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Macroevolutionary dynamics of parasite diversification: A reality check

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Abstract

Parasitism is often invoked as a factor explaining the variation in diversification rates across the tree of life, while also representing up to half of Earth's diversity. Yet, patterns and processes of parasite diversification remain mostly unknown. In this study, we assess the patterns of parasite diversification and specifically determine the role of life-history traits (i.e. life cycle complexity and host range) and major coevolutionary events in driving diversification across eight phylogenetic datasets spanning taxonomically different parasite groups. Aware of the degree of incomplete sampling among all parasite phylogenies, we also tested the impact of sampling bias on estimates of diversification. We show that the patterns and rates of parasite diversification differ among taxa according to life cycle complexity and to some extent major host transitions. Only directly transmitted parasites were found to be influenced by an effect of major host transitions on diversification rates. Although parasitism may be a main factor responsible for heterogeneity in diversification among the tree of life, the high degree of incomplete parasite phylogenies remains an obstacle when modelling diversification dynamics. Nevertheless, we provide the first comparative test of parasite diversification, revealing some consistent patterns and insight into the processes that shape it.

KEYWORDS
antagonistic interactions, coevolution, diversification rates, ecological opportunity, macroevolution, parasitism

1 | INTRODUCTION

Decades of research reconstructing species phylogenetic histories have shown that relationships between species, their distribution and worldwide biodiversity patterns are anything but homogeneous (Jetz et al., 2012; Sanderson & Donoghue, 1996). The advancement of techniques and analyses has resulted in the focus shifting from reconstructing species systematic relationships to determining what causes the heterogeneity that is ubiquitous along and among phylogenetic trees (Brennan & Oliver, 2017; Rabosky, 2014). Research effort has centred on identifying historical patterns of species diversification and the processes and causes of these patterns in order to understand how and why speciation and extinction rates vary through time, space and between clades of phylogenetic trees (Barker et al., 2012; Rabosky, 2009; Sanderson & Donoghue, 1996; Stadler, 2011). A range of ecological and environmental factors such as climate (e.g. Brennan & Keogh, 2018) and ecological opportunity, whether mediated through the habitat (e.g. Foster & Piller, 2018; Testo et al., 2019) or trophic-based (e.g. Price et al., 2012), has been linked to differential speciation and extinction rates. Antagonistic ecological interactions such as parasitism and competition (e.g. Ehrlich & Raven, 1964; Rabosky, 2013; Ricklefs, 2010), as well as mutualistic associations (e.g. Aubier et al., 2017; Jablonski, 2007), have also been found to have an effect on diversification. But whether or not species-level interactions promote diversification or restrict it appears to be dependent on the level of specificity, the role each species plays, the degree of species association (Chomicki et al., 2019; Yoder & Nuismer, 2010) and even evolutionary time (Aguilée et al., 2018).

Parasitism is one of the most successful modes of life, having evolved independently in over 200 lineages throughout the animal tree of life alone (Weinstein & Kuris, 2016). Parasites evolved as exploiters, selected to overcome host defences and exerting fitness costs in their associations with hosts. By overcoming host defences, parasites may develop key innovations driving increases in diversification rates (Braga et al., 2018), and by exploiting new ecological opportunities may undergo rapid lineage diversification (Gavrilets & Losos, 2009). As such, parasitism has been repeatedly associated as a promoter of diversification (Jezkova & Wiens, 2017; Yoder & Nuismer, 2010), and although the patterns and the mechanisms of parasite diversification have been extensively speculated (Morand, 2015; Morand et al., 2015; Poulin, 1995), they still remain vastly unknown. The multiple independent transitions to parasitism provide a unique opportunity to study the patterns and processes of diversification across groups that convergently evolved to explore a similar lifestyle. Given that parasitism evolved convergently along the tree of life, are the diversification patterns similar across multiple parasite groups or are they taxon-dependent? And, is there a common process driving diversification among parasitic taxa? Here, we set to investigate these questions using a comparative evolutionary approach exploring the macroevolutionary dynamics of diversification of phylogenetically unrelated parasite taxa.

Parasitism is a very diverse mode of life, with parasites possessing a remarkable variety of life-history traits, such as life cycle complexity (simple one host, to complex multihosts), and host range (i.e. niche width). In theory, an increase in life cycle complexity is related with the potential for increased diversification (Calcagno et al., 2017; Doebeli & Ispolatov, 2010; Svardal et al., 2014). However, whether differences in life cycle complexity, that is the use of multiple hosts across the parasite ontogeny, correlates with differential macroevolutionary patterns remains to be investigated. In regard to host range, the incorporation of new hosts has commonly been associated with lineage diversification (Janz et al., 2006, 2016), but the extent to which it impacts diversification (speciation and extinction) remains equivocal. In some studies, the number of hosts used (i.e. specialists versus generalists) has been positively correlated with diversification rates (Braga et al., 2018; Janz et al., 2006), with other studies finding the opposite (Weber & Agrawal, 2014; but see Janz et al., 2016).

Whether coevolutionary interactions promote diversification remains to be tested across the tree of life (Althoff et al., 2014). Nonetheless, in host–parasite antagonistic interactions there is an expectation that it does given the imposed costs (Hembry et al., 2014; Yoder & Nuismer, 2010). As a consequence, coevolution has been a key theoretical foundation of host–parasite associations, as the main evolutionary process driving parasite diversification. As a parasite evolves alongside its host, a range of coevolutionary events can occur: they can switch to new hosts, cospeciate with their host, speciate within a host or become extinct resulting in different cophylogenetic patterns (de Vienne et al., 2013). Many host–parasite coevolutionary studies have suggested that events, such as switches to a new host, or rate of host switching, may promote increased diversification or speciation (Huyse & Volckaert, 2005; Navaud et al., 2018; Ricklefs et al., 2014; Sato et al., 2017). This fits with the assumption in free-living organisms that new ecological opportunities lead to increased lineage diversification as open adaptive zones get filled (Braga et al., 2018; Herrera, 2017). This is one of the main predictions under the escape and radiate model of coevolution (Ehrlich & Raven, 1964; Thompson, 1994). However, under the escape and radiate model, coevolution is not the direct mechanism of diversification, but instead it is a sporadic event driving host defences and parasite counter-defences creating new adaptive landscapes, which in turn may promote isolation and divergence (Althoff et al., 2014). Nevertheless, not all new host associations may represent equal ecological opportunities, and not all may promote speciation (Kaczvinsky & Hardy, 2020). Other host–parasite coevolutionary events such as host tracking through codispersal, codivergence and cospeciation can also lead to parasite lineage diversification; if hosts experience radiations by exploring ecological opportunities, isolation and divergence of parasite populations can occur.

Although we have the questions and the analytical tools (e.g. Rabosky, 2014; Silvestro et al., 2011; Stadler, 2013) to investigate patterns and potential drivers of parasite diversification, we are still limited by a simple fact: we do not know the true diversity of parasites (Dobson et al., 2008; Jorge & Poulin, 2018). Most (if not all) of the available phylogenies have a large percentage of incomplete coverage, not accounting for knowledge of the fossil record. Such bias is likely not random, which when not taken into consideration can influence and bias estimates of diversification rates (Höhna, 2014), or even change the conclusions (Cusimano & Renner, 2010). However, empirical studies investigating the impacts of sampling bias are still scarce.

Here, we investigate the macroevolutionary dynamics of parasite diversification while accounting for nonrandom incomplete sampling, by estimating clade-specific sampling fractions based on available taxonomic data. We focus on the following questions: (a) Do patterns of diversification differ across parasites with different life-history traits (i.e. life cycle complexity and host range)? (b) Is there any evidence that major coevolutionary events, specifically major host transitions, drive parasite diversification? (c) How may the current degree of incomplete sampling influence our ability to answer the above questions? We predict that major host transitions will be correlated with shifts in parasite diversification rates. However, we also predict this will only be found for parasites with simple life-history traits, since increased complexity in life-history traits may have led to complex macroevolutionary dynamics making it difficult to disentangle patterns of diversification associated with coevolutionary events.

2 | METHODS

2.1 | Taxa selection and data collection

Data on molecular phylogenies were collected for eight parasite groups covering simple and complex life cycles, including a diverse set of eukaryotic parasite taxa. This compilation was based upon (but not limited to) a search in ISI Web of Science^{TM} using the keywords string, ("Parasite AND Phylogeny AND Diversification"). Studies were selected according to taxonomic depth (i.e. phylogenies estimated for above species-level relationships, with the lowest level being Family and the highest level being Class), sampling bias (i.e. the completeness of the phylogeny according to the number of recognized and identified species for the studied taxonomic level, not being restricted to a particular geographic region), the availability of the data (e.g. time-calibrated phylogenetic trees, xml files, sequence alignments) and information on host–parasite associations and respective coevolutionary events. If no files were made publicly available, an effort was made to contact the authors and directly request data. From each study, we recorded information on the parasites' life cycle, host range level, major host transitions (shift to a new host belonging to at least a different nonrelated genus), as well as any other major life-history events used by the authors to explain diversification of the studied taxa. Parasites' life cycles were classified as simple whenever only one host is required to complete an entire generation, or as complex if more than one host is required. Parasites' host range was classified as narrow (specialized parasites that only infect a limited number of closely related host species), or as broad (generalist parasites that infect several unrelated host species).

2.2 | Phylogenetic tree inference

Time-calibrated trees had to be inferred for three of the eight studies. To do so, we used Bayesian Markov chain Monte Carlo (MCMC) joint estimation of phylogeny and divergence times in BEAST v.2.3.0 (Bouckaert et al., 2014). Estimates of all three components of the site model were inferred during the MCMC analysis, using reversible jump. The method was implemented in the bModelTest package of BEAST (Bouckaert & Drummond, 2017). The birth–death constant speciation and extinction rates model (Gernhard, 2008; Nee et al., 1994) was set as a tree prior, with an uncorrelated lognormal relaxed model for the rate variation among branches. Calibration points were used as described by the authors or based on recent divergence times estimates. For each analysis, three independent MCMC analyses were run for 100 million generations with a sampling frequency of 10,000. For the Myxozoa dataset, two analyses were run for 200 million generations with sampling frequencies of 20,000. We checked for posterior convergence in Tracer v.1.6 (Rambaut et al., 2014) and combined the sampled trees in LogCombiner v.2.3.0 (Bouckaert et al., 2014) discarding the first 10% of samples in each tree file. A maximum clade credibility tree and 95% confidence intervals of ages were calculated using TreeAnnotator v.2.3.0 (Bouckaert et al., 2014). For time-calibrated trees already available online, where appropriate, outgroups were removed using the function *drop.tip* from the ape package (Paradis et al., 2004) in R (R Core Team, 2018). Diversification analyses were performed over the maximum clade credibility tree from the log-combined BEAST analysis.

2.3 | Diversification analysis

Diversification rates were estimated for each time-calibrated tree using two Bayesian methods; BAMM (Bayesian analysis of macroevolutionary mixtures; Rabosky, 2014; Rabosky, Donnellan et al., 2014) and BayesRate (Silvestro et al., 2011). Both of these methods allow for variable rate birth–death models and are able to account for nonrandom taxon sampling, but also employ different likelihood functions. For each of our eight phylogenies, we first explored speciation and extinction dynamics across the entire tree using BAMM and the R package BAMMtools (Rabosky, Grundler et al., 2014). We then directly tested the hypothesis that clades resulting from either host-specific associations or major coevolutionary events, that is host switch and codivergence, had increased net diversification rate using BayesRate (Silvestro et al., 2011). The main advantage of BAMM is that it allows for the detection of heterogeneity by modelling rates through time and among clades, without a priori definition of clades, estimating possible shifts in diversification rate by exploring by default a wide range of models. When coupled with BAMMtools functionalities, it provides a wide range of analysis and visualization of the inferred diversification dynamics. BayesRate, on the other hand, was specifically designed for hypothesis-based testing of diversification regimes, allowing for clade-specific rate estimation for predefined clades. Although there have been concerns raised regarding BAMM's performance (Moore et al., 2016; Meyer & Wiens, 2018; Meyer et al., 2018; but see Rabosky et al., 2017; Rabosky, 2018), estimating diversification rate shifts is a complex task to say the least, with different methods implementing different likelihood functions, each of them having their own limitations regarding accurate estimates of speciation and extinction rates (Stadler, 2013). By implementing these two complementary approaches, we aim at finding robust inferences based on the data while acknowledging their limitations and strengths. To generate comparable metrics between BAMM and BayesRate, we focused on estimating speciation and extinction rates across the whole tree, and then, when relevant, for specific clades, while taking into account the influence of nonrandom incomplete sampling.

We started by estimating shifts in diversification dynamics through time across the whole tree with BAMM v.2.5 which implements a birth–death model using the reversible jump MCMC. Appropriate prior values were determined for each tree using the function *setBAMMpriors* from BAMMtools package. We used the default value on the prior probability of the number of diversification rate shifts ($\gamma = 1$). BAMM analyses were run for 10 million generations, sampling parameters every 2,000. MCMC convergence was assessed by plotting the log-likelihood trace after discarding 10% and estimating the ESS values using the coda package (Plummer et al., 2006). We then estimated the number of rate shifts and analysed the effect of the prior on the posterior. The overall best model was determined by assessing the model with the highest Bayes factor (BF) relative to the model with zero rate shifts. A Bayes factor between 3.2 and 10 was considered substantial support, whereas values above 10 were interpreted as a strong support, in favour of model M1 (Kass & Raftery, 1995; but see Mitchell & Rabosky, 2017). Results were summarized by means of the Bayesian credible set of shift configurations (CSS), mean phylorate plot and shift configuration with the maximum a posteriori (MAP) probability. All analyses performed with functions of the BAMMtools package were conducted in the R statistical computing environment.

We then used BayesRate, a Python implemented Bayesian MCMC testing variation in diversification rates among predefined tree partitions. For each tree, partitions were defined according to information given in each study on either host-specific associations or the occurrence of major coevolutionary events; these included major host transitions, codispersal events and differential host switching rates among clades. Whenever information regarding these events was missing, partitions were defined according to the different major host lineages exploited by the parasite; however, the origin of the host–parasite associations in those cases could have resulted from a host switch or host tracking (see Table S1; Figures S1–S9). Models were defined by linking or unlinking tree partitions in order to test for heterogeneity in diversification rates. The marginal likelihoods of different diversification models were calculated using thermodynamic integration with six beta distributed scaling classes. A search of one million generations was performed, sampling parameters every 50th generation after 10,000 generations of burn-in. Adequacy of MCMC performance was confirmed using Tracer, and for cases where MCMC performed poorly (i.e. low efficiency of the sampling values, ESS), 10 million generations were sampled every 100th generation. For the myxozoa dataset, analyses were run for 20 to 50 million generations. Relative support of each alternative model was assessed using BF calculated between the model of higher marginal likelihood (M1) and all the other models as BF = 2(M1–M2). BF values were interpreted as described above.

Both BAMM and BayesRate have the ability to model taxon absence, which is known to affect the accuracy of speciation and extinction rate estimates (Höhna, 2014). We incorporated bias based on described taxonomic diversity. However, we acknowledge that when it comes to parasites, even described taxonomic diversity is also likewise biased since species coverage is highly uneven (Jorge & Poulin, 2018; Pappalardo et al., 2020). Estimates of the extant known diversity of each taxon were collected from a variety of sources, including most recent publications and/or available databases (Files S1–S8 for additional details). BAMM enables us to account for bias in two different ways, using a single global sampling proportion, which assumes random incomplete taxa sampling across the phylogeny, or by specifying clade-specific proportions including a backbone sampling fraction, thus taking into account nonrandom incomplete taxa sampling. To infer the impact of sampling bias and the different ways this can be considered, we ran models in BAMM accounting for different sampling strategies: (a) global sampling fraction = 1 (a.k.a. no bias), (b) backbone sampling proportions as estimated by higher taxonomic levels sampled (number of genera) and (c) compared inferences to the species-level sampling bias. In comparison, BayesRate accounts for incomplete sampling bias by assigning clade-specific sampling proportions; here, we followed a similar approach to BAMM and repeated analyses assuming no bias (complete sampling for each clade) and compared this with clade-specific sampling estimates. To minimize incongruences between models, we specified bias proportions in BAMM for the same clades as defined in BayesRate.

3 | RESULTS

In total, we analysed eight datasets covering a wide range of parasitic groups (from unicellular to multicellular organisms), varying in life-history traits, that is different life cycles and variable level of host range. Each dataset included between 65 and 649 parasite taxa (Table 1), summing up to a total of 1,403 terminal branches. Estimates of speciation and extinction were very similar between the two used methods (Table 1). For the parasitic fungi tree, there were significant differences in rate estimates between the two methods. But this tree had also the highest sampling bias (i.e. 8% of known species were represented in the tree). When we did not account for any sampling bias, there was no significant difference in rate estimates between the two methods.

3.1 | Patterns of parasite diversification

Parasite diversification differed across the studied parasite taxa both in terms of rates and in terms of patterns. Older groups were found to have lower diversification rate estimates, and these groups also presented lower speciation rates (Table 1). Heterogeneity in diversification rates across the various trees was only detected in parasites with simple life cycles, as none of the methods found support for a model with shift in rates for complex life cycle parasites. According to BAMM, which estimates rate heterogeneity across a phylogeny without having to prespecify the number or location of rate regimes, in three of the four groups with a simple life cycle BF favoured a model with a rate shift (albeit not too high), relative to the null model of 0 rate shifts (Table 2). According to BayesRate, where we prespecify clade-specific partitions, BF favoured only two datasets as having significant shifts in diversification rates. However, one of them, that is the feather mites where BayesRate supported a model with heterogeneity in diversification rates, was not supported by BAMM estimates (Table 2).

TABLE 1 Parasite groups included in this study, life-history traits (i.e. life cycle and host specificity), number of taxa included in the analysis, level of bias (number of species in the study/number of known species) and mean age of the most recent common ancestor (MRCA, in million years ago), along with the speciation, and extinction rates estimates identified across the entire tree from BAMM and BayesRate (estimates were derived from the null model where all clades in the partition are assumed to have the same rate of evolution)

	Life-history traits							
Parasite group	Life cycle	Host range	No. taxa	Bias	MRCA	Method	Speciation rate	Extinction rate
Avian body lice	**Simple**	**Narrow**	**75**	**0.22**	**29.348**	BAMM	0.365 (0.296–0.458)	0.079 (0.015–0.192)
						BayesRate	0.375 (0.270–0.511)	0.111 (5.29E^{-6}–0.273)
Feather mites	**Simple**	**Narrow**	**133**	**0.29**	**85.434**	BAMM	0.173 (0.119–0.245)	0.089 (0.014–0.182)
						BayesRate	0.208 (0.137–0.283)	0.134 (0.047–0.225)
Fungi	**Simple**	**Narrow**[a]	**105**	**0.08**	**69.711**	BAMM	0.253 (0.176–0.410)	0.124 (0.029–0.313)
						BayesRate	0.732 (0.468–1.014)	0.672 (0.400–0.969)
Parasitic wasps	**Simple**	**Narrow**	**195**	**0.24**	**72.046**	BAMM	0.204 (0.156–0.267)	0.096 (0.032–0.175)
						BayesRate	0.258 (0.186–0.336)	0.166 (0.076–0.258)
Myxozoa	Complex	Narrow[a]	649	0.25	589.503	BAMM	0.120 (0.104–0.135)	0.100 (0.082–0.117)
						BayesRate	0.130 (0.112–0.149)	0.110 (0.091–0.131)
Nematoda	Complex[b]	Broad	65	0.08	325.268	BAMM	0.085 (0.057–0.118)	0.068 (0.036–0.103)
						BayesRate	0.103 (0.053–0.162)	0.085 (0.030–0.150)
Haemosporidia (Vertebrate Host)	Complex	Broad[c]	102	0.19	76.587	BAMM	0.228 (0.163–0.304)	0.148 (0.068–0.236)
						BayesRate	0.257 (0.160–0.355)	0.183 (0.074–0.303)
Haemosporidia (Invertebrate Host)						BAMM	0.223 (0.157–0.297)	0.143 (0.060–0.229)
						BayesRate	0.233 (0.145–0.326)	0.147 (0.041–0.258)
Cestoda	Complex	Broad[c]	79	0.20	192.128	BAMM	0.097 (0.069–0.130)	0.070 (0.037–0.108)
						BayesRate	0.101 (0.060–0.148)	0.072 (0.022–0.125)

Note: Parasite groups where evidence for heterogeneity in diversification rates was found are highlighted in bold.

[a] Majority of the taxa in the group are specialist; however, some taxa are generalist.

[b] Majority of the taxa in the group use more than one host; however, some groups have simple life cycles.

[c] Majority of the taxa in the group are generalist; however, some taxa are specialist.

3.2 | Major host transitions and parasite diversification

To investigate whether major host transitions were associated with parasite diversification, we conducted a series of clade-specific diversification analyses using BayesRate, while taking into account BAMM estimates across the whole tree and respective CSS. As presented above, there was no evidence for shifts in diversification rate for any of the complex life cycle parasites included in this study. Although the original authors of each study have identified several major host transitions shaping parasites' evolutionary history, based on our estimates, none of these major events seem to have influenced their diversification patterns. Among the trees of parasites where we found evidence of heterogeneity in diversification rates, we found some level of support for major host transitions events being associated with shifts in diversification.

In the avian body lice, there was congruence between the location of the main host transition event shaping their evolutionary history and a shift in diversification rates. The phylogeny of avian body lice of the family Goniodidae presents a major host switch from Galliformes to Columbiformes (Johnson et al., 2011), which was used to define the two partitions tested: (1) lice infecting Galliformes and (2) lice infecting mainly Columbiformes (Figure 1a). BayesRates supported the model with different rates between the clades associated with the major host transition as the best model, and there was a significant difference in net diversification between the two partitions (Figure 1a; Table S1). BAMM analysis also supported the model with one shift in rates, with the shift located along the branch that originated from the host switch as having the configuration with the highest posterior probability within the 95% CSS configurations sampled with BAMM ($f = 0.31$; Figure S1).

The proctophyllodid feather mites that infect passerine birds have a complex evolutionary history with several inferred major coevolutionary events including major host transitions and codispersion, where the parasite was a passenger on host intercontinental dispersals and thus disperses alongside its host (Klimov et al., 2017). Following Klimov et al.'s (2017) cophylogenetic analyses, seven partitions were defined: (I) clade that originated after the ancient host shift from the ancestor of passerines to hummingbirds, (II) sister clade to that host shift that infects Passeriformes but also other birds, (III)

TABLE 2 Model comparisons based on Bayes Factor (BF) for both BAMM and BayesRate analyses with and without accounting for bias

	Species-level sampling bias			No sampling bias		
	BAMM		BayesRate	BAMM		BayesRate
	No. of rates (BF)	CSS (No. of shifts)	No. of rates (BF)	No. of rates (BF)	CSS (No. of shifts)	No. of rates (BF)
Avian body lice	**2 (13.10)**	5 (0:2)	2 (2.63)	**2 (2,802)**	2 (1)	**2 (8.75)**
Feather mites	2 (1.87)	6 (0:2)	**2 (9.29)**	**2 (996.8)**	6 (1:2)	**2 (66.86)**
Fungi	**3 (213.12)**	9 (1:2)	**2 (17.04)**	**3 (215.6)**	20 (1:2)	**2 (7.25)**
Parasitic wasps	**2 (15.61)**	4 (0:1)	1[a]	1	3 (0:1)	1[a]
Myxozoa	1	4 (0:1)	1[c]	**20 (22,153.0)**	2,977 (0:5)	1[b]
Nematoda	1	1 (0)	1	1	1 (0)	1
Haemosporidia (vertebrate host)	1	1 (0)	1	1	1 (0)	1
Haemosporidia (invertebrate host)	1	2 (0:1)	1			1
Cestoda	1	1 (0)	1	1	1 (0)	1

Note: For BAMM, the number of rates of the best model and respective BF are shown, together with the number of distinct shift configurations composing the 95% credible rate shift configuration sampled including the range of core shifts (lowest: highest). For BayesRate, the number of rates of the model with highest marginal likelihood and the respective BF are shown. BF is shown relative to a null model with 0 shifts for cases of BF > 1. See Methods for details on BF calculation for each method. Parasite groups where evidence for heterogeneity in diversification rates (BF > 3.2) was found are highlighted in bold.

[a] Although the null model has the lowest marginal likelihood, net diversification and speciation were significantly different between partitions.

[b] Although the null model has the lowest marginal likelihood, the net diversification is significantly different between partitions.

[c] Although the null model has the lowest marginal likelihood, speciation and extinction rates are significantly different between partitions.

clade infecting Suboscine passeriform birds in Old World, (IV) clade infecting oscine birds (Passerida and Corvida) in New World, (V) clade infecting the superfamilies Muscicapoidea and Passeroidea in Old World, but also one lineage that originated from a host switch to an unrelated host, (VI) clade resulting from parasite codispersal with their hosts from Old World to New World, (VII) mites mainly infecting finch hosts, but also including a host switch to unrelated hosts (Figure 1b). Although in BayesRate estimates the model with equal rates among clades was rejected in favour of a model with different rates among clades (Table 2), the best model included two different rates (I + II+III + IV+V + VI, VII) with a shift in rates being associated only with the one of the major host associations (Table S1). BAMM did not find support for a model with variable rates; however, the same clade VII was associated with the second highest shift configuration estimated in the 95% CSS ($f = 0.23$; Figure S2).

A group with support from both methods for heterogeneity in rates was the Sclerotiniaceae fungal plant parasites. Navaud et al. (2018) estimated diversification regimes with BAMM and performed cophylogenetic analyses and defined three macroevolutionary events which they have associated with the degree of host range association patterns. However, their estimates did not account for nonrandom sampling bias, and in fact, the species present in the phylogeny represent only 8% of the known species. The regimes defined by the authors also correspond to differences in rate of host switches, and the same three clades were defined for the clade-specific analysis with BayesRate: (I) clade with the lowest level of host switches, (II) clade with intermediate level host switches, and higher level of sorting or loss, (II) clade with higher levels of host switches (Figure 1c). The model with two different rates between clade III, with the highestnumber of host switches and lower congruence (having a higher rate), and the other clades (clade I and II), had higher support than the null model and the one where the three clades have a different rate (Table 2; Table S1). For BAMM, the best model was one with two shifts in rates, and according to the 95% CSS, all configurations included shifts basal to clade II (intermediate level of host switching) and clade III (higher host switch rates) (Figure 1c; Figure S3).

The last group with support for variable rates were the wasp parasitoid of ants, belonging to the family Eucharitidae. Murray et al. (2013) inferred several major host shifts. We defined five partitions accordingly: (I) an early wasp clade infecting the ancestral Formicinae hosts, (II) clade originated from host switch from Formicinae to Myrmicinae ant hosts, (III) clade originated from host switch from Formicinae to Ponerinae, (IV) clade including wasps infecting the ancestral Formicinae hosts, (V) clade originated from host switch from Formicinae to Ponerinae or Ectatomminae and that displays wider host range. There was no support for a model with variable rates according to BayesRate for the defined clades, but there were significant differences in net diversification and speciation between some clades (Table S1). BAMM analyses supported a model with variable rates across the tree, favouring a model with one rate shift (Figure 1d). The location of the shift with the highest probability within the 95% CSS was estimated along the branch from which originated clade V after a main host switch (f = 0.53; Figure S4). A second most frequently sampled configuration had a switch within that group associated with the colonization of New

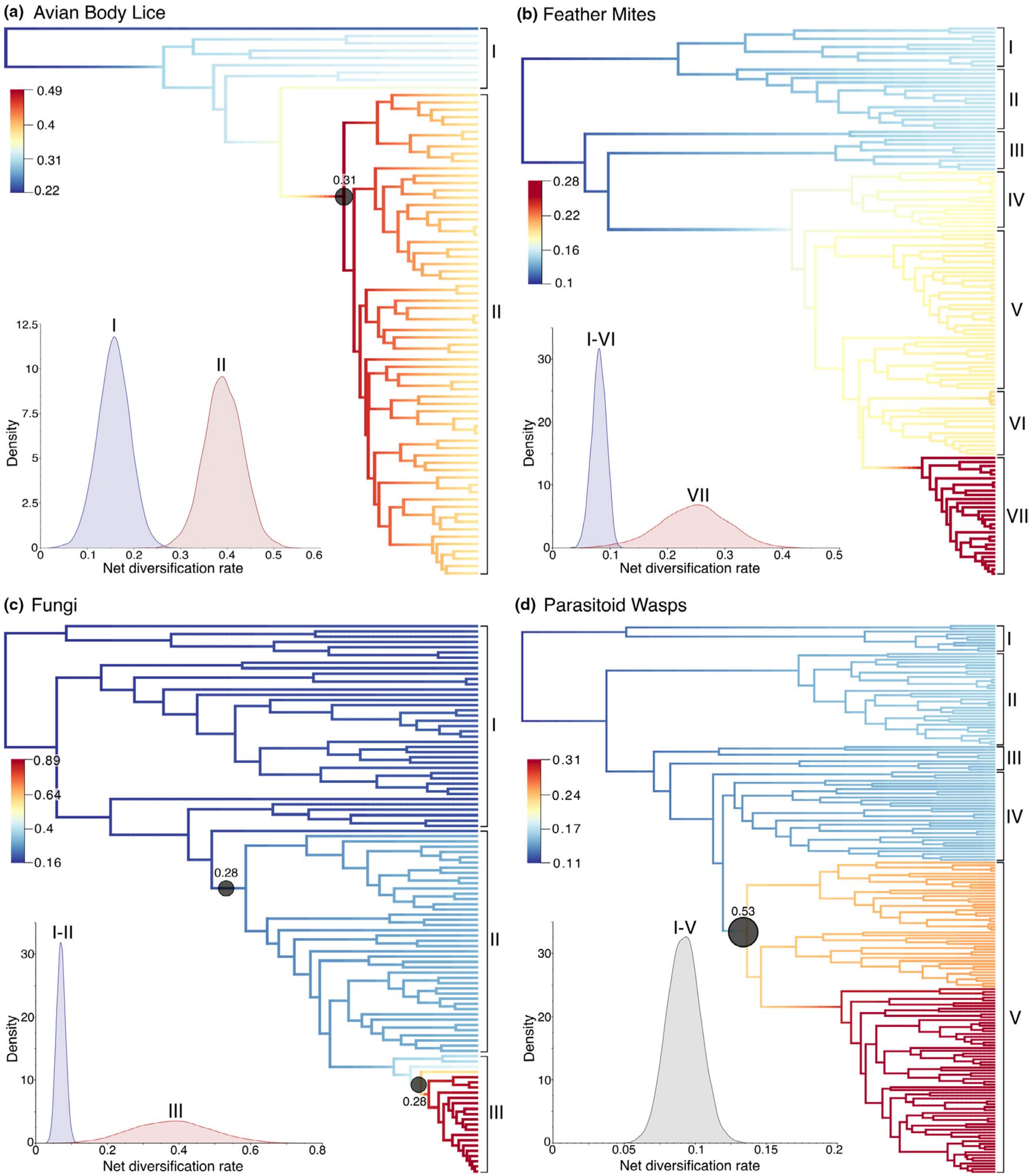

FIGURE 1 Summary of the results obtained for diversification estimates in BAMM and BayesRate for datasets in which heterogeneous rates of diversification were detected. (a) Avian body lice, (b) feather mites, (c) fungi, (d) parasitoid wasps. The phylogenetic trees are mean phylorate plots obtained from BAMM analysis, the colours of these display the mean diversification rate across all shift configurations sampled during simulation of the posterior along each branch of the phylogeny (cool colours = slow, warm colours = fast). The rates of these are indicated by the rainbow legend. Black dots on the trees (a, c and d) indicate the distinct shift configurations with the highest posterior probability, the frequency of which is given next to the black dot. Clades identified (to the right of the tree) are labelled according to partitions in BayesRate. These are based on either coevolutionary events or host associations derived from the original studies. At the bottom left of each tree is the marginal distribution of net diversification rate (speciation minus extinction) with posterior rate estimates (relative densities) relative to the best model from BayesRate analysis, or the model with significant differences in net diversification between clades (see Results for details)

World Neotropical regions ($f = 0.3$). No other host switch seemed to be linked to shifts in diversification in this group.

3.3 | Sampling bias

All the datasets only represented a small fraction of the total known species in the taxa they were meant to cover, with backbone values as low as 8% and the most complete phylogeny having a sampling proportion of 29% (Table 1). Failing to account for sampling bias led to a clear underestimation of rates in both methods. Additionally, there were also differences in the estimated patterns of diversification. When neglecting incomplete sampling bias, we found a difference in BAMM estimates (Figure S10). For the cases where previously we did not find support for a shift in rates, that is parasites with a complex life cycle, for one group, the Myxozoa, there was support for several shifts across the tree (Table 2). For the trees of parasites with a simple life cycle, there was a strong support for a model with a shift in rates for the feather mites (BF = 996.8, with bias BF = 1.87). On the other hand, for the parasitoid wasps there was no support for a shift in rates, contrary to what was found when considering sampling bias. For BayesRate estimates, apart from the differences in rate estimates which were significantly lower when bias was not accounted for, there was no difference in the number of rates detected when considering sampling bias.

4 | DISCUSSION

Although studies on parasite evolutionary history often make claims about the main drivers of parasite diversification, the number of studies that in fact quantify the rate of diversification is almost nonexistent. Here, we have provided the first comparative study investigating common drivers of parasite diversification rates. Although the dynamics of parasite diversification appear to reflect a mosaic pattern of different macroevolutionary histories, and not all groups display heterogeneity in diversification rates across the tree, we have highlighted the role that life-history traits, such as the level of complexity of the parasite life cycle, play on a macroevolutionary scale. Indeed, a consistent pattern uncovered through our analysis is that lifecycle complexity appears to constrain the effects, if any, of major host transitions on macroevolution. We have also highlighted the importance of accounting for random and nonrandom sampling bias, and the influence this has upon speciation and extinction estimates across a range of phylogenetic trees.

4.1 | Do patterns of diversification differ across parasites with different life-history traits?

We found support that life cycle complexity may be linked to differences in patterns of parasite diversification. Parasites requiring multiple hosts to complete their ontogenetic development did not display any shift in rates of diversification among clades of the tree, whereas parasites that use only one host did, suggesting that host range and use had an influence upon speciation and extinction dynamics. Although we found support for the importance of biotic interactions on diversification (Jezkova & Wiens, 2017; Yoder & Nuismer, 2010), we must acknowledge that this is not the only factor in play, the outcome of this impact on diversification is ultimately shaped by abiotic factors (Aguilée et al., 2018) and also clade-specific diversity-dependence (Condamine et al., 2018). With an increase in complexity of a parasite life cycle, there is an increase in the number of biotic and abiotic interactions which could potentially interact and shape macroevolution. There are suggestions that narrower niches may increase speciation without impacting extinction and support higher long-term diversity (Aguilée et al., 2018), which is compatible with the notion of simple and specialized life cycles.

Where we found no evidence for heterogeneous rates of diversification the possibility exists that there are differences in diversification rates but these have been eroded through time. Such patterns are consistent with the notion of temporal stages of diversification where after an initial period of adaptive radiation where species are formed, in a later stage when species fill their niche, speciation rate decreases whereas extinction increases (Aguilée et al., 2018). However, in the case of parasites, successful host switches could potentially break such a cycle even if not all host switches are followed by shifts in diversification. The observed variation in the number of species among clades of parasite trees can be the result of differences in speciation, extinction or both, but can also be due to random variation (Ricklefs, 2007). Such random variation is not a process of diversification but can result in differences in diversity among clades. If there is in fact heterogeneity and we failed to detect it, one reason could be the size of the phylogenetic tree, which affects the accuracy of diversification estimates (Silvestro et al., 2011). Another factor, probably more relevant, is the estimation of extinction which complicates the model of diversification. Extinction may have dampened the signal of past diversification dynamics, and information on extinct lineages may be necessary to properly infer diversification (Herrera, 2017). Notably, older parasite clades displayed lower diversification rates, and with the exception of haemosporidian parasites, all complex life cycle groups dated back more than 190 Ma. The pattern of time dependency of diversification rates is a known feature of the tree of life (Diaz et al., 2019; Moen & Morlon, 2014). However, this is also a common issue of using extant time trees to infer past evolutionary histories (Louca & Pennell, 2020).

4.2 | Major host transitions as the main driver of parasite diversification?

The expectation that coevolution can be an important promoter of parasite diversification has been assumed for a long period of time (e.g. Ehrlich & Raven, 1964). However, it has proven difficult to link patterns of diversification with direct mechanisms linked to coevolution (Althoff et al., 2014). Indeed, the role of coevolution in diversification may vary depending on the type of interaction and its scale (Althoff et al., 2014; Hembry et al., 2014; Yoder & Nuismer, 2010). Under the model of escape and radiate coevolution, coevolution is not the direct mechanism driving diversification, but rather an indirect link, where counteradaptation of the parasite to the new host could initiate population-level processes generating diversification. The incorporation of a new host followed by speciation as a consequence of a major host transition representing a new ecological opportunity can result in an increase in parasite richness due to local adaptation, genetic divergence and habitat (aka host) fragmentation. Moreover, by overcoming host defences, parasites develop key innovations which in turn can drive increases in diversification rates (Braga et al., 2018). We found limited support for this hypothesis, since not all major host transitions were followed by a shift in rates of diversification. On top of this, we also identified other coevolutionary events that occur in parasites, namely codispersion, where a parasite undergoes continental dispersion alongside its host, and can also contribute to patterns of parasite diversification. Thus, whether or not parasite diversification actually occurs through speciation and diversification of the parasite, or is simply a by-product of host tracking and codiversification with the host is important to consider in parasite evolutionary studies. This is not surprising given that by tracking its host the parasite may also become isolated, and the same population-level process named under the escape-radiate hypothesis may also take place. New ecological opportunities promoting diversification in free-living organisms may indirectly promote diversification in their associated parasites, which could be especially true for directly transmitted parasites.

Our results suggest that interactions between life-history traits and major host transitions during parasite evolutionary history may result in different patterns of diversification across parasitic groups. Life-history traits may dictate the extent to which species-level processes add up to produce macroevolutionary changes. New ecological opportunities such as transitions to a new host influence both within and between species-level processes. Intimate associations and their coevolutionary interplay influence population dynamics (gene flow, migration, mutation, extinction) and higher-level dynamics associated with cospeciation and shifts in resource use (key innovations, extinction and speciation). Life cycle complexity and the level of specialization also influence species-level processes, for example higher gene flow in generalists (e.g. Archie & Ezenwa, 2011) versus population fragmentation in specialists with a simple life cycle (e.g. Clayton & Johnson, 2003). Furthermore, our results indicate that life-history traits may in turn influence the outcome of new ecological opportunities and could possibly even restrict it (Poulin, 2007; Ricklefs, 2010; Yoder & Nuismer, 2010). For example, the evolutionary history of haemosporidian parasites comprises several examples of host switches producing new species (Pacheco et al., 2018; Ricklefs et al., 2014), but we did not detect any shift in rates of diversification among clades. Pacheco et al. (2018) detected clade differences in mtDNA rates, which could have been affected by major vector switches. Although there seems to be a causal link between rates of molecular evolution and net diversification (Lanfear et al., 2010, but see ref. Goldie et al., 2011), we found no correlation between diversification and vector host switches.

Altogether, the only predictable outcomes of complex host–parasite associations are taxon-dependent differences in evolution, resulting in taxon-dependent patterns of parasite diversification. Further studies investigating the patterns of diversification of a higher number of parasites varying in life-history traits are required to support or refute our findings on the possible correlates of parasite diversification.

4.3 | How incomplete sampling may influence our ability to answer the above questions

One of the main impacts of the low proportion of species sampled in any diversification analysis is that it can restrict our ability to detect diversification rate shifts. The completeness of a phylogeny is constrained by both the number of recognized or identified species and by sampling. We have to acknowledge that for parasites, studies on diversification are mainly limited by our knowledge of species-level diversity and sampling effort. Ultimately, there are two main barriers, the unknown species diversity and the genetic characterization of the known diversity, which in both cases lag far behind our knowledge of free-living organisms on Earth (Jorge & Poulin, 2018; Pappalardo et al., 2020; Poulin et al., 2019). So, although we have tried to uncover some general patterns of parasite diversification dynamics, we still have a long way to go until we can confidently support the inferences made here. Despite this, we have shown the importance of accounting for nonrandom incomplete sampling bias on real data, and the influence this has upon diversification rate estimates. We have demonstrated that accounting for bias can change the outcome of an analysis. We detected significant increases in rate estimates when comparing to estimates based on analysis that did not account for sampling bias. This is unsurprising given the low proportion of sampling and that there was large bias between clades within phylogenies. By using a comparative framework, we highlighted common patterns among the investigated trees, some of which are consistent across analyses with or without accounting for sampling bias and suggest a real biological generality.

The study of the patterns and processes of diversification, while very engaging for evolutionary biologists, has proven highly challenging. Inferring extinction rates for a group of organisms such as parasites is fraught with uncertainty, given that we have only very rough estimates of the number of extant parasite species and an almost nonexistent fossil record. In this study, we have demonstrated how to approach such limitations by taking advantage of different methods to infer diversification rates across trees. Common to all datasets, those where we uncovered heterogeneity in diversification rates were defined by life-history traits relating to the number of hosts used to complete the life cycle, that is one-host life cycle. Parasites with complex life histories and multihost life cycles may be under different evolutionary pressures shaping their diversification process. Although the results presented in this study may not confirm causality between life-history traits and major host transitions on diversification patterns, congruence in results provide new insights into the complex dynamics that shape parasite diversification. Ultimately, parasite life-history traits provide important clues regarding the likely patterns of diversification. Our study also supports the notion that diversification is not a product of a simple factor but the joint outcome of multiple factors. We provide the first comparative investigation of parasite diversification patterns, revealing their complex nature and insight into the influence life-history traits and major coevolutionary events have upon diversification rates.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data supporting this study have been uploaded as part of the Tables S1-S2, Files S1–S8 and Figures S1–S9.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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