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The role of phylogeny, ecological opportunity, and adaptive radiation in host-parasite interactions: network metrics, host repertoire, and network link prediction

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Abstract

Many species-rich ecological communities result from adaptive radiation events. The effects of these explosive speciation events on community assembly remain poorly understood. Here, we explore the well-documented radiations of African cichlid fishes and interactions with their flatworm gill parasites (*Cichlidogyrus* spp.) including 10529 reported infections and 477 different host-parasite combinations collected through a survey of peer-reviewed literature. We assess the evolutionary, ecological, and morphological parameters on meta-communities partially affected by adaptive radiation events using network metrics, host repertoire measures, and network link prediction (NLP). The hosts' evolutionary history mostly determined host repertoires. Ecological and evolutionary parameters predicted host-parasite associations, but many interactions remain undetected according to NLP. Parasite meta-communities under host adaptive radiation are more specialised and stable while ecological opportunity and ecological fitting have shaped interactions elsewhere. The cichlid-*Cichlidogyrus* network is a suitable eco-evolutionary study system but future studies should validate our findings in other radiating host-parasite systems.

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Statement of authorship

AJCL conceptualised the study and conducted the literature survey. AJCL performed all analyses and produced tables and graphs. AJCL produced host phylogenies with input from SK. AJCL and MPMV wrote the manuscript with input from TA, SK, AP, KS, and MVS.

Conflict of interest

The authors declare that they have no conflict of interest.

Data accessibility statement

Species interaction, host ecological, and community membership data as well as DNA sequence alignments underlying this article are available in Zenodo at www.zenodo.org, at <https://dx.doi.org/10.5281/zenodo.4075171>. Abstract

Many species-rich ecological communities result from adaptive radiation events. The effects of these explosive speciation events on community assembly remain poorly understood. Here, we explore the well-documented radiations of African cichlid fishes and interactions with their flatworm gill parasites (*Cichlidogyrus* spp.) including 10529 reported infections and 477 different host-parasite combinations collected through a survey of peer-reviewed literature. We assess the evolutionary, ecological, and morphological parameters on meta-communities partially affected by adaptive radiation events using network metrics, host repertoire measures, and network link prediction (NLP). The hosts' evolutionary history mostly determined host repertoires. Ecological and evolutionary parameters predicted host-parasite associations, but many interactions remain undetected according to NLP. Parasite meta-communities under host adaptive radiation are more specialised

and stable while ecological opportunity and ecological fitting have shaped interactions elsewhere. The cichlid-*Cichlidogyrus* network is a suitable eco-evolutionary study system but future studies should validate our findings in other radiating host-parasite systems.

Graphical Abstract

Many species-rich ecological communities result from adaptive radiation events. Here, we investigate interactions of African cichlids and their flatworm parasites belonging to *Cichlidogyrus* (a) through network analyses (b), host repertoire estimation, and network link prediction (heatmaps) (c). The hosts' evolutionary history and environment determine observed host repertoires and network structure (b). Cichlid radiations in Eastern Africa have formed more specialised meta-communities (c).

Introduction

Evolutionary processes are a major factor in how ecological communities are formed (Toju *et al.* 2017) at both the ancient (Algar *et al.* 2009) and recent (Fussmann *et al.* 2007) timescale. Many species-rich communities are the result of adaptive radiations (Glor 2010), a form of explosive species formation. Adaptive radiation stem from ecological opportunity arising from a great variety of newly available ecological niches (Losos 2010). This mechanism has produced several diverse and well-known species flocks including Darwin's finches (Petren *et al.* 2005), Caribbean anole lizards (Losos 2009), and cichlid fishes (Salzburger *et al.* 2014). Despite this species diversity, ecological research has focused mostly on the feeding ecology of radiating lineages (e.g. Guerrero & Tye 2009; Takahashi & Koblmüller 2011) with few studies investigating parasitic (e.g. Karvonen & Seehausen 2012) or mutualistic interactions (e.g. Litsios *et al.* 2012).

Metazoan parasites can be of particular interest in this context due to their intimate associations that profoundly affect host fitness (Kutzer & Armitage 2016) and shape biological communities (Gómez & Nichols 2013). For instance, host range, a key characteristic of parasite ecology (Poulin *et al.* 2011), is influenced by environmental factors as well as the hosts' evolutionary history (Poulin *et al.* 2011). Integrative measures account for host ecology as well as evolutionary history (Clark & Clegg 2017), e.g. functional-phylogenetic distance metrics (FPDist) (Cadotte *et al.* 2013). However, the frequency of recorded host switches (see Agosta *et al.* 2010) suggests that such metrics fail to fully grasp the niche limitations of parasites. Host repertoires observed today have likely resulted from alternating phases of host range expansions and isolation (*oscillation hypothesis*) (Janz & Nylin 2008). Parasites expand their host range through their capacity to access novel resources (*ecological fitting*) (Agosta *et al.* 2010), i.e. host species, and through the opportunity emerging from the rise and fall of ecological barriers (D'Bastiani *et al.* 2020), e.g. after anthropogenic introductions (Brooks *et al.* 2021). Therefore, *realised host repertoires* do not equate to the full repertoires of host species that can potentially be infected (*fundamental host repertoires*) (Braga *et al.* 2020). The oscillation of host repertoires resulting from ecological fitting and opportunity has been termed the *Stockholm Paradigm* (Brooks *et al.* 2019) and is considered a major source of parasite biodiversity (Agosta & Brooks 2020).

One of the aspects highlighted by the *Stockholm paradigm* is the potential of predicting future host-parasite interactions in the context of emerging parasitic diseases. Understanding the mechanisms behind these diseases is increasingly relevant in a world where environmental degradation promotes host switches between previously unconnected hosts (Brooks *et al.* 2019). Host switches may present threats to human health and food security (Fitzpatrick 2013; Jenkins *et al.* 2015; Ekroth *et al.* 2019; Brooks *et al.* 2021). To understand parasitic interactions (Bogich *et al.* 2013; Bordes *et al.* 2017), ecological research has put forward network theory (Poulin 2010) through which species are represented as discrete interacting units, e.g. in plant-pollinator (Soares *et al.* 2017; Vizentin-Bugoni *et al.* 2018), predator-prey (Allesina & Pascual 2008), and plant-mycorrhiza systems (Simard *et al.* 2012). Ecologists widely employ network analyses to characterise and visualise species interactions (Pocock *et al.* 2016). Furthermore, increasing computational capacities have promoted the use of network link prediction (NLP) algorithms to model undetected interactions. These methods originating in social network studies (Wang *et al.* 2015), have lately been optimised for biological systems (Martínez *et al.* 2016) including ecological networks (Dallas *et al.* 2017; Zhao *et al.* 2017; Fu *et al.* 2019). Few recent studies on the *Stockholm paradigm* have integrated network analyses (but see D'Bastiani

et al. 2020; Braga *et al.* 2021). Instead, the focus has remained on inferring ancestral host-parasite interactions (Braga *et al.* 2020, 2021) rather than predicting undetected links. The distinction between undetected and unrealised links remains a major hurdle for network studies as observed interactions will often present an underestimation of the real interaction diversity (Fu *et al.* 2019). Furthermore, previous studies (Braga *et al.* 2020, 2021) treated interactions as discrete states, e.g. as non-hosts, potential hosts, and real hosts, despite the literature on network analyses substantiating that some host-parasite interactions are more prevalent than others (Blüthgen *et al.* 2008; Poulin *et al.* 2011). Many of the metrics describing the structure of species networks, such as nestedness, connectance, and specialisation, have been optimised to account for interaction strength, i.e. the frequency of interactions (see Blüthgen *et al.* 2008). Undetected links and interaction strengths could be addressed through NLP as the algorithms account for both of these issues (Dallas *et al.* 2017; Fu *et al.* 2019).

Here, we investigate host-parasite networks of multiple host lineages evolved through adaptive radiation using network theory and NLP. As model system, we selected one of the best-known examples for explosive speciation: African cichlid fishes. The approximately 2000 species residing in the East African Great Lakes are the result of multiple adaptive radiation events (Salzburger *et al.* 2014). Cichlid science has been at the forefront of evolutionary (e.g. Salzburger 2018; Ronco *et al.* 2021) and behavioural (see Koblmüller *et al.* 2019) research. Outside of feeding behaviour (e.g. Cooper *et al.* 2010; Hulseley *et al.* 2019), and fish-fish (e.g. Blažek *et al.* 2018; Marshall 2018) and human-fish interactions (Irvine *et al.* 2019), studies on interactions of cichlids with non-cichlid organisms have focused mostly on parasitic interactions (Cruz-Laufer *et al.* 2021a). One parasite lineage infecting African cichlids, monogenean flatworms belonging to *Cichlidogyrus* Paperna, 1960 sensu Wu *et al.* (2007) (including *Scutogyrus* Pariselle & Euzet, 1995), is particularly species-rich. Currently, 143 species are described that infect the gills of 139 cichlid and five non-cichlid species (see Cruz-Laufer *et al.* 2021a). Monogenean parasites of cichlids were proposed as model system for host-parasite interaction studies (Pariselle *et al.* 2003; Vanhove *et al.* 2016) (Fig. 1).

We explore cichlid-*Cichlidogyrus* interactions comparing meta-communities of the African Great Lakes that are strongly shaped by adaptive radiation events to those outside these lakes. First, we use network metrics to characterise the structure of the observed networks and meta-communities. Second, we assess host repertoires considering both functional and phylogenetic host diversity (Poulin *et al.* 2011; Esser *et al.* 2016) and discuss the limitations of this traditional approach to host repertoires. Third, we assess the performance of two recently proposed NLP models for predicting host-parasite interactions. We aim to address the following questions on the ecology and evolution of parasites using the cichlid-*Cichlidogyrus* network as a model system: (i) Do observed host repertoires correlate with functional or phylogenetic host diversity, (ii) what can network link prediction models reveal about predictors of these interactions, (iii) how are cichlid-*Cichlidogyrus* meta-communities structured when hosts evolve through adaptive radiation?

Materials & methods

Data assembly: Infection data, niche modelling, phylogenies

We assembled infection data through a survey of peer-reviewed literature. This survey resulted in an updated version (Supporting Information) of the list published by Cruz-Laufer *et al.* (2021a). For abundance weighting, we also assembled infection parameters including the number of examined hosts, infected hosts, and parasites. Yet if no infection parameters were reported (59% of reports, 61% of interaction), we considered these reports singular observations to take them into account but minimise their impact on downstream analyses (eventually constituting 9.6% of infections).

We built host niche dendrograms based on ecological, geographical, and morphological data (Table 1) accessed on FishBase (Froese & Pauly 2000) through the *R* package *rfishbase* (Boettiger *et al.* 2012). Missing trophic level and habitat data were added through a literature survey (see Supporting Information). Dendrograms were built through hierarchical clustering in *R* (Pavoine *et al.* 2009) based on a Gower's distance matrix (Gower 1971). Gower's distances were calculated using the function *dist.ktab* in the *R* package *ade4* v1.7.16 (Pavoine *et al.* 2009). As in Clark & Clegg (2017), we accounted for uncertainty of the host niche by applying

several clustering algorithms implemented in the function *hclust* in *R* (incl. *ward.D2* , *single* , *complete* , *average* , *mcquitty* , *median* , and *centroid*) (R Core Team 2022). We tested for topological congruence of the resulting dendrograms using the congruence among distance matrices (CADM) test (Legendre & Lapointe 2004; Campbell *et al.* 2011) in the package *ape* v5.4 (Paradis & Schliep 2019).

As no previous phylogenetic study covers all the species known to host members of *Cichlidogyrus* , we conducted a new analysis (see Appendix S1.1) based on DNA sequence data accessed on GenBank (Appendix S2) to infer phylogenetic distances between hosts. For the parasites, we included morphometric and phylogenetic data from Cruz-Laufer *et al.* (2021b), i.e. morphological measurements and 100 randomly sampled Bayesian tree topologies from the post-burn in fraction.

Network metrics and meta-community structure

The infection data assembled here originate from different ecosystems. Therefore, we considered all communities inferred from these data as meta-communities of cichlids and species of *Cichlidogyrus* . To investigate the effects of adaptive radiation, we compared the meta-communities of species infecting hosts from Lake Tanganyika (LT) and the region inhabited by the Lake Victoria superflock (LV) (see Verheyen *et al.* 2003) with the whole cichlid-*Cichlidogyrus* network. We also inferred meta-communities through the Louvain community detection algorithm, an approach based on optimisation of network modularity (see Blondel *et al.* 2008) implemented in the *R* package *igraph* v1.2.6 (Csardi & Nepusz 2006). The algorithm was applied to the entire (natural and invasive) documented host ranges with hosts and parasites treated equally as nodes. To characterise meta-community structure, we inferred several network metrics that are widely applied to weighted links, including the weighted nestedness based on overlap and decreasing fill (NODF_w) (Almeida-Neto & Ulrich 2011), weighted connectance (C_w) (Bersier *et al.* 2002), specialisation asymmetry (SA) (Blüthgen *et al.* 2007), interaction evenness (E_i) (Bersier *et al.* 2002), and the standardised interaction diversity (H_2') (Blüthgen *et al.* 2006) using *R* package *bipartite* v2.15 (Dormann *et al.* 2008, 2009; Dormann 2011).

We calculated network metrics for meta-communities including more than 10 species (Fig. 2) both for the natural ranges and the full realised host repertoire and geographical distribution (including the result of anthropogenic translocations). To correct for varying sampling intensity, we produced two null distributions (NM): Patefield's algorithm (Patefield 1981), which randomly redistributes rows and columns of the interaction matrix (NM₁) and the redistribution algorithm proposed by Vázquez *et al.* (2007) (NM₂), which maintains the network connectance, i.e. only realised interactions are redistributed. We generated 1000 null matrices through the function *nullmodel* in *bipartite* and assessed significance as proportion of null estimates greater than the observed estimates.

Host repertoire

We investigated the effects of host environment and phylogeny on the host repertoire of the parasites. Host repertoires were quantified as mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) of host species to investigate ancient and recent evolutionary relationships respectively (Clark & Clegg 2017). We calculate MPD and MNTD from functional-phylogenetic distance (FPDist) matrices. These matrices are derived from functional (FDist) and phylogenetic (PDist) distance matrices of the host species infected by each parasite species. We inferred the FDist matrices from the host niche dendrograms and the PDist matrices from the host phylogenetic trees and scaled the matrices by dividing the values through the respective maximum distance. We accounted for uncertainty in the host niche/tree topology by drawing random samples of dendrograms/trees every time we calculated $FPDist = (aPDist^p + (1 - a)FDist^p)^{1/p}$ (Cadotte *et al.* 2013) with $p = 2$ to calculate Euclidean distances (see Cadotte *et al.* 2013; Burbrink *et al.* 2017; Clark & Clegg 2017). Finally, we applied 100 incremental increases from 0 to 1 to the weighting parameter a . We calculated FPDist through the function *FPDist* in the *R* package *funphylocom* v1.1 (Walker 2014). For the null model (NM₃), we generated null distributions by randomly redistributing the labels of the FPDist matrices resulting from 1000 random draws from FDist and PDist matrices. We calculated MPD, MNTD, and 1000 null estimates through the functions *mpd* , *mntd* , and *taxaShuffle* in the *R* package *picante* v1.8.2 (Kembel *et al.*

2010). For interpretation of the FPDist plots, we followed Cadotte *et al.* (2013).

Network link prediction

We applied the following network link prediction (NLP) algorithms:

The *plug-and-play* algorithm (Dallas *et al.* 2017) predicts missing links based on conditional probability estimation and was developed to infer the probabilities of unobserved links being undetected through sets of input parameters.

The *Poisson N-mixture* link prediction model (Fu *et al.* 2019) combines the Poisson N-mixture model used in ecological research with a low-rank collaborative filtering approach. Poisson N-mixture models are used in ecological research to account for imperfect detection in field observations (Royle 2004). Meanwhile, low-rank matrix completion-based collaborative filtering methods are a popular approach for NLP in social network studies. Missing entries in a data matrix are completed based on a low number of known entries (low rank matrix), e.g. to predict consumer preferences (Candes & Plan 2010).

We provided ecological, morphological, and phylogenetic input parameters to these models (Table 1). Both models do currently not account for phylogenetic uncertainty. Therefore, we included only the majority-rule consensus host and parasite BI phylogenies and the *ward.d2* dendrograms (Murtagh & Legendre 2014), one of the most widely used clustering algorithms (Murtagh & Legendre 2014). To avoid overfitting, we reduced the number of input variables per parameter through principal coordinate analyses (PCoA) of the distance matrices of each parameter resulting in 9 input parameters consisting of 24 variables (Table 1). Distance matrices were computed through the *cophenetic* function in *R* applied to dendrograms that were built for each parameter separately through the clustering methods also employed for the host niche dendrograms. We imputed missing data through a k-nearest neighbour algorithm (kNN) in the *R* package *caret* (Kuhn 2008, 2020).

We assess model performance through the Area Under the Receiver Operating Characteristic curve (AU-ROC) and 10-fold cross validation. Each time, the algorithms were trained on 80% of the interaction matrix to predict the remaining 20%. We implemented the models in *Rv4.1.2* (R Core Team 2022) and *MATLAB* v9.11.0 (MathWorks, Natick, USA) using published codes (doi: 10.6084/m9.figshare.4965038; <https://github.com/Hutchinson-Lab/Poisson-N-mixture>). Following Dallas *et al.* (2017), we assessed variable importance of the *plug-and-play* algorithm by measuring the reduction in model performance resulting from 500-fold permutation of each parameter. For variable importances and link prediction, the algorithm was trained on the full dataset. These analyses were not performed for the *Poisson N-mixture* model due to lacking implementation.

Graphing

We plotted the species network through the *R* package *igraph* v1.2.6 (Csardi & Nepusz 2006), chord diagrams through *circlize* v0.4.13 (Gu *et al.* 2014), dendrograms and phylogenetic trees through *ggplot2* v3.3.5 (Wickham 2016) and *ggtree* v3.2.1 (Yu *et al.* 2017, 2018), and heatmaps in *ComplexHeatmap* v2.10.0 (Gu *et al.* 2016).

Results

Data assembly

Across their natural and anthropogenically expanded host and geographical ranges, we found reports of 10529 infected host specimens and 477 different host-parasite interactions in 183 publications. The resulting species network comprises 144 host and 143 parasite species (including species not officially described yet, i.e. cheironyms). We assembled environmental and morphometric data for 133 and DNA sequence data for 117 host species (Appendix S1.1). Niche dendrograms resulting from the clustering algorithms (Appendix S3) were congruent (CADM, Kendall's $W = 0.66$, $\chi^2 = 34944$, $p < 0.01$). The BI host tree topology showed no deviation from recent phylogenetic hypotheses likely to affect downstream analyses (see discussion in Appendix S1.1).

Network metrics and community structure

We identified 42 meta-communities in the cichlid-*Cichlidogyrus* network through the Louvain algorithm. Several detected meta-communities that included only few species and were completely unconnected to the other communities formed part of *LT* (Fig. 2a). Four meta-communities other than *LT* and *LV* (Fig. 2b) included 10 or more species (Fig. 2c; Appendix S4): the ‘*Coptodon zillii*’ (*CZ*), ‘*Oreochromis niloticus*’ (*ON*), ‘*Hemichromis*’ (*He*), and ‘*Tilapia sparrmanii*’ (*TS*) clusters. These names reflect the host taxa accounting for a majority of reported infections (Appendix S1.2). Network structure differed between meta-communities but anthropogenic introductions had only a limited effect (Fig. 3; Appendix S1.2).

Host repertoire

Functional-phylogenetic distances (FPDist) were calculated for all species of *Cichlidogyrus* with more than one host species (Appendix S5) with the weighting parameter a between 0 and 1. Plots for some species are shown in Fig. 4 to illustrate main patterns observed throughout the lineage. Generally, FPDist decreased with increasing phylogenetic weight (MPD or MNTD) as indicated by the falling trend of FPDist estimates (Fig. 4). Observed MPD and MNTD showed a significant pattern of underdispersion (clustering) compared to 1000 random simulations in some cases. Specifically, MPD metrics of FPDist became mostly significant if the weight of phylogenetic distances (PDist) increased (i.e. $a - 1$) (Fig. 4). In contrast, MNTD estimates were largely non-informative regardless of a . One exception is *Cichlidogyrus* sp. ‘nyanza’ (Gobbin *et al.* 2021) with MNTD estimates being lowest for $a - 0$ (Fig. 4).

Network link prediction

Overall, the NLP algorithm performed solidly (*plug-and-play* : mean AUROC = 0.72, full model AUROC = 0.85; *Poisson N-mixture* : mean AUROC = 0.62) despite missing data (Fig. 5a). Several input parameters improved performance of the *plug-and-play* algorithm significantly (Fig. 5c) including the basin/basin type, host phylogenies, trophic level, and life style whereas the parameters for parasite morphology and phylogeny decreased the performance. A substantial amount of species interactions remains undetected, albeit less for *LT* and *LV* (Fig. 5b; Appendix S6). For *LV*, model performances were slightly better (0.78, 0.87; 0.76) but with the host phylogeny as the most important predictor. For *LT*, the models showed little discriminatory power (0.41, 0.87; 0.62).

Discussion

We investigated the patterns of host-parasite interaction of African cichlid fishes and their gill parasites belonging to *Cichlidogyrus*, a proposed model system for macroevolutionary research (Pariselle *et al.* 2003; Vanhove *et al.* 2016). This study is the first to empirically investigate the effects of adaptive radiation events on species interactions [but see Maynard *et al.* (2018) for simulations]. The size of this species network (10529 infections, 477 interactions) is comparable to widely used host-parasite datasets in terms of species richness, e.g. the Global Mammal Parasite Database (GMPD) (Nunn & Altizer 2005), the Sevillata interaction network (Dallas & Presley 2014), and other fish-parasite (Lima Jr *et al.* 2012; Bellay *et al.* 2015) and plant-arthropod systems (Lopez-Carretero *et al.* 2014; de Araujo *et al.* 2020; Oliveira *et al.* 2020; de Araujo & Maia 2021). The system is also the first to encompass closely related parasite species infecting a host system that is a model for speciation research (Seehausen 2006). Therefore, our dataset could be an asset for comparative studies in network ecology and ecological parasitology.

Host repertoire: Host evolution shapes community structure

We inferred two main predictors of cichlid-*Cichlidogyrus* interactions: host phylogenetic relationships and host environment. The hosts’ evolutionary history can have a significant impact on the structure of host-parasite networks (e.g. Mouillot *et al.* 2008a; Braga *et al.* 2014, 2020). Here, we show that the realised host repertoire of most species of *Cichlidogyrus* is determined more by the hosts’ evolutionary history than their environment. First, host repertoires differed more regarding the ecological niche than the phylogenetic relationships as evidenced by a reduction of the mean functional-phylogenetic distances (FPDist) with increasing phylogenetic weight (Fig. 4). Second, FPDist estimates rarely differed from the null distribution for increasing functional

weight (but see *C. sp.* ‘nyanza’; Fig. 4). Third, estimates outside the null distribution were underdispersed (clustered), i.e. lower than expected at random at both the ancient and recent evolutionary scale (measured as MPD and MNTD respectively). The strong phylogenetic influence and underdispersion are associated with co-divergent evolution (Clark & Clegg 2017). Co-divergence assumes that host and parasite phylogenies are phylogenetically congruent (Page 2003; Hoyal Cuthill & Charleston 2012), a pattern that has already been observed for a number of species of *Cichlidogyrus* (Vanhove *et al.* 2015). Congruence might arise especially in younger parasite lineages that have experienced a phase of isolation resulting in co-divergence (Agosta & Brooks 2020), e.g. species of *Cichlidogyrus* infecting tropheine cichlids (Vanhove *et al.* 2015), which arose 4.5–6.5 MYA (Schedel *et al.* 2019).

Additionally, phylogenetic tracking might explain the role of the host phylogeny on host repertoires. Even within the same ecosystem, parasites are constrained to compatible ecological niches created by host speciation (Russo *et al.* 2018). Consequently, phylogenetic relationships are determinants of neotropical (Braga *et al.* 2014) and Mediterranean (Desdevises *et al.* 2002) monogenean-fish communities but also plant-pollinator, plant-frugivore (Rezende *et al.* 2007), plant-mycorrhiza (Jacquemyn *et al.* 2011), and other host-parasite networks (Mouillot *et al.* 2008). Yet natural (Birgi & Euzet 1983; Birgi & Lambert 1986) and invasion-induced (Jimenez-Garcia *et al.* 2001; Šimková *et al.* 2019; Jorissen *et al.* 2020) host switches of species of *Cichlidogyrus* highlight that fundamental host repertoires might differ considerably from the realised host repertoires estimated here. Monogeneans have the capacity to infect new hosts and adapt to new environments (Braga *et al.* 2014; Messu Mandeng *et al.* 2015; Nack *et al.* 2016). Thus, conclusions drawn based solely on analyses of host repertoires should be treated with caution.

Network link prediction: Ecological factors shape community structure

Despite the uncertainty in the host repertoires, network link prediction (NLP) models confirmed the influence of the hosts’ evolutionary history on fish-monogenean community structure. The host phylogeny contributed considerably to the performance of the *plug-and-play* algorithm. However, host-parasite links appear to be mostly predicted by ecological parameters as the basin/basin type-parameter (Table 1) contributed the most (Fig. 5c). Therefore, ecological opportunity might play a major role in the assembly of cichlid-*Cichlidogyrus* communities similar to neotropical teleost-monogenean communities (Braga *et al.* 2014), and these opportunities are predicted by host presence in rivers and lakes.

The uncovered significance of opportunity is highly relevant for aquaculture and fish conservation efforts. This study is the first to quantify host-pathogen interactions in tilapias, Nile tilapia (*Oreochromis niloticus* L.) being one of the most widely farmed fish worldwide (FAO 2019). Introductions of infectious diseases can have devastating effects on native ecosystems (Thompson 2013). Concerning tilapia, co-introductions of the tilapia-lake virus have caused significant economic losses (Eyngor *et al.* 2014; Fathi *et al.* 2017). Moreover, introductions of tilapias have led to co-introductions of their monogenean parasites in continental Africa (Jorissen *et al.* 2020), Madagascar (Šimková *et al.* 2019), Asia (Paperna 1960; Duncan 1973; Wu *et al.* 2006), Australia (Wilson *et al.* 2019), and the Americas (Jiménez-García *et al.* 2001; Azevedo *et al.* 2006), with occasional spillover to native fishes (Jiménez-García *et al.* 2001; Šimková *et al.* 2019), albeit with little changes to the respective meta-community structures (Fig. 3). Our results suggest that anthropogenic introductions might promote further host switches in the future. In this context, network predictions could present key tools for understanding and possibly minimising the risk of emerging diseases (Albery *et al.* 2021).

Our results underline that NLP can verify traditional statistical analyses and provide further insight into ecological and evolutionary mechanisms shaping host-parasite interactions. For instance, we inferred that life style, trophic level, and host size are among the more informative predictors of cichlid-*Cichlidogyrus* interactions whereas parasite phylogenetic relationships and morphological parameters mostly failed to improve model performance (Fig. 5b). Therefore, host switches might more likely occur between ecologically similar hosts and emerging diseases in aquaculture could be avoided through culturing native fishes (Ju *et al.* 2020; Nobile *et al.* 2020). Previous studies on fish parasites have delivered inconclusive results for the role of host and parasite traits on host-parasite community composition. No studies investigated the effects of *life style* as coded here (Table 1), but host habitat preference can affect parasite communities (Locke

et al. 2013). Parasite community composition correlated with the host *trophic level* in some cases, e.g. for shelf fish off Buenos Aires (Timi *et al.* 2011), but not in others, e.g. for freshwater fish in Canada (Locke *et al.* 2013) and marine fish in Finland (Locke *et al.* 2014). *Host size* was suggested as important predictor for the community composition of ectoparasitic monogeneans (Guégan *et al.* 1992; Sasal & Morand 1998; Sasal *et al.* 1999; Šimková *et al.* 2001; Desdevises *et al.* 2002; Morand *et al.* 2002). However, these correlations might reflect phylogenetic patterns of host size (Poulin 2002) explaining the variable importance of host size here. Lastly, no correlation of *attachment* or *reproductive organ morphology* with community composition was found for species of *Cichlidogyrus* unlike for species of *Dactylogyrus* (Šimková *et al.* 2001; Jarkovský *et al.* 2004). Instead, the morphology mostly reflects phylogenetic relationships of the parasites (Vignon *et al.* 2011; Cruz-Laufer *et al.* 2021b). The results of these studies highlight the challenge of linking host and parasite traits with community composition parameters and generalising observed patterns as sampling biases (Fründ *et al.* 2016) (Fig. 5a) and character coding (Pavoine *et al.* 2009) influence the results. NLP provides an accessible path to start uncovering the role of various parameters (Fig. 5c) and predicting undetected interactions (Fig. 5b).

The East African lakes: specialised and saturated communities?

Explosive speciation in cichlids has resulted in distinctively structured cichlid-*Cichlidogyrus* communities in Eastern Africa. Meta-communities in Lake Tanganyika (*LT*) and the Lake Victoria region (*LV*) are more specialised, and less nested and connected than those inferred for species elsewhere (Fig. 3; Appendix S1). Few additional interactions were predicted (Fig. 5b) suggesting that most are already known for the sampled species. This saturation of interactions might be expected as new ecological opportunities, an important determinant of interactions at the global scale, arise less in comparatively stable lake ecosystems such as *LT* (Salzburger *et al.* 2014). Newcomers to these systems might find little opportunity to radiate (e.g. Koch *et al.* 2007). Furthermore, simulations suggest that specialisation in a network can be a by-product of adaptive radiation (Maynard *et al.* 2018).

Specialisation was particularly high for *LT*. Notably, host repertoires were frequently not estimated for these parasite species as many infect only single host species. These restricted host repertoires (Fig. 5b) might also be an explanation for the poor performance of NLP for the *LT* network as the input variables are by design identical for duplicate interactions. The algorithms performed well for *LV* likely because of the higher nestedness (Fig. 3). For instance, only one recorded monogenean species infects deepwater cichlids from the *LT* tribe Bathybatini (Kmentová *et al.* 2016) whereas co-infections for 36 host species in the *LV* community are reported (Fig. 2b, Appendix S1.2). Species of *LV* might be more interconnected than *LT* due the younger age of the host radiation (0.4 M years; see, Salzburger *et al.* 2014), which left the network less saturated. The Lake Victoria region has also experienced rapid ecosystem degradation over the past century including the introduction of a novel predator, *Lates niloticus* (L.), and eutrophication causing the decline and extinction of many native fishes (Marshall 2018). Environmental disturbance might have promoted the expansion of host repertoires as new ecological opportunities arise and parasites increase their change of survival through ecological fitting (Brooks *et al.* 2019). For instance, *Cichlidogyrus* sp. ‘nyanza’ is one of the few species with a host repertoire more determined by ecological parameters than the host evolution at least at the recent evolutionary scale (Fig. 4), although this pattern might emerge from the comparatively low genetic differentiation of the *LV* radiation (Salzburger *et al.* 2014). In conclusion, cichlid-*Cichlidogyrus* communities in the East African lakes appear more stable and saturated than those elsewhere. Yet the younger age and environmental degradation might make *LV* a less stable system than *LT*. Limitations of the dataset call for more extensive sampling of host-parasite communities in these lakes to better understand these interactions. Other lake systems, e.g. Lake Malawi could be of particular interest for future comparative studies mirroring the research conducted on the cichlid radiations in this region (e.g. Duponchelle *et al.* 2008).

Opportunities and limitations: sampling bias, missing data, and databases

We produced the most extensive study on species interaction of cichlid fishes or any other lineage with adaptive radiations to date. Patterns of community structure were inferred through a series of network analytical methods ranging from more traditional to new approaches. Limitations could be addressed through

the following measures:

- Because of the sampling bias in cichlid-*Cichlidogyrus* interactions studies towards economically relevant hosts (Cruz-Laufer *et al.* 2021a), the data likely give an incomplete picture as confirmed by NLP (Fig. 5b). Null models can account for this issue, but taxonomic research remains ultimately essential for closing knowledge gaps. Data generated from such studies should be gathered in online databases, e.g. the Global Interaction Database GLOBI (Poelen *et al.* 2014), to improve access to interaction data for research communities worldwide (Molloy 2011; Upham *et al.* 2021).
- The basin/basin-type parameter analysed here only summarises the entire geographical range of the hosts. Future studies should also account for geographical distribution as geocoordinates to infer local interaction patterns as we expect climates to vary across basins and species ranges.
- New models for NLP are being developed and employed in an increasing number of fields (Martínez *et al.* 2016). We suggest that a streamlined software package or library targeted at ecological research could simplify implementation for ecologists.
- The NLP algorithms applied here differentiate between true (impossible or ‘forbidden’ links) and false negatives (undetected links) (Dallas *et al.* 2017; Fu *et al.* 2019) among unobserved interactions. Wildlife host-parasite infection data regularly include prevalence data, i.e. ratios of uninfected host specimens. This information could be incorporated into future models.

Generally, the cichlid-*Cichlidogyrus* data serves as a study system eco-evolutionary studies because of a substantial amount of interaction, molecular, and morphological data for hosts and parasites. Addressing the limitations listed above might increase this potential. We were able to detect key mechanisms of ecology and evolution. First, the realised host repertoire is phylogenetically constrained as host range parameters are determined more by the host evolutionary history than by ecological parameters. However, recent host switches indicate that fundamental host repertoires might be more extensive than currently known. Second, network link prediction algorithms show that network structure is shaped by ecological opportunity induced by habitat sharing but host evolution, life style, and trophic level are also influential factors. Third, adaptive radiations of host lineages in Eastern Africa have created more specialised and potentially saturated meta-communities. Future studies should investigate whether our findings also apply in other host-parasite systems shaped by adaptive radiation. Therefore, we encourage researchers to reuse data provided here to diversify the portfolio of host-parasite interaction research in the future.

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List of table headers

Table 1. Evolutionary, ecological, and morphological parameters of hosts and parasites used for calculation of host habitat niche dendrogram and network link prediction (NLP) models. Host parameters were accessed in FishBase (Froese & Pauly 2000) and parasite parameters were reused from Cruz-Laufer *et al.* (2021b). To avoid overfitting NLP models, variable numbers per parameter were reduced through principal coordinate analyses (*PCoA*) based on distance matrices of phylogenetic trees or *dendrograms* built through clustering methods (see number of *PCoA* axes used for NLP and their proportion of parameter variation in brackets).

List of figure captions

Figure 1. Ecological and evolutionary processes shape the structure of the cichlid-*Cichlidogyrus* network consisting of cichlid fishes, a model system for explosive speciation research, and the parasitic flatworms belonging to *Cichlidogyrus* infecting the gills of cichlid and few non-cichlid fishes. Species presented in the figure are *Coptodon guineensis* (Günther, 1862) and *Cichlidogyrus gallus* Pariselle & Euzet, 1995.

Figure 2. Cichlid-*Cichlidogyrus* species network. (A) Whole network with unweighted links and Lake Tanganyika (*LT*), Lake Victoria regions (*LV*), inferred species-rich communities ($n > 10$) highlighted in colours. Circles indicate host species and squares species of *Cichlidogyrus* . Meta-communities were detected using the Louvain cluster algorithm including the Lake Victoria (*LV*), ‘*Coptodon zillii*’ (*CZ*), ‘*Oreochromis niloticus*’ (*ON*), ‘*Hemichromis*’ (*He*), and ‘*Tilapia sparrmanii*’ (*TS*) cluster. Many small unconnected clusters belong to *LT* . (B) Chord diagrams of the *LT* and *LV* clusters. (C) Four other species-rich meta-communities

involving species of *Cichlidogyrus* and *Scutogyrus* with links weighted by number of observed infections communities. Unlike *LT* and *LV*, meta-communities *CZ*, *ON*, *He*, and *TS* are characterised by sampling bias towards few, economically relevant host species, e.g. *Coptodon zillii*, *Oreochromis niloticus*, *Hemichromis fasciatus*, and *Tilapia sparrmanii*. Species names were omitted from (B) and (C) but are included in Appendix S4.

Figure 3. Changes of network metrics when only including natural host repertoires and geographical ranges of cichlid-*Cichlidogyrus* meta-communities including Lake Victoria region (*LV*), '*Oreochromis niloticus*' (*ON*), '*Hemichromis*' (*He*), and '*Coptodon zillii*' (*CZ*). Most values of the weighted nestedness based on overlap and decreasing fill (NODF_w) (Almeida-Neto & Ulrich 2011), weighted connectance (C_w) (Bersier *et al.* 2002), specialisation asymmetry (SA) (Blüthgen *et al.* 2007), interaction evenness (E_i) (Bersier *et al.* 2002), and the standardised interaction diversity (H_2') (Blüthgen *et al.* 2006) that differed significantly from the null distributions (NM₁, NM₂) remained unchanged (see Appendix S1.2 for detailed discussion).

Figure 4. Functional-phylogenetic distances (FPDist) inferred from host repertoires of selected species of *Cichlidogyrus* calculated as mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) weighted by abundance of interactions (blue). FPDist matrices are a function of functional (FDist) and phylogenetic (PDist) distance matrices of the host species weighted by the parameter a . Shaded areas (grey) indicate 5% and 95% quantiles of 1000 null distributions resulting from taxon shuffling. If estimates fall outside the null distribution, they can be considered informative. Smaller values indicated higher functional-phylogenetic similarities of host repertoires. A decreasing trend for FPDist estimates indicates that host communities are more phylogenetically than ecologically similar. For plots of other species infecting at least two host species, see Appendix S6.

Figure 5. Network link prediction based on host [H] and parasite [P] data in the cichlid-*Cichlidogyrus* network, and Lake Tanganyika (*LT*) and Lake Victoria regions (*LV*) subnetworks including missingness map of input variables for whole networks (a), heat maps of host-parasite links (b), and bar plot of variable importances (c) predicted by the *plug-and-play* algorithm (Dallas *et al.* 2017). The missingness map illustrates significant gaps in the taxon coverage of phylogenetic data and host standard lengths. The heat maps shows that a large proportion of cichlid-*Cichlidogyrus* interactions likely remain undetected (highlighted in colour) (for taxon labels, see Appendix S6) although most interactions of the studied organisms are most likely known for *LT* and *LV*. The variable importance graph indicates that the basins/basin types inhabited by the hosts are the most important predictor of cichlid-*Cichlidogyrus* interactions, but less so for *LT* and *LV*. Supporting information

Appendix S1. Other methods and results including phylogenetic reconstruction and structure of species-rich meta-communities in the cichlid-*Cichlidogyrus* system.

Appendix S2. GenBank accession numbers of DNA sequences used to render host phylogenetic distances.

Appendix S3. Host niche dendrograms resulting from different clustering algorithms.

Appendix S4. Chord diagrams of meta-communities presented in Fig. 2 with additional species labels. Host species names are abbreviated with the first three characters of the genus name and the first four characters of the species epithet. Parasite species names are abbreviated with the first character and first six characters respectively.

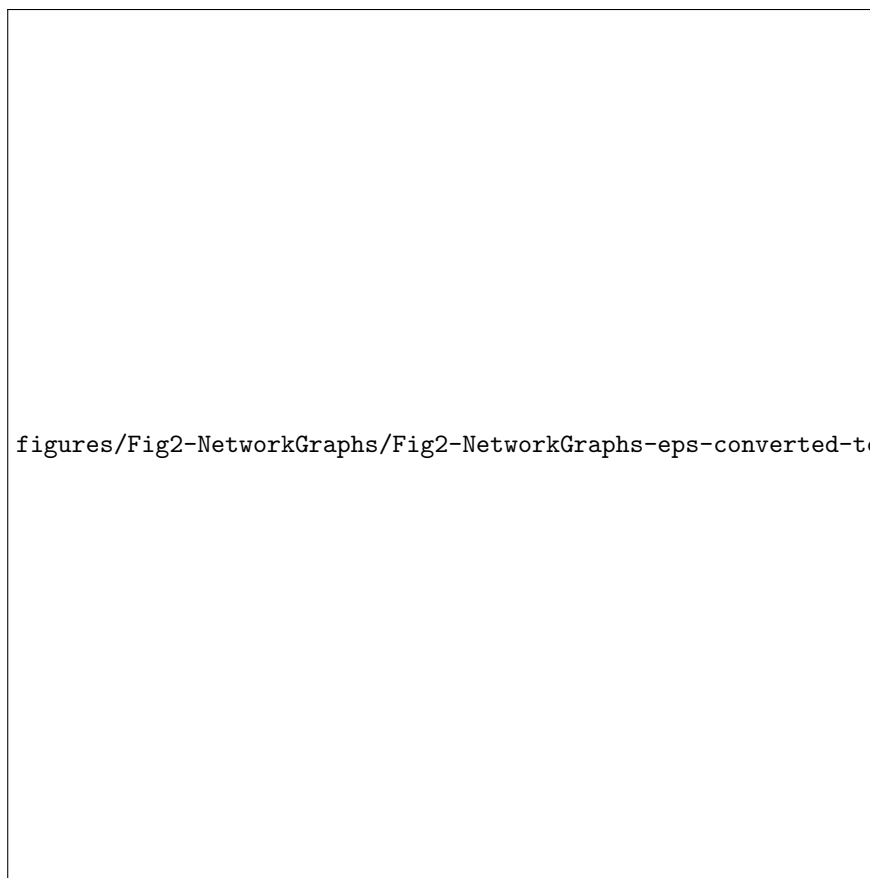
Appendix S5. Functional phylogenetic distance (FPDist) plots of host repertoires of all species of *Cichlidogyrus* not included in Fig. 4.

Appendix S6. Heat maps of links predicted by the *plug-and-play* algorithm with complete taxon labels. See Fig. 5c for simplified version.

Hosted file

Fig1_overview.eps available at <https://authorea.com/users/438073/articles/554279-the-role-of-phylogeny-ecological-opportunity-and-adaptive-radiation-in-host-parasite->

interactions-network-metrics-host-repertoire-and-network-link-prediction



figures/Fig2-NetworkGraphs/Fig2-NetworkGraphs-eps-converted-to.pdf

figures/Fig3-NetworkMetrics/Fig3-NetworkMetrics-eps-converted-to.pdf

figures/Fig4-FPDistPlots/Fig4-FPDistPlots-eps-converted-to.pdf

figures/Fig5-NLP/Fig5-NLP-eps-converted-to.pdf