Worms of change: anthropogenic disturbance changes the ectoparasite community structure of Lake Victoria cichlids

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Abstract

Host-parasite interactions increase the complexity, and thus robustness and resilience, of an ecosystem. This role is particularly relevant in global change times. Environmental changes cause biodiversity loss and shifts in community compositions of free-living organisms, but how these changes affect parasite communities is still unclear. We tested how parasites respond to anthropogenic perturbations, using the Lake Victoria case (East Africa), after 40 years of their onset. Lake Victoria experienced multiple human-induced invasions (e.g. Nile perch), eutrophication, which heavily affected haplochromine cichlid fishes (whose species richness decreased from 500 to 250 species in a decade). We compared gill macroparasite communities of 13 haplochromine species before and after perturbations, using historical and recent fish collections. The host-parasite network re-arranged in a way that buffers the impact of perturbations, indicating resilience. However, the host range of parasites, which is linked to resilience ability, decreased and thus we expect a decreased resilience ability in the future. We also found a decrease in infection parameters, co-infection occurrence, and biodiversity indices highlighting the urgent need of a conservation plan for wildlife parasites, to preserve their ecosystem services in face of global change. This study serves as a proof-of-concept of how often overlooked aspects of host-parasite interactions provide a tool to monitor the health status of an ecosystem.

1. Introduction

A more complex ecosystem is more robust to change(s) than a simple one (Pimm 1984, Landi et al. 2018). Host-parasite interactions increase ecosystem complexity and thereby its robustness and resilience (Lafferty et al. 2006, Lafferty et al. 2008, Dunne et al. 2013), which are particularly valuable in the current global change era. Parasite abundance and diversity are expected to change in response to anthropogenic perturbations, however, the direction of that change is still object of debate, let alone its consequences for ecosystem robustness and resilience.

For parasites, environmental changes encompass changes in host ecology and/or communities (as hosts represent the environment for parasites) in addition to abiotic changes (e.g. drought, temperature rise, pollutants). Ecosystem changes may create new opportunities for free-living organisms and, as consequence, also for parasites: they may face an altered host availability (e.g. hosts becoming rare, or encountering new host species). Ecosystem changes may lead to native host species decline or extinction, potentially causing parasite (co-)extinction (Mey 1990, Faust et al. 2018, Šimková et al. 2019), parasite switching to new host species (Roche et al. 2010, Kafle 2018, Jorissen et al. 2020) and shifts in host range

(Ricklefs et al. 2004, Weckstein 2004), and even lead to zoonotic spillovers (Jones et al. 2013, Allen et al. 2017, Faust et al. 2018, Johnson et al. 2020). These events can constitute a **conservation risk** for parasites (co-extinction) and a **disease outbreak risk** for hosts (changes in host use), including humans (spillovers). Knowing how parasite communities are varying across time can indicate how ecosystem complexity changed, even before we can observe changes in free-living organisms, and thus inform us on the health status of an ecosystem (**indicator potential**) (Shea et al. 2012, Hernández-Camacho and Zamora-Ledesma 2023).

We may expect environmental changes to cause a decline in parasite diversity, directly (e.g. pollutants decreasing survival of parasite transmission stages, Khan and Thulin 1991, Pietrock and Marcogliese 2003, Blanar et al. 2009) or indirectly (e.g. decline in host abundance, Carlson et al. 2020). On the other hand, we may also expect a rise in parasite abundance: increase in temperature positively affects parasite development (Scharsack et al. 2021), ecosystem degradation has been linked to emerging host-parasite pairs (Keesing & Ostfeld 2021; Harvell 2019) and to host immune defence erosion (Lehtinen et al. 1984). Long-term parasite data can shed light on the direction of change in parasitism, but these are lacking, as the average dataset has a time span of 12 years (Fiorenza et al. 2020a). Parasitological dissections of specimens from natural history collections can provide the necessary time coverage to reconstruct changes in parasite abundance and diversity in response to ecosystem degradation. Indeed, each host specimen harbours a parasite community.

We aim to investigate how parasite infection and host-parasite interactions change in response to ecosystem perturbations, using the case of Lake Victoria, in eastern Africa. Since the 1950s, human activities started to heavily impact Lake Victoria and, often with a cascade effect, these resulted in drastic ecosystem changes. The exotic Nile perch (*Lates niloticus*) was introduced in the northern part of Lake Victoria in the 1950s-1960s from Lakes Turkana and Albert (Pringle 2005, Goudswaard et al. 2008) and became an **invasive species** in the 1980s. In Lake Victoria, the Nile perch switched diet to haplochromine cichlid fishes, the locally most abundant prey (Gee 1969), negatively impacting their populations. Concomitantly, **eutrophication** (i.e. water enrichment in inorganic nutrients) increased in Lake Victoria, due to urban/agricultural pollution and soil erosion through deforestation (Verschuren et al. 2002). This altered phytoplankton composition (Hecky 1993, Verschuren et al. 2002), increased water turbidity (Seehausen et al. 1997), reduced dissolved oxygen hence expanding deep anoxic zones (Wanink et al. 2001) and caused algal blooms (Witte et al. 1992a, Sitoki et al. 2010). These anthropogenic factors led to shifts in community compositions (e.g. fish, Witte et al. 2007b, Witte et al. 2007c; phytoplankton, Sitoki et al. 2012; zooplankton, Gophen et al. 1995) and biomass (increased in phytoplankton, Wakwabi et al. 2006; decreased in benthic macroinvertebrates, Ngupula and Kayanda 2010) and an overall rapid and drastic **biodiversity loss** in Lake Victoria (Witte et al. 1992b, Seehausen et al. 1997, Witte et al. 2007a). Haplochromine cichlid fish were particularly affected, as their decline is estimated from 500 to 250 species in a few decades (Witte et al. 1992). Niches previously occupied by haplochromines were taken over by other species, making Lake Victoria dominated by non-haplochromine fishes, simplifying considerably the food web (Witte et al. 1992a, Witte et al. 1992b).

Such anthropogenic perturbations provide a natural experiment, allowing us to study how parasite communities respond to ecosystem changes and whether they can be used as indicators of changing ecosystem health. The aforementioned drastic changes in Lake Victoria, especially in the host community composition, may influence the host-parasite interactions by leading parasites to change their host usage. Parasites may expand their host range by ecological fitting (Kritsky and Boeger 2003, Brooks et al. 2006) in response to ecosystem perturbations or, alternatively, may reduce

it in response to decreased host availability. We screened for ectoparasites 13 haplochromine species from recent and historical fish collections to test whether and how parasite communities changed in response to (anthropogenic) ecosystem perturbations in Lake Victoria. We expect a decrease in parasite numbers and a change in host usage following the ecosystem changes in Lake Victoria. Because of reduced abundance and diversity of haplochromine species, we expect a reduction in the abundance of their parasites, especially for those with high host specificity, and a change in host usage.

2. Materials and methods

2.1. Study system

Lake Victoria is the youngest, shallowest and most turbid of the three major African Great Lakes. It harbours a young adaptive radiation of haplochromine cichlids (Cichlidae: Haplochromini), well-known in evolutionary research because of its young age and fast speciation rate (Meier et al. 2017, McGee et al. 2020). Most of the current Lake Victoria haplochromine fauna evolved *in situ* in the past 14'600 years (Johnson et al. 2000, Stager and Johnson 2008, Wagner et al. 2013, Meier et al. 2017), following the refilling of the lake (Stager and Johnson 2008) and the subsequent colonization and hybridization of at least four cichlid lineages (Seehausen et al. 2003, Meier et al. 2017). Lake Victoria also harbours older haplochromine lineages, distantly related to radiation members, that did not radiate (e.g. *Astatoreochromis alluaudi*, *Pseudocrenilabrus multicolor*; Seehausen 2006, Wagner et al. 2012, Wagner et al. 2013). The cichlid diversity in African Great Lakes is also associated with parasite diversity (Raeymaekers et al. 2013, Vanhove et al. 2015, Karvonen et al. 2018, Gobbin et al. 2020).

We focus on gill parasites of haplochromines, because, contrary to many internal parasites: they display higher host-specificity (Poulin et al. 2011), they can be easily morphologically identified to species level, and they mostly have a direct life cycle (i.e. no intermediate hosts that may cloud the target host-parasite interaction). In Lake Victoria, haplochromine gill parasitofauna is composed by monogenean flatworms (Monogenea) and crustacean copepods (Copepoda), both with a direct life cycle. Monogenean species show high host specificity, whereas copepods are generalists. In particular, the monogenean *Cichlidogyrus* is an emerging model for the evolution of host-parasite interactions (Cruz-Laufer et al. 2021). It is the most species-rich parasite taxon of African freshwater fish (Scholz et al. 2018), it radiated in another African Great lake (Vanhove et al. 2015), and is of known abundance in Lake Victoria (Gobbin et al. 2020). Haplochromine species in Lake Victoria vary in their parasite community composition (Gobbin et al. 2020) and one species of *Cichlidogyrus* (*C. longipenis*) shows indications of expansion to new host species between 1960s and 2010s (comparing Gobbin et al. 2020 and Paperna and Thurston 1969). The link between ecosystem disturbance and host switches has been observed in the cichlid-*Cichlidogyrus* system: in the Congo basin, invasion of introduced tilapia is linked to an increase in host range of *Cichlidogyrus* parasites (Jorissen et al. 2020).

The use of historical museum collections is heavily underexploited in parasitology (Harmon et al. 2019) although it has a great potential (Wood and Vanhove 2022). Historical collections have already been used to detect host switches in African cichlids (Jorissen et al. 2020), to reconstruct invasion routes in African Great Lakes (Kmentová et al. 2019) and to track abundance variation of an economically important nematode off the U.S. coast (Howard et al. 2019). This approach can be applied to reconstruct changes in gill parasite assemblages infecting fish because: *i)* each host individual harbors a parasite community, allowing community analysis, *ii)* parasite detectability is not influenced by museum preservation protocols (Fiorenza et al. 2020a), *iii)* gill parasites are physically protected by the fish operculum thus infection levels are unlikely to be altered during host manipulation (Kvach et al. 2016).

2.2. Fish collection

Cichlid fish (n=565) were obtained from the ichthyological collections of the Naturalis Biodiversity Center (Leiden, the Netherlands) and of the Swiss Federal Institute of Aquatic Science and Technology (EAWAG, Kastanienbaum, Switzerland). These specimens were originally sampled during different field campaigns at different locations in Lake Victoria between 1973 and 2014. In particular, most fish were collected during the HEST expedition (Haplochromis Ecological Survey Team) in 1978-9, and the Bern University-EAWAG campaigns in 2010 and 2014 (Karvonen et al. 2018, Gobbin et al. 2020, Gobbin et al. 2023). Both took place in the Speke Gulf and Mwanza Gulf (southern part of the lake). Most fish (n=327) were preserved in 4% formalin and subsequently transferred to 70% ethanol, other fish (n=95) were directly preserved in 100% ethanol for future genetic analysis.

We selected 13 common haplochromine species (nomenclature following Fricke and Eschmeyer 202) representing 7 trophic groups (based on teeth morphology and/or stomach content, Seehausen 1996, Seehausen and Bouton 1998; **Table 1**), with specimens available from both before and after ecosystem perturbations in Lake Victoria. We set 1980 as the temporal cut-off, because in this year the Nile perch became invasive also in southern Lake Victoria and water eutrophication became apparent (Ochumba and Kibaara 1989, Sitoki et al. 2010). All haplochromine species sampled belong to the Lake Victoria radiation lineage, except *Astatoreochromis alluaudi* that represents an older and distantly related lineage that never radiated in Lake Victoria. We screened for gill macroparasites at least 10 fish individuals per species and per time period (before vs. after perturbations). Each fish individual was also measured (SL, standard length, to the nearest mm) and sexed.

2.3. Parasite collection

We examined gill arches (right side of the fish only) under a dissecting stereoscope for gill macroparasites. The right side only was screened to minimize damage to collection specimens (left-side is usually used for fish taxonomy) and to allow inter-studies comparability (as this is standard procedure, e.g. MacColl 2009, Gobbin et al. 2023). No differences have been detected in parasite abundance between the two gill sides (Roux et al. 2011). Formalin-fixed monogenean parasites (from both recent and historical fish collections) were directly mounted on slides in Hoyer's medium and examined with a microscope (Leica DM 2500 LED and Olympus BX41TF) under 1000x magnification. Ethanol-fixed monogenean specimens (from recent fish collection only) were first cut into three parts: the two body extremities with sclerotized organs were mounted as described, the central body part was preserved in ethanol at 4°C for future molecular analysis. Monogenean species were identified following relevant literature (Paperna 1996, Vanhove et al. 2011, Gobbin et al. 2021) based on shape and size of sclerotized parts of the attachment organ (haptor) and of the male copulatory organ (MCO) (e.g. Grégoir et al. 2015, Gobbin et al. 2020), and counted. Other gill macroparasites were identified following Paperna (1996) and counted.

2.4. Statistical analysis

All statistical analyses were performed in R statistical software version 4.3.1 (R Core Team 2023), except ANOSIM posthoc tests (performed in PAST3; Hammer et al. 2001). Since host species *Pundamilia nyererei* was disproportionately represented in the time period after perturbations (104 vs. 11 fish individuals, respectively), we randomly sampled 15 individuals from that time period (sample_n – dplyr package).

2.4.1 Prevalence and intensity

We fit a Hurdle mixed model (glmmTMB – glmmTMB package; Magnusson et al. 2017) to simultaneously explore how parasite **prevalence** (proportion of infected hosts) and **intensity** (number of parasites per infected host individual) differed before vs. after perturbations and how it was influenced by parasite species. Hurdle models allow to handle zero-inflation, a common issue in parasitological analyses. Hurdle models are two-component models: a binary model fits data as zeroes or non-zeroes (prevalence) and, once this hurdle is crossed, a zero-truncated negative binomial model fits non-zero values (intensity, Zuur et al. 2009). Since the binary model predicts the probability of obtaining zeroes, negative estimates represent an increase in the probability of fish being infected (in plots, these are converted to positive values for the sake of readability). Rank deficient parasite species were excluded from the hurdle models (i.e. *Gyrodactylus sturmbaueri*, cestode sp. I without data for one time period). Overdispersion was assessed by comparing the dispersion of simulated residuals to the observed residuals (testDispersion – DHARMa package; Hartig 2018) and inspecting quantile-quantile plots. Zero-inflation was assessed by comparing the distribution of expected and observed zeroes (testZeroInflation – DHARMa package; Hartig 2018). The initial model included the following fixed effects: time period (before vs. after perturbations), parasite species, and their interaction term. Random effects initially included are: host species, fish individual identity (to account for individual variability in infection), fish length as an offset term (to account for the fact that bigger fish carry more parasites, Roux et al. 2011). Fish length was scaled prior to analysis (scale – base R, then adding 2 to avoid negative values) to balance fish interspecific differences in size. The optimal random effect structure of the model was determined by Akaike information criterion (AIC) and Bayesian information criterion (BIC) comparisons (Schwarz 1978, Sakamoto et al. 1986). We used ANOVA (Anova – car package; Fox and Weisberg 2019) to estimate the parameters of significant fixed effects for both model components and thus select for the Minimum Adequate Model (MAM) (Nakagawa and Cuthill 2007). To compare parasite species before and after perturbations, we computed Estimated Marginal Means (emmeans – emmeans package) with custom contrasts and Benjamini-Hochberg correction for multiple comparisons (Benjamini and Hochberg 1995).

2.4.2 Biodiversity metrics

We characterized gill parasite communities using parasite species richness per individual host (hereafter referred to as individual species richness) and **five biodiversity metrics** (so that each host individual is considered a living habitat for parasites): Shannon diversity index (accounting for parasite species richness and equitability; Shannon and Weaver 1949), Pielou's evenness index (measuring the relative abundance of the different parasite species in a host community; Pielou 1977), Jaccard index (based on species presence/absence; Jaccard 1912), Simpson's diversity index (accounting for species richness and species relative abundance; Simpson 1949), and Bray-Curtis distances (compositional dissimilarity based on parasite counts of infected hosts; Bray and Curtis 1957). We used linear mixed-effects models (lmer – lme4) to test whether parasite species richness, Shannon-Weaver, Pielou's evenness and Simpson indices changed after ecosystem perturbations. The initial model included: time period (before vs. after perturbations), host species and their interaction term as fixed effects. Initial random effects were: host length and sampling effort per year (both as a regular random term or as an offset term). The optimal random effect structure and the MAM were determined as detailed above.

Since the Jaccard index and Bray-Curtis distances are expressed as a matrix, we used Analysis of Similarities (anosim – vegan) to test whether they changed after perturbations. To test whether temporal changes in parasite community composition varied among host species, we performed pairwise comparisons in PAST3 (as this is currently unavailable in R), with Benjamini-Hochberg correction (p.adjust – base R).

2.4.3 Host range and co-infections

The **host range** (number of host species infected by a given parasite species) was calculated per sampling year, excluding uninfected host individuals. Using generalized linear models (glm – base R) we tested host range for the influence of: perturbations (before vs. after perturbations), parasite species, and their interaction. We also included an offset term, to account for the fish sampling effort of each year. We followed the same procedure detailed above to determine the MAM and to perform post-hoc tests.

We tested whether **coinfections** of host individuals were more frequent before or after ecosystem perturbations, using generalized linear models (glmer.nb – lme4). First, we calculated the number of parasite species per infected host individual and classified the infection as single- or multiple-species (expressed as 0 or 1, respectively). The initial model included: time period (before vs. after perturbations), host species and their interaction term as fixed effects; fish identity as random effect, and host length as an offset (as described above). The optimal random effect structure and the MAM were determined as mentioned above.

2.4.4 Network analyses

We performed **network analyses** at host-individual level (infected host individuals only), rather than at species level, to consider the host intraspecific variation in parasite communities. Indeed, a host individual often interacts with more than one parasite species (polyparasitism) and thus its role within the network varies depending on how many parasites it can transmit to other hosts. For each network, before and after perturbations, we calculated three indices: *i)* connectance (C, Dunne et al. 2002), *ii)* modularity (Q; Newman and Girvan 2004), and *iii)* weighted nestedness based on overlap and decreasing fill (WNODF; Almeida-Neto and Ulrich 2011). **Connectance** (C) is the proportion of realized links among all possible links (estimated with networklevel – bipartite package). It ranges from 0 (no realized links) to 1 (all realized links). **Modularity** (Q) measures how well the network can be grouped into different modules (estimated with computeModules – bipartite package). It ranges from 0 (prevalent links between modules) to 1 (prevalent links within modules) (Miranda et al. 2019). **Nestedness** measures the hierarchical organization of the community (Almeida-Neto and Ulrich 2011). We used WNODF, which describes the degree to which parasites interact with subsets of host species. Nestedness and modularity usually correlate with each other, with the direction and magnitude of this correlation depending on network type and on its connectance (Fortuna et al. 2010). In antagonistic networks (e.g. host-parasites), the network stability is enhanced by increasing nestedness and/or decreasing modularity (Thébault and Fontaine 2010).

Network size influences WNODF and Q values, but not C values (Dunne et al. 2002). In order to compare WNODF and Q between the two time periods, we generated 1000 null model replicates of the real matrices (nullmodel – bipartite package; Dormann et al. 2009) using the swap.web algorithm to standardize initial estimates of these two indices. Then, we used bootstrap replicates by rows (host individuals) to generate 1000 random networks of each original matrix. The 95% confidence intervals for each index were calculated (following Llopis-Belenguer et al. 2020). We tested differences of the three indices (C, Q, WNODF) between the period before and after perturbations using non-parametric Mann–Whitney–Wilcoxon (wilcox.test – base R).

3. Results

We found 654 monogeneans belonging to seven species (*Cichlidogyrus bifurcatus*, *C.* sp. 'furu', *C. longipenis*, *C.* sp. 'nyanza', *C.* sp. 'pseudodossoui', *C.* sp. 'vetusmolendarius', *Gyrodactylus sturmbaueri*), 301 copepods belonging to two species (*Lamproglena monodi*, *Ergasilus lamellifer*), and 15 cestodes (larval stages) belonging to an unidentified taxon (cestode sp. I). Eight parasite species were shared among the two time periods, whereas *G. sturmbaueri* was observed only once after perturbations and the larval cestode sp. I was observed only before perturbations. We identified to species level 91.3% of monogeneans and 93% of copepods (the remaining 8.7% and 7% specimens were damaged and thus not suitable for identification). These parasites unidentified to species level were included in quantitative (e.g. prevalence, intensity) but not in qualitative analyses (e.g. network analyses), because there is no reason to assume these represent additional different species.

3.1. Prevalence and intensity

Overall, infection **prevalence** decreased from 88.73% to 69.70% after perturbations in Lake Victoria ($ChiSq_1$=28.747, p<0.001). The decrease in prevalence tended to vary across parasite species, although this was probably due to one parasite species (*C. longipenis*) deviating from the overall prevalence decrease pattern (**Figure 1a**, **Table S1**). Different parasite species differed in their overall prevalence in both time periods combined ($ChiSq_9$=279.781, p<0.001, pooling time periods): *Ergasilus lamellifer* had the highest infection prevalence (38.23%), whereas *C. bifurcatus* had the lowest one (2.06%, **Table S1**).

Infection **intensity** decreased from 5.80 to 4.63 after perturbations ($ChiSq_1$=46.870, p<0.001) and this decrease varied across parasite species ($ChiSq_9$=49.506, p<0.001). After ecosystem perturbations, three parasite species decreased or tended to decrease (*E. lamellifer* z=3.557, p<0.001; *C.* sp. 'nyanza' z=1.909, p=0.056; *C.* sp. 'pseudodossoui' z=1.816, p=0.069) whereas two parasite species increased in intensity (*C.* sp. 'vetusmolendarius' z=-2.871, p=0.004; *L. monodi* z=-2.912, p=0.0043). Infection intensity also differed among parasite species ($ChiSq_{14}$=830945, p<0.001): *C. longipenis* had the highest infection intensity (7.00), whereas *G. sturmbaueri* and *C. bifurcatus* had the lowest one (1.00, 1.14, respectively, **Table S1**).

3.2. Biodiversity indices

The species richness per individual host (1.9 vs. 1.1; $Chisq_1$=47.312, p<0.001), the Shannon-Wiener index ($Chisq_1$=38.100, p<0.001) and Pielou's evenness index ($Chisq_1$=29.794, p<0.001) decreased after perturbations, whereas the Simpson index did not change ($Chisq_1$=0.199, p=0.655; **Figure 2**). This decrease varied within host species (individual species richness $Chisq_{12}$=31.169, p=0.001; Shannon-Wiener index Chisq=36.534, p<0.001; Pielou's evenness index $Chisq_1$=26.426, p=0.009). Out of 13 host species, seven showed a decrease in both individual species richness and Shannon-Wiener index, while six decreased in Pielou's evenness index (**Table S2**). All indices also varied between host species (individual species richness $Chisq_1$=76.445, p<0.001; Pielou's evenness index $Chisq_{12}$=48.831, p<0.001; Shannon-Wiener $Chisq_{12}$=65.028, p<0.001; Simpson index $Chisq_{12}$=34.897, p<0.001).

Gill parasite communities differed between time periods (before vs. after perturbations, Bray-Curtis R2=0.017, F_1=6.899, p=0.001; Jaccard R2=0.015, F_1=6.187, p=0.001). This temporal variation in parasite communities varied across host species (Bray-Curtis R2=0.415, F_{24}=7.15, p=0.001; Jaccard R2=0.431, F_{24}=7.620, p=0.001): it was significantly different in nine host species (**Table S3**).

3.3. Host range and co-infection

The **host range** of parasites decreased significantly after perturbations ($Chisq_1$=9.525, p=0.002), after accounting for the variation between parasite species ($Chisq_{11}$=42.207, p<0.001). This decrease did not vary across parasite species ($Chisq_9$=4.376, p=0.885). On average, the two copepod species had the largest host range in both time periods combined (*L. monodi* 3.6, *E. lamellifer* 3.1 host species), whereas *C. longipenis* had the smallest one (1 host species in this dataset, *A. alluaudi*).

Occurrence of co-infection decreased after ecosystem perturbations from 66.4% to 43.8% (**Figure 2**, $Chisq_1$=13.771, p<0.001), after accounting for the variation between host species ($Chisq_{12}$=25.927, p=0.011). Variation in parasite co-occurrence among host species did not differ between the two time periods ($Chisq_{12}$=10.376, p=0.583).

3.4. Network analysis

The host-parasite networks differed between time periods (i.e. before and after perturbations) in their nestedness and modularity (both $p<0.001$), but they did not differ in their connectance, both when considering all identified parasite species (**Figure 3**) and monogenean species only. Standardized modularity was higher (0.51 vs. 0.35) and standardized nestedness was lower (14.16 vs. 24.56) after perturbations, than before perturbations. Connectance was low in both periods (0.23 before and 0.18 after perturbations), which is due to low species richness of the network.

4. Discussion

Environmental changes cause biodiversity loss and shifts in community compositions of free-living organisms, but how these changes affect parasite communities is still unclear. Parasites are an important component of biodiversity and provide many ecosystem services. We tested how parasites respond to anthropogenic perturbations in Lake Victoria, a biodiversity hotspot that experienced human-induced Nile perch invasion and eutrophication. For this, we compared parasite communities before and after the peak of these perturbations, using recent and historical collections. Host-parasite interactions were affected by anthropogenic perturbations: infection parameters (intensity, prevalence, co-infections), host range, and biodiversity indices (individual species richness, Shannon-Wiener, Pielou's evenness) decreased and the host-parasite network rearranged.

Gill parasites have been co-introduced to Lake Victoria with Nile perch (e.g. the diplectanid monogenean *Dolicirroplectanum lacustre*, Thys et al. 2022). Among Nile perch parasites, no monogeneans have been found on any African freshwater fish other than species of *Lates* (Scholz et al. 2018, Kmentová et al. 2020), and three crustaceans also infect haplochromines elsewhere but were never reported in Lake Victoria (not on *L. niloticus* nor on haplochromines, Outa et al. 2021). Unsurprisingly, gill parasites of the Nile perch did not switch to haplochromines in Lake Victoria. This indicates that changes observed in parasite communities of Victorian cichlids, even though they accompanied anthropogenic host introductions, are not driven by parasite (co-)introductions, but rather driven by other ecological changes as human-induced perturbations.

Most parasite species showed a declining pattern in both prevalence and intensity, while these parameters increased for few others. This is in line with the "few winners, many losers" paradigm, which was already observed in other host-parasite systems (e.g. bat flies in response to different levels of anthropogenic disturbance, Pilosof et al. 2012). It is unclear why the winners are *L. monodi* and *C.* sp. 'vetusmolendarius', but we speculate it may be because *L. monodi* has a wide host range combined with high prevalence and potentially high dispersal, whereas *C.* sp. 'vetusmolendarius' showed the ability to switch host species. The change in prevalence and intensity was always mirrored by a change in the same direction in the relative occurrence of a given parasite within the parasite community (**Figure S1**), suggesting that parasite species declining in intensity and prevalence are also representing a smaller part of the infection; whereas parasites increasing in intensity (*C.* sp. 'vetusmolendarius', *L. monodi*) are expanding into these emptied niches.

The aforementioned changes in infection parameters, and in the host-parasite network occurred despite the consistent parasite species composition (i.e. same parasite species were observed before and after perturbations, excepted cestode sp. I and one *Gyrodactylus sturmbaueri*). This highlights that the absence of changes in species richness does not imply ecosystem stability. It is therefore necessary to consider hidden facets – as host range, multispecies infection, bipartite network – to detect changes in interspecific interactions. These aspects are "hidden" because parasites are often simply

numerically counted, without species-level identification (except for a limited number of already known host-parasite interactions). Therefore, changes in interspecific interactions in the ecosystem will not be apparent if parasites are not taken into account. Since these aspects are typically not considered in free-living organisms, it is important to monitor parasite communities and their interactions with hosts to be able to detect ecosystem changes.

The one individual of *Gyrodactylus* recorded after perturbations may be an accidental infection, or it may represent the low extremity of these worms' wide variability in prevalence in African cichlids (Zahradníčková et al. 2016, Jorissen et al. 2020). Cestode sp. I was observed only before perturbations. Cestodes have indirect life cycles (i.e. more than one host), thus they face a higher conservation risk when a step of the cycle is disrupted (e.g. if a host goes extinct or its population declines; Rohr et al. 2011) and are more dependent on host trophic connections than parasites with direct life cycles (e.g. monogeneans and copepods of this study). The decline in host diversity and abundance that followed perturbations in Lake Victoria may have led to a decline of this cestode taxon. On the other hand, cestodes generally have low host specificity, making them prone to switch host species. It is therefore possible that it switched to a host species not surveyed in this study. Since the cestode larvae were not identified to finer resolution, we can depict two alternative scenarios: *i)* the taxon is endemic to Lake Victoria, thus it may be threatened or extinct (if it does not infect or did not switch to other hosts), *ii)* the taxon is not endemic to Lake Victoria and persists in other host species and other lakes of the region. Either way, we can speculate that the Lake Victoria populations of cestode sp. I have been heavily impacted by perturbations and/or that it had a lower resilience than other parasite species (as parasites with indirect life cycles are less resilient, Wood et al. 2023).

Lake Victoria is a young system; therefore, its host-parasite network is expected to be simple and relatively small, as we observed. This is supported by the comparison of the *Cichlidogyrus*-cichlid network in Lake Victoria and Lake Tanganyika, which is a much older system (Cruz-Laufer et al. 2022), thus confirming the ideas of Pariselle et al. (2015) on the differences between the monogenean communities infecting cichlids in these two lakes. Host-parasite networks are usually modular and not nested (Fortuna et al. 2010, Thébault and Fontaine 2010, Morrison and Dirzo 2020). Disruption of the network structure has already been observed after biological invasions (Runghen et al. 2021, Llaberia-Robledillo et al. 2022). Even if in Lake Victoria the parasite species richness mostly remained the same over time, the network rearranged: modularity increased and nestedness decreased after perturbations. This pattern is the opposite of those observed in seed-dispersal networks following global warming (Takemoto and Kajihara 2016) and other human impacts (Sebastián-González et al. 2015). However, caution is needed in comparing different network types, as they often differ in their characteristics (Takemoto and Iida 2019). An increase in modularity in response to anthropogenic perturbations was previously observed in host-parasite networks (Gilarranz et al. 2016, Lula Costa et al. 2023). These findings corroborate the idea that increased modularity and decreased nestedness act as impact buffers (Bordes et al. 2015, Gilarranz et al. 2017). The observed increase in modularity was not linked to an increase in infection intensity, as found by Lula Costa et al. (2023) suggesting that both changes are an effect of perturbations rather than being one the effect of the other. The observed nestedness decrease is in contrast with previous studies (nestedness increased after biological invasion, Llaberia-Robledillo et al. 2022) and with the concept that a low nestedness is promoted when parasite niches are well established (Almeida-Neto and Ulrich 2011). Gill parasite taxa are shared among haplochromines of Lake Victoria, rather than being specialized to only one or few host species (Gobbin et al. 2020). Thus, interactions may be less vulnerable to perturbations than highly specialized interactions, making the network relatively resistant to perturbations considering its simplicity.

The ecological niche of parasites (i.e. host range) narrowed after perturbations. This is in line with a distribution range contraction driven by human activities observed in many mammal taxa (Laliberte and Ripple 2004, Pacifici et al. 2020). The current narrow niche likely results from a loss of host availability (both in terms of abundance and species richness), rather than from a real specialization process of the parasite. The "forced" narrow niche poses an increased conservation risk: if more host species disappear, parasites may not be able to maintain a viable population. Thus, a niche contraction implies a decrease in resilience. With many parasite species narrowing their niches, we may infer a general decrease in Lake Victoria ecosystem resilience. Parasites in Lake Victoria experiencing a contracting host range became more vulnerable and require at least monitoring of their conservation status. It is important to notice that a host range shift differs from a host shift: the former implies a quantitative change in host species exploited (decrease/increase in numbers) whereas the latter focuses on qualitative changes in host species exploited (colonization of different host species). While host shifts are often considered in disease literature (zoonosis and spillovers), changes in host range are overlooked. We highlight here the importance of monitoring changes in host range for early detection of ecosystem changes.

Parasitic infections are often studied in isolation, whereas in nature different parasite species commonly co-occur in the same host individual (Petney and Andrews 1998). Co-infections can have evolutionary (e.g. on virulence, Rigaud et al. 2010) and ecological consequences (e.g. on competition and niche distribution, Gobbin et al. 2021). Reversely, co-infections might be influenced by ecological changes and thus they need to be monitored in the context of global change. We observed a decrease in the occurrence of co-infections after perturbations. This may be linked to the decrease in parasite prevalence and intensity, which leads to a decrease in chances of multi-infection. The decrease of co-infections may also be due to *i)* parasites becoming less competitive and thus less able to infect host individuals in which another parasite species occurs and/or *ii)* a decreased facilitating effect (i.e. infection subsequent to mechanical damage, Bandilla et al. 2006; or through immunosuppression of the host, Zhi et al. 2018). Competition has been observed among species of *Cichlidogyrus* and hypothesized to have caused their niche distribution within host gills (Gobbin et al. 2021). The few parasite species that increased in intensity (*C.* sp. 'vetusmolendarius', *L. monodi*) were not more likely to outcompete other parasite species, because their probabilities to occur in co-infections were not higher than those of parasites declining in intensity.

Parasite populations are declining in Lake Victoria and elsewhere (Russell et al. 2015, MacKenzie and Pert 2018, Wood et al. 2023). However, this trend cannot be generalized, as the direction of change (if any) can vary between parasite taxa even within the same study (Howard et al. 2019, Fiorenza et al. 2020b, Quinn et al. 2021, Welicky et al. 2021). A decline in abundance is mostly observed in ectoparasites and in parasites with more than one host than endoparasites and parasites with one host (Carlson et al. 2017, Vanhove et al. 2022, Wood et al. 2023). It is therefore important to monitor each ecosystem, as different parasites can respond differently in different ecosystems and to different perturbations. The decline in parasitism in Lake Victoria is detectable already in a 40-years period (20 years after the onset of perturbations). This 40-years' timeframe is similar to that of previous studies in fish parasites (90 years in Welicky et al. 2021; 50 years in Fiorenza et al. 2020b). Further studies are needed to assess at higher temporal resolution how long it actually took for these changes in parasite communities to manifest.

The overall decline in parasitism in Lake Victoria and elsewhere, and the potential loss of one parasite taxon (cestode sp. I) stresses the urgent need for a conservation plan of parasites infecting wildlife (as already highlighted by Carlson et al. 2020). In response to this need, two of the authors recently established, together with other parasitologists worldwide,

the IUCN Species Survival Commission's Parasite Specialist Group, aiming at assessing the conservation status of parasite species globally (Hopkins and Kwak 2023).

5. Conclusion

In a relatively short period, human-induced perturbations in Lake Victoria affected not only free-living organisms, but also their parasites. Although the parasite community mostly maintained the same species, we observed a change in community composition and an overall decline in infection and biodiversity metrics. The decrease in infection intensity, prevalence and host range poses a conservation risk for parasites. The host-parasite network re-arranged in a way that buffers the impact of perturbations (i.e. modularity increased, nestedness decreased), showing some resilience. However, the host range of parasites, which is linked to resilience ability, decreased and thus we expect a decreased resilience in the future. We showed the complementarity of two approaches, bipartite network and infection parameters, in detecting temporal variation in host-parasite interactions. Parasites contribute to biodiversity and increase enormously the number of connections between organisms, which is crucial for ecosystem resilience (especially in face of current global change). It is therefore important to monitor these metrics of parasitism across time, rather than merely assess species richness, to evaluate both the conservation status of parasite species and the health status of ecosystems, and subsequently enforce conservation policies.

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7. References

Allen, T., K. A. Murray, C. Zambrana-Torrelio, S. S. Morse, C. Rondinini, M. Di Marco, N. Breit, K. J. Olival, and P. Daszak. 2017. Global hotspots and correlates of emerging zoonotic diseases. Nature Communications **8**:1124.

Almeida-Neto, M., and W. Ulrich. 2011. A straightforward computational approach for measuring nestedness using quantitative matrices. Environmental Modelling & Software **26**:173-178.

Bandilla, M., E. T. Valtonen, L. R. Suomalainen, P. J. Aphalo, and T. Hakalahti. 2006. A link between ectoparasite infection and susceptibility to bacterial disease in rainbow trout. International Journal for Parasitology **36**:987-991.

Benjamini, Y., and Y. Hochberg. 1995. Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing. Journal of the Royal Statistical Society: Series B (Methodological) **57**:289-300.

Blanar, C. A., K. R. Munkittrick, J. Houlahan, D. L. MacLatchy, and D. J. Marcogliese. 2009. Pollution and parasitism in aquatic animals: A meta-analysis of effect size. Aquatic Toxicology **93**:18-28.

Bordes, F., S. Morand, S. Pilosof, J. Claude, B. R. Krasnov, J.-F. Cosson, Y. Chaval, A. Ribas, K. Chaisiri, K. Blasdell, V. Herbreteau, S. Dupuy, and A. Tran. 2015. Habitat fragmentation alters the properties of a host–parasite network: rodents and their helminths in South-East Asia. Journal of Animal Ecology **84**:1253-1263.

Bray, J. R., and J. T. Curtis. 1957. An Ordination of the Upland Forest Communities of Southern Wisconsin. Ecological Monographs **27**:325-349.

Brooks, D. R., V. León-Règagnon, D. A. McLennan, and D. Zelmer. 2006. Ecological Fitting as a Determinant of the Community Structure of Platyhelminth Parasites of Anurans. Ecology **87**:S76-S85.

Carlson, C. J., K. R. Burgio, E. R. Dougherty, A. J. Phillips, V. M. Bueno, C. F. Clements, G. Castaldo, T. A. Dallas, C. A. Cizauskas, G. S. Cumming, J. Doña, N. C. Harris, R. Jovani, S. Mironov, O. C. Muellerklein, H. C. Proctor, and W. M. Getz. 2017. Parasite biodiversity faces extinction and redistribution in a changing climate. Sci Adv **3**:e1602422.

Carlson, C. J., S. Hopkins, K. C. Bell, J. Doña, S. S. Godfrey, M. L. Kwak, K. D. Lafferty, M. L. Moir, K. A. Speer, G. Strona, M. Torchin, and C. L. Wood. 2020. A global parasite conservation plan. Biological Conservation **250**:108596.

Cruz-Laufer, A. J., T. Artois, S. Koblmüller, A. Pariselle, K. Smeets, M. Van Steenberge, and M. P. M. Vanhove. 2022. Explosive networking: The role of adaptive host radiations and ecological opportunity in a species-rich host–parasite assembly. Ecology Letters **25**:1795-1812.

Cruz-Laufer, A. J., T. Artois, K. Smeets, A. Pariselle, and M. P. M. Vanhove. 2021. The cichlid–*Cichlidogyrus* network: a blueprint for a model system of parasite evolution. Hydrobiologia **848**:3847-3863.

Dormann, C., J. Frund, N. Bluthgen, and B. Gruber. 2009. Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks. Open Journal of Ecology **2**:7-24.

Dunne, J. A., K. D. Lafferty, A. P. Dobson, R. F. Hechinger, A. M. Kuris, N. D. Martinez, J. P. McLaughlin, K. N. Mouritsen, R. Poulin, K. Reise, D. B. Stouffer, D. W. Thieltges, R. J. Williams, and C. D. Zander. 2013. Parasites Affect Food Web Structure Primarily through Increased Diversity and Complexity. PLoS Biology **11**:e1001579.

Dunne, J. A., R. J. Williams, and N. D. Martinez. 2002. Food-web structure and network theory: The role of connectance and size. Proceedings of the National Academy of Sciences **99**:12917-12922.

Faust, C. L., H. I. McCallum, L. S. P. Bloomfield, N. L. Gottdenker, T. R. Gillespie, C. J. Torney, A. P. Dobson, and R. K. Plowright. 2018. Pathogen spillover during land conversion. Ecology Letters **21**:471-483.

Fiorenza, E. A., K. L. Leslie, M. E. Torchin, K. P. Maslenikov, L. Tornabene, and C. L. Wood. 2020a. Fluid preservation causes minimal reduction of parasite detectability in fish specimens: A new approach for reconstructing parasite communities of the past? Ecol. Evol. **10**:6449-6460.

Fiorenza, E. A., C. A. Wendt, K. A. Dobkowski, T. L. King, M. Pappaionou, P. Rabinowitz, J. F. Samhouri, and C. L. Wood. 2020b. It's a wormy world: Meta-analysis reveals several decades of change in the global abundance of the parasitic nematodes Anisakis spp. and Pseudoterranova spp. in marine fishes and invertebrates. Global Change Biology **26**:2854-2866.

Fortuna, M. A., D. B. Stouffer, J. M. Olesen, P. Jordano, D. Mouillot, B. R. Krasnov, R. Poulin, and J. Bascompte. 2010. Nestedness versus modularity in ecological networks: two sides of the same coin? Journal of Animal Ecology **79**:811-817.

Fox, J., and S. Weisberg. 2019. An R Companion to Applied Regression. 3rd edition. Sage, Thousand Oaks CA.

Fricke, R., and W. N. Eschmeyer. 2024. Eschmeyer's Catalog of Fishes: genera, species, references. W. N. & Van der Laan, R. (eds.)

Gee, J. M. 1969. A comparison of certain aspects of the biology of *Lates niloticus* (Linne) in some East African lakes. Revue de Zoologie et Botanique Africaines **80**:244-262.

Gilarranz, L. J., C. Mora, and J. Bascompte. 2016. Anthropogenic effects are associated with a lower persistence of marine food webs. Nature Communications **7**:10737.

Gilarranz, L. J., B. Rayfield, G. Liñán-Cembrano, J. Bascompte, and A. Gonzalez. 2017. Effects of network modularity on the spread of perturbation impact in experimental metapopulations. Science **357**:199-201.

Gobbin, T. P., M. P. M. Vanhove, A. Pariselle, M. E. Maan, and O. Seehausen. 2020. Temporally consistent species differences in parasite infection but no evidence for rapid parasite-mediated speciation in Lake Victoria cichlid fish. Journal of Evolutionary Biology **33**:556-575.

Gobbin, T. P., M. P. M. Vanhove, O. Seehausen, and M. E. Maan. 2021. Microhabitat distributions and species interactions of ectoparasites on the gills of cichlid fish in Lake Victoria, Tanzania. International Journal for Parasitology **51**:201-214.

Gobbin, T. P., M. P. Vanhove, O. Seehausen, M. E. Maan, and A. Pariselle. 2021. Four new species of *Cichlidogyrus* (Platyhelminthes, Monogenea, Dactylogyridae) from Lake Victoria haplochromine cichlid fishes, with the redescription of *C. bifurcatus* and *C. longipenis*. bioRxiv:2021.2001.2029.428376.

Gobbin, T. P., M. P. M. Vanhove, R. Veenstra, M. E. Maan, and O. Seehausen. 2023. Variation in parasite infection between replicates of speciation in Lake Victoria cichlid fish. Evolution **77**:1682-1690.

Gophen, M., P. B. O. Ochumba, and L. S. Kaufman. 1995. Some aspects of perturbation in the structure and biodiversity of the ecosystem of Lake Victoria (East Africa). Aquat. Living Resour. **8**:27-41.

Goudswaard, K. P. C., F. Witte, and E. F. B. Katunzi. 2008. The invasion of an introduced predator, Nile perch (*Lates niloticus*, L.) in Lake Victoria (East Africa): chronology and causes. Environmental Biology of Fishes **81**.

Grégoir, A. F., P. I. Hablützel, M. P. M. Vanhove, A. Pariselle, J. Bamps, F. A. M. Volckaert, and J. A. M. Raeymaekers. 2015. A link between host dispersal and parasite diversity in two sympatric cichlids of Lake Tanganyika. Freshwater Biology **60**:323-335.

Hammer, O., D. A. T. Harper, and P. D. Ryan. 2001. PAST: Paleontological Statistics Software Package for Education and Data Analysis. Paleontologia Electronica **4**:1-9.

Harmon, A., D. T. J. Littlewood, and C. L. Wood. 2019. Parasites lost: using natural history collections to track disease change across deep time. Frontiers in Ecology and the Environment **17**:157-166.

Hartig, F. 2018. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. Page R package version 0.4.6 https://CRAN.Rproject.org/package=DHARMa.

Hecky, R. E. 1993. The eutrophication of Lake Victoria. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie **29**.

Hernández-Camacho, N., and S. Zamora-Ledesma. 2023. The Potential of the Parasite Fauna as an Indicator of Ecosystem Health in the Anthropized Environments of Mexico. Pages 569-579 *in* R. W. Jones, C. P. Ornelas-García, R. Pineda-López, and F. Álvarez, editors. Mexican Fauna in the Anthropocene. Springer International Publishing, Cham.

Hopkins, S., and M. Kwak. 2023. New IUCN Species Survival Commission Parasite Specialist Group launched in 2023. Oryx **57**:283-283.

Howard, I., E. Davis, G. Lippert, T. P. Quinn, and C. L. Wood. 2019. Abundance of an economically important nematode parasite increased in Puget Sound between 1930 and 2016: Evidence from museum specimens confirms historical data. Journal of Applied Ecology **56**:190-200.

Jaccard, P. 1912. The distribution of the flora in the Alpine zone. New Phytologist **11**:37-50.

Johnson, C. K., P. L. Hitchens, P. S. Pandit, J. Rushmore, T. S. Evans, C. C. W. Young, and M. M. Doyle. 2020. Global shifts in mammalian population trends reveal key predictors of virus spillover risk. Proceedings of the Royal Society B: Biological Sciences **287**:20192736.

Johnson, T. C., K. Kelts, and E. Odada. 2000. The holocene history of Lake Victoria. The Holocene History of Lake Victoria **29**:2-11.

Jones, B. A., D. Grace, R. Kock, S. Alonso, J. Rushton, M. Y. Said, D. McKeever, F. Mutua, J. Young, J. McDermott, and D. U. Pfeiffer. 2013. Zoonosis emergence linked to agricultural intensification and environmental change. Proceedings of the National Academy of Sciences **110**:8399-8404.

Jorissen, M. W. P., T. Huyse, A. Pariselle, S. Wamuini Lunkayilakio, F. Muterezi Bukinga, A. Chocha Manda, G. Kapepula Kasembele, E. J. Vreven, J. Snoeks, E. Decru, T. Artois, and M. P. M. Vanhove. 2020. Historical museum collections help detect parasite species jumps after tilapia introductions in the Congo Basin. Biological Invasions **22**:2825-2844.

Kafle, P. 2018. Climate Change and Range Expansion of Protostrongylid Nematodes in the Canadian Arctic. Doctoral Thesis.

Karvonen, A., C. E. Wagner, O. M. Selz, and O. Seehausen. 2018. Divergent parasite infections in sympatric cichlid species in Lake Victoria. Journal of Evolutionary Biology **31**:1313-1329.

Khan, R. A., and J. Thulin. 1991. Influence of Pollution on Parasites of Aquatic Animals. Pages 201-238 *in* J. R. Baker and R. Muller, editors. Advances in Parasitology. Academic Press.

Kmentová, N., M. Van Steenberge, D. F. E. Thys van den Audenaerde, T. Nhiwatiwa, F. Muterezi Bukinga, T. Mulimbwa N'sibula, P. Masilya Mulungula, M. Gelnar, and M. P. M. Vanhove. 2019. Co-introduction success of monogeneans infecting the fisheries target *Limnothrissa miodon* differs between two

non-native areas: the potential of parasites as a tag for introduction pathway. Biological Invasions **21**:757-773.

Kmentová, N., S. Koblmüller, M. Van Steenberge, T. Artois, F. Muterezi Bukinga, T. Mulimbwa N'sibula, D. Muzumani Risasi, P. Masilya Mulungula, M. Gelnar, and M. P. M. Vanhove. 2020. Failure to diverge in African Great Lakes: The case of *Dolicirroplectanum lacustre* gen. nov. comb. nov. (Monogenea, Diplectanidae) infecting latid hosts. Journal of Great Lakes Research **46**:1113-1130.

Kritsky, D., and W. Boeger. 2003. Phylogeny of the Gyrodactylidae and the phylogenetic status of *Gyrodactylus* Nordmann, 1832 (Platyhelminthes: Monogenoidea). Taxonomy, Ecology and Evolution of Metazoan Parasites **2**:37-58.

Kvach, Y., M. Ondračková, M. Janáč, and P. Jurajda. 2016. Methodological issues affecting the study of fish parasites. II. Sampling method affects ectoparasite studies. Diseases of Aquatic Organisms **121**:59-66.

Lafferty, K. D., S. Allesina, M. Arim, C. J. Briggs, G. De Leo, A. P. Dobson, J. A. Dunne, P. T. J. Johnson, A. M. Kuris, D. J. Marcogliese, N. D. Martinez, J. Memmott, P. A. Marquet, J. P. McLaughlin, E. A. Mordecai, M. Pascual, R. Poulin, and D. W. Thieltges. 2008. Parasites in food webs: the ultimate missing links. Ecology Letters **11**:533-546.

Lafferty, K. D., A. P. Dobson, and A. M. Kuris. 2006. Parasites dominate food web links. Proceedings of the National Academy of Sciences **103**:11211-11216.

Laliberte, A. S., and W. J. Ripple. 2004. Range Contractions of North American Carnivores and Ungulates. BioScience **54**:123-138.

Landi, P., H. O. Minoarivelo, Å. Brännström, C. Hui, and U. Dieckmann. 2018. Complexity and stability of ecological networks: a review of the theory. Population Ecology **60**:319-345.

Lehtinen, K.-J., M. Notini, and L. Landner. 1984. Tissue damage and parasite frequency in flounders, *Platichtys flesus* (L.) chronically exposed to bleached kraft pulp mill effluents. Annales Zoologici Fennici **21**:23-28.

Llaberia-Robledillo, M., J. A. Balbuena, V. Sarabeev, and C. Llopis-Belenguer. 2022. Changes in native and introduced host–parasite networks. Biological Invasions **24**:543-555.

Llopis-Belenguer, C., I. Blasco-Costa, J. A. Balbuena, V. Sarabeev, and D. B. Stouffer. 2020. Native and invasive hosts play different roles in host–parasite networks. Ecography **43**:559-568.

Lula Costa, A. P., J. Bascompte, and A. Andrian Padial. 2023. Modularity in host-parasite mixed networks: interaction configuration shifts based on human perturbation and parasitism form. International Journal for Parasitology **53**:585-594.

MacColl, A. D. C. 2009. Parasite burdens differ between sympatric three-spined stickleback species. Ecography **32**:153-160.

MacKenzie, K., and C. Pert. 2018. Evidence for the decline and possible extinction of a marine parasite species caused by intensive fishing. Fisheries Research **198**:63-65.

Magnusson, A., H. J. Skaug, A. Nielsen, C. W. Berg, K. Kristensen, M. Maechler, K. J. van Bentham, B. M. Bolker, and M. E. Brooks. 2017. glmmTMB: Generalized Linear Mixed Models using Template Model Builder.

McGee, M. D., S. R. Borstein, J. I. Meier, D. A. Marques, S. Mwaiko, A. Taabu, M. A. Kishe, B. O'Meara, R. Bruggmann, L. Excoffier, and O. Seehausen. 2020. The ecological and genomic basis of explosive adaptive radiation. Nature **586**:75-79.

Meier, J., D. A. Marques, S. Mwaiko, C. Wagner, L. Excoffier, and O. Seehausen. 2017. Ancient hybridization fuels rapid cichlid fish adaptive radiations. Nature Communications **8**:14363-14374.

Mey, E. 1990. Eine neue ausgestorbene Vogel-Ischnozere von Neuseeland, *Huiacola extinctus* (Insecta, Phthiraptera. Zoologischer Anzeiger:49-73.

Miranda, P. N., J. E. L. d. S. Ribeiro, P. Luna, I. Brasil, J. H. C. Delabie, and W. Dáttilo. 2019. The dilemma of binary or weighted data in interaction networks. Ecological Complexity **38**:1-10.

Morrison, B. M. L., and R. Dirzo. 2020. Distinct responses of antagonistic and mutualistic networks to agricultural intensification. Ecology **101**:e03116.

Nakagawa, S., and I. C. Cuthill. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. Biological Reviews **82**:591-605.

Newman, M. E. J., and M. Girvan. 2004. Finding and evaluating community structure in networks. Physical Review E **69**:026113.

Ngupula, G. W., and R. Kayanda. 2010. Benthic macrofauna community composition, abundance and distribution in the Tanzanian and Ugandan inshore and offshore waters of Lake Victoria. African Journal of Aquatic Science **35**:185-192.

Ochumba, P. B. O., and D. I. Kibaara. 1989. Observations on blue-green algal blooms in the open waters of Lake Victoria, Kenya. African Journal of Ecology **27**:23-34.

Ogutu-Ohwayo, R. 1990. The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, Lates niloticus, and the Nile tilapia, Oreochromis niloticus. Environmental Biology of Fishes **27**:81-96.

Outa, J. O., Q. M. Dos Santos, A. Avenant-Oldewage, and F. Jirsa. 2021. Parasite diversity of introduced fish Lates niloticus, Oreochromis niloticus and endemic Haplochromis spp. of Lake Victoria, Kenya. Parasitology Research **120**:1583-1592.

Pacifici, M., C. Rondinini, J. R. Rhodes, A. A. Burbidge, A. Cristiano, J. E. M. Watson, J. C. Z. Woinarski, and M. Di Marco. 2020. Global correlates of range contractions and expansions in terrestrial mammals. Nature Communications **11**:2840.

Paperna, I. 1996. Parasites, infections and diseases of fishes in Africa, an update. Food and Agriculture Organization of the United Nations **CIFA Technical Paper**:220.

Petney, T. N., and R. H. Andrews. 1998. Multiparasite communities in animals and humans: frequency, structure and pathogenic significance. International Journal for Parasitology **28**:377-393.

Pielou, E. C. 1977. Mathematical ecology. Wiley, New York.

Pietrock, M., and D. J. Marcogliese. 2003. Free-living endohelminth stages: at the mercy of environmental conditions. Trends in Parasitology **19**:293-299.

Pilosof, S., C. W. Dick, C. Korine, B. D. Patterson, and B. R. Krasnov. 2012. Effects of Anthropogenic Disturbance and Climate on Patterns of Bat Fly Parasitism. PLOS ONE **7**:e41487.

Pimm, S. L. 1984. The complexity and stability of ecosystems. Nature **307**:321-326.

Poulin, R., F. Guilhaumon, H. S. Randhawa, J. L. Luque, and D. Mouillot. 2011. Identifying hotspots of parasite diversity from species–area relationships: host phylogeny versus host ecology. Oikos **120**:740-747.

Pringle, R. M. 2005. The Origins of the Nile Perch in Lake Victoria. BioScience **55**:780-787.

Quinn, J., S. Lee, D. Greeley, A. Gehman, A. M. Kuris, and C. L. Wood. 2021. Long-term change in the parasite burden of shore crabs (Hemigrapsus oregonensis and Hemigrapsus nudus) on the northwestern Pacific coast of North America. Proceedings of the Royal Society B: Biological Sciences **288**:20203036.

R Core Team. 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Raeymaekers, J. A. M., P. I. Hablützel, A. F. Grégoir, J. Bamps, A. K. Roose, M. P. M. Vanhove, M. Van Steenberge, A. Pariselle, T. Huyse, J. Snoeks, and F. A. M. Volckaert. 2013. Contrasting parasite communities among allopatric colour morphs of the Lake Tanganyika cichlid *Tropheus*. BMC Evolutionary Biology **13**:41-57.

Ricklefs, R. E., S. M. Fallon, and E. Bermingham. 2004. Evolutionary Relationships, Cospeciation, and Host Switching in Avian Malaria Parasites. Systematic Biology **53**:111-119.

Rigaud, T., M.-J. Perrot-Minnot, and M. J. F. Brown. 2010. Parasite and host assemblages: embracing the reality will improve our knowledge of parasite transmission and virulence. Proceedings of the Royal Society B: Biological Sciences **277**:3693-3702.

Roche, D. G., B. Leung, E. F. Mendoza Franco, and M. E. Torchin. 2010. Higher parasite richness, abundance and impact in native versus introduced cichlid fishes. International Journal for Parasitology **40**:1525-1530.

Rohr, J. R., A. P. Dobson, P. T. J. Johnson, A. M. Kilpatrick, S. H. Paull, T. R. Raffel, D. Ruiz-Moreno, and M. B. Thomas. 2011. Frontiers in climate change-disease research. Trends in Ecology & Evolution **26**:270-277.

Roux, L. E. l., A. Avenant-Oldewage, and F. C. v. d. Walt. 2011. Aspects of the Ecology of *Cichlidogyrus philander* Collected from *Pseudocrenilabrus philander philander* from the Padda Dam, Gauteng, South Africa. African Zoology **46**:103-116, 114.

Runghen, R., R. Poulin, C. Monlleó-Borrull, and C. Llopis-Belenguer. 2021. Network Analysis: Ten Years Shining Light on Host-Parasite Interactions. Trends in Parasitology **37**:445-455.

Russell, C., T. Casson, C. Sump, K. Luth, M. Zimmermann, N. Negovetich, and G. Esch. 2015. Catastrophic Collapse of the Larval Trematode Component Community in Charlie's Pond (North Carolina). Journal of Parasitology **101**:116-120, 115.

Sakamoto, Y., M. Ishiguro, and G. Kitagawa. 1986. Akaike information criterion statistics., Dordrecht.

Scharsack, J. P., B. Wieczorek, A. Schmidt-Drewello, J. Büscher, F. Franke, A. Moore, A. Branca, A. Witten, M. Stoll, E. Bornberg-Bauer, S. Wicke, and J. Kurtz. 2021. Climate change facilitates a parasite's host exploitation via temperature-mediated immunometabolic processes. Global Change Biology **27**:94-107.

Scholz, T., M. P. M. Vanhove, N. Smit, Z. Jayasundera, and M. Gelnar. 2018. A Guide to the Parasites of African Freshwater Fishes.

Schwarz, G. 1978. Estimating the Dimension of a Model. The Annals of Statistics **6**:461-464, 464.

Sebastián-González, E., B. Dalsgaard, B. Sandel, and P. R. Guimarães Jr. 2015. Macroecological trends in nestedness and modularity of seed-dispersal networks: human impact matters. Global Ecology and Biogeography **24**:293-303.

Seehausen, O. 1996. Lake Victoria Rock Cichlids: taxonomy, ecology and distribution. Verduyn Cichlids, Zevenhuizen, Netherlands.

Seehausen, O. 2006. African cichlid fish: a model system in adaptive radiation research. Proceedings of the Royal Society of London B: Biological Sciences **273**:1987-1998.

Seehausen, O., and N. Bouton. 1998. The community of rock-dwelling cichlids in Lake Victoria. Bonner Zoologische Beiträge **47**:301-311.

Seehausen, O., E. Koetsier, M. Schneider, L. Chapman, C. Chapman, M. Knight, G. Turner, J. J. M. van Alphen, and R. Bills. 2003. Nuclear markers reveal unexpected genetic variation and a Congolese-Nilotic origin of the Lake Victoria cichlid species flock. Proceedings of the Royal Society B: Biological Sciences **270**:129-137.

Seehausen, O., J. J. M. van Alphen, and F. Witte. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. Science **277**.

Shannon, C. E., and W. Weaver. 1949. The Mathematical Theory of Communication. University of Illinois Press.

Shea, J., G. J. Kersten, C. M. Puccia, A. T. Stanton, S. N. Stiso, E. S. Helgeson, and E. J. Back. 2012. The use of parasites as indicators of ecosystem health as compared to insects in freshwater lakes of the Inland Northwest. Ecological Indicators **13**:184-188.

Šimková, A., E. Řehulková, J. R. Rasoloariniaina, M. W. P. Jorissen, T. Scholz, A. Faltýnková, Š. Mašová, and M. P. M. Vanhove. 2019. Transmission of parasites from introduced tilapias: a new threat to endemic Malagasy ichthyofauna. Biological Invasions **21**:803-819.

Simpson, E. H. 1949. Measurement of Diversity. Nature **163**:688-688.

Sitoki, L., J. Gichuki, C. Ezekiel, F. Wanda, O. C. Mkumbo, and B. E. Marshall. 2010. The Environment of Lake Victoria (East Africa): Current Status and Historical Changes. International Review of Hydrobiology **95**:209-223.

Sitoki, L., R. Kurmayer, and E. Rott. 2012. Spatial variation of phytoplankton composition, biovolume, and resulting microcystin concentrations in the Nyanza Gulf (Lake Victoria, Kenya). Hydrobiologia **691**:109-122.

Stager, J. C., and T. C. Johnson. 2008. The late Pleistocene desiccation of Lake Victoria and the origin of its endemic biota. Hydrobiologia **596**:5-16.

Takemoto, K., and M. Iida. 2019. Ecological Networks. Pages 1131-1141 *in* S. Ranganathan, M. Gribskov, K. Nakai, and C. Schönbach, editors. Encyclopedia of Bioinformatics and Computational Biology. Academic Press, Oxford.

Takemoto, K., and K. Kajihara. 2016. Human Impacts and Climate Change Influence Nestedness and Modularity in Food-Web and Mutualistic Networks. PLOS ONE **11**:e0157929.

Thébault, E., and C. Fontaine. 2010. Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. Science **329**:853-856.

Thys, K. J. M., M. P. M. Vanhove, J. W. J. Custers, N. Vranken, M. Van Steenberge, and N. Kmentová. 2022. Co-introduction of Dolicirroplectanum lacustre, a monogenean gill parasite of the invasive Nile perch *Lates niloticus*: intraspecific diversification and mitonuclear discordance in native versus introduced areas. International Journal for Parasitology **52**:775-786.

Vanhove, M. P. M., N. Kmentová, W. J. Luus-Powell, E. C. Netherlands, I. de Buron, and M. A. Barger. 2022. Chapter 15 - A snapshot of parasites in tropical and subtropical freshwater wetlands: modest attention for major players. Pages 417-485 *in* T. Dalu and R. J. Wasserman, editors. Fundamentals of Tropical Freshwater Wetlands. Elsevier.

Vanhove, M. P. M., A. Pariselle, M. Van Steenberge, J. A. Raeymaekers, P. I. Hablützel, C. Gillardin, B. Hellemans, F. C. Breman, S. Koblmüller, C. Sturmbauer, J. Snoeks, F. A. Volckaert, and T. Huyse. 2015. Hidden biodiversity in an ancient lake: phylogenetic congruence between Lake Tanganyika tropheine cichlids and their monogenean flatworm parasites. Scientific reports **5**:13669-13684.

Vanhove, M. P. M., J. O. S. Snoeks, F. A. M. Volckaert, and T. Huyse. 2011. First description of monogenean parasites in Lake Tanganyika: the cichlid *Simochromis diagramma* (Teleostei, Cichlidae) harbours a high diversity of *Gyrodactylus* species (Platyhelminthes, Monogenea). Parasitology **138**:364-380.

Verschuren, D., T. C. Johnson, H. J. Kling, D. N. Edgington, P. R. Leavitt, E. T. Brown, M. R. Talbot, and R. E. Hecky. 2002. History and timing of human impact on Lake Victoria, East Africa. Proceedings. Biological Sciences **269**:289-294.

Wagner, C. E., L. J. Harmon, and O. Seehausen. 2012. Ecological opportunity and sexual selection together predict adaptive radiation. Nature **487**:366-370.

Wagner, C. E., I. Keller, S. Wittwer, O. M. Selz, S. Mwaiko, L. Greuter, A. Sivasundar, and O. Seehausen. 2013. Genome-wide RAD sequence data provide unprecedented resolution of species boundaries and relationships in the Lake Victoria cichlid adaptive radiation. Molecular Ecology **22**:787-798.

Wakwabi, E. O., J. Balirwa, and M. J. Ntiba. 2006. Aquatic biodiversity of Lake Victoria basin. Pages 77-121 *in* O. D. O. O. W. O. Odada E.O., editor. Environment for development : an ecosystems assessment of Lake Victoria basin environmental and socio-economic status, trends and human vulnerabilities. United Nations Environment Programme (UNEP), Pan African START Secretariat (PASS), Nairobi, Kenya.

Wanink, J. H., J. J. Kashindye, P. C. Goudswaard, and F. Witte. 2001. Dwelling at the oxycline: does increased stratification provide a predation refugium for the Lake Victoria sardine *Rastrineobola argentea*? Freshwater Biology **46**:75-85.

Weckstein, J. D. 2004. Biogeography Explains Cophylogenetic Patterns in Toucan Chewing Lice. Systematic Biology **53**:154-164.

Welicky, R. L., W. C. Preisser, K. L. Leslie, N. Mastick, E. Fiorenza, K. P. Maslenikov, L. Tornabene, J. M. Kinsella, and C. L. Wood. 2021. Parasites of the past: 90 years of change in parasitism for English sole. Frontiers in Ecology and the Environment **19**:470-477.

Witte, F., T. Goldschmidt, P. C. Goudswaard, W. Ligtvoet, M. J. P. Van Oijen, and J. H. Wanink. 1992a. Species extinction and concomitant ecological changes in Lake Victoria. Netherlands Journal of Zoology **42**:214-232.

Witte, F., T. Goldschmidt, J. Wanink, M. van Oijen, K. Goudswaard, E. Witte-Maas, and N. Bouton. 1992b. The destruction of an endemic species flock: quantitative data on the decline of the haplochromine cichlids of Lake Victoria. Environmental Biology of Fishes **34**:1-28.

Witte, F., J. H. Wanink, and M. Kishe-Machumu. 2007a. Species Distinction and the Biodiversity Crisis in Lake Victoria. Transactions of the American Fisheries Society **136**.

Witte, F., J. H. Wanink, M. Kishe-Machumu, O. C. Mkumbo, P. C. Goudswaard, and O. Seehausen. 2007c. Differential decline and recovery of haplochromine trophic groups in the Mwanza Gulf of Lake Victoria. Aquatic Ecosystem Health & Management **10**:416-433.

Wood, C. L., and M. P. M. Vanhove. 2022. Is the world wormier than it used to be? We'll never know without natural history collections. Journal of Animal Ecology **n/a**:1-13.

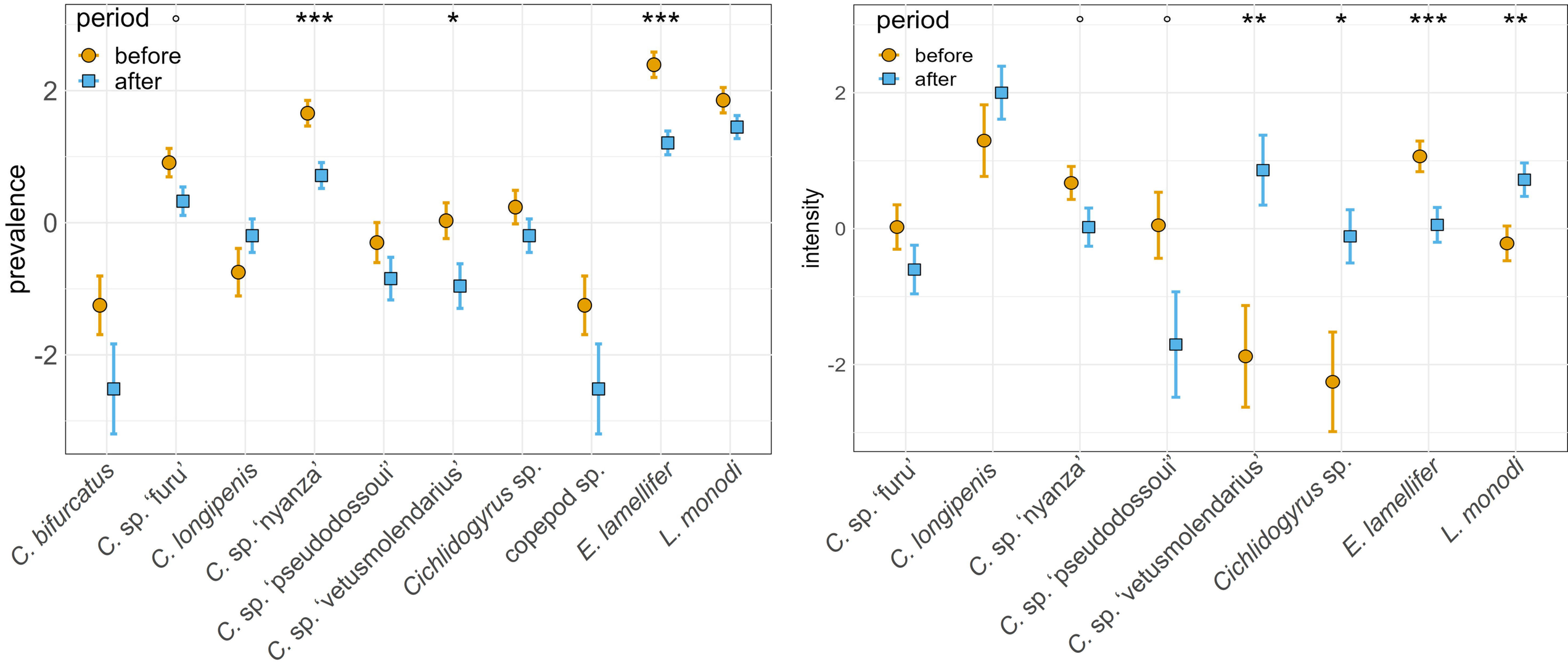
Wood, C. L., R. L. Welicky, W. C. Preisser, K. L. Leslie, N. Mastick, C. Greene, K. P. Maslenikov, L. Tornabene, J. M. Kinsella, and T. E. Essington. 2023. A reconstruction of parasite burden reveals one century of

climate-associated parasite decline. Proceedings of the National Academy of Sciences **120**:e2211903120.

Zahradníčková, P., M. Barson, W. J. Luus-Powell, and I. Přikrylová. 2016. Species of *Gyrodactylus* von Nordmann, 1832 (Platyhelminthes: Monogenea) from cichlids from Zambezi and Limpopo river basins in Zimbabwe and South Africa: evidence for unexplored species richness. Systematic Parasitology **93**:679-700.

Zhi, T., X. Xu, J. Chen, Y. Zheng, S. Zhang, J. Peng, C. L. Brown, and T. Yang. 2018. Expression of immune-related genes of Nile tilapia *Oreochromis niloticus* after *Gyrodactylus cichlidarum* and *Cichlidogyrus sclerosus* infections demonstrating immunosupression in coinfection. Fish & Shellfish Immunology **80**:397-404.

Zuur, A. F., E. N. Ieno, A. A. Saveliev, G. M. Smith, and N. Walker. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York, NY, United States.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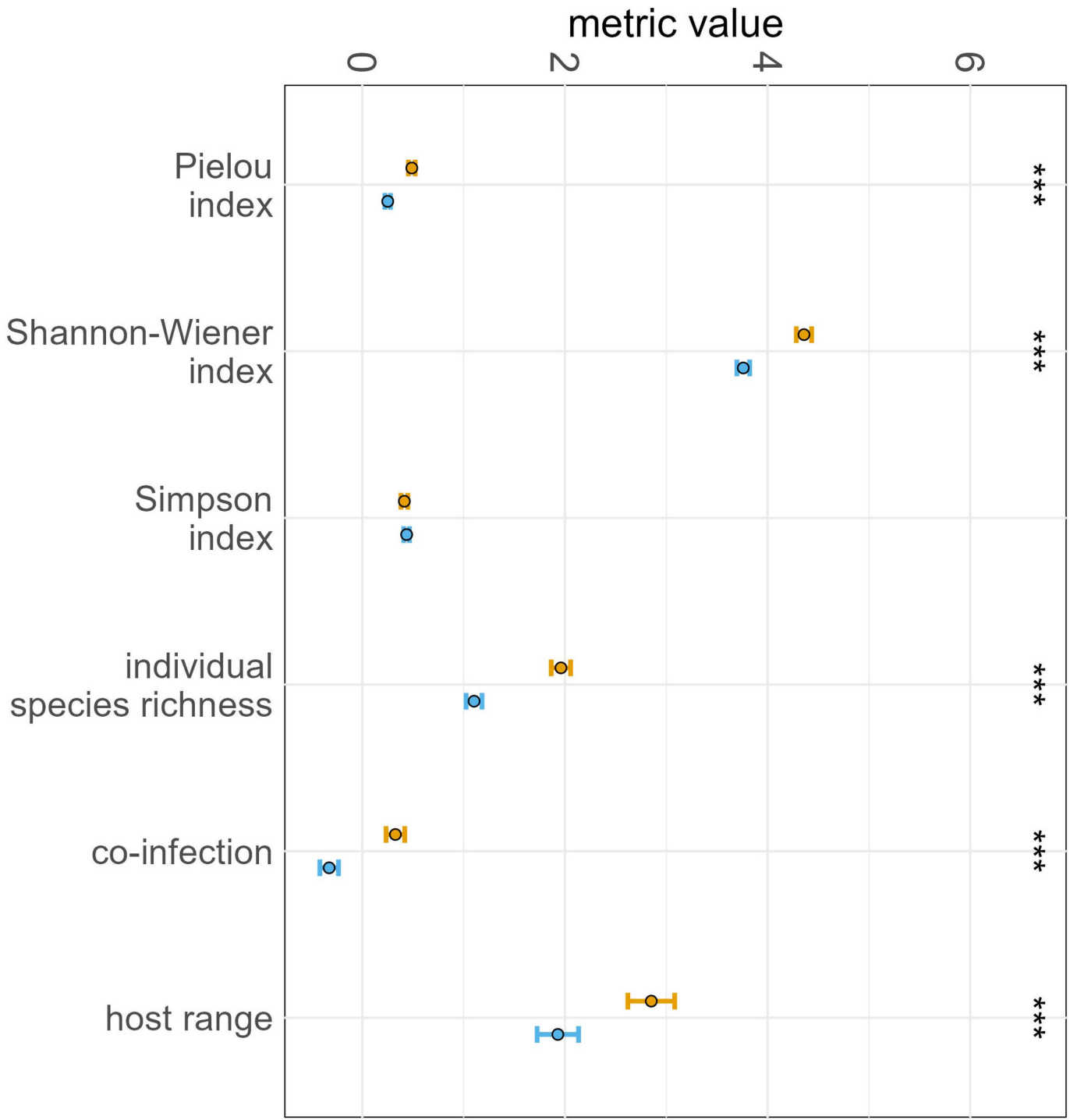
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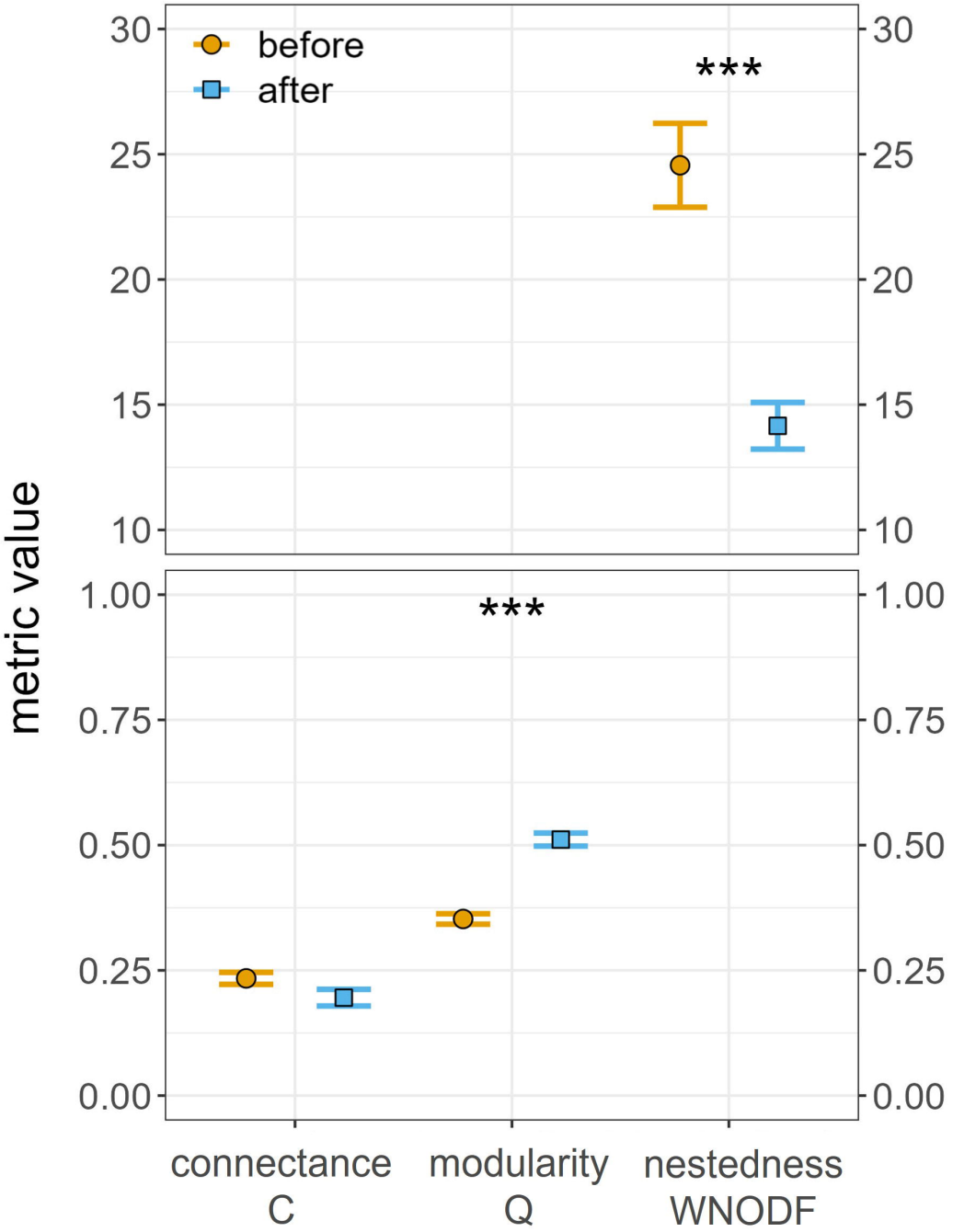
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Table 1 - Host species (Cichlidae: Haplochromini) sampled before and after perturbations in Lake Victoria. N = number of fish individuals; SL = standard length (mm), indicated as mean and range (minimum-maximum).

				SL (mm)	
	Host species	**Trophic group**	**N**	**mean**	**(min-max)**
before perturbations	*Mbipia mbipi*	algivore epilithic	10	76.9	(66.5-83.3)
	Haplochromis obliquidens	algivore epiphitic	10	72.7	(67.8-78.2)
	Haplochromis antleter	detritivore	11	64.4	(59.8-70.2)
	Haplochromis riponianus	insectivore	10	104.3	(91.4-112.9)
	Lithochromis sp. 'yellow chin pseudonigricans'	insectivore	10	79.5	(69.5-86.0)
	Haplochromis chilotes	insectivore	11	93.1	(70.3-110.3)
	Haplochromis sauvagei	insectivore	10	74.6	(57.7-83.4)
	Astatoreochromis alluaudi	molluscivore	18	70.8	(48.9-129.0)
	Haplochromis ishmaeli	molluscivore	10	107.6	(94.8-121.5)
	Haplochromis xenognathus	molluscivore	10	78.9	(59.0-100.5)
	Haplochromis spekii	piscivore	11	176	(144.9-191.4)
	Pundamilia nyererei	planktivore	11	61.9	(50.0-70.0)
	Haplochromis pyrrhocephalus	zooplanktivore	10	71.4	(66.0-78.8)
after perturbations	*Mbipia mbipi*	algivore epilithic	20	92.5	(73.9-113.2)
	Haplochromis obliquidens	algivore epiphitic	10	68.3	(59.7-104.1)
	Haplochromis antleter	detritivore	10	55.2	(47.6-61.7)
	Haplochromis riponianus	insectivore	10	90.2	(76.6-101.5)
	Lithochromis sp. 'yellow chin pseudonigricans'	insectivore	10	92.1	(79.7-113.0)
	Haplochromis chilotes	insectivore	20	102.4	(65.9-126.5)
	Haplochromis sauvagei	insectivore	22	102.8	(88.0-115.4)
	Astatoreochromis alluaudi	molluscivore	21	94.3	(48.2-133.7)
	Haplochromis ishmaeli	molluscivore	15	79.1	(0.0-112.9)
	Haplochromis xenognathus	molluscivore	11	105.3	(80.8-115.4)
	Haplochromis spekii	piscivore	4	145.3	(130.8-170.7)
	Pundamilia nyererei	planktivore	15	83.9	(74.2-106.7)
	Haplochromis pyrrhocephalus	zooplanktivore	30	49.9	(41.7-58.7)

Figure 1 - Infection prevalence **(a)** and intensity **(b)** ±SE were higher before (orange points) than after (blue squares) perturbations in Lake Victoria, overall and for some parasite species (significance level ° 0.1, * 0.05, ** 0.01 *** 0.001). Only one parasite species (*Cichlidogyrus longipenis*) increased in prevalence, and two others (*C.* sp. 'vetusmolendarius'*, Lamproglena monodi*) increased in intensity.

Figure 2 - Infection prevalence, diversity metrics (Pielou's evenness index, Shannon-Wiener index, individual species richness), occurrence of co-infections and host range (number of host species exploited by a given parasite species) decreased after perturbations in Lake Victoria. As an exception, the Simpson index did not change. Orange points: before perturbations, blue squares: after perturbations. ±SE

Figure 3 - After perturbations, modularity (Q) increased whereas nestedness (WNODF) decreased in the host-gill parasite network. Connectance (C) did not change. Modularity and nestedness were standardized based on null.swap algorithm. Orange points: before perturbations, blue squares: after perturbations. ±SE.

Figure S1 - Relative occurrence of each parasite taxon infecting haplochromines hosts before and after perturbations in Lake Victoria.

Table 1 - Host species (Cichlidae: Haplochromini) sampled before and after perturbations in Lake Victoria. N = number of fish individuals; SL = standard length (mm), indicated as mean and range (minimum-maximum).

Table S1 - Infection prevalence and intensity overall and for each parasite species, before and after perturbations in Lake Victoria. *Cichlidogyrus* spp. are specimens of *Cichlidogyrus* that were not suitable for identification to species level, but there is no reason to assume these represent additional different species. $\chi 2$: Chi square for overall comparison, z: z-ratio for parasite species comparisons.

Table S2 - Infection diversity measures (individual species richness, Pielou's evenness index, Shannon-Wiener index overall and for each host species. Simpson index not shown because it did not change after perturbations. $\chi 2$: Chi square for overall comparison, z: z-ratio for host species comparisons.

Table S3 - Comparison of Jaccard index and Bray-Curtis distances before and after perturbations within host species. Bray-Curtis distances differed in nine host species, whereas Jaccard index differed in three host species.