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# Understanding the influence of host radiation on symbiont speciation through parasites of species flocks

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#### SHORT TITLE: Host radiation and symbiont speciation

#### **ABSTRACT:**

(Adaptive) radiations have attracted evolutionary biologists since a long time as ideal model systems to study patterns and processes of often rapid speciation. But, whereas a wealth of (sometimes already genome-scale) data is available for host radiations, very few studies target the patterns of diversification in their symbionts, even though they would be excellent models to study symbiont speciation. Our review summarizes what little is known about general patterns of symbiont diversification in often iconic adaptive host radiations and to what extent these patterns are dependent on the evolutionary trajectories of their hosts. We identify research gaps that need to be addressed in the future and discuss the potential of approaches not yet typically employed in these study systems, such as epidemiological disease modeling and new omics technologies, for significantly advancing our understanding of these complex eco-evolutionary relationships.

## **1.** Introduction: species flocks taught us much about the history of species but less about the history of interspecific associations

Studying and comparing species flocks, and the closely intertwined mechanisms of adaptive and non-adaptive radiation, have contributed to understanding speciation since Charles Darwin wrote about the tanager finches of the Galápagos Islands more than 150 years ago (Bowen et al. 2020). Since then, research into species flocks has overwhelmingly focused on free-living taxa. It often overlooks the phenomenon of symbiosis, in which two or more organisms of different species are associated intimately and for a protracted time, one of them being the symbiont and the other one the host (Margulis 1999, Smith and Smith 2015). In their overview of aquatic species radiations drawing from cases across invertebrates and vertebrates, Bowen et al. (2020) only mention a handful of radiating symbiont taxa but stress the importance of host-symbiont relationships in diversification processes, in two different contexts. Firstly, the peculiar diversification mechanisms of symbionts (e.g., host-switching, Fig. 1) make them conducive to speciation, and secondly, symbionts may drive radiation in their hosts. Given this importance of host-symbiont interactions in speciation, it is remarkable that research efforts on radiation have overlooked most parasites (symbionts that benefit from exploiting their host, which is in turn harmed: Smith and Smith 2015) and other symbionts. The latter include commensals (which benefit from a host in an otherwise benign relationship) and mutualists (mutualism being a form of symbiosis in which both species benefit) (Smith and Smith 2015). This is especially unfortunate since parasites were proposed for decades to have undergone extensive radiation processes (e.g., Price 1977; Poulin 1999).

On the topic of parasite radiation, Price (1977) asserts that "[a]daptive radiation can be most extensive when many related species of host are available for colonization, particularly if the hosts within a taxon differ in an important way relative to the requirements of the parasites." This would seem an interesting argument to zoom in on parasites of host species flocks. Surprisingly, however, studying parasite speciation explicitly in a context of host radiation is uncommon (Vanhove et al. 2016), even though radiations have been proposed as disease models (e.g., in cichlid fishes: Parsons et al. 2021). To the contrary, although there is indeed (scarce) empirical evidence of symbiont radiation across parasite taxa from different kingdoms (see Supplementary Methods for Web of Science search methodology), these are not typically associated with host radiations, as exemplified by the initial radiation of *Plasmodium*, one of the most important parasitic disease agents worldwide (Liu et al. 2010, 2014); downy mildew parasites of plants belonging to Asteraceae (Choi and Thines 2015); fungal plant pathogens of Sclerotiniaceae (Navaud et al. 2018); mikrocytid parasites of various aquatic invertebrates including economically important ones (Hartikainen et al. 2014); species of Ceratomyxa (Myxozoa) infecting clinid fishes in intertidal habitats (Bartošová-Sojková et al. 2018); and the parasitic finches belonging to Vidua (Viduidae) (Jamie et al. 2021).

The diversification mechanisms of parasites and other symbionts, by virtue of their niche being a living organism, are diverse and often result in higher species richness than their hosts (Fig. 1) (see, e.g., de Meeûs et al. 1997, Thompson 1999, Huyse et al. 2005). This makes them ideal models in speciation research and makes it all the more regrettable that their potential to help shed light on species formation is underexplored (Huyse et al. 2005). Elucidating these complex diversification mechanisms is expected to be more fruitful at fine-grained phylogenetic scale, by comprehensively sampling a set of closely related hosts, rather than studying symbionts of phylogenetically more distant host lineages (Page et al. 1995; Clark et al. 2000). This is hence a methodological reason why parasites and other symbionts of radiating hosts deserve more scientific attention. Moreover, better understanding of speciation in a context of parasitism and other interspecific associations is also important in more applied fields like infectious disease research and phytopathology (Huyse et al. 2005; Schulze-Lefert and Panstruga 2011; Brooks and Boeger 2019).

Perhaps, the most compelling reason for wanting to better understand symbiont speciation is straightforward. Even if the assertion that the majority of species on earth are parasites (Windsor 1998) should not hold true, it appears safe to argue that the impressive body of speciation literature dealing with radiations actually turned a blind eye to a substantial proportion of the planet's biodiversity. With the current review, we hope to offer some clues about how to help fill this research gap.

## 2. Are species flocks conducive to symbiont radiation?

In a first, explorative, literature study of the link between host species flocks and symbiont speciation (see Supplementary Methods for Web of Science search methodology), a total of 130 articles were retained. Most of these studies (n = 85) targeted parasites belonging to the

animal kingdom (Figs. 2, 3). Only about half of all studies included a comparison of diversity or species richness between symbionts and hosts (Table 1). In the original studies, different approaches were applied for different symbiont taxa (e.g., diversity of lineages *versus* species), which reflect differences between the respective fields and between micro- and macroevolutionary angles. While animal taxa have been studied in their roles as both symbionts and hosts, a symbiotic role is reported for most bacteria and fungi, in contrast to plant taxa that are most often considered as hosts. A general conclusion on the relative diversity of symbiotic and host lineages is difficult to draw given the relatively small number of studies directly comparing symbiont and host species richness, but in animals, parasite diversity estimates tend to lie above those for hosts (26 studies versus 19, Table 1).

## 2.1 Examples of species flocks with a high species richness of symbionts

Some of the better studied host-symbiont systems include clown fishes and anemones, parasitoid wasps and various insect hosts, fruit flies and fig trees, gall-inducing insects and their host plants, and more recently, monogenean flatworms and their fish hosts.

An adaptive radiation process driven by mutualistic interaction was proposed to explain the high species richness of clown fishes (30 species). They show an increased rate of species diversification and morphological evolution compared to their closest relatives without anemone mutualistic associations (Litsios et al. 2012). The high diversity of clown fishes seems to be further maintained by their ability to cohabitate (Camp et al. 2016).

The biodiversity and speciation of parasitoid wasps seem to follow host biodiversity patterns, and high host specificity is reported. As such, the evolution of parasitoid wasps supports the theory of biodiversity promoting speciation (Emerson and Kolm 2005). Contemporary African non-pollinating fig wasp diversity is seen as a legacy of ancient fig tree diversification and recent ecological opportunities (Jousselin et al. 2006; McLeish et al. 2010). Ecological barriers to reproduction, resulting from the host flies' adaptation to their host plants, have promoted the sequential radiation of the parasitic braconid wasp *Diachasma alloeum* (Forbes et al. 2009).

Radiation within a radiation was also suggested for gall-inducing sawflies of Asteromyia, with a remarkably high speciation rate (88 species per million years) comparable with some of the most rapid adaptive radiations known in plants (Stireman et al. 2010). Host-associated mating and oviposition have likely played a role in the sequential radiation of the gall-boring mordellid beetle Mordellistena convicta, which is attracted to galls of the tephritid gall fly Eurosta solidaginis on different species of Solidago (Asteraceae) (Rhodes et al. 2012). Niche diversification has promoted speciation resulting in high species richness in willow-galling sawflies (Hymenoptera: Tenthredinidae) (Nyman et al. 2007). In the context of plants and herbivores, and in turn also plant-feeding insects and their parasitoids, the escape-and-radiate (EAR) hypothesis proposes a cyclic coevolutionary process: a prev lineage acquires a new defensive trait, proliferates, and with time, the new clade's defences are overcome by antagonists. The latter, in turn, diversify to exploit the species of the hitherto antagonist-free clade of prey. In the context of willows, their gallers, and these gallers' parasites, Nyman et al. (2007) consider the EAR hypothesis too simplistic for explaining reciprocal diversification effects in such complex food webs. They propose a scenario of stepwise antagonistic coevolution: temporary relief from parasitism continuously drives prey lineages to colonize new niches, and consequently, some of the associated antagonists evolve and thereby bring mortality levels back to normal.

Cichlid fishes are a prime model for speciation research and a well-studied example of adaptive radiation processes. Recent studies indicate that the species richness of monogenean flatworms belonging to *Cichlidogyrus* (Dactylogyridae) is linked to that of their fish hosts: the diversity of these obligate parasites was proposed to be driven by a combination of high host-specificity, host-switching, and within-host speciation. They were proposed to form the first parasite radiation discovered in the African Great Lakes (Vanhove et al. 2015). The cichlid-*Cichlidogyrus* network was suggested as a model system of parasite evolution (Vanhove et al. 2016; Cruz-Laufer et al. 2021).

## 2.2 Examples to the contrary: species flocks with a low species richness of symbionts

Contrary to the general pattern of high species richness of the monogenean flatworm radiation in Lake Tanganyika (Cruz-Laufer et al. 2022), a particular cichlid lineage, Bathybatini, is infected by a single species of *Cichlidogyrus*. In this case, lower host availability combined with long-distance migration in the pelagic zone are proposed to have restricted parasite diversification (Kmentová et al. 2016, 2021). Similar patterns were observed in flatworm parasites of marine fishes (Schoelinck et al. 2012). Other reasons, notably recent host diversification, were proposed for a limited parasite species richness even in species-rich host radiations (e.g., Gobbin et al. 2021).

# **3.** A view from evolutionary parasitology: parasite speciation processes in radiating host lineages

In what follows, in view of space limitations, we focus on parasitism only, singling out parasitological studies of host species flocks in search of potentially generalizable patterns in the mechanisms of symbiont speciation in a context of host radiations. We therefore take stock of the state of parasitology in a list of well-known host radiations sourced from the literature. To this end, we compare how well-studied their parasites are – in general, in a speciation context – with the extent to which literature on the host radiation is available (Table 2).

## 3.1 Case studies from animal parasitology

Contrary to previous hypotheses that speciation in (host-specific) parasites generally follows that of their hosts, there is increasing evidence that host-switching is much more common than strict co-speciation (e.g., Huyse et al. 2005). Nonetheless, it has been suggested that host radiations induce parallel radiations in their parasites (Losos and Mahler 2010). Yet, little is known about the patterns and mechanisms of speciation in parasites from adaptive host radiations. Indeed, our literature search on parasite speciation in some of the most iconic adaptive host radiations yielded few publications that tackle this topic (Table 2). This lack of studies, and thus insights, into the generalities and idiosyncrasies of parasite speciation in these systems is surprising: many of these adaptive radiations are well-studied with respect to host phylogenetic relationships and species distributions, making them ideal systems for studying speciation also in their parasites.

In both nematode (subfamilies Cloacininae and Phascolostrongylinae) and cestode (subfamily Anoplocephalinae) parasites of kangaroos, wallabies, and rat-kangaroos (all species within the family Macropodidae), host-switching plus some within-host diversification is the predominant mode of speciation, while co-speciation plays a negligible role (Beveridge and Chilton 2001; Beveridge et al 2002; Hardman et al. 2012; Chilton et al. 2012, 2016, 2017; Beveridge et al. 2019). This has been attributed to the particular life history of the parasites and the ecology of their macropodid hosts (Beveridge and Spratt 1996). Typically, several macropodid species share their habitat, and larvae deposited by one macropodid species might be ingested together with plants (or intermediate hosts) by another species. As host-switches are only possible with hosts occurring in sufficient proximity, (past) host geography is important in explaining phylogenetic relationships among parasite species (Hardman et al. 2012; Chilton et al. 2016, 2017). A predominant role of host-switching in diversification was also found in streblid flies (*Trichobius phyllostomae* group) on phyllostomid bats (Graciolli and de Carvalho 2012). Although these species are typically host-specific, which should favour co-speciation, the latter was found to be rare. As female streblid flies deposit pupae around the bat roosting sites, host-switching might occur when more than one bat species is present at the same roosting site.

In nematodes of Caribbean *Anolis* lizards, host specificity determines population structure in the parasite (Falk and Perkins 2013). A broad host range implies more possibilities for dispersal, whereas high host specificity allows for population differentiation and diversification of the parasites in line with the population divergence of their hosts, a pre-requisite for eventual co-speciation.

Arguably the best-explored host parasite system among adaptive host radiations is the Lake Tanganyika cichlid species flock (Teleostei: Cichlidae) and its parasites belonging to *Cichlidogyrus* (Monogenea: Dactylogyridae), even though only part of the actual diversity of *Cichlidogyrus* is known. Both host phylogeny and host ecology determine diversity and phylogenetic relationships among the parasites (Cruz-Laufer et al. 2022; Rahmouni et al. 2022). The strong influence of host phylogeny on patterns of parasite divergence in this system indicates a significant role of co-divergent host-parasite evolution, either by (recent) allopatric divergence (Agosta and Brooks 2020) or by phylogenetic tracking (Russo et al. 2018). Co-speciation prevails in recently diverged parasite taxa and in taxa inhabiting the shallow littoral zone, where host species adapted to this particular niche are typically very abundant (Vanhove et al. 2015; Rahmouni et al. 2022). On the larger scale, host-switching was also found to be important in the diversification of *Cichlidogyrus* from Lake Tanganyika cichlids (Rahmouni et al. 2022). Parasite species from habitats with low host density appear to be less host-specific, utilizing a range of related host species and "failed" to speciate further (Kmentová et al. 2016, 2021; Rahmouni et al. 2022; Section 2.2).

## 3.2 Case studies from plant parasitology

Although there is no shortage of species-rich plant lineages that probably underwent adaptive radiation, only about 10% of studies on adaptive radiation have a botanical focus (Schenk 2021). Accordingly, Schenk (2021) states that the role of antagonistic and other interspecies interactions in plant radiations is "virtually unknown". Indeed, in our sample of plant radiation studies, the proportion mentioning parasites is just about negligible (Table 2). In those taxa for which symbiont diversity was studied, such as Oncidiinae (Orchidaceae), *Platanthera* (Orchidaceae), and *Schiedea* (Caryophyllaceae), the scant research attention seems focused on mutualistic interactions, such as mycorrhiza (e.g., Pereira et al. 2005; Valadares et al. 2015; Esposito et al. 2016; Oja et al. 2017; Kaur et al. 2019) and pollination (e.g., Medeiros 2015; Young et al. 2017). Species in the radiation of *Brocchinia* (Bromeliaceae) are highly diverse in strategies for nutrient capture (Givnish 2015). For the carnivorous pitcher-forming species of *Brocchinia*, Adlassnig et al. (2011) mention a far

lower number of inquilines than for members of the unrelated carnivorous pitcher plant (CPP) genera *Nepenthes* (Nepenthaceae) and *Sarracenia* (Sarraceniaceae). Of the inquilines in CPPs, few are parasitic in general, and the authors do not mention them in a speciation context.

The revision by Kobayashi et al. (2021) of the taxonomy of the leaf-mining gracillariid moth genus *Philodoria*, endemic to Hawaii, provides interesting ideas about the extent to which its members use silverswords (*Argyroxiphium*, *Dubautia*, and *Wilkesia*: Landis et al. 2018) as host plants. Although these leaf miners commonly feed on plants belonging to Asteraceae, *Philodoria wilkesiella* is one of the few leaf miners on species of *Argyroxiphium*, reported only from *Argyroxiphium grayanum*; chemical, physiological, or structural features of the plant may determine which species are mined by these moths. Several members of *Dubautia*, though, are utilised by several species of *Philodoria*, and *Wilkesia gymnoxiphium* hosts *Philodoria funkae*. Among the scarce examples of host-parasite systems investigated in the context of plant radiations, this endemic silversword-leaf miner system clearly is a promising candidate for studying the drivers of symbiont specificity and species richness. The study of plant-feeding insects has proven highly informative for our understanding of host-parasite interactions and infectious diseases (Agosta et al. 2010). Therefore, despite the traditionally mostly separate literature in plant and animal parasitology, we highly recommend more (comparative) research into the diversification of parasites in host plant radiations.

# 4. The potential of epidemiological disease modelling to understand symbiosis and parasite diversification in species flocks

For medically important pathogens such as *Plasmodium* (malaria agent) or *Borrelia* (lyme disease agent), the historical pathways (Ricklefs and Outlaw 2010; Cornuault et al. 2013) and future expansions of their distributions or host ranges have been inferred (Jamison et al. 2015). (Molecular) evolutionary approaches have contributed to a better understanding of the epidemiology of human infectious diseases (e.g., Nelson and Holmes 2007), found their way into integrated outbreak responses (e.g., Ho et al. 2017), and offer potential for predictive models (e.g., Stockdale et al. 2022). Also, while epidemiology often focuses on one-host-one-pathogen settings, a multi-host-multi-pathogen perspective is more realistic (Rigaud et al. 2010; Evison 2015; Pilosof et al. 2015). In this respect, studying symbioses in species flocks is promising.

Conversely, epidemiology may also contribute to a fundamental understanding of parasite biology. For example, epidemiological modelling was used to identify the black pea aphid *Aphis fabae* as the vector responsible for an outbreak of *Potato virus Y* in a zone of seed potato production in Finland (Döring 2011). There are obvious limitations to a purely epidemiological approach, given the complex interactions between a pathogen, its various host species, and the environment (Döring 2011), but in combination with genomic and experimental approaches, epidemiological modelling is well-suited to improve our understanding of disease emergence (Pepin et al. 2019). What is its potential for understanding the diversification of symbionts?

## 4.1 Role of host contact and behaviour

Epidemiological disease modelling is used to study infectious and non-infectious diseases. While infectious diseases are transmissible between hosts, non-infectious diseases are not (Keeling and Rohani 2008). Epidemiological models of non-infectious diseases often focus on studying trends in time or geography and associations between the probability of developing the disease and risk factors. Infectious-disease models, on the other hand, characterize the complex biological and environmental interactions between hosts (humans, animals, or plants) and infectious agents (White 2017). There exist many models for studying infectiousdisease dynamics, which often fall somewhere in between compartmental and phenomenological models (Abrams et al. 2020). Phenomenological models are a more generic regression-type of models, which are helpful to estimate key characteristics of the disease (Bretó 2018). In compartmental models, the host population is subdivided into separate classes according to the disease status of hosts, such as being susceptible to the disease, exposed to the pathogen, infectious to other susceptible hosts, and recovered from the disease. Functional forms are used to represent the knowledge and assumptions on the underlying biological processes, typically represented by a set of differential equations.

Effective contacts, i.e., contacts between hosts that cause transmission of the pathogen from an infectious host to a susceptible host, are crucial in infectious-disease epidemiology. Compartmental models are based on the law of mass action, which assumes that the number of new infections is proportional to all effective contacts between infectious and susceptible hosts (Wilson and Wocester 1945). While the original model formulations assume a homogeneous mixing of hosts, there is considerable heterogeneity in host mixing for several disease examples. Host behaviour impacting the processes involved in effective contacts is thus key in infectious-disease studies.

Similar modelling approaches can be used when studying symbiosis in species flocks: modelling the mechanisms of host-symbiont interactions by adapting compartmental models to describe the biological mechanisms in species interactions. For example, in parasitology, many parasitic organisms have a complex life cycle that requires transmission between different hosts (Section 4.2) or environmental reservoirs. The frequency and proximity of interactions between hosts can strongly influence the transmission of parasites. Phenomenological models describing the symbiosis in species flocks in relation to the environment or to genetic differences between species can provide an opportunity to better understand the symbioses in species flocks.

## 4.2 Role of symbiont life history

Symbiont life histories vary in complexity, with some symbionts completing their life cycle on or in a single host and others obligately requiring multiple hosts. That a single-host parasite would acquire a dependence on additional hosts appears counterintuitive at first glance; yet, parasites with complex life cycles have evolved independently in various parasitic groups, and interesting theoretical work examines the selective advantages of increasing lifecycle complexity for symbionts (Choisy et al. 2003; Parker et al. 2003; Gandon 2004; Auld and Tinsley 2015).

A wide range of studies have explored how the multiplicity of potential hosts may affect the dynamics of infectious diseases (e.g., Anderson and May 1991; Hess 1996; Haydon et al. 2002), with few focusing on the evolutionary consequences of complex life cycles on virulence in particular (Gandon 2004). The compartmental modelling framework employed by these studies, using, e.g., the susceptible-infected-recovered (SIR) model (Kermack and McKendrick 1927) or one of its variants (see Brauer et al. 2019 for a summary), has long been a well-established pillar in infectious-disease modelling. An essential concept in studying an infectious-disease model is the basic reproduction number, usually denoted as  $R_0$ , which is

defined as the number of secondary infections caused by an average infective agent introduced into a wholly susceptible population over the course of the disease (Brauer et al. 2019). If  $R_0 < 1$ , the infection will die out, whereas if  $R_0 > 1$ , it will establish itself. Interestingly, the mathematical expression of  $R_0$  in parasites that sequentially exploit two different types of hosts but do not transmit within each host type, as is often the case in vector-borne parasites (see below), is very similar to that obtained for scenarios where parasites infect a single host but produce free-living stages. These scenarios are thus considered analogous by some authors (Gandon 2004).

Vector-borne diseases are characterised by the pathogen having a complex life cycle with at least two host types, one of which commonly is an invertebrate (e.g., mosquitoes, flies, snails, or ticks) that usually is highly abundant in the environment and within which the pathogen develops before infecting the other host type, which usually is a vertebrate. One can further distinguish between vector-borne disease systems where the transmission between host types either requires free-living infective stages in the environment (as, e.g., in *Schistosoma*) or is direct, which means that pathogens only survive in the internal environment of the two hosts (Garira and Chirove 2020). A recent theoretical study developed an SIR model to explore the dynamics of a multi-strain pathogen with differing strain-specific transmission mechanisms (direct transmission *versus* a combination of direct and environmental transmission). Applied to a two-strain framework for the avian influenza virus, the results suggest that environmental transmission is a more fragile evolutionary strategy than direct transmission (Breban et al. 2010).

Since symbioses are inherently complex multiscale systems, i.e., symbionts may replicate within hosts, transmit between host individuals, and/or spread between host populations, selection may operate and trade-offs may occur at different levels (Garabed et al. 2019). As compared to traditional compartmental models, multiscale modelling approaches explicitly aim to link or couple scales (with respect to, e.g., organism size, population level, or time), to translate the often detailed knowledge at the individual scales into integrated knowledge about the overall dynamics (Garabed et al. 2019). Recent examples in the context of complex pathogen life histories are multiscale models for schistosomiasis (Garira et al. 2014) and human onchocerciasis (Garira and Chirove 2020). The latter study in particular has been praised as providing a paradigm for other ecological studies, with the modelling approach developed specifically with a number of control points in mind, which can be translated into clinical and environmental interventions (Garabed et al. 2019). For a general take on multiscale models in infectious disease, we refer to Garira (2020).

Given the complexity of these systems, it is essential that phenomenological models to understand symbiosis in species flocks include co-infection (Sofonea et al. 2015), age of infection (Kenne et al. 2021), and microbiome (Hahn et al. 2022). Only then will we gain a better understanding of how host radiation contributes towards parasite speciation.

## 4.3 Role of individual host physiological traits

The complex dynamics of host-parasite associations is intimately linked to the physiological state of the host. Specific individual host traits affecting this complex symbiotic relationship include sex and reproductive status, ontogeny stage, and immunocompetence. Also, interactions between behaviour and immunity are well-established, but it is unknown how parasites come into play. Integrating parasite transmission into these aspects of host competence would enhance our understanding of host-parasite dynamics and may be a fruitful

area for experimental research (Barron et al. 2015).

Many fish species exhibit sex-related differences in behaviour and metabolic status, including the production of hormones that act as chemoattractants for parasites (Buchmann et al. 2004). Hence, sex and reproductive condition can affect the abundance, species richness, and diversity of parasites in a particular host (Santoro et al. 2020). In Nile tilapia (*Oreochromis niloticus*), females tend to be more susceptible to the gill monogeneans *Cichlidogyrus tilapiae* and *C. sclerosus* than males and sexually undifferentiated fish (Akoll et al. 2012), but this is by no means a rule for all host-parasite systems. For example, *Gyrodactylus* spp. was found to be equally abundant in male and female Nile tilapia kept in mixed-sex groups (Tadiri et al. 2016). The variation in susceptibility within host species and specialisation of parasites to particular groups of host species should reinforce the diversification among parasite species. However, studies explicitly targeting this issue are lacking.

Interactions between parasites and the host immune system, including the parasite's potential ability to dampen or circumvent the host response, are key elements in a long-term symbiotic relationship (Ilgová et al. 2021). Of particular importance are the host mucosal immunity and its ability to recognize the parasite. The constitutive expression of immune-related genes and their up- or downregulation upon infection depend on the host genotype (Ilgová et al. 2021; Hahn et al. 2022). Following exposure to *G. cichlidarum*, there is an upregulation of cytokines (IL-1 $\beta$ , TGF- $\beta$ , and TNF- $\alpha$ ) in Nile tilapia gills and an increase in the contents of specific immunoglobulin IgM in skin (Zhi et al. 2018, 2020). The major histocompatibility complex (MHC) genes encode cell-surface glycoproteins that recognize parasite antigens and activate the adaptive immune response (Yamaguchi and Dijkstra 2019). These hypervariable genes show large allelic and functional diversity between hosts, and they have been implicated in parasite-mediated host divergence in the Midas cichlid species flocks (*Amphilophus* spp.) across Nicaraguan lakes (Bracamonte et al. 2022).

Modulation of the host neural, endocrinal, neuromodulatory, and immunomodulatory systems by the parasite (reviewed by Lafferty and Shaw 2013) creates an additional dimension of complexity, since the parasite can change the corresponding physiological traits in the host. These changes are dependent on the host genotype and can even impact the microbiome (Hahn et al. 2022), which further affects the host phenotype. Albeit not a trivial task, it is important to consider these individual physiological traits when defining susceptible, infected, and non-competent hosts in infectious-disease models.

Species flocks as special cases of complex parasite systems have not yet received broad attention in the modelling context. Recent work considers, for example, a pathogen newly introduced into a metapopulation of hosts with two genotypes exhibiting different migration rates and different levels of disease-induced mortality in the context of evolutionary rescue (Jiao et al. 2020) and – in multi-host-multi-pathogen communities, specifically – how the presence of generalist pathogens, alternative hosts, and within-host priority effects affect the risk of focal hosts being infected with a specialist pathogen (Jiao and Cortez 2022). These models can incorporate parameters such as host population size, parasite transmission rates, host specificities, and ecological variables. By running simulations, researchers can explore how these factors influence the diversification of parasites and the dynamics of host-parasite coevolution over time (e.g., Schenk 2019).

## 5. Perspectives: priority research gaps in monitoring and molecular approaches

Monitoring and quantifying symbiont diversity is inherently difficult, since symbionts are often among the smallest and most cryptic species known. In this respect, it is worrisome that training, hiring, and financing of taxonomists are dwindling in general (e.g., Borkent 2020), and the situation for symbiont taxonomy is unlikely to be an exception (see, e.g., Keune et al. 2017 for recommendations on parasitological training in the Global South and Poulin and Presswell 2022 for the state of fish parasite taxonomy). The sheer detection of symbionts and the subsequent species identification, particularly when based on morphological characteristics, require considerable skills and expertise. Advanced imaging methods have been demonstrated to enable the morphological distinction of similar species of minute parasites, e.g., confocal fluorescence microscopy (Marchiori et al. 2015) and scanning electron microscopy (Fannes et al. 2017) for fish-infecting dactylogyrid monogeneans. These techniques have also been explored, albeit to a very limited extent, for representatives of the same parasite family infecting cichlids of the Lake Tanganyika assemblage (Fannes et al. 2015; Cruz Laufer 2023).

However, as in most other areas of biodiversity research, molecular methods have become commonplace to supplement morphological identification. Particularly exciting developments are reaching symbiont diversity research from the rapidly developing field of environmental DNA (eDNA), which seeks to gain insights into species distribution and diversity through molecular markers and techniques applied to DNA obtained directly from environmental samples, mostly water or soil, containing, for example, mere shed cells, extracellular (free floating) DNA, or microscopic organisms. The rich and diverse applications of eDNA in symbiont research and the associated challenges, e.g., concerning the translation of eDNAinformed monitoring results into assessment of disease risk, were summarised recently (Bass et al. 2015). eDNA approaches determine the presence or absence of specific taxa via speciesspecific (targeted) assays, often using quantitative PCR, or characterise overall diversity via so-called metabarcoding techniques relying on the amplification of common DNA barcoding markers via universal primer sets that ideally work for all taxa of interest in the sample and subsequent high-throughput sequencing of amplicons. A targeted eDNA protocol for the detection of Gyrodactylus salaris in water samples has been published (Rusch et al. 2018), and many more examples are listed in a recent review (Sengupta et al. 2022). Metabarcoding has recently been applied to assess parasite diversity (Lamellodiscus spp.) in several sparid host fishes (Scheifler et al. 2022). This approach holds great promise to scale up to large numbers of samples, to gain unprecedented insights into symbiont host specificity and preference, particularly in species flocks.

Besides monitoring, recent molecular techniques will also allow us to advance our understanding of functional and evolutionary aspects of host-symbiont interactions. In the last decade, there has been a remarkable advance in new omics technologies, including, most recently, single-cell sequencing (Nam et al. 2021). It is now feasible to obtain whole transcriptome, genome, and even epigenome sequences from single cells, which opens up the possibility of identifying genomic variants within hosts and parasites and to understand the influence of parasites on host genotypes and vice versa. We are also starting to realize that epigenetic changes, such as DNA methylation and hydroxymethylation (Konstantinidis et al. 2020), potentially drive genome evolution through elevated nucleotide transversion rates. Since little is known about the effects of parasite exposure on the epigenomes of species flocks, it would be very relevant to investigate if these epigenetic mechanisms play a role in host-parasite coevolution.

## 6. Concluding remarks

Studying adaptive radiations has greatly contributed to our current understanding of the factors and processes underlying diversification and speciation. Yet, to what extent host and symbiont diversification in adaptive radiations are interdependent has received only little attention in the past and thus remains largely unclear. Now, with recent methodological advances in various fields of research and well-resolved phylogenomic trees with (almost) full taxon coverage of adaptive host radiations becoming available (e.g., Ronco et al. 2021), the next logical step is to make use of these recent developments, ideally in an integrative approach, to also target the hitherto largely neglected symbiont part of these radiations. Only then will we get closer to a full understanding of how hosts and symbionts shape each other's diversification processes (not only) in adaptive radiations.

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## Tables

Table 1: Overview of symbiont-host relationships with numbers of literature records from the Web of Science database sorted by kingdom. The search and selection criteria of studies are described in Section 2, with further details described in the Supplementary Methods and Supplementary Results.

Kingdom	Symbiont/host	Number of symbiont families	Symbiont diversity lower/higher/equal/not compared	Parasitic/parasitoid/mutualistic
Animalia	88/74	44	11/26/8/42	70/10/7
Archaea	1/0	1	0/0/0/1	0/0/0
Bacteria	12/0	7	1/3/1/7	8/0/1
Fungi	18/2	9	5/3/1/11	12/0/5
Myzozoa	5/0	3	2/0/0/3	5/0/0
Plantae	2/0	2	0/0/0/2	2/0/0
SAR	2/0	1	0/0/0/2	1/0/1
Viruses	6/0	5	1/1/1/3	6/0/0

Table 2: The state of parasitology literature for well-established host radiations, with number of articles from the Web of Science database, number of articles on parasites, and number of articles on parasite speciation (see Supplementary Table S1 for Web of Science search strings).

	Number of parasitological studies combined with					
	Number	Number of	speciation, species	Number of studies on		
	of	parasitological	richness, or	parasite speciation, species		
Host radiation <sup>a</sup>	studies⁵	studies	<b>biodiversity</b> <sup>d</sup>	richness, or biodiversity <sup>e</sup>		
ANIMALS						
Marsupials	12613	716	77	13		
New World monkeys	1963	86	5	0		
Old World fruit bats	703	23	2	0		
North American tiger beetles	17	1	0	0		
Lake Tanganyika cichlid fishes	666	67	35	6		
Lake Malawi cichlid fishes	652	11	3	0		
Lake Victoria cichlid fishes	526	10	4	0		
Hawaiian Drosophila	114	13	5	0		
Anolis	3404	137	14	1		
Darwin's finches	488	99	15	0		
red crossbill	202	18	2	0		
Phylloscopus	757	40	3	0		
Parus	3880	360	12	0		
Ctenotus	103	1	0	0		
Centrarchus	14	1	0	0		
Coregonus	2652	115	13	0		
Cancer	60	2	0	0		
Hawaiian honeycreepers	54	7	0	0		
Hawaiian crickets	50	18	1	0		
Lake Baikal sculpins	50	4	0	0		
Lake Barombi Mbo cichlid fishes	16	2	0	0		
Vangidae	21	3	0	0		

Lake Lanao barbs	4	0	0	0
Antarctic icefish	422	8	2	0
Lake Baikal amphipods	209	19	1	0
Phyllostomidae	1387	106	30	1
lemurs	4826	211	29	0
PLANTS				
silverswords	172	7	0	0
Pontederiaceae	443	3	0	0
Brocchinia	30 <sup>f</sup>	2	1	0
Oncidiinae	152	6	1	0
Aquilegia	476	3	0	0
Argyranthemum	121	2	0	0
Platanthera	358	38	5	0
Schiedea	72	1	0	0
Dalechampia	152	1	0	0
Encelia	163	4	0	0

<sup>a</sup> Host taxa included all radiations featured in Givnish and Sytsma (1997), Schluter (2000), Seehausen (2004), and Martin and Richards (2019). Since speciation mechanisms are best inferred based on the symbionts of closely related hosts (Page et al. 1995; Clark et al. 2000), radiations from a phylogenetic level of order onwards were omitted. Radiations only including one or two host species were also not considered in view of our focus on speciation in the context of species flocks.

<sup>b</sup> Query: TOPIC = [the scientific name(s) of the host taxon/taxa in question – see first column]

° Query: TOPIC = [the scientific name(s) of the host taxon/taxa in question – see first column] AND TOPIC = (parasite OR symbio\*)

<sup>d</sup> Query: TOPIC = [the scientific name(s) of the host taxon/taxa in question – see first column] AND TOPIC = (parasite OR symbio\*) AND TOPIC = (speciation OR richness OR biodiversity)

<sup>e</sup> After qualitative assessment of the article's content.

<sup>f</sup> This excludes 4 articles on the cancellariid gastropod genus *Brocchinia* Jousseaume, 1887.

### **Figure legends**

Figure 1: Diversification mechanisms of symbionts, A: Co-divergence/co-speciation (also called induced speciation), B: Duplication (also called within-host speciation or synxenic speciation), C: Host-switch (also called ecological transfer, lateral transfer, host transfer, parasite sharing, species jump, cross-species transmission, or host transition), D: Duplication in allopatry with "magnifying-glass effect" (symbionts diversifying faster than their respective host populations), E: lineage sorting through extinction, F: Failure to diverge, G: lineage sorting through "missing the boat" (symbionts absent from one of the host founder populations at a speciation event). Mechanisms A-D increase symbiont diversity; in mechanisms E-G, symbiont diversity does not increase, or decreases. Terminology follows Euzet and Combes (1980), Paterson and Gray (1997), Pariselle (2003), Nieberding et al. (2004), Vanhove and Huyse (2015), and Hay et al. (2020).

Figure 2: Summary of diversity comparison between symbionts and their respective hosts. The search and selection criteria of studies are described in Section 2, with further details described in the Supplementary Methods and Supplementary Results.

Figure 3: Cumulative curve of the number of studies focusing on symbiont diversity over the last 30 years. The search and selection criteria of studies are described in Section 2, with further details described in the Supplementary Methods and Supplementary Results.

## Text box: Open questions for further research

- Are the symbionts of host lineages that underwent radiation more prone to form radiations themselves?
- What can we learn from the comparison between symbionts that are more *versus* less species-rich than their host species flocks?
- Do speciation mechanisms of symbionts of host radiations fundamentally and consistently differ between parasites, commensals, and mutualists?
- Does variation in susceptibility within host species impact diversification of their parasites?