The cichlid-*Cichlidogyrus* network: A blueprint for a model system of parasite evolution

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Abstract

Species interactions are a key aspect of evolutionary biology. Parasites, specifically, are drivers of the evolution of species communities, and impact biosecurity and public health. However, when using interaction networks for evolutionary studies, interdependencies between distantly related species in these networks are shaped by ancient and complex processes. We propose using recent interacting host-parasite radiations, e.g. African cichlid fishes and cichlid gill parasites belonging to *Cichlidogyrus* (Dactylogyridae, Monogenea), as macroevolutionary model of species interactions. The cichlid-*Cichlidogyrus* network encompasses 138 parasite species and 416 interactions identified through morphological characteristics and genetic markers in 160 publications. We discuss the steps required to develop this model system based on data resolution, sampling bias, and reporting quality. In addition, we propose the following steps to guide efforts for a macroevolutionary model system for species interactions: First, evaluating and expanding model system outcome measures to increase data resolution. Second, closing knowledge gaps to address underreporting and sampling bias arising from limited human and financial resources. Identifying phylogenetic and geographic targets, creating systematic overviews, enhancing scientific collaborations, and avoiding data loss through awareness of predatory journal publications, can accelerate this process. Third, standardising data reporting to increase reporting quality and to facilitate data accessibility.

Key words

Cichlid parasites; Dactylogyridae; Monogenea; host-parasite network; taxonomic bias; data reporting.

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Conflict of interest

The authors declare that they have no conflict of interest.

Author contributions

AJCL had the idea for this review, and performed literature search and data analysis. AJCL and MPMV wrote this article with input from TA, AP, and KS.

A model system for parasite evolution: The blueprint

Species interactions such as predators-prey or host-symbiont, and host-parasite interactions are a key factor of the evolution of species communities (terHorst et al., 2018). Interactions are the foundation of ecosystems (Duffy et al., 2007; terHorst et al., 2018) and a crucial aspect for conservation efforts in the light of global ecosystem degradation (Heleno et al., 2012; Tylianakis et al., 2010). However, traditional evolutionary biologists have mainly focused on evolutionary processes in single species or pairwise interactions instead of the complex interaction networks that ecologists have investigated extensively (terHorst et al., 2018). Study systems specifically used to investigate evolutionary processes in species-rich interaction networks remain scarce (Toju et al., 2017) despite 'eco-evolutionary feedbacks', i.e. the interplay of ecological and evolutionary processes, recently becoming a focus point of evolutionary research (Toju et al., 2017). The root of this issue lies in the grouping of the species (A) by their ecosystem function in relation to the other set (B) (e.g. A as a 'pollinator', 'predator', 'prey', 'host', 'symbiont', or 'parasite' of B). Bipartite networks, one of the most common representations of interacting species communities, frequently involve two such sets of interacting species groups (e.g. set A and set B) (Harvey et el., 2017) such as plants and pollinators (Campbell et al., 2011), plants and phytophagous insects (Nylin et al., 2018), conifers and granivorous birds (Benkman et al., 2010), plants and mycorrhizal fungi (Selosse et al., 2006), or corals and dinoflagellates (Ziegler et al., 2018). As a consequence, the evolutionary distances amongst the species is considerably larger than if A and B each formed recently evolved monophyletic taxa (e.g. Wilson et al., 2012). Established bipartite networks frequently lack the power to integrate eco-evolutionary feedbacks as the extensive period of time passed since the last common ancestor means that a multitude of factors might have affected the diversification process of a species set. These factors can generate high levels of uncertainty for the detection of evolutionary patterns.

Recent species radiation or even co-radiations, i.e. two co-evolving species radiations (Losos & Mahler, 2010), could present a solution (Benkman et al., 2010) as the number of factors driving diversification processes is likely lower due to the relatively short time frame since the last common ancestor. Species radiations are characterised by explosive diversification events resulting in species-rich assemblages, and in some cases, replicate radiations (Rabosky & Glor, 2010; Salzburger et al., 2005). Some model radiations such as the Caribbean lizard genus *Anolis* (Squamata: Dactyloidae) (Mahler et al., 2013), Darwin's finches (Passeriformes: Thraupidae) (Grant, 1999), and cichlid fishes (Teleostei: Cichlidae) (Seehausen, 2006), have been explored in depth during decades of expansive ecological, evolutionary, developmental, and behavioural research (Abzhanov, 2010; Koblmüller et al., 2015; Sanger et al., 2008). However, the interactions of these models have only been explored from an ecological perspective including studies on feeding strategies (Hata et al., 2014; Heleno et al., 2013) and predatory pressure (Pringle et al., 2019). Co-radiations in general have been the subject of few evolutionary study systems (fungal endophytes: Saikkonen et al., 2016; phytophagous insects: Wilson et al., 2012). Species-poor interaction networks remain the norm for 'eco-evolutionary' studies (Toju et al., 2017). A model system involving metazoan co-radiations has not been established to date.

Obligate parasite radiations and their hosts could be one of the most promising candidates for a macroevolutionary model system for species interactions as host-parasite interactions are frequently preserved in natural history collections of the host (Harmon et al., 2019) due to the close nature of parasitic interactions. Such a model system for macroevolutionary study could shed light on patterns of disease evolution (Harmon et al., 2019) such as expansions and reductions of host ranges and geographical ranges (Hoberg & Brooks, 2008), e.g. Jorissen et al. (2020) especially because metazoan parasites account for a significant portion of all animal species worldwide (Poulin, 2014) and are key drivers of evolutionary and ecological processes in species-rich communities (Gómez & Nichols, 2013; Lefèvre et al., 2009). Furthermore, parasites are the cause of an increasing number of diseases in humans, livestock (Thompson, 2013), and crops (Ekroth et al., 2019), an effect that is amplified by the current process of global environmental degradation (Brooks et al., 2019). But despite the pool of historical records and the integral role of parasites in ecosystem health, biosecurity, and public health, only few bipartite host-parasite networks have been investigated to date as the small body sizes of most parasites complicates identifying species (de Meeûs et al., 2007). Similar to other bipartite network systems, proposed metazoan parasite models have focused on microevolutionary questions to minimise model complexity, i.e. systems involving few species and species interactions, such as the water flea–bacterium network with *Daphnia magna* Straus, 1820 and *Pasteuria ramosa* Metchnikoff, 1888 (Bento et al., 2017), the mammal-cestode network with several mammalian hosts and species of *Echinococcus* Rudolphi, 1801 (Thompson & Jenkins, 2014), the legume–pea aphid network with leguminous plants and several pea aphid subspecies (Peccoud & Simon, 2010), and several fish-flatworm networks involving gyrodactylid monogenean parasites (Bakke et al., 2007), e.g. the salmonid-*Gyrodactylus* (Ziętara & Lumme, 2002) or goby-*Gyrodactylus* (Huyse & Volckaert, 2005) networks, but see species-rich plant parasite networks, e.g. Wilson et al. (2012). To investigate the macroevolution of host-parasite interactions, the flatworm parasites belonging to *Cichlidogyrus* Paperna, 1960 (Platyhelminthes: Monogenea, Dactylogyridae) [including *Scutogyrus* Pariselle & Euzet 1995 (Platyhelminthes: Monogenea, Dactylogyridae) (Wu et al., 2007)] infecting the gills of mainly African cichlid fish have been proposed as a study system for metazoan parasites (Pariselle et al., 2003; Vanhove et al., 2016). Arguments expressed in favour of a cichlid-*Cichlidogyrus* model system can be summarised as follows [according to the model system criteria of Kellog & Shaffer (1993)]:

- *Variability*. Monogeneans are the most species-rich group of cichlid parasites alongside digeneans (Vanhove et al., 2016) with *Cichlidogyrus* being the most species-rich African freshwater fish parasite genus (Kuchta et al., 2018). The cichlid-*Cichlidogyrus* network currently comprises 138 parasite species infecting fish species belonging to fifteen cichlid tribes and two non-cichlid families resulting in 416 host-parasite interactions (Online Resource 1). This known species diversity is higher than the diversity of all parasitic nematodes in African fish (Moravec, 2019) and provides the cichlid-*Cichlidogyrus* system with an advantage over other systems involving host model systems with a less diverse parasite fauna such as helminth parasites of anoles (Falk & Perkins, 2015) or feather mites of Darwin's finches (Bulgarella & Palma, 2017).
- *Tractability*. Sample availability and, therefore, data availability and quality of host parameters are high due to the model system status of African cichlids (Kornfield & Smith, 2000) rooted in the extensive library of scientific publications (see Koblmüller et al. 2015). In addition, a simple life cycle of the parasites in the absence of intermediate hosts, a lower infection and attachment site diversity of fish gills as opposed to internal organs (Bellay et al., 2015), and a predicted neutral effect on the natural selection of the host species (Pariselle et al., 2003), minimise the number of parasite-related parameters (Pariselle et al., 2003). The gill flap protects the gill parasites from physical damage during the host sampling process that can potentially skew the recorded infection levels of a host specimen (Kvach et al., 2016). Furthermore, the ectoparasitic lifestyle protects samples from degradation as the parasite is instantly exposed to any fixative media (e.g. formaldehyde or ethanol), in which the host specimens are fixed, stored, and preserved. In contrast, the preservation of

endoparasites is delayed by the host's body, which the fixative has to penetrate to reach the infection site. This delay can result in a deteriorated state of morphological characteristics and DNA molecules (Tkach et al., 2019) unless the parasite samples are extracted immediately after the death of the host.

- *Accessibility.* Due to the sympatric speciation of cichlids in Africa, most host species are found in the biodiversity hotspots of the Great East African Lakes. This focused geographical range (Pariselle et al., 2003) and the availability of host specimens from natural-history collections worldwide (Harmon et al., 2019) increase the accessibility to host samples.
- *Representativeness.* As flatworms (Platyhelminthes), species of *Cichlidogyrus* are representatives of one of the groups with the highest parasite diversity alongside arthropods (Poulin & Morand, 2004). In addition, their cichlid hosts have the biodiversity hotspot in the East African Lakes. This hotspot is also a global biodiversity hotspot. Hence, understanding interactions of cichlids and non-cichlids in multispecies networks should be considered key for conserving diverse species communities as a whole especially because climate change (Cohen et al., 2016; Olaka et al., 2010), biological invasion (Witte et al., 2013), pollution (Odada et al., 2003), and overfishing (Kayanda et al., 2010) threaten the unique ecosystems of the East African lakes. Only few studies have investigated cichlid–non cichlid interactions such as with flatworm parasites (Mendlová & Šimková, 2014), algae (Hata et al., 2014) and hydrozoans (Bose et al., 2019). While no replicate radiations have been described to date, natural (Messu Mandeng et al., 2015) and invasion-induced (Jorissen et al., 2018b; Roche et al., 2010; Šimková et al., 2019) host shifts have occurred in multiple cases. Investigating these events could provide insight into pattern of disease evolution as novel pathogens frequently emerge from host shifts (Woolhouse et al., 2005).

Despite these arguments, the model system quality of the cichlid-*Cichlidogyrus* network has never been evaluated systematically. Numerous studies have produced a broad but scattered insight into the diversity, ecology, epidemiology, and evolution of cichlid-monogenean interactions (see Vanhove et al., 2016). Data of morphological, phylogenetic, and ecological studies are published with varying quality. Therefore, this review will assess shortcomings of literature data and discuss and propose solutions of three common issues regarding these data. We will first give an overview on the issues and solutions related to data resolution, i.e. which measurements and markers are being used and could be used in the future as 'the model system toolbox'. Second, we will characterise the sampling bias and data loss, identify causes, and propose a range of solutions for publications on cichlid parasites to 'create a stable model system architecture'. Third, we will assess reporting quality and propose a framework to optimise reporting quality of data, the 'foundations of model system architecture'. We will estimate whether and how improvements in these areas can enhance model system aspects of the two–trophic level network. This review aims to guide future efforts to develop a bipartite model system to analyse macroevolutionary mechanisms of host-parasite interaction networks.

Measurements and markers: The model system toolbox

A key tool for measuring and describing mechanisms in a model system are endpoints. Endpoints are outcome measures of a model system commonly applied in ecosystem health assessment (Cairns et al., 1992). If we apply this concept to the cichlid-*Cichlidogyrus* system, morphological, ecological, and genetic parameters included in typical reports of *Cichlidogyrus* spp. could constitute model endpoints. However, the parameters commonly considered in these reports fail to provide enough data resolution as they are limited to a few morphological characteristics (see Fig. 1 for a typical drawing), genetic markers, and ecological measures. To build the cichlid-*Cichlidogyrus* model system and increase the system's tractability, the systematic and ecological informativeness of established endpoints should be assessed and novel endpoints should be established as follows.

First, past studies have characterised species of *Cichlidogyrus* and other monogenean species mainly with morphometric measures of the sclerotised structures in the attachment (haptor) and reproductive organs (see Fig. 1 for measures included in typical species descriptions and standard terminology), e.g. in Fannes et al. (2017), and few partial nuclear and mitochondrial DNA markers, e.g. in Igeh et al. (2017). Some haptor measures coincide with phylogenetic clades (Vignon et al., 2011) as demonstrated by some studies using ancestral states reconstruction of morphological characters of species of *Cichlidogyrus* (Mendlová et al., 2012; Vignon et al., 2011). However, these results appear questionable as undersampling of specimens and distortion of those morphological characters as a result of sample fixation (Fankoua et al., 2017; Vignon, 2011) might produce biased results and systematic errors. Some measures might also be highly correlated, i.e. multicollinear, and, therefore, redundant (Vignon, 2011). To maximise systematic and ecological informativeness, the scale of undersampling, distortion, and redundancy of measures should be quantified through a statistical assessment of these morphological characteristics. This assessment could increase statistical power of data analyses in the future. Additional measures should be added to include shape variations that are not covered by current methods, e.g. the width and shaft lengths of the hooks (Geraerts et al., 2020), the membranous extension of the ventral bar (Mendlová et al., 2012), and the interspecific shape variations of penis and accessory piece in the male copulatory organ (Geraerts et al., 2020). Similar to a previous study on the anchor shape variations in species of the genus *Ligophorus* Euzet & Suriano, 1977 (Rodríguez-González et al., 2017), geometric morphometric analyses could be used to maximise the phylogenetic signal of the measures. Furthermore, new imaging and staining techniques such as three-dimensional images resulting from scanning electron microscopy (Fannes et al., 2015), confocal microscopy (Galli et al., 2006; Marchiori et al., 2015; Rossin et al., 2017) or soft tissue staining (Mair et al., 1998) might enhance morphological and anatomical descriptions and, thus, increase data resolution.

Second, most phylogenetic analyses have been based on few genetic markers including the partial 28S and 18S nuclear ribosomal DNA, partial internal transcribed spacer 1 (ITS1) region of nuclear ribosomal DNA, and mitochondrial cytochrome *c* oxidase subunit I (COI) DNA regions. These studies have resulted in mostly modest support values (Messu Mandeng et al., 2015; Mendlová et al., 2012) leaving questions on the systematics of *Cichlidogyrus* unanswered. Furthermore, the systematic application of other genetic markers such as 16S nuclear ribosomal DNA (Plaisance et al., 2005), and the histone 3 (H3), the elongation factor 1 α (EF1α) (Perkins et al., 2009), and the mitochondrial cytochrome *c* oxidase subunit II (COII) DNA region (Bueno-Silva & Boeger, 2014) remains restricted to certain other monogenean taxa. New mitochondrial and nuclear DNA markers might soon increase resolution of phylogenetic and population-level analyses in future studies especially because of recent advances in assembling DNA sequences of specimens of *Cichlidogyrus* resulting from next-generation sequencing techniques (Vanhove et al. 2018).

Third, infection parameters, e.g. prevalence, i.e. ratio of infected hosts, and infection intensity, i.e. parasites per infected hosts, are the most common quantifiers of cichlid-*Cichlidogyrus* interactions as these parameters are essential and accessible quantifiers of parasite ecology (Poulin, 2006). However, beyond infection levels, ecological parameters are mostly absent from typical taxonomic reports despite several studies demonstrating that host size and sex (Akoll et al., 2012), seasonality (Akoll et al., 2012; Hirazawa et al., 2010), and inorganic and organic pollutants (Poléo et al., 2004; Sanchez- Ramirez et al., 2007; Šebelová et al., 2002) affect the physiology and host interactions of flatworm parasites. To improve current data sets, related to the host (e.g. Akoll et al., 2012) or the immediate environment (e.g. Fannes et al., 2017; Huyse et al., 2004) should be included in full in the respective publication if the data collection does not inflate the research effort as even few observations can provide information for meta-analyses. Additional host endpoints will further increase the data resolution of the proposed model system, and can be found in studies focussing on the pathology (e.g. Igeh & Avenant- Oldewage, 2020) and immunology (e.g. Zhi et al., 2018) of monogenean infections or the effects of human activity on the disease ecology (e.g. Madanire-Moyo et al., 2012). More insight into the health of cichlids is needed as infrastructure and human resources addressing the biosecurity of these species remains poor (Opiyo et al., 2018) with little disease monitoring of cultured (Opiyo et al., 2018) and wild (Mugimba et al., 2018) populations of 'tilapias' despite the economic relevance of these cichlids for fisheries and aquaculture in Africa, Asia, and the Americas (FAO, 2019). We also recommend the deposition of 'symbiotypes', i.e. host vouchers of parasite types, in natural history collection because similar to other diseases (Bradley et al., 2020) this deposition would have the advantage that many host parameters are preserved in these collections long-term. For environmental parameters, *in-vitro* culturing methods, i.e. cultures without living hosts, might facilitate investigating the effects of environmental factors in controlled laboratory environments in the near future as these methods are becoming available for an increasing number of parasite species (Hutson et al., 2018), some of which are relatively closely related to monogeneans, e.g. the cestode *Schistocephalus solidus* Müller, 1776 (Wedekind et al., 1998), or also have a similar ectoparasitic lifestyle, e.g. gnathiid isopods (Grutter et al., 2020).

Sampling bias: Creating a stable model system architecture

Cichlid-*Cichlidogyrus* interactions constitute the most extensively described host-parasite network based on an adaptive radiation of host species. Decades of research (Online Resource 2) have provided a valuable insight into the biodiversity and ecology of these parasites. Yet the knowledge on the cichlid parasite diversity remains incomplete, biased, and insufficient for conclusive genus-wide evolutionary analyses as the discovery of new species is constrained by limited human and financial resources. The dominance of a few researchers in novel reports of parasite-host interactions (Fig. 2) and a rapid increase of new species of *Cichlidogyrus* highlight these constraints. Since the last taxonomic revision of dactylogyridean parasites of African cichlids (Pariselle & Euzet, 2009), 59 new species of *Cichlidogyrus* have been recorded, a 75% increase. Some of these species have been reported from cichlid hosts belonging to seven previously neglected tribes (Online Resource 2). At the same time, new discoveries of host-parasite interactions have continued to increase exponentially, i.e. the discovery rate shows no sign of deceleration and appears unrestrained due to the extensive numbers of interactions remaining to be found. However, this increase (generalised linear model with negative binomial distribution, $\chi^2 = 243.41$, df = 1, $p < 0.001$) (see Fig. 2) suggests that the discovery of cichlid parasite species and host-parasite interactions remains at the characteristic early exponential stage of a typical cumulative species discovery curve (Bebber et al., 2007). Therefore, estimating the total number of extant interactions is currently impossible. Many more interactions could be discovered in the future if restricting factors are addressed.

One of these restricting factors is research capacity. Like other biodiverse regions (Fisher & Christopher, 2007), challenging political and economic conditions surrounding the East and Central African cichlid biodiversity hotspots continue to limit funding opportunities and the access to sampling locations despite a growing scientific impact of publications from developing countries (see Gonzalez-Brambila et al., 2016). For researchers in Africa, these restrictions inhibit the access to specimens in biorepositories, e.g. natural history collections, as samples are frequently moved to and stored in developed countries (The H3Africa Consortium, 2014), see 'parachute science' (Barber et al., 2014). Financial limitations also restrict the access to scientific literature as commercial interests of publishers (Fuchs & Sandoval, 2013) result in high access fees for readers or, alternatively, high publication fees for the authors of open access articles (Veríssimo et al., 2020). These disparities between high and low-income countries cause structural and financial dependencies (Dahdouh-Guebas et al., 2003) and inhibit the growth of research capacity as demonstrated by the higher percentage of foreign institutions in the collaborative networks of research institutions in developing countries compared to industrialised nations (Banerjee, 2017). Consequently, societal preferences in both developing and developed countries drive a positive and taxonomic publication bias: positive and novel results are favoured over negative and repeat observations whereas cichlid hosts relevant to consumption, i.e. species belonging to the tilapia-like tribes Coptodonini Dunz and Schliewen, 2013 (22% of publications) and Oreochromini Dunz and Schliewen, 2010 (65% of publications), are favoured over less economically relevant hosts belonging to other tribes (33% of publications) (Fig. 3; Online Resource 2). This research impact-driven approach, which focuses on novelty and economic relevance, is reminiscent of publication (Song et al., 2010) and taxonomic biases (Troudet et al., 2017) in global biodiversity data and research biases in other fields such as conservation research (Trimble & Van Aarde, 2010; Ford et al., 2017), epidemiology (Siddiqi, 2011), and invasion ecology (Pyšek et al., 2008). Because of this 'bias', most evolutionary research concerning *Cichlidogyrus* remains purely descriptive or limited to a subset of species of *Cichlidogyrus*, e.g. exclusively to parasites infecting tropheine (Vanhove et al., 2015) or bathybatine (Kmentová et al., 2016) cichlids. Taxonomic biases in genus-wide studies can lead to misleading results as the ecology of species of *Cichlidogyrus* can vary in the same ecosystem depending on the host species (Kmentová et al., 2016). Thus, an observed correlation could reflect a sampling bias rather than causation, e.g. Mendlová & Šimková (2014) detected a correlation of parental care behaviour and host specificity because of a study bias towards cichlid species expressing a specific type of parental care, namely mouth brooding.

Both publication and taxonomic biases are amplified by data that continue to be lost through low quality publishing. In the light of the exponential growth of scientific publishing (Bornmann & Mutz, 2015), assuring research quality has become a discussion that exceeds the scope of this review. However, one prominent phenomenon arising from publication pressure in taxonomic research (e.g. Raghavan et al., 2014) is predatory publishing, i.e. exploitative publications that demand high fees with no attached peer-review process (Beall, 2013). Data arising from predatory publishing are effectively 'lost science' (Clark & Smith, 2015) as research quality cannot be guaranteed. Cichlid research forms no exemption as predatory journals specifically target researchers from low-income countries (Xia et al., 2015), where most cichlid species are sampled. Predatory publishing can further boost the stigma for publications from these countries, which can already face a lack of valorisation (Lee et al., 2013). A potential bias of peer-reviews against early-career researchers (Lee et al., 2013) from low-income countries [see 'matata effect' in Van der Stocken et al. (2016)] might enhance the success of this targeting strategy.

To address sampling bias and data loss, closing knowledge gaps is key. Recent studies on the parasites of host species belonging to the underrepresented cichlid tribes including Bathybatini Poll, 1986 (Kmentová et al., 2016); Cyprichromini Poll, 1986; Ectodini Poll, 1986; Eretmodini Poll, 1986 (Rahmouni et al., 2017); Haplochromini

Poll, 1986 (Van Steenberge et al., 2015); Hemichromini Hoedeman, 1947; and Tylochromini Hoedeman, 1947 (Muterezi Bukinga et al., 2012; Jorissen et al., 2018a; Pariselle et al., 2014; Rahmouni et al., 2018) have expanded the taxonomic coverage concerning examined host specimens of *Cichlidogyrus*. However, knowledge gaps can be addressed more systematically taking the following approaches:

- *Targeting*: Databases of literature data (Online Resource 2) with taxonomic (Online Resource 1) and geographical inventories of reported samples should be created, and the deposition of voucher specimens in biorepositories close to the sample locations should be encouraged to increase data access and availability in low-income countries. These measures could outline gaps in host taxonomic and geographic coverage (Jones et al., 2009) and support decision-making on taxonomic and geographic targets (Stephenson et al., 2017) similar to the handbooks for the general parasite diversity (see Scholz et al., 2018) and nematode parasite diversity (Moravec, 2019) of African fish.
- *Systematic revision*: The 2009 systematic revision of *Cichlidogyrus* and the identification key (Pariselle & Euzet, 2009) should be updated to facilitate identifying species despite the relatively small sizes of these parasites.
- *Collaboration*: 'Parachute' science, i.e. research in developing countries that side-lines local scientific communities (Barber et al., 2014), can be avoided through North-South and South-South collaborative networks involving African institutions (Chu et al., 2014; Klopper et al., 2002). North-South collaboration can, e.g., facilitate the access for local academics to distant learning resources to make acquiring research skills more affordable (Chu et al., 2014). Promoting South-South collaborations through an improved research infrastructure for genomic research including African-based biorepositories and standardised protocols for sharing these resources might also reverse the 'brain drain' of African experts to high-income countries (The H3Africa Consortium, 2014). These networks could enable the whole research community to tap into local scientific and traditional knowledge (Drew, 2005) while increasing the academic capacity in the region and the whole field (Barber et al., 2014; Van der Stocken et al., 2016). The need for capacity development in monitoring and identifying parasites in the Global South has also been observed in a One Health or EcoHealth context (Keune et al., 2017).
- *Awareness building*: Increasing awareness of predatory publishing (Beall, 2013) and reforming the current systems for evaluating and funding science (Edwards & Roy, 2017) are ideas to reduce data loss. Systemic changes could include enforcing ethical codes in peer-review reports to avoid 'bad faith' reviews (Atjonen, 2018), double-blind (Tomkins et al., 2017) or open review (Ross-Hellauer, 2017) processes to address reviewer biases (see references for more detailed information), and publications in academic journals that follow Fair Open-Access principles (Veríssimo et al., 2020) to ease financial restrictions in low-income countries.

In conclusion, taking a more targeted, systematic, and awareness-building approach will enhance the tractability of the *Cichlidogyrus*-cichlid network whereas the collaborative aspect might additionally enhance model accessibility due to an increased academic capacity for parasitological research in Africa.

A standard for reporting data: The foundations of model system architecture

As data from cichlid gill parasites reach back 80 years, data reporting has undergone considerable changes from basic taxonomic descriptions in the 1930s (Markewitsch, 1934) to modern data sheets and DNA sequence data deposited in online databases (e.g. Igeh et al., 2017). However, data accessibility varies across current publications due to barriers working against data dissemination such as varying reporting quality. Out of 163 publications on *Cichlidogyrus* and *Scutogyrus*, approximately a third report prevalence data and somewhat fewer report infection intensity data across the three most studied tribes (Fig. 3, Online Resource 2). This lack of data accessibility should be addressed by increasing reporting quality in future publications and, thus, tractability of the network. We propose a standardised reporting framework (Table 1).

Varying data accessibility inhibits data dissemination (Molloy, 2011) and prolongs data extraction (Dasu & Johnson, 2003). For cichlid parasite literature, data extraction frequently requires manual copying of hidden data from non-modifiable formats such as in running text or portable document format (pdf) tables. Furthermore, varying reporting quality hampers data analyses due to missing data and laborious calculations of parameters from raw data. In taxonomic publications on cichlid parasites, data ranges (Dossou, 1982; Paperna & Thurston, 1969; Rahmouni et al., 2018) and qualitative data (Pariselle et al., 2015) for ecological and morphological parameters are traditionally accepted for describing and, consequently, identifying species. Hence, infection parameters, and mean values of infection parameters and morphometric data are frequently absent despite these quantifiers being essential and accessible descriptors of parasite ecology (Poulin, 2006). Epidemiological publications include infection parameters prominently (Firmat et al., 2016; Otachi et al., 2014) but frequently lack species names as the species are only identified on genus level due to the focus of these studies on the disease ecology rather than the parasite biodiversity.

A standardised reporting framework can improve data reporting quality (see Table 1). Reported morphological and ecological measurements ought to include mean values and descriptors of data distribution such as minimum, maximum, standard deviation, and sample size, and descriptors of host-parasite interactions, i.e. infection parameters, including examined host individuals, infected host individuals, and mean parasite load. Data ought to be reported in 'tidy' data tables (Wickham, 2014), i.e. one variable per column and one observation per row, saved in open formats such as comma-separated values (csv) or tab-delimited text files (txt). These raw data should be openly accessible in supplementary files or, preferably, public repositories (Molloy, 2011) to support the data summarised in the main article. We recommend this framework for data reporting to increase tractability of the network by optimising data accessibility for future studies.

Work in progress: A conclusion

We demonstrated that cichlid fishes and the gill-infecting flatworm parasites belonging to *Cichlidogyrus* are uniquely suitable for being bipartite macroevolutionary model system due to the presence of historical collections and the range of different fields that have started exploring these interactions from different perspectives including evolutionary, epidemiological, ecological, and genomic research. The combination a species-rich clade of parasites with a single-host lifecycle and a host diversity that has been studied for decades are unique for a metazoan parasite model. However, the low data resolution, the sampling bias towards economically relevant host species, and the inconsistent data quality demonstrate that many of these fields have only recently started to explore the parasites of cichlids. Therefore, many model system criteria cannot currently be met but the present model aspects might be enhanced in the future if the measures are taken to address shortcomings with additional research. To do so, we proposed a range of approaches, some of which have taken first steps in recent years including genomics and 'tidy' data, and others which appear futuristic such as the possibility of *in vitro* cultures. With these proposals, we have aimed to highlight the different perspectives on host-parasite networks or species interactions in general ranging from taxonomic, evolutionary, ecological standpoints to pathological, epidemiological, immunological, and data science perspectives. We also addressed underlying social aspects of parasitological research in low-income countries. These systemic problems of scientific publishing and research in the Global South might be discussed more thoroughly elsewhere. However, we have demonstrated that these issues often lie at the root of many 'scientific' problems at a second glance.

Overall, this review has highlighted the importance of data science to building a macroevolutionary model system for species interactions. All bipartite systems ranging from symbiotic and predator-prey interactions to viral and bacterial diseases are at their core networks of interacting species. Nonetheless, 'eco-evolutionary feedback' studies with bipartite models have lagged behind their 'unipartite' counterparts. With this review, we would like to encourage researchers working on other species interactions to evaluate data resolution, sampling biases, and reporting quality of the respective system to detect shortcomings. Naturally, priorities on the data that are collected and published differ amongst taxonomists, evolutionary biologists, epidemiologists, and ecologists. For example, taxonomic and epidemiological perspectives have shaped the reporting of metazoan parasites and their animal hosts in flatworm research, i.e. the data are presented to meet the requirements of the field. Yet any raw data should be published even if those are not directly relevant to the respective publication as this simple effort can create opportunities for researchers in high and low-income countries. Researchers should also consider adding their raw data to openly accessible databases. To characterise a host-parasite system, morphological data, interaction data, and DNA sequences data can be uploaded to MorphoBank, Global Biotic Interactions (GloBI), and NCBI GenBank. An open exchange of data could multiply the impact of study systems and increase the interconnectivity of research groups and fields.

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List of figures

Figure 1 Schematic overview of typical morphological structures and measurements in reports of *Cichlidogyrus* spp. A Overview of organism with haptor sclerites and male copulatory organ. B Anchor. C Hook. D. Ventral bar. E Dorsal bar. F Male copulatory organ. Measurements: a, anchor total length; b, anchor blade length; c, anchor shaft length; d, anchor guard length; e, anchor point length; U1-U7, hook lengths; w, bar width; x, bar length; h, auricle length; y, distance between auricles; AP, accessory piece length; Pe, penis length; He, heel length; sclerotised vagina not included as only observed in some species

Figure 2 Cumulative count of host-parasite interactions reported between 1934 and 2019 for species of *Cichlidogyrus* and *Scutogyrus*, grouped by first authors of publications first recording these combinations. The increase of discovered combinations mainly relates to the works of I. Paperna and A. Pariselle. Furthermore, the exponential growth of the discovery curve (grey) indicates that these discoveries remain at an early stage, independent of overall species number (Bebber et al., 2007). Discoveries are not independent as new accounts are published in groups (Bebber et al., 2007). To account for the overdispersion caused by this dependency, a discovery curve was fitted using a generalised linear model with a negative binomial distribution ($\chi^2 = 243.41$, df = 1, $p < 0.001$) using the 'MASS' package (Venables & Ripley, 2002) in the statistical software R v3.6.1 (R Core Team, 2019). Graphing was performed using the 'ggplot2' package from R (Wickham, 2016)

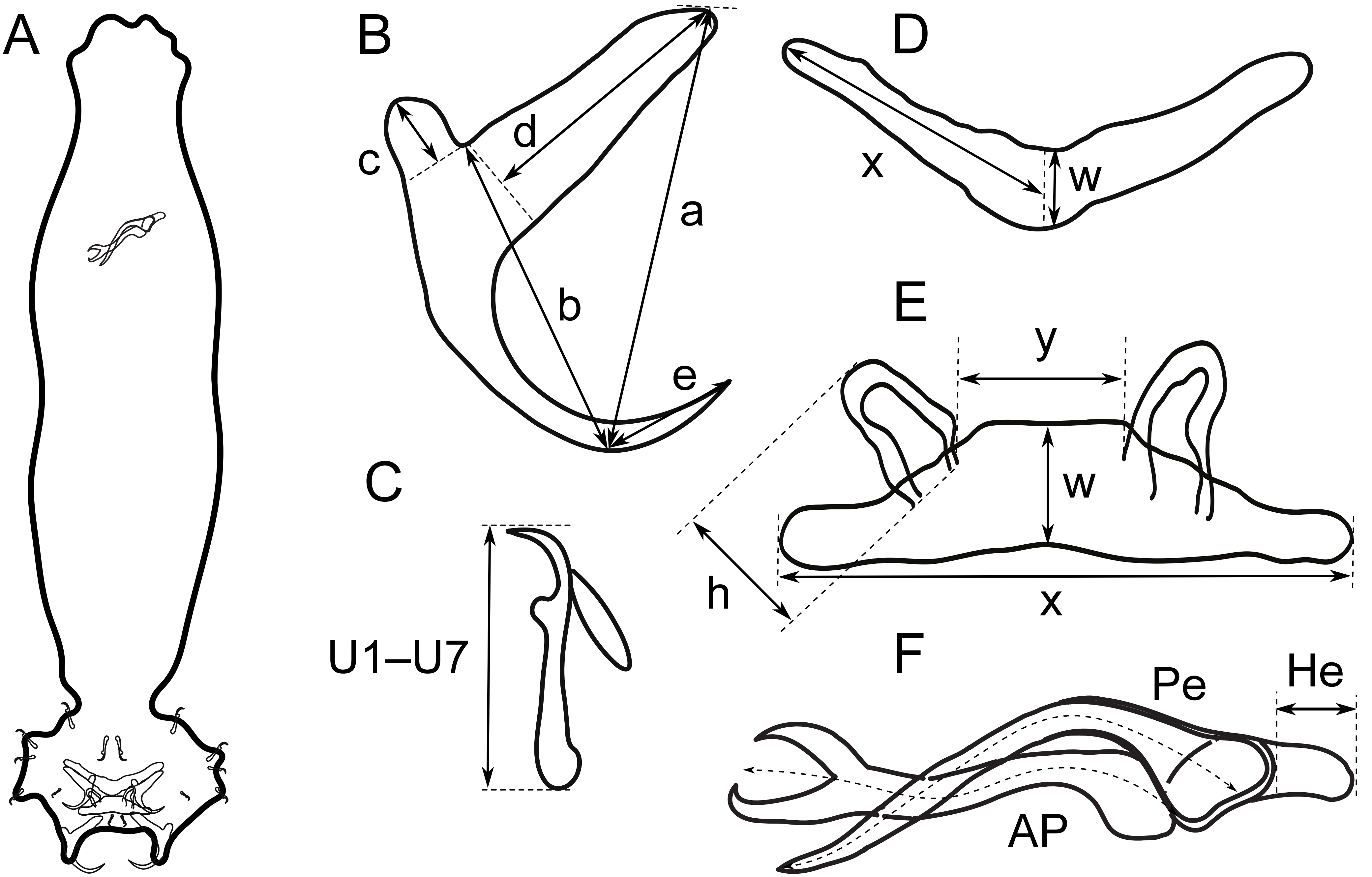
Figure 3 Number of peer-reviewed publication (until July 2020) on *Cichlidogyrus* and *Scutogyrus* infecting the three most examined cichlid tribes (All), and number of those publications reporting infection parameters such as prevalence (P) and infection intensity (I). *Pooled data from other cichlid tribes also include *Cichlidogyrus* spp. infecting non-cichlids. Graphing was performed using the 'ggplot2' package (Wickham, 2016) in the statistical software R v3.6.1 (R Core Team, 2019)

List of electronic supplementary material

Online Resource 1 List of first records of host-parasite interactions of parasitic flatworms belonging to *Cichlidogyrus* (Dactylogyridae, Monogenea) and their cichlid (Cichlidae, Teleostei) and non-cichlid host fishes.

Online Resource 2 List of records of host-parasite interactions of parasitic flatworms belonging to *Cichlidogyrus* (Dactylogyridae, Monogenea) and their cichlid (Cichlidae, Teleostei) and non-cichlid host fishes in peer-reviewed publications, and presence of infection parameters for those records.

Figure 1



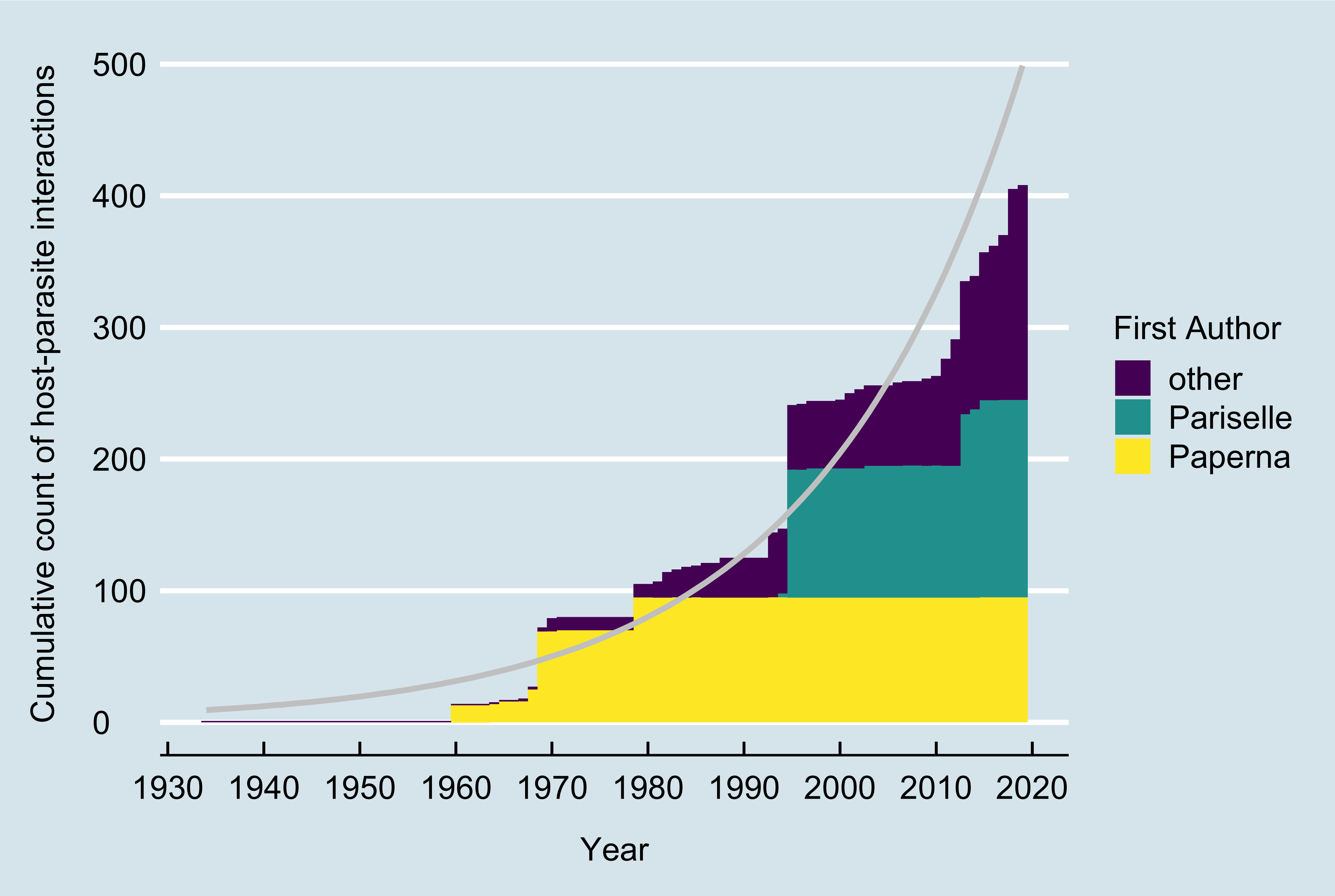

Cumulative count of host-parasite interactions
0
100
200
300
400
500
1930
1940
1950
1960
1970
1980
1990
2000
2010
2020
Year
First Author
other
Pariselle
Paperna

Figure 3

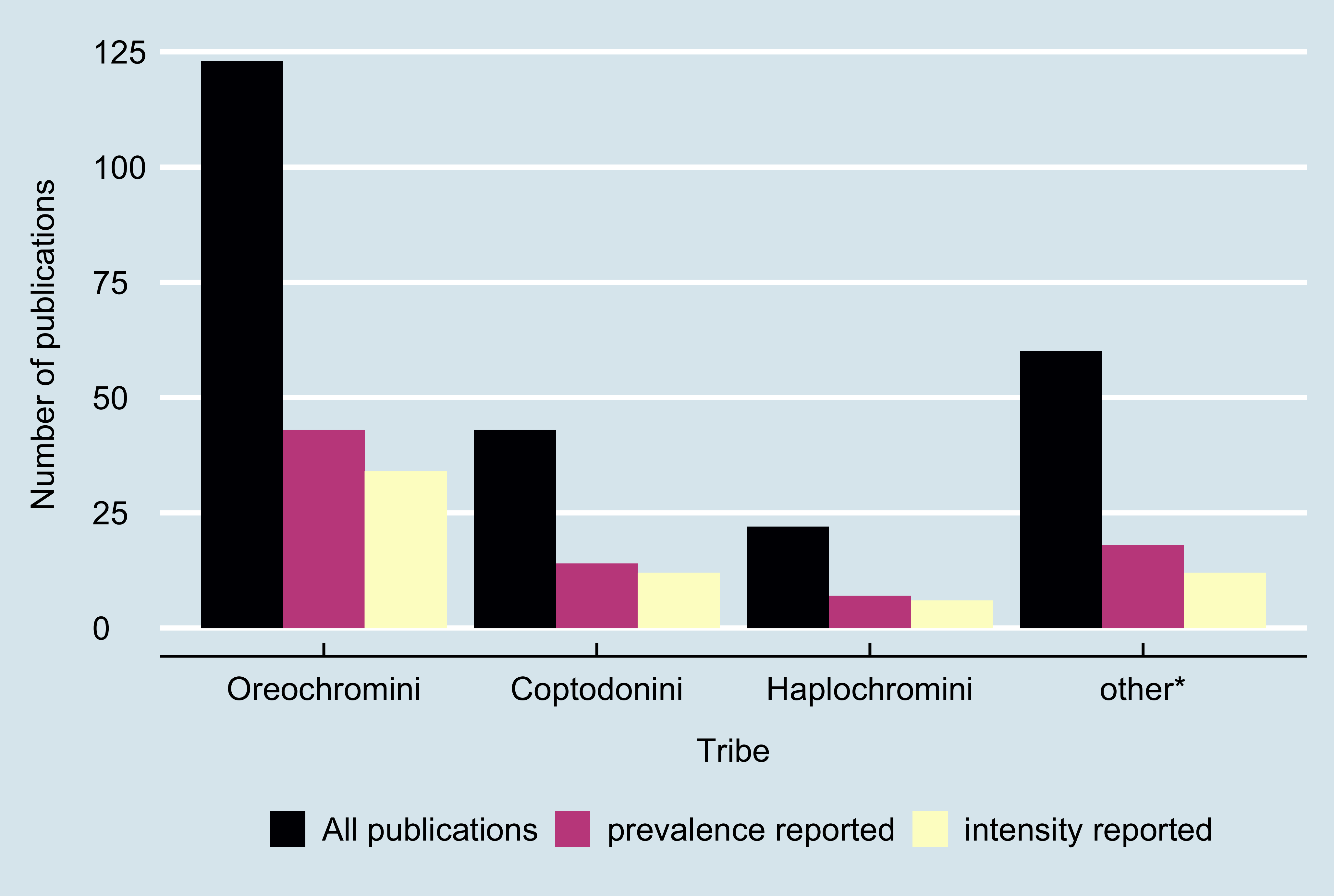

Number of publications
125
100
75
50
25
0
Oreochromini
Coptodonini
Haplochromini
other*
Tribe
All publications
prevalence reported
intensity reported

Table 1 Proposed standardised framework for reporting host-parasite network data, common reporting practice (examples in italics), and consequences of the common practice for data analysis: enhanced number and data formatting can increase reporting quality in future publications.

Standardised framework	**Common practice**	**Consequence of common practice**
Number formatting		Lost data: Usefulness for quantitative analyses limited
• All measurements incl. mean and data distribution (n > 30) *mean: 23 µm* *min: 20 µm* *max: 25 µm* *standard deviation: 2.4 µm*	• Incomplete reporting, e.g. as range *17-23 µm*	
• Fully reported infection parameters *examined hosts: 29* *infected hosts: 10* *parasites (total): 45*	• Qualitative reporting *"We found parasite A infecting host B."* • Incomplete reporting *Intensity: 1-20*	
• Host parameters (with mean and data distribution if applicable) *Size: 15 cm* *Sex: Male/female*	• No reporting	
• Physico-chemical parameters (with mean and data distribution if applicable) *e.g. temperature: 29*	• No reporting	
Data formatting		Time intensive extraction of data
• Data in tables	• Data in running text	
• Tidy data table (1 variable per column, 1 observation per row) *mean: 23 µm* *min: 20 µm* *max: 25 µm* *standard deviation: 2.4 µm*	• 'Messy' data table *(20-)21-24(-25) µm*	
• Open formats in supplementary file or public repositories *'table.csv'* *'table.txt'*	• Non-modifiable formats *'article.pdf'*	