Life-histories as determinants of infection prevalence for trypanosomatids: A meta-analysis

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Abstract

Trypanosomatids are a diverse family of protozoan parasites, some of which cause devastating human and livestock diseases. There are two distinct infection life-cycles in trypanosomatids; some species complete their entire life-cycle in a single host (monoxenous) while others infect two hosts (dixenous). Dixenous trypanosomatids are mostly vectored by insects, and the human trypanosomatid diseases are transmitted mainly by vectored parasites. While infection prevalence has been described for subsets of hosts and trypanosomatids, little is known about whether monoxenous and dixenous trypanosomatids differ in infection prevalence. Here, we use meta-analyses to synthesise all published evidence of trypanosomatid infection prevalence for the last two decades. We employed a semi-automated screening protocol, using machine learning algorithms and natural language processing, resulting in the qualitative inclusion of 569 citations and quantitative inclusion of 261 citations. We find striking difference in infection prevalence with monoxenous species having twice the infection prevalence (19.8%) than dixenous species (8.68%) in both insect and non-insect hosts and are more than three-fold more prevalent in insects (20.9%) compared to their dixenous kins (6.61%). We also find that dixenous trypanosomatids have lower infection prevalence among insects compared to their definitive hosts, which is consistent across dixenous genera. Within the monoxenous trypanosomatids, genera infecting bees are characterised with the highest prevalence, which does not vary between wild and managed bees. To our knowledge, these results reveal for the first time, a fundamental difference in infection prevalence according to host specificity where vectored species suffer from lower infection prevalence as a result of a 'jack of all trades, master of none' style trade-off between the vector and definitive host.

Introduction

Trypanosomatids are Kinetoplastid protozoan parasites that infect a diverse range of hosts including vertebrates, invertebrates and plants. Among trypanosomatids, there are two distinct life-histories with some infecting only a single host for their whole life-cycle (monoxenous), and others that require two hosts to complete their development (dixenous). The dixenous lifestyle is thought to be evolutionarily derived and has evolved independently multiple times among the Kinetoplastids.[1] Dixenous trypanosomatids invariably include an insect vector that then transmits infection to a vertebrate or plant definitive host. Dixenous trypanosomatids consist of four main genera: *Leishmania, Trypanosoma, Endotrypanum and Phytomonas*. The vast majority of epidemiological and empirical evidence for all trypanosomatids comes from the former two genera (*Leishmania and Trypansoma*) as they are the most medically relevant. At least 20 species of *Leishmania*, cause cutaneous, mucocutaneous and visceral leishmaniasis; *Trypanosoma cruzi* causes Chagas disease and *Trypanosoma brucei* is the etiological agent of African sleeping sickness. These diseases cause more than 830,000 infections every year[2], causing significant disease burden, and their control is challenging. Estimates of incidence and mortality vary but some studies predict that more than 1 million people contract leishmaniasis annually, including up to 700,000 visceral cases (which is fatal in 95% of cases), and a further 1 billion people are at risk of infection.[3–5]

Monoxenous trypanosomatids not only have a simpler life-cycle and narrower host specificity, usually in a single invertebrate host, but they are also more common, more ancient (but see),[6] and more diverse than dixenous trypanosomatids.[7] There are 17 currently described monoxenous trypanosomatids genera: *Angomonas, Blastocrithidia, Blechomonas, Crithidia, Herpetomonas, Jaenimonas, Kentomonas, Lafontella, Leptomonas, Lotmaria, Novymonas, Paratrypanosoma, Rhynchoidomonas, Sergeia, Strigomonas, Wallacemonas,* and *Zelonia* in contrast to the four dixenous genera. Despite the overwhelming diversity of monoxenous trypanosomatids we know comparatively little about their natural history and prevalence, due to their perceived lack of medical relevance - although this has been called into question recently by opportunistic vertebrate infections by some monoxenous trypanosomatids.[8–10]

Monoxenous and dixenous trypanosomatids also appear to differ in their infection prevalence. Despite the substantive health burden of vectored trypanosomatids, they have surprisingly low infection prevalence in the vector insects. For instance, fewer than 3% of *Phlebotomus* sand flies carry *Leishmania*[11] and as few as 0.1% of adult tsetse flies have transmissible *Trypanosoma* cells in their saliva.[12] In contrast, trypanosomatids with only a single insect host can reach extremely high prevalence. In the bumblebee *Bombus terrestris* up to 35% of workers can be infected by its trypanosomatid parasite, *Crithidia bombi*.[13] These data hint at something crucial: that perhaps the major limiting factor for trypanosomatid infection transmission is the vector, not the vertebrate host. Therefore, a detailed understanding of insect-parasite interactions, and how they can be manipulated, will be vital to the control and potential eradication of these diseases.

Here, we set out to systematically test whether monoxenous and dixenous trypanosomatids indeed have different infection prevalences, and whether this is

consistent among hosts. While some systematic reviews have attempted to examine trypanosomatid pooled prevalence they have only done so in the context of either individual trypanosomatid or host taxa,[14,15] or summarised evidence across hosts but were restricted to one geographic region.[16-18] This is the first review of its type at this scale aimed to describe how fundamental aspects of parasite life-history influence disease prevalence in an important group of human, livestock, and wildlife parasites. We hope that our findings will help clarify the link between parasite life-history and infection in turn, potentially shed light onto better control strategies to combat the spread of trypanosomatid infections.

Methodology

Literature search

We searched Scopus and all available databases in Web of science, to identify all published studies that describe trypanosomatid prevalence in non-human hosts. Full search terms can be found in Supplementary Table 1. During the literature search, we did not apply any year or publication type restrictions (search stopped Jan 2020). To exhaustively find studies of neglected trypanosomatids, we further checked the references in relevant papers and added candidate citations to screening list of studies. All duplicate references were identified and removed.

Relevant screening stages and design

References were initially screened based on titles and abstracts manually by a single reviewer (HA) using Rayyan website as outlined in (Supplementary appendix). We further employed an automated second review protocol using Machine Learning Algorithm (MLA) and Natural Language Processing (NLP) during the initial screening phase, as has previously been suggested for large datasets[19] (and detailed in (Supplementary appendix). All studies that received a manual or an automated "include" decision were subsequently subjected to further eligibility assessment by full-text review by two different reviewers (Figure.1). Inclusion and exclusion criteria, as well as detailed protocol of study selection and data extraction can be found in (Supplementary appendix).

Selection of studies for meta-analysis

After filtering, 569 studies, with 1031 prevalences, were included in subsequent analyses. As expected, fewer (16%) of these were on non-human parasites. We included all of these studies in our meta-analysis. The remaining studies (84%) were on vector-borne human parasites such as *Leishmania* and *Trypanosoma* species. To capture all of the information about the less commonly studied trypanosomatids but without processing all of the over-represented parasites, we opted to qualitatively include only studies with > 400 sampled individuals. To confirm that this did not introduce any bias, we randomly selected 20 citations with fewer than 400 individuals. We made this selection approach based on the following considerations: (I) studies with larger sample size would be closer to the true population prevalence, (II) have stronger impact on the meta-analysis and (III) when

broken down to host and parasite taxa level they will remain statistically informative. As an additional confirmatory step, we compared the outcome and the fit of models with 261 studies (as per our selection strategy) or all of the studies (n= 569). To our assurance, while both models showed similar outcome, models with 265 studies had a better fit than the alternatives (i.e. lower AIC value:Δ153).

Meta-analysis

Estimates of proportion of infections were calculated using "metaphor" package[20] with the variance stabilised by Freeman-Tukey double arcsine transformation. Pooled estimates were back-transformed for each analysis and multiplied by 100 to get the pooled prevalence. Publication bias was assessed using a funnel plot with trim and fill method and Egger's test. We employed a random effect multilevel model (rma.mv) with a nested random design to account for the heterogeneity of evidence either due to different study protocols and/or different host/parasite taxa within and between studies. We assigned "study ID" as an outer random factor, and both "host type: 19 levels" and "parasite taxa: 47 levels" were considered inner-random factors. This was done for the general model with no moderator applied as well as meta-regression models with the following moderators: diagnostic method (3 levels [molecular, microscopic, serological]), life-history traits of the parasite (3 levels[dixenous, monoxenous, mixed trypansomatids), host groups (insects and non-insects), parasite taxa (47 levels), host taxa (19 levels). We also ran similar meta-regression models to assess pooled prevalence but in a subgroup of interest excluding some levels of the moderator as necessary . For instance, when comparing diagnostic methods among hosts we excluded serological approaches as they only apply to vertebrates. Between-study variation was assessed using the Higgins I^2 statistic, which usually indicates substantial heterogeneity if exceeding 50%. Q_M statistic, an omnibus test of all model coefficients except for the intercept, was conducted to conclude if a moderator significantly influences the mean effect size. All meta-regression models were run with and without the model intercept to statistically compare effect size of factors and generate pooled estimate for each factor respectively. Forest plots were presented using "orchaRd" package with "tanh" transformation as traditional forest plot will fail to present the large number of included citations.[21]

Figure1: *Selection and screening stages*

A) The overall protocol utilised for literature search and screening, wherein (n) represents the number of studies included/excluded at each stage and (K) represents the number of data extracted from qualitatively or quantitatively included studies. All steps of the systematic review were in concordance with PRISMA guidelines.[22]

Results

Exploring the impact of host-parasite traits on prevalence patterns

Out of 6046 unique citations, we have qualitatively included 569 studies[23–591] and quantitatively included 261 studies.[23–283] Overall, these results demonstrate a growing number of trypanosomatids studies over the last two decades (Supplementary Fig.2). Additional information about the geographic distribution of trypanosomatids can also be found in (Supplementary appendix).

A summary of the pooled prevalence and the main features of included citations, stratified by parasite species, can be found in Table 1. We found that monoxenous parasites that usually infect the same host-order, show similar infection prevalence across hosts. This is the case both for monoxenous species with high prevalence (e.g. bees) and parasites with low pooled prevalence (e.g. monoxenous and dixenous species infecting flies)(Fig.2C). Subsequent analysis of various host-groupings show similar trends in infection prevalence in bees and flies to that presented in Table 1, though the latter remains influenced by both monoxenous and dixenous species (Supplementary Fig.6). In addition, fish, raccoons and buffaloes have high pooled prevalence although they are comparatively rarely studied (Supplementary Fig.3). In spite of the low number of studies, their total sample size indicates comparable robustness of analysis to that of other host groups, which supports our estimates of prevalence (Supplementary Fig.3B).

Infection prevalence is further stratified into within host prevalence in (Fig.2A). As expected, dogs and cats appear to be the main vertebrate-reservoirs for *Leishmania* and *Trypanosoma cruzi*. Additionally, the *Trypanosoma congolense* group seem to heavily infect certain domesticated animals such as pigs, sheep, and goats. Buffaloes, camels, and cattle appear to be the main reservoirs for Surra (*Trypanosoma evansi*). Some hosts have similar infection prevalence to various parasites of Trypanosomatidae (i.e. flies and rodents) while other parasite-groups show similar prevalence among various hosts (e.g. *Trypanosoma simia*).

Multiple analysis of monoxenous versus dixenous infections

We set out to test whether pooled prevalence of monoxenous infections differ from dixenous infections (both among insect and non-insect hosts). We find a strongly significant difference between pooled prevalence of monoxenous (19.8%) and dixenous infections (8.68%) (Fig.3A). Introducing "host-traits" as a sole moderator (i.e. insects and non-insects) reveals no significant difference between pooled prevalence of the two groups, 11.5% and 9.45% respectively (Fig.3B). Limiting the analysis to insects alone revealed an even stronger effect with monoxenous infections- three-fold more prevalent (20.9%) than dixenous infections (6.61%) (Fig.4, Table 2). We then compared prevalence in the groups of insects that had both dixenous and monoxenous parasites (true bugs and

flies). Here however, we find non-significantly higher pooled prevalence for dixenous infections in flies and similar pooled prevalence in true bugs (Table 2).

Notably, dixenous parasites consistently infect 4.54-8.00% of their insect hosts with no significant difference among parasite genera (Fig.4B). Common dixenous parasites, with prevalence data from both insects and non-insects, were significantly more prevalent in their non-insect hosts (9.38%) than their insect hosts (5.51%) (Table 2).

Monoxenous genera exhibit two alternative trends: high pooled prevalence for *Lotmaria*, *jaculum* and *Crithidia* species, but low pooled prevalence for *Herpetomonas*, *Leptomonas*, *Agomonas*, and *Blastocrithidia* groups (Fig.4 B). Taking into consideration that a considerable amount of monoxenous data (80%) were on bee infections, we performed an in depth sub-group analysis to further understand the main drivers of bee infection prevalence. While the majority of included data represent natural infection among wild bees, the remaining evidence describes spillover of infections e.g. by sampling non-native/commercial bees. We do not find any difference in trypanosomatid infection prevalence between wild-bees and commercial/managed bees for bumblebees or honeybees (Table 2).

Honeybee infections seem to predominantly occur in Western/European honeybees (e.g. *Apis mellifera Linnaeus*) compared to Asian honeybees (e.g. *Apis dorsata Fabricius* and *Apis cerana Fabricius*). We also noted a significant reduction in heterogeneity of evidence across all honeybee-infections due to spatial variations only (46% heterogeneity). However, a much higher diversity of infection prevalence was found in bumblebee taxa. Accounting for spatial and temporal factors failed to significantly reduce the heterogeneity in evidence for bumblebee infections, suggesting a unique impact of various bumblebee-trypanosomtids systems on different patterns of prevalence (Fig.2.B) and likely the greater diversity of bumblebees.

Diagnostic approach also affected infection prevalence but differ according to host. Microscopic diagnostics revealed higher infection prevalence in insects whereas molecular assays report higher infection prevalence in non-insects (Table 2).

Figure 2: *Infection prevalence among host-trypanosomatid systems*

A heat-map of prevalence of all host-parasite systems (A), of bumblebee-trypanosomatids (B). A phylogenetic representation of all host taxa examined here. The first (inner) ring (R1) illustrates the parasite taxon's life-history (dixenous, monoxenous or both), the second ring (R2) highlights the abundance of prevalence data for each taxon, and the third ring (R3) is host order. Prevalence of infection (%) is shown in the outer scaled ring, which is coloured according to parasite life-history.

Figure 3: *Forest plots of main meta-regression models*

A) Pooled estimate of infection prevalence of dixenous (0.310, 95% CI:0.285, 0.335), monoxenous (0.467, 95% CI:0.404, 0.530), and mixed trypanosomatids (0.427, 95% CI:0.313, 0.551) with significant difference between them (P<0.05). These pooled estimates back-transform to 8.68%, 19.8%, and 17.0%, respectively. B) There is no overall significant difference between the pooled estimate of infection prevalence of insect (0.354, 95% CI: 0.313, 0.396) and non-insect (0.320, 95% CI:0.292, 0.353) hosts (P>0.05). These pooled estimates correspond to 11.5% and 9.45%.

Figure 4: *Forest plots of meta-regression models based on parasites-grouping among insects*

A) Pooled estimate of infection prevalence of monoxenous genera, representing a pooled estimate of 0.395 (95% CI:-0.201, 0.992), 0.566 (95% CI:0.332, 0.801), 0.235 (95% CI:-0.1764, 0.6468), 0.197 (95% CI:-0.415, 0.8085), 0.524 (95% CI:0.4118, 0.6371), 0.158 (95% CI:-0.2545, 0.5707), 0.125 (95% CI: -0.469, 0.720) and 0.557 (95% CI:0.012, 1.10) for *monoxenous, Lotmaria, Leptomonas, Herpetomonas, Crithidia, Blastocrithidia, Angomonas and 'jaculum'* species respectively with no significant difference between them (P>0.05). These pooled estimates were back-transformed to a prevalence of 13.4%, 27.9%, 3.70%, 2.13%, 24.0%, 0.882%, 0.185% and 27.0%. B) Pooled estimates of infection prevalence in dixenous genera, of 0.293 (95% CI:0.2407, 0.3458), 0.269 (95% CI:0.0786, 0.4597) and 0.223 (95% CI:0.1586, 0.2868) for *Trypanosoma, Phytomonas* and *Leishmania* respectively with no significant difference between subgroups (P>0.05) corresponding to prevalence of 8.00%, 6.76% and 4.543%.

Discussion

Trypanosomatid parasites have two distinct life-histories that vary in the number of host species and the complexity of their life-cycle. This difference is profound and will have commensurately profound effects on the evolution of parasite traits, including their ability

to establish infection. How these alternative life-history strategies influence infection prevalence, however, is poorly understood. To our knowledge, this is the first comprehensive study designed to test for differences in infection prevalence. Our semi-automated screening protocol, resulted in the qualitative inclusion of 569 citations and quantitative inclusion of 261 citations.

We find that monoxenous trypanosomatids are far more prevalent in their hosts than are dixenous species. Across all hosts, we find at least two-fold higher prevalence in monoxenous species (Fig.3A) and more than three-fold higher when we examine infection prevalence in insects alone (Table 2). Taken together, one cannot escape the impression that complex parasite life-cycles have a cost to infection prevalence. In line with such speculation, high prevalence for monoxenous species was mainly notable among genera that infects bees such as *Crithidia* and *Lotmaria* with pooled prevalence of 24.0% and 27.9% respectively; ranking bees with the highest pooled prevalence among all insects (26.3%). It is striking to realise that greater than a quarter of surveyed bees are infected by trypanosomatid pathogens. This is of a particular concern considering the crucial role of bees as pollinators, which, with other insect pollinators, account for the fertilisation of 83% of flowering plants[592] including nutritionally and economically important crop species[593,594]. Bees and other pollinators have been declining. Among the presumed causes of pollinator declines are infectious diseases.[595] Despite the attention that bee-trypanosomatid infection has attracted, the distribution of interest remains uneven. Infection prevalence of trypanosomatids is largely unexplored outside of Europe and North America (Supplementary Fig.4)

The relationship between wild and managed bees, and the risk of spillover in either direction, has received particular attention and concern in the literature. While managed bees have been blamed for parasite transmission to wild bees,[74,596] we find no significant difference between managed and wild honeybees and bumblebees (either independently or combined) in trypanosomatid infection prevalence. Whether this reflects shared susceptibility to infection or ongoing spillover to and from wild pollinators remains unknown.

To our knowledge this is the first study to provide such concise statistical summary of prevalence data among all host-trypanosomatids systems. Encouragingly, our findings recapitulate those of several other, taxon- or geographically-restricted, systematic reviews. For instance, A similar range of prevalence (2.4-9.2%) for trypanosomatids was reported in sand-flies (*Phlebotomus* spp.) in Iran,[597] which largely agrees with our finding of 2.02%. Another meta-analysis on trypanosomatids in tsetse flies revealed a prevalence of 10%, which is somewhat higher than we find in flies (5.51%).[15] The variation between these prevalence data could be due to different study design, year of publications of included studies and data analysis. Unlike our study, all prevalence data from[15] were uncovered using microscopic examination and the analysis was done using STAT. Thus, although biting flies are responsible for most human trypanosomatids, our results seem to comport with previous studies revealing low infection prevalence in flies as a group, with no significant difference between monoxenous and dixenous parasites within flies (Table 2). Meanwhile, pooled prevalence for trypanosomosis in cattle, sheep and goats was reported

as ranging between 1-9%, which is comparable to what we find (Table 2. and Supplementary Fig.6).[17,18,598]

We also reveal significantly higher prevalence in the definitive vertebrate hosts than vector flies which is consistent among dixenous genera. This brings to the fore a possibility that dixenous trypanosomatids infect more of their vertebrate hosts than their insects vectors. Evolutionary theories predict a life history trade-off between investment in survival (within-host persistence and growth) and reproduction (between-host transmission). For dixenous trypanosomatids, such relationship is amplified by the number of host species needed to complete the life-cycle.[599] This trend warrants further investigations as understanding how these species are maintained in the metapopulation holds great potential in managing the spread of vector-borne diseases. For instance, if the prevalence of infection in vectors is low, further reduction in insect hosts may better control infection in the metapopulation than suppression in vertebrate hosts.

In this study, we find that microscopic diagnostics revealed higher infection prevalence in insects but greater infection prevalence was revealed from molecular assays in non-insects (Table 2). This result does not necessarily indicate greater accuracy for either assay, but may rather indicate the preferred methodology of researchers working with insect versus vertebrate hosts. In line with this explanation, Abdi and researchers[15] concluded that microscopic diagnostics were more common in surveys of tsetse flies than molecular assays and Aregawi *et al.*[14] reported a higher range of prevalence (6–28%) by molecular tests in vertebrates compared to microscopic tests (2–9%) for the detection of *Trypanosoma evansi*. Standardising the diagnostic method applied for the detection of trypanosomatids within insects and non-insects is crucial consideration for future research to enable accurate comparisons of prevalence that is unlikely due variations in diagnostic protocols. We took this factor into consideration while doing all sub-group analysis (meta-regression models) presented in this study to ensure that the difference in prevalence is real and not due to variable diagnostics. To our assurance, in all of the main subgroup analysis, there was no significant difference in pooled prevalence due different diagnostic tools. This is true for monoxenous or dixenous trypanosomatids in insects and dixenous trypanosomatids among vertebrate hosts (e.g. cats, dogs, rodents, goats, pigs, bats and buffaloes).

The key takeaway from this study is the unique pattern of infection prevalence in association with different life-history traits of trypanosomatids: revealing both (I) higher pooled prevalence for monoxenous species in insects and across all hosts, and (II) significantly lower prevalence among vectors compared to definitive hosts for dixenous species. We present three non-mutually exclusive arguments that could explain this finding:

- First, monoxenous species are subject to selection pressure from only one host, thereby affording these species more opportunity to adapt to this host than parasites that must co-evolve with both a vector and definitive host. We would thus expect to see greater parasite fitness in specialized monoxenous parasites than in dixenous parasites as the monoxenous parasites would arrive closer to their

evolutionary optima. Dixenous parasites, in contrast, may be forced to trade-off infection relevant traits in one host for traits in the second host.

- Second, our finding may be the result of an equal force of infection shared among differing numbers of host species. Here, we offer a numerical explanation, where the same hypothetical number of infectious units are simply shared among more host species in dixenous parasites, thus diluting the infection prevalence in any one host species - to approximately half. This explanation is more than passingly similar to the "dilution effect" which is often, and sometimes controversially, used to describe infection risk in human populations when the natural host is not usually the human - eg. Lyme disease,[600-602] although to our knowledge it has not been invoked to explain variation in infection prevalence among vectored and non-vectored parasites.

- Finally, host characteristics such as lifespan, recruitment rate, sociality, and physiology may explain some of the variation in infection prevalence. For instance, social bees, which have higher infection prevalence, differ from the rest of insect hosts not only in their sociality but also in their lifespan. The biological unit for social bees is the colony, which can extend the lifespan of an infection to at least a year (bumblebees) and to several years in honeybees. The other insect hosts live for up to a few months, and have high birth and death rates which, along with rarer direct interactions can reduce the overall prevalence of infection regardless of the parasite life-cycle strategy. Consistent with this view, we found low pooled prevalence among flies with no significant difference between monoxenous and dixenous species. Furthermore, flies might be physiologically harder to infect by trypanosomatids than bees as genomic studies have described a reduced immune repertoire in bees relative to dipterans.[603,604]

While this study was ambitious in scope and exhaustive in design, there are limitations. Foremost is the small number of studies describing prevalence in monoxenous species. But, as our analyses demonstrate earlier, this is more likely due to scarcity of publications for neglected trypanosomatids rather than study selection/handling approaches employed here. Finally, although this study is far-reaching and inclusive to all reported trypanosomatids systems contributing to slyvatic transmission cycles, it does not include humans as vertebrate hosts. Despite the exclusion of human infections, their impact and contribution to the transmission cycles either directly (to insects) or indirectly (to non-insects) have been accounted for by including studies surveying animals living nearby to humans. This includes pets (dogs, cats), domesticated animals, and the vectors, such as true bugs (tritomines), which are particularly found in houses. Thus, although the direct interaction in humans-trypanosomatids systems fall beyond the scope of this study, what we show here (i.e. how trypanosomatids differ in their infection prevalence among various non-human hosts) is particularly important to enable effective prevention plans for neglected tropical diseases of humans and livestock. Understanding the fundamental processes that determine infection prevalence will help us better understand trypanosomatids in general and identifying "weak-links" in the infection chain of vectored parasites - here in the vectored species, will enable better tailored control strategies for

trypanosomatid diseases relevant to human, livestock, and wildlife health as well as food-security.

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Table1. *Summary of all included studies based on parasite groupings*

Trypanosomatid groups	Parasite grouping	Host order	Infected hosts	Geographic distribution	systematic studies	meta-analysis studies	Kmeta	sig	pooled estimate (ci.il, ci.ul)	SE	pooled prevalence
'jaculum'_spp.	monoxenous_spp.	Hemiptera	Insects {True bugs}	South America	1	1	4	***	0.563 (0.227, 0.889)	0.170	28.2
Agomonas_spp.	monoxenous_spp.	Diptera	Insects {flies}	South and Central America, Africa	1	1	3		0.123 (-0.271, 0.521)	0.202	0.9
Blastocrithidia_spp.	monoxenous_spp.	Hemiptera, Chiroptera	Insects {True bugs}, none_insects {bats}	South and North America	3	3	5	*	0.234 (0.039, 0.429)	0.100	4.62
Crithidia_bombi	monoxenous_spp.	Hymenoptera	Insects {bees}	South and North America, Europe	18	18	80	***	0.569 (0.475, 0.663)	0.048	23.7
Crithidia_expoeki	monoxenous_spp.	Hymenoptera	Insects {bees}	North America	2	2	10		0.569 (0.474, 0.664)	0.0483	28.7
Crithidia_mellificae,_Lotmaria_passim	monoxenous_spp.	Hymenoptera	Insects {bees}	Europe, South and North Amarica , Asia and Africa	7	7	7	***	0.149 (0.10, 0.394)	0.125	1.53
Crithidia_mexicana	monoxenous_spp.	Hymenoptera	Insects {bees}	North America	1	1	8	.	0.335 (-0.002, 0.673)	0.171	10.0
Crithidia_spp.	monoxenous_spp.	Hymenoptera, Diptera	Insects {bees, flies}	North America, Europe, Asia	3	3	8	*	0.286 (0.073, 0.499)	0.108	7.3
fish_trypanosomes	dixenous_spp.	Acipenseriformes	none_insects {fish}	Europe	2	2	2	***	0.729 (0.449, 1.01)	0.143	44.36
Herpetomonas_spp.	monoxenous_spp.	Diptera	Insects {flies}	South America	1	1	1		0.244(-0.176, 0.624)	0.204	4.26
Leishmania_amazonensis	dixenous_spp.	Diptera	Insects {flies}	South America	1	1	1		0.174 (-0.166, 0.513)	0.173	2.30
Leishmania_braziliensis	dixenous_spp.	Diptera, Carnivora	Insects {flies}, none_insects {dogs}	South and North America and Asia	12	7	7	***	0.308 (0.165, 0.4450)	0.073	8.54
Leishmania_donovani	dixenous_spp.	Diptera, Carnivora and others	Insects {flies}, none_insects {dogs, and multiple other hosts}	Asia and Africa	5	3	3	*	0.272 (0.040, 0.503)	0.118	6.56
Leishmania_guyanensis	dixenous_spp.	Diptera, Carnivora	Insects {flies}, none_insects {dogs}	South America	2	1	2	*	0.357 (0.0418, 0.671)	0.161	11.6
Leishmania_infantum	dixenous_spp.	Diptera, Carnivora, Chiroptera and others	Insects {flies}, none_insects {dogs, cats, rodents, equids, bats, oppossums, other animals}	South and North America, Europe, Africa, Asia	119	41	45	***	0.359 (0.298, 0.421)	0.031	11.8
Leishmania_major	dixenous_spp.	Diptera, Carnivora, Rodentia and others	Insects {flies}, none_insects {dogs, cats, rodents, birds, other animals}	South America, Asia, Africa	14	5	9	**	0.252 (0.0926, 0.412)	0.082	5.60
Leishmania_mexicana	dixenous_spp.	Carnivora, Chiroptera, Rodentia	none_insects {rodents, bats,	South and North America	4	2	2	***	0.444 (0.195, 0.692)	0.127	18.0

			dogs}							
Leishmania_spp.	dixenous_spp.	Diptera, Carnivora, Rodentia and others	insects{flies}, none_insects {dogs, cats, rodents, other animals}	South America, Africa, Europe	62	30	57	***	0.335 (0.267, 0.403)	0.035	10.2
Leishmania_tropica	dixenous_spp.	Diptera, Carnivora	insects{flies}, none_insects {dogs, cats}	Asia and Africa	5	4	4	.	0.182 (-0.002, 0.367)	0.094	2.60
Leishmania_turanica	dixenous_spp.	Rodentia	none_insects {rodents}	Asia and Africa	1	NA	NA		NA	NA	NA
Leptomonas_spp.	monoxenous_spp.	Siphonaptera, Hemiptera	Insects {true bugs, fleas}	South America	2	2	5	.	0.241 (-0.02, 0.503)	0.134	5.04
Lotmaria_passim	monoxenous_spp.	Hymenoptera	Insects {bees}	South and North America, Asia and Africa	8	8	11	***	0.549 (0.393, 0.705)	0.080	26.8
monoxenous_spp.	monoxenous_spp.	Hymenoptera, Hemiptera	Insects {bees, true bugs}	Asia	2	2	2	***	0.567 (0.239, 0.896)	0.168	28.5
Phytomonas_spp.	dixenous_spp.	Hemiptera	Insects {true bugs}	South America, Asia	3	3	6	**	0.253 (0.05, 0.455)	0.101	5.60
Trypanosoma_avium	dixenous_spp.	Siphonaptera, Passeriformes	Insects {fleas}, none_insects {birds}	Australia, Europe, North America	4	3	3	.	0.198 (-0.0214, 0.418)	0.112	3.26
Trypanosoma_brucei	dixenous_spp.	Diptera, Carnivora, Artiodactyla and others	Insects {flies}, none_insects {dogs, cattle, sheep, goats, equids and others}	Africa and Asia	40	25	43	***	0.161 (0.0943, 0.228)	0.034	1.90
Trypanosoma_chelodinae	dixenous_spp.	NA	none_insects {animals}	Australia	1	NA	NA		NA	NA	NA
Trypanosoma_congolense	dixenous_spp.	Diptera, Carnivora, Artiodactyla and others	Insects {flies}, none_insects {dogs, cattle, sheep, goats, equids and others}	Africa	58	38	78	***	0.261 (0.205, 0.318)	0.029	6.05
Trypanosoma_copemani	dixenous_spp.	NA	none_insects {animals}	Australia	1	1	1	.	0.373 (-0.0239, 0.770)	0.203	12.7
Trypanosoma_cruzi	dixenous_spp.	Hemiptera, Chiroptera, Carnivora	Insects {True bugs}, none_insects {dogs, cats, bats}	South, Central and n North America	50	33	39	***	0.357 (0.290, 0.423)	0.034	11.6
Trypanosoma_culicavium	dixenous_spp.	Diptera	Insects {flies}	Australia	1	1	2		0.218 (-0.114, 0.550)	0.169	4.14
Trypanosoma_dionisii	dixenous_spp.	Chiroptera	none_insects {bats}	South and North America	3	3	5	***	0.423 (0.227, 0.619)	0.100	16.30
Trypanosoma_equiperdum	dixenous_spp.	Perissodactyla	none_insects {equids}	Asia	1	1	1		0.224 (-0.173, 0.621)	0.203	4.30
Trypanosoma_evansi	dixenous_spp.	Artiodactyla, Perissodactyla and others	none_insects {equids, camels, dogs, cattle, goats, sheep, buffaloes and animals}	South America, Africa, Asia and Europe	63	32	46	***	0.339 (0.272, 0.405)	0.034	10.50
Trypanosoma_everetti	dixenous_spp.	Passeriformes	none_insects {birds}	Africa	1	1	1		0.0394 (-0.358, 0.437)	0.203	0.000
Trypanosoma_evotomys	dixenous_spp.	Rodentia	none_insects {rodents}	Europe	1	1	1	*	0.399 (0, 0.798)	0.204	14.60

Trypanosoma_giganteum	dixenous_spp.	NA	none_insects {animals}	Europe	1	NA	NA		NA	NA	NA
Trypanosoma_gilletti	dixenous_spp.	NA	none_insects {animals}	Australia	1	1	1		0.185 (-0.212, 0.582)	0.203	2.70
Trypanosoma_godfreyi	dixenous_spp.	Diptera, Artiodactyla	Insects {flies}, none_insects {pigs}	Africa	4	3	6	.	0.174 (-0.0044, 0.353)	0.091	2.34
Trypanosoma_lewisi	dixenous_spp.	Rodentia	none_insects {rodents}	Asia and Africa	2	2	2	***	0.511 (0.230, 0.792)	0.143	23.5
Trypanosoma_noyesi	dixenous_spp.	NA	none_insects {animals}	Australia	1	1	1		0.206 (-0.191, 0.603)	0.203	3.50
Trypanosoma_rangeli	dixenous_spp.	Hemiptera, Chiroptera	Insects {True bugs}, none_insects {bats}	North and South America	3	2	2		0.158 (-0.0816, 0.398)	0.122	1.80
Trypanosoma_simiae	dixenous_spp.	Siphonaptera, Artiodactyla, Perissodactyla	Insects {fleas}, none_insects {cattle, equids, pigs}	Africa	9	6.00	15	**	0.195 (0.067, 0.323)	0.065	3.08
Trypanosoma_spp.	dixenous_spp.	Diptera, Artiodactyla, Passeriformes, Rodentia, Hemiptera, Chiroptera, Acipenseriformesand others	Insects {True bugs, flies}, none_insects {cattle, rodents, bats, pigs, birds, fish, equids, and others}	South and North America, Europe, Africa, Asia and Australia	47	17	21	***	0.285 (0.192, 0.377)	0.05	7.25
Trypanosoma_theileri	dixenous_spp.	Artiodactyla	none_insects {cattle, animals}	South America, Africa	5	4	6	***	0.343 (0.182, 0.504)	0.082	10.7
Trypanosoma_tungarae	dixenous_spp.	Anura	none_insects {frogs}	South America	1	1	1	*	0.558 (0.133, 0.983)	0.217	27.7
Trypanosoma_vegrandis	dixenous_spp.	Chiroptera and others	none_insects {bats, animals}	Australia	3	1	1	*	0.438 (0.0413, 0.835)	0.203	17.5
Trypanosoma_vivax	dixenous_spp.	Diptera, Artiodactyla, Perissodactyla and others	Insects {flies}, none_insects {cattle, sheep, goats, camels, dogs, other animals}	Africa, South America	63	43	61	***	0.279 (0.225, 0.334)	0.028	7.00
Trypanosomatidae_spp.	mix	Diptera, Hemiptera, Siphonaptera, Chiroptera and others	Insects {true bugs, fleas, flies}, none_insects {reptiles, bats, rodents}	Europe, South America, Asia and Africa	15	12	15	***	0.423(0.305, 0.451)	0.06	16.372
Trypanozoon	dixenous_spp.	Diptera, Artiodactyla and others	Insects {flies}, none_inescts {animals, pigs, camels, dogs, cattle}	Africa	6	4	7		0.222 (0.0681, 0.376)	0.078	4.8

Parasite grouping as extracted from systematically (51 level) and quantitatively (47 level) included studies. Parasite groups ending with "spp." are trypanosomatids with no enough information to break them down to the exact parasite taxa/group. Systematic and quantitative summary of the main features are outlined in for each group.

Table2: *Pooled prevalence for several subgroup analysis*

Analysis 1						
Host grouping	*k*	pooled estimate (Cl.lb, Cl.ub)	Microscopic (%)	pooled estimate (Cl.lb, Cl.ub)	Molecular (%)	(t-test)	Sig
Insects	313	0.409 (0.352, 0.466)	14.9	0.332 (0.282, 0.382)	9.64	0.0002	***
Non-insects	229	0.120 (0.361, 0.448)	0.642	0.405 (0.361, 0.448)	14.9	<.0001	***

Analysis 2						
Host grouping	K	pooled estimate (Cl.lb, Cl.ub)	Dixenous (%)	pooled estimate (Cl.lb, Cl.ub)	Monoxenous (%)	(t-test)	Sig
Insects	313	0.280 (0.228, 0.333)	6.61	0.483 (0.414, 0.552)	20.9	<.0001	***
Flies	155	0.232 (0.194 0.270)	4.80	0.173 (-0.0226, 0.244)	2.45	0.438	
Truebugs	33	0.357 (0.265, 0.449)	11.5	0.358 (0.170, 0.547)	11.6	0.991	

Analysis 3 *						
Parasite grouping	K	pooled estimate (Cl.lb, Cl.ub)	Insects (%)	pooled estimate (Cl.lb, Cl.ub)	Non-insects (%)	(t-test)	Sig
Dixenous spp	390	0.244 (0.216, 0.272)	5.51	0.316 (0.290, 0.342)	9.38	0.0001	***
Leishmania spp.	125	0.162 (0.114, 0.210)	2.02	0.397 (0.357, 0.438)	14.5	0.0001	***
Trypanosoma spp. [1]	226	0.208 (0.177, 0.240)	4.09	0.248 (0.219, 0.277)	5.85	0.0001	***
Trypanosoma cruzi	39	0.394 (0.285, 0.502)	14.51	0.294 (0.201, 0.388)	8.17	0.1731	

Analysis 4						
Bees Groups	K	pooled estimate (Cl.lb, Cl.ub)	Wild (%)	pooled estimate (Cl.lb, Cl.ub)	Managed (%)	(t-test)	Sig
All	123	0.554 (0.440, 0.668)	26.8	0.505 (0.207, 0.804)	22.2	0.754	
Honeybee	17	0.631 (0.448, 0.815)	34.2	0.481 (0.082, 0.880)	20.1	0.502	
Bumblebee	106	0.530 (0.398, 0.663)	24.4	0.527 (0.113, 0.941)	24.2	0.991	

*dixenous species with prevalence data from both insects and non-insects

[1] Prevalence data for *Trypanosoma cruzi* are not included here

All of the analysis were done using meta-regressions with random effect model and an appropriate nested random design.

K is the total prevalence data included in the analysis in each row.