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Parasites of Neotropical Primates: A Review

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Abstract The study of parasites is of great relevance to primatology given their ecological significance and their effects on primate demography, behavior, and evolution. Moreover, assessing the vulnerability of endangered species to parasitic infections is important in developing appropriate conservation strategies. We conducted an intensive bibliographical search to synthesize the available information about the parasites of Neotropical primates. We analyzed the host and parasite taxonomic coverage of the available studies, examined the advantages and disadvantages of the diagnostic techniques employed, identified information gaps that need to be addressed, and recommend future directions in the parasitological research of Neotropical primates. Researchers have reported 276 parasite taxa, including endo- and ectoparasites, in 21 of the 22 genera of Neotropical primates. Of these, 42 parasite species have also been reported in humans, although this number may be inaccurate owing to misidentification. The parasites of 50% of Neotropical primate species are completely unknown, and 32% of the parasites recorded in these hosts have not been identified to the species level. Information regarding ectoparasites is particularly limited. We need to develop methods that enhance parasite diagnosis accuracy when using noninvasive samples, and the incorporation of molecular techniques in routine procedures should be a priority in parasitological studies of Neotropical primates. An integrative approach in which veterinarians, primatologists, and parasitologists collaborate in the identification and treatment of parasites of Neotropical primates is essential to achieve significant progress in this field.

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Introduction

Parasitism is one of the most common forms of life on earth (Windsor 1998). This way of life represents a survival strategy that has evolved independently several times, and is present in organisms from almost every known kingdom (Poulin and Morand 2000). Parasites are important components of natural ecosystems because they can drive the community composition of free-living organisms by acting as agents of natural selection (Gómez and Nichols 2013; Poulin 1999).

Research on primate parasites is of great interest because of their ecological significance, and because the close evolutionary history shared between primates and humans makes primates suitable models for the study of human parasite transmission dynamics and evolution (Phillips *et al.* 2014). The study of parasites can also help us to understand demographic and evolutionary processes in primates (Reed *et al.* 2009; Whiteman and Parker 2005). Moreover, because ca. 60% of the primate species are considered endangered (Estrada *et al.* 2017), parasitological studies are important to assess the health of species and populations, and their vulnerability to infections, to develop accurate management and conservation strategies (Altizer *et al.* 2007).

Currently, there are 171 species of primates included in 22 genera inhabiting forests in the Neotropical biogeographical region (Estrada *et al.* 2017). These Neotropical primate species represent 34% of the total primate species in the world (Estrada *et al.* 2017). Several efforts have been made to determine the parasitic fauna of Neotropical primates; however, this information is published in a scattered manner and sometimes in local bibliographical resources that are difficult to access. Some attempts have been made to gather the published information on the parasite fauna of Neotropical primates (Correa *et al.* 2016; Duszynski *et al.* 1999; Stuart *et al.* 1998; Vitazkova 2009, Yamashita 1963); these compilations focus either on a particular host taxa, on a particular region, or on a specific type of parasites. For example, a compilation of published records of the parasite fauna that infect howlers (*Alouatta* spp.) across their distributional range found 78 taxa of parasites infecting this genus (Stuart *et al.* 1998; Vitazkova 2009). A checklist of the helminth parasites of primates from Brazil based on the database of the Helminthological Collection of the Oswaldo Cruz Institute (CHIOC), Brazil, and updated information from the literature, included 50 species of helminths in 46 primate species (Correa *et al.* 2016). A review of the coccidian parasites in primates reported six species of these protozoans in Neotropical primates (Duszynski *et al.* 1999). The Global Mammal Parasite Database (GMPD) provides a more inclusive effort and contains a large number of records of parasites in nonhuman primate species (Nunn and Altizer 2005; Stephens *et al.* 2017).

We aimed to complement and enrich existing compilations of primate parasitological information by summarizing current knowledge of the parasitic fauna of Neotropical primates, including data on three major groups of eukaryote parasites: protozoans, helminths, and ectoparasitic arthropods. We identify information gaps that need to be addressed in the near future to achieve a better understanding of the host–parasite relationship, and the way this can be used to propose more reliable strategies in primate health and conservation. We address four main issues: 1) host taxonomic coverage and geographic distribution of parasite records, i.e., how many Neotropical primates species have been reported as hosts of at least one parasite species, and where the records were made; 2) diagnostic methods employed in parasitological studies of Neotropical primates and their advantages and limitations; 3) the representation of the main parasitic groups across the parasitological literature; and 4) future directions in the parasitological study of Neotropical primates.

Methods

We conducted an intensive bibliographical search on primate parasitological studies from 1900 to 2017 on the ISI Web of Knowledge® platform. We conducted the search independently for each genus of Neotropical primates, using the following combination of terms: “parasite” AND the name of the primate genus, e.g., “parasite” AND *Alouatta*. We accessed the platform in May and June 2017. We checked each record individually and retained only those in which a parasite taxon was recorded. We discarded studies performed under laboratory conditions that employed individuals as models for the development of vaccines, or those describing the physiological response of monkeys to experimental infections. We retained only studies that contributed to the description of parasite diversity in Neotropical primates, i.e., those that report the presence of particular parasite species in a primate species.

We complemented the literature search in three ways: 1) using the GMPD (Stephens *et al.* 2017), adding records that we did not find in the literature, such as those from national collections and museums; 2) searching the references cited in other reviews, such as Stuart *et al.* (1998) and Correa *et al.* (2016), that are not listed by the ISI Web of Knowledge because of the time frame; and 3) including papers published in *Neotropical Primates*, a reference journal for the publication of primatological research in this region, and *International Journal for Parasitology: Parasites and Wildlife*, which do not have an impact factor, so are not retrieved in searches of the ISI Web of Knowledge. Some parasitological reports may exist in the gray literature, such as theses, or as unpublished studies presented in scientific meetings. These sources are generally difficult to obtain, and we did not consider them; hence the numbers we present may be underestimated for some Neotropical primates.

From each bibliographical source, we recorded the following information: 1) host species analyzed; 2) parasite taxa recorded; 3) country where the study was performed; 4) host living condition (captive in zoos or primate centers, kept in laboratory facilities, or free-living); and 5) diagnostic methods used, including direct observation (employed mostly in ectoparasite studies), blood tests, coproscopic analysis, necropsy, and molecular analysis. In several papers, data from more than one host species (and genera) were available, or more than one diagnostic method was employed; for example, several studies combine blood tests and molecular methods. In these cases, we reported the estimates for each comparison independently, counting the paper once for each host species and diagnostic method.

We present the data in two ways, as a Host–Parasite list and as a Parasite–Host list. We ordered the Host-Parasite list alphabetically by host family, then host genus and species, following the species of Neotropical primates considered by Estrada *et al.*

(2017). For each primate species, we present parasites by major parasitic group, i.e., protozoans; helminths such as cestodes, trematodes, nematodes, acanthocephalans; and arthropods such as dipterans, ixodids, acariforms, and phthirapterans. In each parasite category, we list species alphabetically by genus and species.

We divided the Parasite–Host list into endo- or ectoparasites. We present each group in phylogenetic order. Parasite taxonomy follows the classification schemes presented in databases such as the World Register of Marine Species (WoRMS) and the Global Biodiversity Information Facility (GBIF). For protozoans, we followed the classification proposed by Cavalier-Smith (2003). Several classification schemes have been developed for protozoans, but our overall analyses consider parasite species richness irrespective of higher rank classifications. Each parasite phylum contains classes, orders, families, genera, and species in alphabetical order. We include species distribution, referring to countries where the parasite was recorded, and the references. Given its length, we included the Parasite–Host list as Electronic Supplementary Material (ESM Table SI). We obtained information on Neotropical primate distribution from Rylands *et al.* (1995) and primate conservation status and general publications per genera from Estrada *et al.* (2017). We used a linear regression test in R (R Development Core Team 2013) to estimate the strength of the association between parasite richness and the number of parasitological studies for each Neotropical primate genus.

Results

We retrieved 877 entries from our search of the ISI Web of Knowledge. Some studies provided information on parasites from more than one primate genus, so we retrieved them more than once. After discarding irrelevant studies and correcting for duplicate entries, we retained 220 studies. We added 11 studies from *Neotropical Primates* and *International Journal for Parasitology: Parasites and Wildlife* and 20 original references from the available checklists, compiling a final database of 251 publications on the parasitic fauna of Neotropical primates.

Of the 22 genera of Neotropical primates, we found at least one parasitological record for 21, with 85 of the 171 species the subject of at least one parasitological survey (Table I). The parasites of 50% of all Neotropical primate species are unstudied. The monotypic *Callibella* (the black-crowned dwarf marmoset) is the only genus lacking any parasitological information.

Most of the parasitological research on Neotropical primates has been conducted in the genus *Alouatta* (Table II), although only 6 of the 12 species have been examined for parasites. Of the other genera with >10 species, *Saguinus*, *Ateles*, *Callithrix*, and *Leontopithecus* have the most complete taxonomic coverage, as almost all the species belonging to these genera have at least one parasitological report, with only the mottle-face tamarin (*S. inustus*), the white-cheeked spider monkey (*Ateles marginatus*), the buffy-headed marmoset (*Callithrix flaviceps*), and the black-faced lion tamarin (*Leontopithecus cassaira*) lacking parasitological information. Genera such as *Callimico*, *Cebuella*, and *Brachyteles* have very low species richness, and all their species have been subject to parasitological research. The least studied genera are *Mico*, *Plecturocebus*, and *Pithecia*; these are highly diverse genera, with only a small number of parasitological studies available for a few species.

Table I Host–parasite list for Neotropical primates based on a literature search in ISI Web of Knowledge, the Global Mammal Parasite database, and additional sources

Host	Parasite group	Parasite taxa
Family Aotidae		
Aotus		
Aotus azarae	Protozoa	*Blastocystis* sp., *B. hominis*, *Endolimax* sp., *E. nana*, *Entamoeba* sp., *Giardia* sp., *Isospora* sp., *Leishmania* sp., *Plasmodium cynomolgi**, *P. vivax**, *Trypanosoma cruzi*, *T, minasense*
	Cestoda	*Taenia* sp.
	Nematoda	*Dipetalonema* sp., *Strongyloides* sp., *Trypanoxyuris* sp., *Uncinaria* sp.
Aotus lemurinus	Protozoa	*Plasmodium cynomolgi**, *P. vivax**
Aotus miconax	Protozoa	*Eimeria* sp.
	Nematoda	*Strongyloides* sp.
Aotus nancymaae	Protozoa	*Plasmodium falciparum**
	Trematoda	*Aototrema dorsogenitalis*, *Athesmia heterolecithoides*, *Phaneropsolus orbicularis*
	Cestoda	*Hymenolepis diminuta*
	Acanthocephala	*Prosthenorchis elegans*
	Nematoda	*Dipetalonema gracile*, *Mansonella* sp., *Primasubulura jacchi*, *Trypanoxyuris* sp., *T. microon*
Aotus nigriceps	Protozoa	*Leishmania* sp., *Plasmodium* sp., *P. brasilianum*, *Trypanosoma cruzi*
Aotus trivirgatus	Protozoa	*Isospora arctopitheci**, *Plasmodium knowlesi**, *Trypanosoma* sp., *T. minasense*
	Trematoda	*Amphistoma emarginatum*, *Athesmia heterolecithoides*, *Phaneropsolus orbicularis*, *Zonorchis goliath*
	Acanthocephala	*Moniliformis moniliformis*
	Nematoda	Ascarididae gen. sp., *Dipetalonema gracile*, *D. marmosetae*, *D. barbascalensis*, *Trypanoxyuris interlabiata*, *T. microon*
	Diptera	*Alouattamyia baeri*
Aotus vociferans	Protozoa	*Iodamoeba* sp., *I. bütschilii; Plasmodium brasilianum*, *P. falciparum**, *P. fragile**, *P. malariae**
	Trematoda	*Schistosoma mansoni*
	Cestoda	*Hymenolepis diminuta*
	Nematoda	*Ascaris* sp., *Mansonella* sp., *Strongyloides* sp., *Trypanoxyuris micron*
Aotus zonalis	Cestoda	Cyclophyllidea gen. sp.
	Nematoda	*Dipetalonema gracile*, *Protospirura muricola*
Aotus sp.	Diptera	*Dermatobia* sp.
	Phthiraptera	*Gyropus ovalis*
Family Atelidae		
Alouatta		
Alouatta belzebul	Protozoa	*Plasmodium brasilianum*, *Toxoplasma gondii*, *Trypanosoma minasense*, *T. mycetae*

Table I (continued)

Host	Parasite group	Parasite taxa
	Cestoda	*Mathevotaenia megastoma*
	Nematoda	*Ascaris elongata*, *Trypanoxyuris minutus*, *T. oedipi*
	Diptera	*Alouattamyia baeri*
	Phthiraptera	*Cebidicola* sp.
Alouatta caraya	Protozoa	*Balantidium aragaoi*, *Chilomastix* sp., *Eimeria* sp., *Entamoeba* sp., *Giardia* sp., *G. inestinalis*, *Plasmodium brasilianum*, *P. falciparum*, *P. malariae*, *P. vivax*, *Retortamonas intestinalis*, *Toxoplasma gondii*, *Trichomonas* sp., *Trypanosoma cruzi*, *T. forestali*, *T. minasense*, *T. mycetae*
	Trematoda	*Controrchis biliophilus*
	Cestoda	*Bertiella mucronata*, *Mathevotaenia megastoma*, *Moniezia rugosa*, *Raillietina alouattae*
	Nematoda	*Ancylostoma quadridentata*, Ascarididae gen sp., *Ascaris lumbricoides*, *Capillaria* sp., *Dipetalonema* sp., *D. gracile*, *Enterobius* sp., *E. vermicularis*, *Filaria* sp., *Longistriata dubia*, *Oesophagostomun* sp., oxyurid fam. Gen. sp., *Parabronema bonnei*, Strongylidae gen. sp., *Strongyloides* sp., Trichostrongylidae gen. sp., *Trichuris* sp., *Trypanoxyuris minutus*, *T. oedipi*, *Viannella dubia*
	Acariformes	*Cebalges gaudi*
	Ixodida	*Amblyomma* sp.
	Phthiraptera	*Cebidicola semiarmatus*, *Pediculus mjobergi*
Alouatta guariba	Protozoa	*Giardia intestinalis*, *Leishmania* sp., *Plasmodium brasilianum*, *P. falciparum*, *P. simium*, *P. vivax*, *Trypanosoma forestali*, *T. hippicum*, *T. minasense*, *T. mycetae*, *T. venezuelense*
	Cestoda	*Moniezia rugosa*
	Nematoda	*Dipetalonema caudispina*, *D. gracile*, microfilaria, *Parabronema bonnei*, *Trichuris dispar*, *Trypanoxyuris minutus*, *T. oedipi*
	Phthiraptera	*Cebidicola semiarmatus*
Alouatta palliata	Protozoa	*Balantidium* sp., *Blastocystis* sp., *Chilomastix* sp., coccidian fam. Gen. sp., *Cyclospora* sp., *Dientamoeba* sp., *Eimeria* sp., *Endolimax* sp., *Entamoeba* sp., *E. coli*, *Giardia* sp., *Iodamoeba* sp., *Isospora* sp., *I. arctopitheci*, *Leishmania mexicana*, *Plasmodium brasilianum*, *P. falciparum**, *P. malariae*, *P. simium**, *Retortamonas* sp., *Toxoplasma* sp., *Trichomona* sp., *Trypanosoma cruzi*, *T. mycetae*
	Trematoda	*Controrchis* sp., *C. biliophilus*
	Cestoda	*Raillietina* sp., *R. demerariensis*
	Acanthocephala	*Prosthenorchis elegans*
	Nematoda	Ancylostomatidae gen. sp., Ascarididae gen. sp., *Ascaris* sp., *A. lumbricoides*, *Capillaria* sp., *Dipetalonema marmosetae*, *Enterobius* sp., oxyurid fem. Gen. sp., *Parabronema* sp., *P. bonnie*, Strongylidae gen. sp., *Strongyloides* sp., *Trypanoxyuris* sp., *T. minutus*,

Table I (continued)

Host	Parasite group	Parasite taxa
		T. multilabiatus
	Acariformes	*Listrocarpus alouattae*
	Diptera	*Alouattamyia baeri*, *Dermatobia hominis*
Alouatta pigra	Protozoa	*Balantioides coli*, *Blastocystis* sp., *Cryptosporidium* sp., *Cyclospora* sp., *Eimeria* sp., *Endolimax nana*, *Entamoeba* sp., *E. coli*, *E. hartmanii*, *E. polecki*, *Giardia* sp., *G. intestinalis*, *Iodamoeba bütschilii*, *Isospora* sp., *Leishmania mexicana*, *Trypanosoma cruzi*
	Trematoda	*Controrchis* sp., *C. biliphilus*
	Cestoda	*Raillietina* sp.
	Nematoda	Ascarididae gen. sp., *Ascaris* sp., *Capillaria* sp., *Enterobius* sp., oxyurid fam. Gen. sp., *Parabronema* sp., Strongylidae gen. sp., Trichostrongylidae gen. sp., *Trichostrongyloides* sp., *Trichuris* sp., *Trypanoxyuris* sp., *T. minutus*, *T. pigrae*
Alouatta seniculus (syn. *A. puruensis*)	Protozoa	*Balantidium* sp., *Blastocystis* sp., *Chilomastix* sp., *Endolimax nana*, *Entamoeba* sp., *E. coli*, *E. histolytica*, *E. polecki*, *Giardia itestinalis*, *Iodamoeba* sp., *Plasmodium* sp., *P. brasilianum*, *P. falciparum*, *P. simium*, *Toxoplasma* sp., *T. gondii*, *Trypanosoma* sp., *T. cruzi*, *T. hippicum*, *T. lambrechti*, *T. minasense*, *T. mycetae*, *T. rangeli*, *T. venezuelense*
	Trematoda	*Controrchis biliophilus*
	Cestoda	*Raillietina alouattae*, *R. demerariensis*
	Nematoda	Ancylostomatidae gen. sp., *Ascaris* sp., *A. lumbricoides*, *Dipetalonema gracile*, *Enterobius* sp., *Filariopsis asper*, *Mansonella* sp., *Parabronema bonnei*, *Physaloptera dilatata*, Strongyloididae gen. sp., *Strongyloides* sp., *Trichostrongylus* sp., Trichuridae gen. sp., *Trichuris dispar*, *T. trichiura*, *Trypanoxyuris* sp., *T. minutus*
	Acariformes	*Listrocarpus alouattae*
	Ixodida	*Amblyomma* sp., *A. cajenennse*
	Phthiraptera	*Cebidicola extrarius*, *C. semiarmatus*
	Diptera	*Alouattamyia baeri*, *Cochliomyia hominivorax*
Alouatta sp.	Trematoda	*Athesmia foxi*
Ateles		
Ateles belzebuth	Protozoa	*Blastocystis* sp., *Chilomastix* sp., *Entamoeba* sp., *E. histolytica*, *Iodamoeba* sp., *I. bütschilii*, *Trypanosoma cruzi*
	Nematoda	*Strongyloides* sp., *Trichuris trichiura*
Ateles chamek	Protozoa	*Plasmodium* sp.
	Nematoda	*Dipetalonema yatesi*
Ateles fusciceps	Protozoa	*Cryptosporidium* sp., *Endolimax* sp., *Entamoeba* sp., *Plasmodium brasilianum*, *P. simium**, *Trypanosoma cruzi*, *T. minasense*
	Nematoda	Ascarididae gen. sp., *Ascaris lumbricoides*, *Dipetalonema gracile*, *D. marmosetae*, *Necator americanus*, *Protospirura muricola*, *Strongyloides* sp., *Trypanoxyuris atelis*, *T. atelophora*

Table I (continued)

Host	Parasite group	Parasite taxa
Ateles geoffroyi	Protozoa	*Cryptosporidium* sp., *Endolimax* sp., *Entamoeba* sp., *Isospora* sp., *Plasmodium brasilianum*, *P. malariae*, *P. simium**, *Trypanosoma cruzi*, *T. minasense*
	Trematoda	*Controrchis* sp., *C. biliophilus*
	Cestoda	*Mathevotaenia megastoma*
	Nematoda	Ancylostomatididae gen. sp., *Ascaris* sp., *Dipetalonema gracile*, *D. marmosetae*, Strongyloididae gen. sp., *Strongyloides* sp., *S. fuelleborni*, Trichuridae gen. sp., *Trypanoxyuris* sp., *T. atelis*, *T. atelophora*, *T. minutus*, *T. trypanuris*
Ateles hybridus	Protozoa	Balantididae gen. sp., *Entamoeba* sp.
	Cestoda	Cestode fam. Gen. sp.
	Nematoda	*Necator* sp., *Strongyloides* sp., *Trichostrongylus* sp., *Trichuris* sp., *Trypanoxyuris* sp.
Ateles paniscus	Protozoa	*Balantioides coli*, *Leishmania amazonensis*, *Plasmodium brasilianum*, *Trypanosoma advieri*, *T. lesourdi*, *T. minasense*
	Nematoda	*Dipetalonema caudispina*, *D. gracile*, oxyurid fam. Gen. sp., *Physaloptera multiuteri*, *Strongyloides* sp., *Trypanoxyuris minutus*, *T. atelis*
Ateles sp.	Cestoda	*Moniezia rugosa*
	Acanthocephala	*Prosthenorchis elegans*
Brachyteles		
Brachyteles arachnoides	Protozoa	*Entamoeba hartmanni*, *Plasmodium brasilianum*, *P. simium*
	Trematoda	Digenean fam. Gen. sp. .
	Cestoda	*Mathevotaenia megastoma*, *Moniezia rugosa*
	Nematoda	*Dipetalonema caudispina*, *D. gracile*, *Graphidiodes berlai*, *Strongyloides cebus*, *Trypanoxyuris brachytelesi*
Brachyteles hypoxanthus	Protozoa	*Balantioides coli*, *Entamoeba* sp., *Giardia* sp.
	Trematoda	Digenean fam. Gen. sp.
	Cestoda	*Hymenolepis* sp., *Moniezia* sp., *M. rugosa*
	Nematoda	Ancylostomatidae gen. sp.
Lagothrix		
Lagothrix cana	Protozoa	*Plasmodium* sp.
	Nematoda	*Strongyloides cebus*, *Trypanoxyuris lagothricis*
Lagothrix lagotricha	Protozoa	*Plasmodium brasilianum*, *Trypanosoma minasense*
	Acanthocephala	*Prosthenorchis elegans*
	Nematoda	*Ancylostoma braziliense*, *Ascaris lumbricoides*, *Dipetalonema gracile*, *Necator* sp., *Physaloptera dilatata*, *Trichuris* sp., *Trypanoxyuris lagothricis*
	Acariformes	*Listrocarpus lagothrix*
Lagothrix flavicauda (syn. *Oreonax flavicauda*)	Protozoa	*Eimeria* sp., *Endolimax* sp., *Isospora* sp.
	Nematoda	*Strongyloides* sp., *Trichuris* sp.
Family Callithrichidae		
Callibella	No records	
Callimico		

Table I (continued)

Host	Parasite group	Parasite taxa
Callimico goeldii	Protozoa	*Isospora callimico*, *I. endocallimici*
	Trematoda	*Conspicuum conspicuum*, *Platynosomum amazonensis.*
	Cestoda	*Sparganum* sp.
	Nematoda	*Angiostrongylus dujardini*, *Gongylonema* sp., *Trypanoxyuris goeldii*, *T. oedipi*
	Acariformes	*Listrocarpus cosgrovei*
Callithrix		
Callithrix aurita	Nematoda	*Primasubulura jacchi*
Callithrix geoffroyi	Protozoa	*Plasmodium brasilianum*, *Trypanosoma cruzi*
	Acanthocephala	*Oncicola juxtatesticularis*, *Pachysentis lenti*
	Nematoda	*Rictularia nycticebi**
	Acariformes	*Fonsecalges johnjadini*
Callithrix jacchus	Protozoa	*Sarcocystis* sp., *Giardia* sp., *Giardia intestinalis*, *Leishmania chagasi*, *Plasmodium malariae*, *Toxoplasma gondii*, *Trypanosoma cruzi*, *T. minasense*
	Trematoda	*Athesmia foxi*, *Leiptertrema foxi*,*Platynosomum amazonensis*, *Schistosoma mansoni*
	Acanthocephala	Acantocephalus fam. Gen. sp., *Oncicola sigmoides*, *Prosthenorchis elegans*, *P. spirula*
	Nematoda	*Dipetalonema gracile*, *D. marmosetae*, *Filariopsis barretoi*, *Molineus verxillarius*, *Necator americana*, *Primasubulura distans*, *P. jacchi*, *Subulura* sp., *Trichospirura leptostoma*, *Trypanoxyuris callithricis*
	Pentastomida	*Armillifer* sp.
Callithrix kuhlii	Acanthocephala	*Prosthenorchis elegans*
Callithrix penicillata	Protozoa	*Cryptosporidium* sp., *Isospora arctopitheci*, *Leishmania* sp.*, *L. braziliensis**, *L. amazonensis**, *Trypanosoma cruzi*, *T. minasense**
	Trematoda	*Fasciola hepática**, *Platynosomum illiciens*
	Acanthocephala	Acantocephalus fam,. gen. sp.
	Nematoda	*Physaloptera dilatata*, *Primasubulura jacchi*, *Strongyloides stercoralis**, *S. venezuelensis**, *Trichospirura leptostoma*
	Acariformes	*Fonsecalges* sp., *Listrocarpus hapalei*
Callithrix sp.	Cestoda	Dilepididae gen. sp.
	Nematoda	Ancylostomatidae gen. sp.
Cebuella		
Cebuella pygmaea	Protozoa	*Toxoplasma gondii*, *Trypanosoma cruzi*, *T. minasense*
	Acanthocephala	*Prosthenorchis elegans*, *P. spirula*
	Nematoda	*Filariopsis cebuellae*, *Primasubulura jacchi*, *Trichospirura leptostoma*
Leontocebus		
Leontocebus fuscicollis (syn. *Saguinus fuscicollis*)	Protozoa	*Entamoeba* sp., *Iodamoeba* sp., *Sarcocystis* sp., *Trypanosoma cruzi*, *T. devei*, *T. minasense*, *T. rangeli*
	Trematoda	*Athesmia foxi*, *Neodiplostomum tamarini*, *Phaneropsolus* sp., *Platynosomum amazonensis*, *P. marmoseti*
	Cestoda	*Hymenolepis* sp., *Paratriotaenia* sp., *Sparganum* sp.

Table I (continued)

Host	Parasite group	Parasite taxa
	Acanthocephala	*Prosthenorchis elegans*
	Nematoda	*Dipetalonema* sp., *D. gracile*, *D. marmosetae*, *Filaroides* sp., *F. barretoi*, *Longistriata* sp., *Mansonella* sp., *Molineus elegans*, *M. vexillarius*, nematode fam. Gen. sp., *Primasubulura jacchi*, *Rictularia* sp., *Spirura guianensis*, spirurid fam. Gen. sp., Strongylidae gen. sp., *Strongyloides* sp., *Trichospirura leptostoma*, *Trichuris trichiura*, *Trypanoxyuris callithricis*, *T. tamarini*, *Viannaia* sp.
	Pentastomida	*Armillifer* sp. *Porocephalus* sp.
Leontocebus nigricollis (syn. *Saguinus nigricollis*)	Protozoa	*Trypanosoma cruzi*, *T. minasense*
	Trematoda	*Conspicuum conspicuum*, *Neodipostomum tamarini*, *Platynosomum amazonensis*, *P. marmoseti*
	Cestoda	*Hymenolepis* sp., *Mathevotaenia* sp., *Sparganum* sp.
	Ancanthocephala	*Prosthenorchis elegans*
	Nematoda	*Dipetalonema gracile*, *Longistriata dubia*, *Mansonella tamarini*, *Primasubulura jacchi*, *Spirura tamarini*, *Trypanoxyuris tamarini*
	Acariformes	*Fonsecalges* sp.
Leontocebus weddelli	Protozoa	*Trypanosoma minasense*
	Nematoda	*Dipetalonema* sp., *Mansonella mariae*
Leontopithecus		
Leontopithecus chrysomelas	Protozoa	*Leishmania* sp., *Plasmodium brasilianum*, *Trypanosoma cruzi*
	Acanthocephala	*Prosthenorchis elegans*
	Nematoda	*Gongylonema* sp., Spiruridae gen. sp., Trichostrongylidae gen. sp.
Leontopithecus chrysopygus	Protozoa	*Trypanosoma cruzi*
	Acanthocephala	*Prosthenorchis elegans*
	Nematoda	*Dipetalonema caudispina*, *D. gracile*
Leontopithecus rosalia	Protozoa	*Plasmodium brasilianum*, *Toxoplasma gondii*, *Trypanosoma cruzi*
	Acanthocephala	*Oncicola* sp., *O. spirula*, *Prosthenorchis elegans*, *P. spirula*
	Nematoda	Ancylostomatidae gen. sp., Ascarididae gen. sp., *Dipetalonema caudispina*, *D. gracile*, *Gongylonema* sp., *Mansonella zakii*, *Physaloptera dilatata*, *Rictularia nycticebi**, Spiruridae gen. sp., Strongylidae gen. sp., Trichostrongylidae gen. sp., *Trypanoxyuris minutus*
	Acariformes	*Euschoengastia* sp., *Microtrombicula brennani*, *Rhyncoptes anastosi*, *Speleocola tamarina*
	Ixodida	*Amblyoma* sp.
Leontopithecus sp.	Acanthocephala	*Oncicola sigmoides*
Mico		
Mico argentatus	Protozoa	*Trypanosoma cruzi*
	Nematoda	*Dipetalonema marmosetae*, *Primasubulura jacchi*
Mico chrysoleucus	Protozoa	*Trypanosoma cruzi*
	Acanthocephala	*Prosthenorchis elegans*
	Nematoda	*Primasubulura distans*

Table I (continued)

Host	Parasite group	Parasite taxa
Mico emiliae	Protozoa	*Trypanosoma cruzi*, *T. devei*
Mico humeralifer	Protozoa	*Plasmodium brasilianum*
Mico melanurus	Cestoda	*Sparganum* sp., *Mathevotaenia megastoma*
	Nematoda	*Primasubulura distans*, *P. jacchi*
Saguinus		
Saguinus bicolor	Protozoa	*Trypanosoma cruzi*, *T. rangeli*
	Cestoda	*Mathevotaenia megastoma*
	Nematoda	*Dipetalonema caudispina*, *D. gracile*, *Primasubulura distans*
Saguinus geoffroyi	Protozoa	*Cryptosporidium* sp., *Endolimax* sp., *Entamoeba* sp., *Isospora arctopitheci*, *Leishmania braziliensis*, *Plasmodium simium**, *Trypanosoma cruzi*, *T. minasense*, *T. rangeli*
	Trematoda	*Athesmia heterolecithoides*, *Echinostoma aphylactum*, *Zonorchis goliath*
	Cestoda	*Spirometra mansonoides*
	Acanthocephala	*Prosthenorchis elegans*, *P. lenti*
	Nematoda	*Allodapa* sp., *Angiostrongylus cantonensis*, Ascarididae gen. sp., *Dipetalonema marmosetae*, *D. obtusa*, *Physaloptera* sp., *Spirura guianensis*, *Strongyloides* sp., *Subulura jacchi*, *Trichospirura leptostoma*, *Trypanoxyuris callithricis*
Saguinus imperator	Protozoa	*Leishmania* sp.
	Nematoda	*Dipetalonema* sp., *Mansonella mariae*
Saguinus labiatus	Protozoa	*Toxoplasma gondii*, *Trypanosoma cruzi*
	Trematoda	*Athesmia heterolecithoides*
	Acanthocephala	*Prosthenorchis elegans*
	Nematoda	*Dipetalonema gracile*, *Filariopsis barretoi*, *Primasubulura jacchi*
Saguinus leucopus	Protozoa	*Endolimax* sp., *Entamoeba* sp., *Trypanosoma* sp., *T. cruzi*
	Acanthocephala	*Prosthenorchis* sp.
	Nematoda	Ancylostomatidae gen. sp., *Ascaris* sp., Filariidae gen. sp., *Trichospirura leptostoma*, *Trichostrongylus* sp.
Saguinus martinsi	Protozoa	*Plasmodium brasilianum*
Saguinus melanoleucus	Protozoa	*Entamoeba* sp.
Saguinus midas	Protozoa	*Plasmodium brasilianum*, *Trypanosoma cruzi*, *T. devei*, *T. minasense*, *T. rangeli*
	Cestoda	*Mathevotaenia megastoma.*
	Acanthocephala	*Prosthenorchis elegans*
	Nematoda	*Dipetalonema gracile*, *D. graciliformis*, *D. marmosetae*, *Molineus midas*
	Ixodida	*Amblyomma humeralcebidice*, *A. longirostris*
	Siphonaptera	*Rhopalopsyllus lugubris*
Saguinus mystax	Protozoa	*Cryptosporidium* sp., *Trypanosoma cruzi*
	Trematoda	*Athesmia heterolecithoides*, *Platynosomum amazonensis.*
	Cestoda	

Table I (continued)

Host	Parasite group	Parasite taxa
		Hymenolepis sp., *H. cebidarum*, *H. diminuta*, *Sparganum* sp., *Spirometra* sp.
	Ancanthocephala	*Prosthenorchis elegans*
	Nematoda	*Dipetalonema gracile*, *D. graciliformis*, *Filariopsis barretoi*, *Mansonella mystaxi*, *Molineus vexillarius*, *Physaloptera* sp., *Primasubulura distans*, *P. jacchi*, *Spirura delicata*, spirurid fam. Gen. sp., Strongylidae gen. sp.
	Diptera	*Dermatobia* sp.
Saguinus niger	Protozoa	*Trypanosoma cruzi*, *T. devei*
	Ancanthocephala	*Oncicola sigmoides*, *Pachysentis septemserialis*, *Prosthenorchis elegan*
	Nematoda	*Dipetalonema graciliformis*
Saguinus oedipus	Protozoa	*Toxoplasma gondii*, *Trypanosoma minasense*
	Trematoda	*Athesmia foxi*, *Neodiplostomum* sp.
	Acanthocephala	*Moniliformis clarki*, *Prosthenorchis elegans*
	Nematoda	*Angiostrongylus dujardini*, *Dipetalonema gracile*, *D. marmosetae*, *Filariopsis barretoi*, *Gongylonema* sp., *Molineus verxillarius*, *Primasubulura jacchi*, *Trichospirura leptostoma*, *Trypanoxyuris callithricis*, *T. oedipi*
Family Cebidae		
Cebus		
Cebus albifrons	Protozoa	*Chilomastix* sp., *Endolimax* sp., *Entamoeba* sp., *Isospora cebi*, *Plasmodium brasilianum*, *Toxoplasma gondii*, *Trypanosoma cruzi*, *T. lambrechti*, *T. minasense*, *T. rangeli*
	Acanthocephala	*Prosthenorchis elegans*
	Cestoda	*Hymenolepis* sp.
	Nematoda	*Capillaria* sp., *Dipetalonema obtusa*, Strongylidae gen. sp., *Strongyloides* sp., *Trypanoxyuris clementinae*
	Acariformes	*Cebalgoides cebi*
Cebus capucinus	Protozoa	*Cryptosporidium* sp., *Endolimax* sp., *Entamoeba* sp., *Giardia* sp., *G. intestinalis*, *Isospora arctopitheci*, *Plasmodium brasilianum*, *P. simium**, *Trypanosoma cruzi*, *T. minasense*, *T. rangeli*
	Trematoda	*Athesmia heterolecithoides*
	Cestoda	*Hymenolepis diminuta*, *Mathevotaenia megastoma*, *Moniezia rugosa*
	Acanthocephala	Acantocephalus fam. Gen. sp., *Prosthenorchis* sp.
	Nematoda	Ascarididae gen. sp., *Dipetalonema caudispina*, *D. gracile*, *D. marmosetae*, *D. obtusa*, *Filariopsis barretoi*, *Molineus torulosus*, *Necator americanus*, *Physaloptera* sp., *P. cebi*, *Protospirura muricola*, spirurid fam. Gen. sp., Strongylidae gen. sp., *Strongyloides* sp., subulurid fam. Gen. sp.
	Acariformes	*Cebalges gaudi*, *Listrocarpus capucinus*
Cebus olivaceus	Protozoa	*Isospora arctopitheci*, *Trypanosoma minasense*
	Nematoda	*Molineus torulosus*

Table I (continued)

Host	Parasite group	Parasite taxa
Cebus sp.	Acathocephala	*Oncicola confusa*, *O. fretasi*
	Nematoda	*Heterakis spumosa*
Cebus versicolor	Nematoda	Ancylostomatididae gen. sp., Oxyuridae gen. sp., Strongyloididae gen. sp.
Saimiri		
Saimiri boliviensis	Protozoa	*Plasmodium brasiliamun*, *P. coatneyi**, *P. cynomolgi**, *P. fragile**, *P. inui**, *P. malariae**, *P. simium**, *P. vivax**, *Trypanosoma cruzi*, *T. minasense*, *T. rangeli*
	Cestoda	*Atriotaenia* sp., *Mathevotaenia* sp.
	Acanthocephala	*Prosthenorchis elegans*
	Nematoda	*Dipetalonema caudispina*, *D. gracile*, *D. marmosetae*, *Filariopsis barretoi*, *Gongylonema pulchrum*, *Molineus elegans*, *Trypanoxyuris sceleratus*
Saimiri oerstedii	Protozoa	*Entamoeba* sp., *Giardia intestinalis*, *Plasmodium brasilianum*, *Trypanosoma minasense*
	Acanthocephala	*Prosthenorchis elegans*
	Nematoda	*Dipetalonema gracile*, *D. marmosetae*, *D. obtusa*, *Filaroides* sp., *Physaloptera multiuteri*, *Trypanoxyuris sceleratus*
	Acariformes	*Listrocarpus costaricensis*
Saimiri sciureus	Protozoa	*Blastocystis* sp., *Chilomastix* sp., *Cryptosporidium hominis*, *Entamoeba* sp., *Giardia intestinalis*, *Isospora arctopitheci*, *I. saimiriae*, *Plasmodium brasilianum*, *P. falciparum**, *P. vivax**, *Toxoplasma gondii*, *Trypanosoma cruzi*, *T. minasense*, *T. rangeli*
	Trematoda	*Athesmia foxi*
	Cestoda	*Mathevotaenia* sp., *M. megastoma*, *Sparganum* sp.
	Acanthocephala	*Oncicola sigmoides*, *O. spirula*, *Prosthenorchis elegans*, *P. spirula.*
	Nematoda	*Baylisascaris potosis*, *Dipetalonema* sp., *D. caudispina*, *D. gracile*, *D. marmosetae*, *D. obtusa*, *Enterobius* sp., *Filariopsis barretoi*, *F. gordius*, *Gongylonema* sp., *Longistriata dubia*, *Mansonella colombiensis*, *M. mariae*, *M. saimiri*, *Microfilaria* sp., *Molineus elegans*, *M. torulosus*, *M. verxillarius*, *Trichuris* sp., *Trypanoxyuris minutus*, *T. sceleratus*, *Viannella dubia*
	Acariformes	*Fonsecalges* sp., *Listrocarpus saimiri*
	Pentastomida	*Porocephalus* sp.
Saimiri ustus	Protozoa	*Plasmodium* sp., *P. brasilianum*, *Trypanosoma cruzi*, *T. minasense*, *T. rageli*
Sapajus		
Sapajus apella (syn. *Cebus apella*)	Protozoa	*Blastocystis* sp., *Cryptosporidium* sp., *Endolimax* sp., *Entamoeba* sp., *Giardia* sp., *Leishmania* sp., *L. amazonensis**, *L. infantum**, *L. shawi*, *Plasmodium* sp., *P. brasilianum*, *Toxoplasma gondii*, *Trypanosoma cruzi*, *T. lambrechti*, *T. minasense*
	Trematoda	*Athesmia heterolecithoides* .
	Cestoda	*Bertiella mucronata*, *Mathevotaenia megastoma*, *Moniezia rugosa*, *Spirometra* sp.

Table I (continued)

Host	Parasite group	Parasite taxa
	Acanthocephala	*Oncicola machadoi*, *O. spirula*, *Prosthenorchis elegans*, *P. spirula*
	Nematoda	*Ascaris* sp., *Dipetalonema caudispina*, *D. gracile*, *Molineus torulosus*, *Filariopsis barretoi*, *Physaloptera* sp., *P. cebi*, *Strongyloides* sp., *Subulura* sp., Trichuroidea gen. sp., *Trypanoxyuris clementinae*
	Acariformes	*Fonsecalges johnjadini*
Sapajus cay (syn. *Cebus cay*)	Acanthocephala	*Pachysentis rugosus*
	Nematoda	*Dipetalonema gracile*
Sapajus libidinosus (syn. *Cebus libidinosus*)	Protozoa	*Trypanosoma cruzi*
	Nematoda	*Ancylostoma* sp., *Dipetalonema gracile*, *Filariopsis* sp., *Molineus* sp., *M. torulosus*, *Physaloptera* sp., *Strongyloides* sp., *Subulura* sp., *Viannella dubia*
Sapajus nigritus (syn. *Cebus nigritus*)	Cestoda	*Mathevotaenia megastoma*
Sapajus robustus (syn. *Cebus robustus*)	Protozoa	*Plasmodium brasilianum*, *P. simium*, *Trypanosoma cruzi*
Sapajus xanthosternos (syn. *Cebus xanthosthernos*)	Protozoa	*Leishmania* sp., *Plasmodium brasilianum*, *P. simium*, *Toxoplasma gondii*, *Trypanosoma cruzi*
	Cestoda	*Mathevotaenia megastoma*
Family Pitheciidae		
Cacajao		
Cacajao calvus	Protozoa	*Isospora arctopitheci**, *Plasmodium brasilianum*, *Trypanosoma cruzi*
	Cestoda	Taeniidae gen. sp.
	Nematoda	*Ancylostoma braziliense*, *Bunostomum* sp., *Necator* sp., *N. americanus*, *Physaloptera* sp., spirurid fam. Gen. sp., Strongyloididae gen. sp., *Trypanoxyuris* sp., *T. cacajo*, *T. ucayalii*
Callicebus		
Callicebus nigrifrons	Protozoa	*Leishmania* sp., *Trypanosoma cruzi*
	Cestoda	*Bertiella mucronata*, *Hymenolepis* sp., *H. cebidarum*, *Mathevotaenia megastoma*
	Nematoda	*Primasubulura jacchi*
Callicebus oenanthe	Cestoda	*Bertiella mucronata*
Callicebus personatus	Protozoa	*Plasmodium brasilianum*, *Trypanosoma cruzi*
	Cestoda	*Bertiella mucronata*, *Hymenolepis cebidarum*, *Mathevotaenia megastoma*
	Nematoda	*Dipetalonema caudispina*
Cheracebus		
Cheracebus torquatus (syn. *Callicebus torquatus*)	Protozoa	*Plasmodium brasilianum*, *Trypanosoma cruzi*, *T. lambrechti*
	Cestoda	*Mathevotaenia megastoma*
	Nematoda	*Trypanoxyuris croizati*
Chiropotes		
Chiropotes albinasus	Protozoa	*Plasmodium* sp.
	Trematoda	*Athesmia heterolecithoides*
Chiropotes chiropotes	Protozoa	*Plasmodium brasilianum*

Table I (continued)

Host	Parasite group	Parasite taxa
	Nematoda	*Trypanoxyuris satanas*
Chiropotes satanas	Protozoa	*Leishmania shawi*, *Plasmodium brasilianum*, *Trypanosoma cruzi*, *T. lambrechti*, *T. mycetae*
	Nematoda	*Physaloptera dilatata*, *Trypanoxyuris satanas*
Pithecia		
Pithecia irrorata	Protozoa	*Leishmania* sp., *Plasmodium* sp., *Trypanosoma cruzi*, *T. devei*, *T. minasense*, *T. mycetae*, *T. rangeli*
	Pentastomida	*Porocephalus* sp.
Pithecia monachus	Nematoda	*Trypanoxyuris trypanuris*
Pithecia pithecia	Protozoa	*Plasmodium brasilianum*, *Toxoplasma gondii*, *Trypanosoma lambrechti*, *T. rangeli*
	Nematoda	*Dipetalonema* sp., *Dirofilaria immitis*, *Mansonella* sp., *Trypanoxyuris trypanuris*
	Ixodida	*Amblyomma longirostris*
	Diptera	*Cochliomyia hominivorax*
Plecturocebus		
Plecturocebus brunneus (syn. *Callicebus brunneus*)	Protozoa	*Chilomastix* sp., *Plasmodium* sp., *P. brasilianum*, *Trypanosoma cruzi*, *T. devei*, *T. minasense*, *T. rangeli*
Plecturocebus caligatus (syn. *Callicebus caligatus*, *C. dubius*)	Protozoa	*Plasmodium* sp.
	Cestoda	*Mathevotaenia megastoma*
	Nematoda	*Primasubulura distans*
	Pentastomida	*Linguatula leptocephalus*
Plecturocebus cupreus (syn. *Callicebus cupreus*)	Protozoa	*Trypanosoma minasense*
	Cestoda	*Mathevotaenia megastoma*, *Raillietina* sp., *R. trinitatae*
	Acanthocephala	*Prosthenorchis elegans*
Plecturocebus modestus (syn. *Callicebus modestus*)	Cestoda	*Bertiella* sp.
	Nematoda	Spirurid fam. Gen. sp., Strongylidae gen. sp., *Strongyloides* sp.
Plecturocebus moloch (syn. *Callicebus moloch*)	Protozoa	*Plasmodium brasilianum*
	Nematoda	*Trichospirura leptostoma*, *Trypanoxyuris callicebi*
Plecturocebus ornatus (syn. *Callicebus ornatus*)	Protozoa	*Plamosdium brasilianum*, *Trypanosoma minasense*

Hosts are ordered by family, genus, and species. Parasites are listed by main parasite groups. * indicates parasites detected only under laboratory conditions. See ESM Table SI for more information on the country and references for each record

Two hundred and seventy-six parasite taxa have been recorded to infect Neotropical primates (ESM Table SI). The number of parasite taxa for each host genus varies from 2 in *Cheracebus* to 106 taxa in *Alouatta* (Table II). Parasite richness in each primate genus positively correlates with the number of parasitological studies, being higher in those genera that have been studied more intensively ($R^2 = 0.894$, $df = 19$, $P < 0.001$). The parasite fauna of Neotropical primates is dominated mainly by nematodes, being the richest parasitic group, followed by protozoans, ectoparasites, cestodes, trematodes, acanthocephalans, and pentastomids (Table II). Sixty-eight percent of all parasitic taxa

Table II Number of parasitological studies and parasite species richness for each genus of Neotropical primates, based on data from a literature search in ISI Web of Knowledge, the Global Mammal Parasite database, and additional sources

Host genus	Number of host species[b]	Studied host species	Number of studies	Number of parasitic taxa recorded/number of parasites identified to species level						
				Protozoa	Helminths				Ecto-parasites[a]	Total
					Trematode	Cestode	Acanthocephala	Nematode		
Alouatta	12	6	105	45/26	5/2	7/5	2/1	40/16	7/ 6	106/56
Aotus	11	8	36	23/13	5/4	3/1	1/1	10/4	0	42/23
Ateles	7	6	25	18/9	2/1	3/2	1/1	19/8	0	43/21
Brachyteles	2	2	6	5/3	1/0	4/2	0	6/5	0	16/10
Cacajao	3	1	8	2/2	0	1/0	0	10/4	0	13/6
Callibella	1	0	0	0	0	0	0	0	0	0
Callicebus	5	3	11	3/2	0	4/3	0	2/1	0	19/6
Callimico	1	1	8	2/2	1/1	0	0	4/3	1/1	8/7
Callithrix	6	5	35	13/10	3/3	1/0	7/5	10/7	2/1	36/26
Cebuella	1	1	3	2/2	0	0	2/2	0	0	4/4
Cebus	14	4	24	14/8	2/1	3/2	5/3	24/11	1/1	49/26
Cheracebus	6	1	2	0	0	1/1	0	1/1	0	2/2
Chiropotes	5	3	7	4/3	1/1	0	0	2/2	0	7/6
Lagothrix	5	3	10	3/2	0	0	0	8/5	1/1	12/8
Leontocebus	10	3	11	4/2	6/5	5/0	1/1	17/8	1/0	34/16
Leontopithecus	4	3	22	4/3	0	0	5/4	11/5	0	20/12
Mico	13	5	5	2/2	0	2/1	1/1	2/2	0	7/6
Pithecia	16	3	10	6/4	0	0	0	4/2	1/1	11/ 7
Plecturocebus	22	6	10	3/0	0	4/2	1/1	6/3	0	14/7
Saguinus	12	11	34	11/7	3/3	5/3	6/5	27/13	3/3	55/34

Table II (continued)

Host genus	Number of host species[b]	Studied host species	Number of studies	Number of parasitic taxa recorded/number of parasites identified to species level						
				Protozoa	Helminths				Ecto-parasites[a]	Total
					Trematode	Cestode	Acanthocephala	Nematode		
Saimiri	7	4	43	22/18	0	3/0	5/4	17/13	3/2	50/37
Sapajus	8	6	38	15/8	2/1	4/3	5/5	13/5	1/1	40/23
Total	171	85	251	66/45	20/15	24/9	17/14	117/80	29/24	276/185

[a] All groups of arthropods, i.e., ticks, mites, lice, and dipterans

[b] Data from Estrada *et al.* (2017)

reported in Neotropical primates have been identified to the species level, leaving 32% of parasitic fauna undetermined at this level (Table II).

Alouatta, *Lagothrix*, *Callithrix*, *Plecturocebus*, *Leontopithecus*, *Saguinus*, *Callicebus*, and *Brachyteles* have parasitological records in >80% of the countries that comprise their distribution range (Fig. 1). Costa Rica, Mexico, and Panama are the only countries with parasitological information available for all the primate genera that occur in their territory. Brazil and Mexico stand out as the countries where more parasitological information has been generated (Fig. 1). Parasitological surveys are needed in Bolivia, Colombia, Ecuador, and Venezuela given the high primate diversity found in these countries (Fig. 1).

Among the most widely distributed parasite species are the protozoan *Trypanosoma cruzi*, reported from Mexico to Brazil, in 14 genera and 30 species of Neotropical primate; the acanthocephalan *Prosthenorchis elegans*, present in 11 genera and 17 species, inhabiting six countries from Mexico to Brazil; the trematode *Controrchis biliophilus*, recorded in 5 species in 5 countries between Mexico and Brazil; and the nematode *Trypanoxyuris minutus*, recorded in 4 genera and 9 species of Neotropical primates, and present in 8 countries from Mexico to Argentina (ESM Table SI).

The majority of the parasitological research in Neotropical primates has focused on endoparasites. Helminths are the most covered group of parasites, with 204 studies, followed by protozoans with 115 studies. In contrast, ectoparasites have been explored only in 19 studies (6%). Moreover, only 15 of the 171 species (9%) of Neotropical primates have been studied for ectoparasites.

The majority of the parasite taxa have been recorded in free-living primates; nevertheless, a significant portion of the parasitological records in *Aotus*, *Callicebus*, *Callithrix*, *Leontopithecus*, *Pithecia*, and *Saimiri* are from captive populations (Table III). All the available information for parasites of *Mico* and *Callimico* is from captive primates (Table III). Of all parasite species recorded in Neotropical primates, 8% have been reported only in captive populations, including five species of

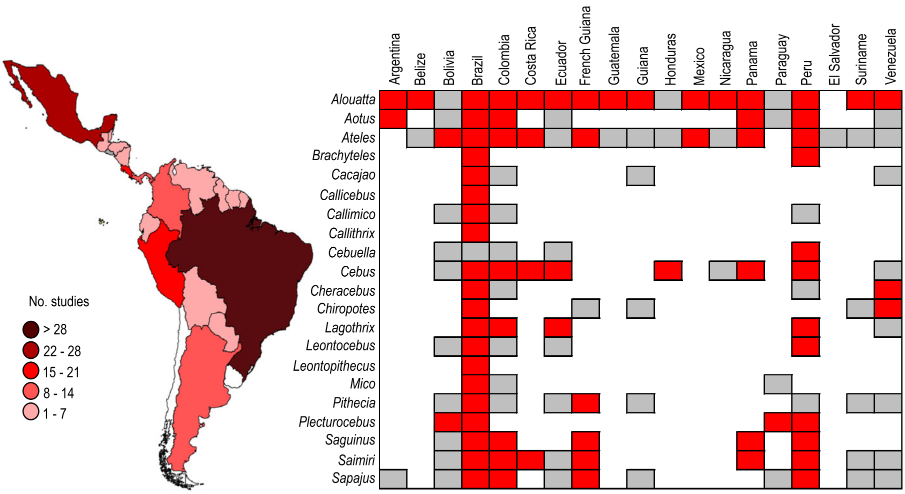

Fig. 1 Geographical distribution of parasitological research in Neotropical primates. The table shows countries where parasitological studies have been carried out for each genus (red). Countries with no available parasitological studies are shown in gray.

Table III Percentage (and number) of parasitological studies of Neotropical primates carried out in different host living conditions and applying different diagnostic methods

Genera	Host living conditions, % (no.)			Diagnostic method, % (no.)				
	Free-living	Zoos	Laboratory	Blood	Fecal	Necropsy	Direct	Molecular
Alouatta	83 (80)	15 (14)	2 (2)	18 (17)	43 (41)	9 (9)	15 (15)	16 (16)
Aotus	26 (12)	17 (8)	57 (26)	52 (15)	28 (8)	3 (1)	0	17 (5)
Ateles	56 (14)	40 (10)	4 (1)	29 (9)	32 (10)	10 (3)	0	29 (9)
Brachyteles	100 (3)	0	0	33 (1)	67 (2)	0	0	0
Cacajao	60 (3)	20 (1)	20 (1)	25 (1)	50 (2)	25 (1)	0	0
Callicebus	43 (3)	57 (4)	0	20 (2)	20 (2)	30 (3)	0	30 (3)
Callimico	0	100 (6)	0	0	0	25 (1)	0	75 (3)
Callithrix	22 (7)	53 (17)	25 (8)	36 (10)	25 (7)	25 (7)	4 (1)	11 (3)
Cebuella	50 (1)	50 (1)	0	67 (2)	0	33 (1)	0	0
Cebus	78 (18)	9 (2)	13 (3)	24 (4)	41 (7)	24 (4)	12 (2)	0
Cheracebus	100 (1)	0	0	0	0	100 (1)	0	0
Chiropotes	80 (4)	20 (1)	0	60 (3)	0	0	0	40 (2)
Lagothrix	89 (8)	11 (1)	0	22 (2)	33 (3)	22 (2)	11 (1)	11 (1)
Leontocebus	83 (5)	17 (1)	0	29 (2)	29 (2)	29 (2)	14 (1)	0
Leontopithecus	37 (7)	63 (12)	0	35 (7)	20 (4)	25 (5)	5 (1)	15 (3)
Mico	0	100 (3)	0	50 (2)	0	25 (1)	0	25 (1)
Pithecia	44 (4)	56 (5)	0	47 (7)	7 (1)	13 (2)	7 (1)	27 (4)
Plecturocebus	100 (8)	0	0	22 (2)	33 (3)	33 (3)	0	11 (1)
Saguinus	38 (14)	43 (16)	19 (7)	31 10)	22 (7)	19 (6)	13 (4)	16 (5)
Saimiri	44 (17)	15 (6)	41 (16)	43 (16)	14 (5)	14 (5)	14 (5)	16 (6)
Sapajus	50 (14)	39 (11)	11 (3)	46 (12)	15 (4)	15 (4)	4 (1)	19 (5)
Total	55 (223)	29 (119)	16 (67)	32 (124)	28 (108)	16 (61)	8 (31)	17 (66)

protozoans (four species of *Plasmodium* and *Cryptosporidium hominis*), two species of Platyhelminthes (*Atriotaenia* sp. and *Fasciola hepatica*), one acanthocephalan (*Moliniformis clarki*), and seven species of nematodes (*Gongylonema pulchrum*, *Angiostrongylus cantonesi*, *A. dujardini*, *Dilofilaria immitis*, *Rictularia nycticebi*, *Strongyloides stercoralis*, *S. venezuelensis*) (ESM Table SI).

The diagnostic methods commonly employed for parasitic surveys in Neotropical primates include analysis of blood and fecal samples, and opportunistic necropsy is performed only in very few cases when a primate individual dies from natural causes or if it is found as a road-kill (Table III). Molecular procedures have been applied as a diagnostic method in only 17% of the parasitological studies (Table III).

Discussion

The bibliographic review presented here shows that parasitological research is moderately common in the study of Neotropical primates; nearly half the primate diversity occurring in this region is the subject of at least one parsitological study. More than 200 taxa of parasites have been reported infecting these hosts, with nematodes as the richest parasitic group. This parasitological diversity has been diagnosed by employing a variety of methods and in multiple host living conditions, each of them representing a set of advantages and limitations regarding host accessibility and parasite diagnosis accuracy. Our review adds parasitological information for 20 primate species and 318 parasitological records that were not included in the GMPD (Nunn and Altizer 2005; Stephens *et al.* 2017).

Host Taxonomic Coverage and its Application to Neotropical Primate Conservation

Although parasitological records exist for almost every genus, the amount of available information is highly biased toward certain genera and particular primate species (e.g., *Alouatta* is the best studied genus, but 6 of the 12 species lack information regarding their parasites), and toward some countries across the host distribution range. This asymmetric sampling effort is also observed in the number of primatological publications for each genus (Table S1 from Estrada *et al.* 2017), suggesting that some species are more appealing to researchers than others, perhaps because they are more charismatic or easier to study. Also, it is possible that these species have been the subject of well-established and long-term research programs.

Sixty one of the 171 species of Neotropical primates are included in a risk category of the IUCN Red List (Estrada *et al.* 2017). In 46% of these threatened species any information regarding their parasite fauna is lacking. Moreover, in 89% of the species whose conservation status has not yet been evaluated information regarding their parasite fauna is also lacking. Parasitological studies conducted in threatened species can shed light on three aspects of host biology that are fundamental for policymakers: 1) determining potential scenarios of coevolutionary history among hosts and parasites; 2) analyzing host–parasite dynamics and determining parasite species richness and transmission routes; and 3) assessing host health status and vulnerability to parasitic infections. For example, in conservation strategies that involve the movement of animals, such as reintroduction or translocation programs, parasites could be also co-reintroduced along with their hosts; such cases must consider the native geographical distribution of the parasite and the strength of the association (Jorgensen 2015). Habitat restoration projects, such as the establishment of biological corridors, also need to consider parasite transmission dynamics and the presence of potential reservoir hosts to assess trade-offs between the benefits of connecting populations and the possible risks of parasite transmission (McCallum and Dobson 2012). Moreover, mortality trends could be related to parasite infections. If this possibility is not considered, it could jeopardize established conservation programs (Zhang *et al.* 2008).

Despite the relevance of parasitological data for species conservation, we found no studies in which such information had been used when designing management strategies for threatened species. Greater efforts are needed to obtain parasitological data from unstudied, endangered Neotropical primates species (ESM Table SII) to assess the role of parasites in population declines, and identify risk zones (i.e., locations of disease outbreaks or highly infested populations). It is also essential to communicate this information to the institutions responsible for the development and application of conservation policies, enabling the design of suitable strategies and management protocols.

Diagnostic Methods Used, and their Advantages and Limitations

Some inherent features of parasites, such as size, location, and morphological variability through their life cycle, make parasitological research challenging. Hence, in addition to the regular usual complications of any primatological study, the observation, collection, and identification of primate parasites face further difficulties. Sampling parasites in wildlife frequently requires capture and manipulation of the host, and in most cases host sacrifice. For Neotropical primates, host sacrifice is unethical and is not an option.

Given the arboreal nature of many Neotropical primate species (Hartwig 2007), host capture and manipulation are highly risky, and probably not feasible, especially for endangered species; thus, noninvasive sampling techniques are required, such as coproscopic analyses. Additional relevant information can be obtained from faecal samples, such as diet and microbiota components, hormones, and immune measures, which may be related to parasitism (Amato and Righini 2015; Lukas *et al.* 2004; Muehlenbein 2009; Wasser *et al.* 1997, 2010). However, noninvasive methods are limited in terms of parasite identification (Solórzano-García and Pérez-Ponce de León 2017), since they rely mostly on morphological features of the eggs or immature stages, which are very similar among closely related species. In many cases parasites can be identified only as far as the family level or even at higher categories of the taxonomic hierarchy such as phylum (ESM Table SI).

Molecular techniques are promising tools for parasite diagnosis, especially when using noninvasive sampling, since they allow more robust species identification and the confirmation of uncertain parasite species (Gasser 2006; Raja *et al.* 2014; Solórzano-García *et al.* 2017). For example, the parasitic nematode *Enterobius* has been recorded in howlers in Brazil (Godoy *et al.* 2004; Holsback *et al.* 2013; Vicente *et al.* 1997), Mexico (García-Serrano 1995; Trejo-Macías *et al.* 2007), and Ecuador (Helenbrook *et al.* 2015b) (Tables I and SI); however, these records require confirmation, as pinworms and primates have a strong coevolutionary association in which *Enterobius* is found only in Old World primates (Catarrhini), *Lemuricola* in lemurs (Strepsirrhini), and *Trypanoxyuris* in Neotropical primates (Platyrrhini) (Hugot *et al.* 1996). Moreover, parasitological studies suggest that *Trypanoxyuris* are highly host specific parasites (Hugot 1999; Solórzano-García *et al.* 2016). Thus reports of *T. oedipi*—a pinworm normally found in *Saguinus*—in *Alouatta* (Correa *et al.* 2016); *T. trypanuris*—a pinworm normally found in *Pithecia*—in *Ateles* (Thatcher and Porter 1968); and *T. minutus*—a pinworm normally found in *Alouatta*—in *Leontopithecus* (Monteiro *et al.* 2007), *Ateles*, and *Saimiri* (Vicente *et al.* 1997) need confirmation.

Molecular methods for parasite diagnosis rely on comparisons of available molecular information for confirmed parasite species to DNA from the unknown parasite species. Necropsies are by far the best method to obtain adult forms of many types of parasites, and present an important opportunity to increase the parasite genetic library. Therefore, each opportunity to perform a necropsy on a primate should include both morphological examinations and DNA extraction for as many parasites species as possible. However, only 8 of 61 necropsies performed in Neotropical primates studies complemented their analyses with molecular information by extracting DNA from the parasites recovered from their hosts (Cedillo-Peláez *et al.* 2011; Malta *et al.* 2010; Pena *et al.* 2011). Collaboration between primatologists with professionals of other disciplines, including veterinarians, parasitologists, and zookeepers, is fundamental to develop postmortem protocols that sample parasites and assess any apparent damage they cause, and to carry out the morphological, genetic, and phylogenetic analysis needed to accurately estimate parasitic richness in Neotropical primates, easing the future of molecular diagnosis through noninvasive techniques in endangered species.

Parasite Taxonomic Coverage

Our Parasite–Host list contains information on 276 taxa of parasites in Neotropical primates. The number of parasitic taxa is higher in those primate species that have been studied more intensively, suggesting that the parasitic richness reported in Neotropical primates may increase as greater research efforts are directed to the less studied primate species. Also, the parasite diversity reported in these hosts might be imprecise owing to difficulties in species identification, incomplete parasite species description, or limitations of diagnostic methods, leading to inconclusive or uncertain records. For instance, some of the parasites identified to family level, such as Strongylidae and Ascariididae, or even those identified to genus level may represent a single parasite species or many species, especially if the same record has been made for several host species, leading to the over- or underestimation of parasite diversity.

A similar inaccurate estimation of parasite diversity could occur with those parasite species that have been reported in a wide distribution range, where different species or local variants may exist, that might not being detected unless close attention is paid. For example**,** *Trypanoxyuris minutus* is a common parasite of howlers (*Alouatta* spp.) recorded almost across their entire distribution (e.g., Amato *et al.* 2002; De Thoisy *et al.* 2001; Pope 1966; Stuart *et al.* 1998; Thatcher and Porter 1968; Trejo-Macías *et al.* 2011). Recent studies have shown that more than one species of *Trypanoxyuris* parasitize howlers in Mexico (*Alouatta palliata* and *A. pigra*) (Solórzano-García *et al.* 2016); thus, it is likely that *Trypanoxyuris*' species other than *T. minutus* infect different howler species. This hypothesis needs to be tested by increasing the sampling effort in understudied areas and host species.

Our review shows that the sampling effort for endo- and ectoparasites parasites is asymmetrical, with most parasitological research focused on endoparasites. One plausible explanation for this disparity is related to the sampling methods required to collect parasites from their hosts. Sampling ectoparasites involves capture and sedation of individuals (Cristobal-Azkarate *et al.* 2012; Troyo *et al.* 2009), while information for most endoparasites is obtained through noninvasive sampling techniques. However, records of blood parasites, which in general also require the manipulation and sedation of the host, are not uncommon (Acardi *et al.* 2013; de Castro Duarte *et al.* 2008; Fandeur *et al.* 2000; Pires *et al.* 2012; Ziccardi and Lourenço-de-Oliveira 1997; among others) (Table III). Unfortunately, most studies of blood parasites of primates did not sample ectoparasites (or did not publish their results). Ectoparasites are important components of the parasitological communities in terms of species richness and abundance; in addition, some species of ectoparasites may cause severe damage to their hosts; for example, heavy loads of bot flies (*Cuterebra baeri*) can compromise howlers through nutritional stress, and even cause their death (Milton 1996). Furthermore, many ectoparasites can act as vectors for pathogens that can cause serious diseases, such as *Rickettsia* spp., *Bartonella* spp., and hemoplasmas. The last two are recorded in Neotropical primates (Bonato *et al.* 2015; Cubilla *et al.* 2017; De Thoisy *et al.* 2001). In contrast, many ectoparasites form intimate and specialized associations with their hosts. Because of their host-specificity patterns, life cycle characteristics, and transmission mode, ectoparasites are considered as potential markers for inferring their host's evolutionary history, and provide insights into host behavior and ecology (OConnor 1987; Reed *et al.* 2009; Zohdy *et al.* 2012).

Studies that survey the entire parasite fauna of Neotropical primates (i.e., endoparasites such as gastrointestinal and blood parasites, and ectoparasites) are scarce in the literature. Most studies focus on a particular group of parasites and a particular geographic area. A more integrative approach is required when designing sampling strategies. To make this plausible, we need collaboration among specialists. This approach will allow us to gather as much information as possible from the same sampling effort, and will considerably increase our knowledge of the parasites of Neotropical primates.

Sampling parasites in captive individuals is easier than sampling in the wild, and can yield valuable information; however, parasites found in hosts under captivity do not necessarily constitute part of their natural parasite fauna, as they may be acquired as an accidental infection given the artificial conditions in which those animals live, resulting in misleading information on primate parasitological diversity and zoonotic risk. Identification of the parasite fauna of free-living populations is essential to fully understand the ecological relations and the evolutionary associations between primates and parasites, and to assess the potential implications of parasitic infections for primate conservation and public health.

Parasites Overlap between Humans and Neotropical Primates

Humans and Neotropical primates seem to share a significant amount of parasite species from every major group of parasites considered in this review. Of the 276 taxa of parasites recorded in Neotropical primates, 42 species have also been reported as parasites of humans (24 species of protozoans, 2 species of trematodes, 3 species of cestodes, 1 species of acanthocephalan, 10 species of nematodes, and 3 species of ectoparasites; ESM Table SI). Some of these parasites are the etiological agents of severe human tropical diseases such as malaria, Chagas disease, and leishmaniasis. Since the same species of *Plasmodium*, *Trypanosoma*, and *Leishmania* that infect humans have apparently been found in Neotropical primates, we can postulate that these primates can serve as potential reservoirs for human infections (de Castro Duarte *et al.* 2008; Fandeur *et al.* 2000; Rovirosa-Hernández *et al.* 2013). However, these statements should be taken with caution, given the difficulties in parasite species identification, and the uncertainty of some records, such as *Enterobius vermicularis*. Parasite species identity should be confirmed using as much evidence as possible, including morphological features, molecular data, and ecological traits, to avoid speculation, especially when investigating potential cross-species transmission events between primates and humans or domestic fauna.

The mechanisms of transmission of parasite species between humans and nonhuman primates are, in most cases, still unresolved and the direction of transfer is controversial. For example, the evolutionary history of *Plasmodium* involves several host-switching events and horizontal transfer of parasites between humans and nonhuman primates, and we do not know the natural host where the parasite originated (Di Fiore *et al.* 2009). Nonetheless, molecular and phylogeographic evidence suggests that *P. brasilianum* and *P. simium*, the two most common species of *Plasmodium* found in Neotropical primates, could be derived from transmission of the human parasites *P. malariae* and *P. vivax* to Neotropical primates (Faust and Dobson 2015; Leclerc *et al.* 2004). The presence of helminths such as *Ancylostoma braziliense*, *Necator americanus*, *Ascaris lumbricoides*, and *Schistosoma mansoni* in Neotropical primates could also be a result of an anthropozoonotic transmission (Michaud *et al.* 2003; Phillips *et al.* 2004), but this hypothesis needs further testing. Molecular data shed light on the genetic variants of parasites shared by humans and nonhuman primates, allowing the assessment of primates as potential source of parasitism in humans (Villanueva-García *et al.* 2017), sometimes supporting the zoonotic transmission of the parasites (Hasegawa *et al.* 2014), and other times showing that humans and nonhuman primates harbor genetically different variants of parasites (Gasser *et al.* 2009; Helenbrook *et al.* 2015a; van Lieshout *et al.* 2005).

Future Directions in Parasitological Research in Neotropical Primates

The inventory of the parasite fauna in Neotropical primates is far from complete, and intensive study is required to better understand primate–parasite associations. Valuable efforts have been made to understand the parasite diversity associated with Neotropical primates, and to determine how environmental characteristics, host features, and habitat perturbation affect the primate–parasite dynamics (i.e., Behie *et al.* 2014; Helenbrook *et al.* 2015a; Parr *et al.* 2013; Santa-Cruz *et al.* 2000; Tavela *et al.* 2013; Wenz *et al.* 2010). However, we need an integrative research program to examine the parasite fauna comprehensively, with complementary studies. This requires an interdisciplinary approach in which veterinarians, primatologists, and parasitologists work together in the determination, description, and treatment of parasites.

Since several species of Neotropical primates are endangered, and in many occasions capturing and handling individuals for parasitological research would not be feasible, especially in free-living populations, we need to develop methods that enhance parasite diagnostic accuracy when using noninvasive sampling. New molecular technologies impose new challenges and provide new opportunities for the study of parasites. The molecular diagnosis of parasite eggs found in primate faeces is an effective method to characterize the parasites of Neotropical primates (Solórzano-García and Pérez-Ponce de León 2017). Moreover, faecal metagenomic analyses can be used to identify parasites in primates (Srivathsan *et al.* 2016). The utility of these methods relies on the completeness of the parasite genetic library; thus, the extraction and publication of molecular data from recovered and identified parasites should be a priority in current and future Neotropical primate parasitological studies.

Conclusions

Parasitological research is an exciting research field with many unanswered questions, including the evolutionary and ecological processes involved in driving parasite–

primate dynamics, and the effects of parasitism on primate conservation and human public health. Despite valuable efforts, our parasitological knowledge of Neotropical primates is still limited. Several Neotropical primate species and geographical regions remain unexplored, and some parasite groups, such as ectoparasites, have been neglected in parasitological surveys. The development of an integrated research program is essential to make further and significant contributions. Furthermore, the generation of molecular data should become part of the regular procedures in parasitological research, particularly when performing a necropsy, to increase the genetic library, hence improving the utility and accuracy of noninvasive sampling surveys. To accomplish this, we suggest that primatologists include parasitologists in their research programs, addressing parasitology from an interdisciplinary approach.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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