disease risk. J Exp Biol 213:961–970. https://doi.org/10.1242/jeb.037721

Jones KE, Patel NG, Levy MA et al (2008) Global trends in emerging infectious diseases. Nature 451:990–993. https://doi.org/10.1038/nature06536

Keesing F, Holt RD, Ostfeld RS (2006) Effects of species diversity on disease risk. Ecol Lett 9:485–498. https://doi.org/10.1111/j.1461-0248.2006.00885.x

Keinath DA, Doak DF, Hodges KE et al (2017) A global analysis of traits predicting species sensitivity to habitat fragmentation. Glob Ecol Biogeogr 26:115–127. https://doi.org/10.1111/geb.12509

Kiene F, Andriatsitohaina B, Ramsay MS et al (2021) Habitat fragmentation and vegetation structure impact gastrointestinal parasites of small mammalian hosts in Madagascar. Ecol Evol 11:6766–6788. https://doi.org/10.1002/ece3.7526

Lafferty KD (2012) Biodiversity loss decreases parasite diversity : theory and patterns. Philos Trans R Soc B Biol Sci 367:2814–2827. https://doi.org/10.1098/rstb.2012.0110

Lafferty KD, Kuris AM (1999) How environmental stress affects the impacts of parasites. Limnol Oceanogr 44:925–931

Landaeta-Aqueveque C, Robles R, Henríquez A et al (2018) Phylogenetic and ecological factors affecting the sharing of helminths between native and introduced rodents in Central Chile. Parasitology 145:1570–1576

Lindenmayer DB, Fischer J (2006) Tackling the habitat fragmentation panchreston. Trends Ecol Evol 22:127–132. https://doi.org/10.1016/j.tree.2006.11.006

Loiseau C, Harrigan RJ, Robert A et al (2012) Host and habitat specialization of avian malaria in Africa. Mol Ecol 21:431–441. https://doi.org/10.1111/j.1365-294X.2011.05341.x

Lyles AM, Dobson AP (1993) Infectious disease and intensive management: population dynamics, threatened hosts, and their parasites. J Zoo Wildl Med 24:315–326

Marcogliese DJ (2016) The distribution and abundance of parasites in aquatic ecosystems in a changing climate: more than just temperature. Integr Comp Biol 56:611–619. https://doi.org/10.1093/icb/icw036

Marcogliese DJ, Pietrock M (2011) Combined effects of parasites and contaminants on animal health: parasites do matter. Trends Parasitol 27:123–130. https://doi.org/10.1016/j.pt.2010.11.002

Martínez-Mota R, Pozo-Montuy G, Bonilla Sánchez YM, Gillespie TR (2018) Effects of anthropogenic stress on the presence of parasites in a threatened population of black howler monkeys (*Alouatta pigra*). Therya 9:161–170. https://doi.org/10.12933/therya-18-572

Martinson HM, Fagan WF (2014) Trophic disruption: a meta-analysis of how habitat fragmentation affects resource consumption in terrestrial arthropod systems. Ecol Lett 17:1178–1189. https://doi.org/10.1111/ele.12305

Mbora DNM, Wieczkowski J, Munene E (2009) Links between habitat degradation, and social group size, ranging, fecundity, and parasite prevalence in the Tana River mangabey (Cercocebus galeritus). Am J Phys Anthropol 140:562–571. https://doi.org/10.1002/ajpa.21113

McCallum H, Dobson A (2002) Disease, habitat fragmentation and conservation. Proc R Soc London Ser B Biol Sci 49:2041–2049. https://doi.org/10.1098/rspb.2002.2079

Merritt JF (2010) The biology of small mammals. John Hopkins University Press, Baltimore

Meyer-Lucht Y, Otten C, Püttker T et al (2010) Variety matters: adaptive genetic diversity and parasite load in two mouse opossums from the Brazilian Atlantic forest. Conserv Genet 11:2001–2013. https://doi.org/10.1007/s10592-010-0093-9

Mortelliti A, Amori G, Boitani L (2010) The role of habitat quality in fragmented landscapes: a conceptual overview and prospectus for future research. Oecologia 163:535–547. https://doi.org/10.1007/s00442-010-1623-3

Nunn CL, Altizer S, Jones KE, Sechrest W (2003) Comparative tests of parasite species richness in primates. Am Nat 162:597–614. https://doi.org/10.1086/378721

Patz JA, Graczyk TK, Geller N, Vittor AY (2000) Effects of environmental change on emerging parasitic diseases. Int J Parasitol 30:1395–1405. https://doi.org/10.1016/S0020-7519(00)00141-7

Patz JA, Daszak P, Tabor GM et al (2004) Unhealthy landscapes: policy recommendations on land use change and infectious disease emergence. Environ Health Perspect 112:1092–1098. https://doi.org/10.1289/ehp.6877

Pedersen AB, Jones KE, Nunn CL, Altizer S (2007) Infectious diseases and extinction risk in wild mammals. Conserv Biol 21:1269–1279. https://doi.org/10.1111/j.1523-1739.2007.00776.x

Poulin R (2001) Interactions between species and the structure of helminth communities. Parasitology 122:S3–S11. https://doi.org/10.1017/s0031182000016991

Poulin R, Morand S (2000) The diversity of parasites. Thle Q Rev Biol 75:277–293

R Development CoreTeam (2011) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. http://www.R-project.org/

Rakotoniaina JH, Kappeler PM, Ravoniarimbinina P et al (2016) Does habitat disturbance affect stress, body condition and parasitism in two sympatric lemurs? Conserv Physiol 4:1–16. https://doi.org/10.1093/conphys/cow034

Resasco J, Bitters ME, Cunningham SA et al (2019) Experimental habitat fragmentation disrupt nematode infections in Australian skinks. Ecology 100:e02547. https://doi.org/10.1002/ecy.2547

Rimbach R, Bisanzio D, Galvis N et al (2015) Brown spider monkeys (*Ateles hybridus*): a model for differentiating the role of social networks and physical contact on parasite transmission dynamics. Philos Trans R Soc B Biol Sci 370:. https://doi.org/10.1098/rstb.2014.0110

Riquelme M, Salgado R, Simonetti J et al (2021) Intestinal helminths in wild rodents from native forest and exotic pine plantations (*Pinus radiata*) in Central Chile. Animals 11:384. https://doi.org/10.3390/ani11020384

RStudio Team (2022) RStudio: integrated development for R. RStudio, PBC. http://www.rstudio.com/. Accessed 28 Nov 2022

Sáez-Durán S, Debenedetti ÁL, Sainz-Elipe S et al (2021) Ecological analysis of the helminth community of the wood mouse, *Apodemus sylvaticus*, along an 18-year post-fire regeneration period in a Mediterranean ecosystem. Animals 11:2926. https://doi.org/10.3390/ani11102926

Saino N, Suffritti C, Martinelli R et al (2002) Immune response covaries with corticosterone plasma levels under experimentally stressful conditions in nestling barn swallows (*Hirundo rustica*). Behav Ecol 14:318–325

Santicchia F, Romeo C, Martinoli A et al (2015) Effects of habitat quality on parasite abundance: do forest fragmentation and food availability affect helminth infection in the Eurasian red squirrel? J Zool 296:38–44. https://doi.org/10.1111/jzo.12215

Schwarzer G (2007) meta: an R package for meta-analysis. R News 7:40–45

Simões RO, Luque JL, Gentile R et al (2016) Biotic and abiotic effects on the intestinal helminth community of the brown rat *Rattus norvegicus* from Rio de Janeiro, Brazil. J Helminthol 90:21–27. https://doi.org/10.1017/S0022149X14000704

Suzán G, Esponda F, Carrasco-Hernández R, Aguirre A (2012) Habitat fragmentation and infectious disease ecology. In: Aguirre A, Ostfeld RS, Daszak P (eds) New directions in conservation medicine. Oxford University Press Inc, New York, Applied Cases of Ecological Health, pp 135–150

Taylor MA, Coop RL, Wall RL (2016) Veterinary helminthology. Veterinary parasitology. 4th edn. Blackwell Science Ltd, Oxford, pp 1–109

Tompkins DM, Dobson AP, Arneberg P et al (2002) Parasites and host population dynamics. In: Hudson PJ, Rizzoli A, Grenfell BT et al (eds) The ecology of wildlife diseases. Oxford University Press, Oxford, pp 45–62

Trejo-Macías G, Estrada A, Mosqueda Cabrera MÁ (2007) Survey of helminth parasites in populations of *Alouatta palliata mexicana* and *A. pigra* in continuous and in fragmented habitat in southern Mexico. Int J Primatol 28:931–945. https://doi.org/10.1007/s10764-007-9137-5

Vandergast A, Bohonak A, Weissman D, Fisher R (2007) Understanding the genetic effects of recent habitat fragmentation in the context of evolutionary history: phylogeography and landscape genetics of a southern California endemic Jerusalem cricket (Orthoptera: Stenopelmatidae: Stenopelmatus). Mol Ecol 16:977–992. https://doi.org/10.1111/j.1365-294X.2006.03216.x

Viana M, Mancy R, Biek R et al (2014) Assembling evidence for identifying reservoirs of infection. Trends Ecol Evol 29:270–279. https://doi.org/10.1016/j.tree.2014.03.002

Walker JG, Morgan ER (2014) Generalists at the interface: nematode transmission between wild and domestic ungulates. Int J Parasitol Parasites Wildl 3:242–250. https://doi.org/10.1016/j.ijppaw.2014.08.001

Warren CP, Pascual M, Lafferty KD, Kuris AM (2010) The inverse niche model for food webs with parasites. Theor Ecol 3:285–294. https://doi.org/10.1007/s12080-009-0069-x

Wells K, Smales LR, Kalko EKV, Pfeiffer M (2007) Impact of rain-forest logging on helminth assemblages in small mammals (Muridae, Tupaiidae) from Borneo. J Trop Ecol 23:35–43. https://doi.org/10.1017/S0266467406003804

Werner CS, Nunn CL (2020) Effect of urban habitat use on parasitism in mammals: a meta-analysis. Proc R Soc B Biol Sci 287:20200397. https://doi.org/10.1098/rspb.2020.0397rspb20200397

Wilcox BA, Gubler DJ (2005) Disease ecology and the global emergence of zoonotic pathogens. Environ Health Prev Med 10:263–272. https://doi.org/10.1265/ehpm.10.263

Wilson K, Bjornstad ON, Dobson AP et al (2002) Heterogeneities in macroparasite infections: patterns and processes. In: Hudson PJ, Rizzoli AP, Grenfell BT et al (eds) The ecology of wildlife diseases. Oxford University Press, pp 6–44