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Host and parasite morphology influence congruence between host and parasite phylogenies ☆

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ABSTRACT

Comparisons of host and parasite phylogenies often show varying degrees of phylogenetic congruence. However, few studies have rigorously explored the factors driving this variation. Multiple factors such as host or parasite morphology may govern the degree of phylogenetic congruence. An ideal analysis for understanding the factors correlated with congruence would focus on a diverse host–parasite system for increased variation and statistical power. In this study, we focused on the *Brueelia*-complex, a diverse and widespread group of feather lice that primarily parasitise songbirds. We generated a molecular phylogeny of the lice and compared this tree with a phylogeny of their avian hosts. We also tested for the contribution of each host–parasite association to the overall congruence. The two trees overall were significantly congruent, but the contribution of individual associations to this congruence varied. To understand this variation, we developed a novel approach to test whether host, parasite or biogeographic factors were statistically associated with patterns of congruence. Both host plumage dimorphism and parasite ecomorphology were associated with patterns of congruence, whereas host body size, other plumage traits and biogeography were not. Our results lay the framework for future studies to further elucidate how these factors influence the process of host–parasite coevolution.

1. Introduction

Congruence between the phylogenies of interacting species such as hosts and parasites can be shaped by a variety of factors. In some cases, parasites are so closely linked to their hosts that when the hosts diverge, the parasites diverge as well, leading to perfect or near-perfect congruence between the host and parasite phylogenetic trees (Hafner et al., 1994; Clayton et al., 2004). Host divergence, however, is not the only factor influencing parasite diversification. Host and parasite morphology, physiology, behaviour, ecology or biogeography may also influence patterns of host–parasite phylogenetic congruence (Weckstein, 2004; Vinarski et al., 2007; Gorrell and Schulte-Hostedde, 2008; Bruyndonckx et al., 2009; du Toit et al., 2013; Bell et al., 2016). These factors can influence host–switching, parasite duplication and parasite extinction, all of which can erode congruence between phylogenies of associated hosts and parasites (Page and Charleston, 1998; Clayton et al., 2016).

Over the last few decades, many studies have indicated that host–parasite systems show enormous variation in levels of phylogenetic congruence (Hoberg and Brooks, 2008; Bochkov et al., 2011; de Vienne et al., 2013). For example, Weiblen and Bush (2002) found that mutualistic fig wasps had more congruent relationships with the fig hosts than did parasitic wasps. Mutualistic fig wasps are responsible for pollinating their host plants, whereas parasitic fig

☆ *Note:* Novel nucleotide sequence data reported in this paper are available in GenBank under the accession numbers KY619306–KY619672. Relevant data files are available from the University of Illinois Data Bank under DOI https://doi.org/10.13012/B2IDB-2011663_V1.

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wasps are not. Weiblen and Bush (2002) hypothesised that host reproductive constraints imposed on mutualistic but not parasitic fig wasps best explained the differences in phylogenetic congruence. In another study, Peterson et al. (2010) showed that biogeographic history may explain variable cophylogenetic patterns between *Nothofagus* (southern beech) trees and parasitic *Cyttaria* fungus. Whereas, Desdevises et al. (2002) argued that ecological factors (e.g. host sociality) best explain the observed cophylogenetic variation between monogenean parasites and their teleost fish hosts.

Although these studies each provide unique insights, they do not each contain replicated variation in congruence required for more robust statistical analyses. A broadly-focused and statistical comparative approach is needed to more rigorously identify potential factors associated with phylogenetically congruent lineages. An ideal study using this approach would investigate a parasite group that exhibits substantial variation in congruence, and is also sufficiently large and diverse to provide statistical power. Such an approach could provide a "roadmap for linking comparative phylogenetic patterns" (Weber and Agrawal, 2012) to causal hypotheses that could be tested at micro-evolutionary time scales by first asking the question: Are there particular biotic or abiotic factors that contribute to host–parasite phylogenetic congruence? Here, we address this question with a novel approach that evaluates whether particular factors are repeatedly associated with phylogenetically congruent host–parasite associations. To statistically evaluate congruence, we use the distance-based method ParaFit (Legendre et al., 2002). This approach assesses the global (overall) congruence between host and parasite phylogenies by testing whether the two groups of taxa are randomly associated with respect to their phylogenetic distances. ParaFit also tests for the statistical contribution of each host–parasite association to the overall congruence, such that individual host–parasite associations can be categorised as those contributing significantly to congruence and those that do not. We then use this categorisation as a dependent variable in a generalised logistic regression that includes host, parasite and biogeographic factors to evaluate which factors contribute the most to predicting whether a host–parasite association will significantly contribute to congruence or not.

In this study, we focus on *Brueelia*-complex lice, a monophyletic and diverse clade of feather lice found mainly on perching birds (Aves: Passeriformes), but also occurring on a few other avian groups such as woodpeckers, toucans and bee-eaters (Price et al., 2003; Bush et al., 2016). With over 400 described species, this complex contains nearly one-tenth of all known species of lice (Phthiraptera). In addition to being speciose, lice in this complex are morphologically and behaviourally diverse (Bartlow et al., 2016). Similar to other feather lice, members of the *Brueelia*-complex are permanent, obligate ectoparasites that complete their entire life-cycle on the surface of their host. They eat downy feathers and skin, and glue their eggs to feathers with a glandular cement (Marshall, 1981; Clayton et al., 2016). Within the *Brueelia*-complex, there are four different louse "ecomorphs" that have morphological and behavioural adaptations specialised for living on different microhabitats of the host (Bush et al., 2016), and some of these lice are phoretic on hippoboscid flies (Bartlow et al., 2016). Differences in dispersal ability likely lead to dramatic differences in host–specificity across this complex, with some species being confined to a single host species and others parasitizing hosts in up to 11 different host families (Price et al., 2003; Bush et al., 2016).

Based on this underlying knowledge of the ecology and natural history of lice, we include host, parasite and biogeographic factors in a statistical model for predicting whether a host–parasite association is likely to contribute significantly to overall phylogenetic congruence. First, several aspects of host morphology potentially influence host–parasite phylogenetic congruence. Host size may influence the level of congruence with associated feather lice because smaller hosts typically harbour fewer lice, increasing the probability of extinction (Rozsa, 1997; Clayton and Walther, 2001), which would in turn erode phylogenetic congruence between the lice and their hosts (Page, 1994; Johnson et al., 2003). Host colour may also influence parasite host specificity. For example, some ectoparasites use cryptic colouration to escape host defense by avoiding visual detection (Bush et al., 2010). However, the ability of ectoparasites to survive across multiple host species may be compromised on hosts with more variable plumage such as those that are sexually dimorphic or have a variety of plumage patches with different colours.

Parasite morphology may also influence phylogenetic congruence. For example, feather lice of birds can be divided into four "ecomorphs" that specialise on different microhabitats of the host: "head", "wing", "body" and "generalist" lice (Johnson et al., 2012). These ecomorphs are morphologically distinct, primarily a reflection of their strategies for avoiding host preening behaviour (Clay, 1951, 1949; Clayton, 1991; Clayton et al., 2003). These ecomorphs also often have different levels of host specificity, which in turn influences congruence between host and parasite trees. For example, a study of wing and body lice of New World doves showed that the phylogeny of body lice is more congruent with host phylogeny than that of wing lice on the same hosts (Johnson and Clayton, 2003). In this case, wing lice are able to disperse amongst host species by hitching rides (phoresis) on highly mobile and generalist hippoboscid flies (Diptera), whereas body lice are not as capable of phoresis (Harbison and Clayton, 2011), which could explain differences in phylogenetic congruence between these two parasite ecomorphs.

Finally, there may be other factors extrinsic to the hosts and parasites that influence congruence between trees, and these may have a biogeographic basis. For example, climatic factors such as humidity can influence parasite population size (Moyer et al., 2002), which in turn may influence extinction (sorting) events (Clayton et al., 2003). The phylogeny of the *Brueelia*-complex is also known to be correlated with biogeography (Bush et al., 2016), so we included this factor in our generalised model to potentially account for any such effects.

To carry out this study, we generated a new phylogenetic tree for the *Brueelia*-complex based on molecular sequence data from 380 lice. This data set builds upon a mitochondrial cytochrome oxidase subunit I *(Cox1)* and nuclear elongation factor 1 subunit alpha (EF-1α) locus data set from Bush et al. (2015, 2016) by incorporating additional louse samples and sequences from three additional nuclear loci to improve and expand the previous phylogeny. Using this phylogenetic hypothesis, we assessed operational taxonomic units (OTUs) in the *Brueelia*-complex, and used this "species tree" for cophylogenetic analysis with ParaFit, to compare the louse phylogeny with host phylogenies from Jetz et al. (2012). As part of the cophylogenetic analysis, we identified particular host–parasite associations that contribute to the pattern of congruence between the two trees. We then generated a generalised multivariate logistic regression model to determine which host, parasite and biogeography factors best predict congruent versus non-congruent host–parasite associations.

2. Materials and methods

2.1. Sample collection and sequencing

Lice were collected from birds in the field using pyrethrin powder dusting or ethyl acetate fumigation methods (Clayton and Drown, 2001), immediately placed in 95% ethanol, and stored at −80 °C. We extracted DNA from louse specimens using a Qiagen

Blood and Tissue Kit or QIAamp DNA Micro Kit (Qiagen, Valencia, CA, USA) adapted from standard protocols: we used a sterilised needle to partially sever the louse head from the body, which exposes the internal body cavity to proteinase K and buffer solution in which the specimen was incubated at 55 °C for ~48 h (Johnson et al., 2003; Valim and Weckstein, 2012). This procedure allows for DNA extraction while preserving the exoskeleton of the louse as a voucher specimen for morphological examination and archival preservation. Using PCR, we amplified the mitochondrial locus *Cox1*, and the following nuclear loci: EF-1α, a hypothetical protein (HYP), di-phosphinositol polyphosphate phosphohydrolase (DIPP), and transmembrane emp24 domain-containing protein 6 (TMEDE6). We used the primers L6225 and H7005 for *Cox1* (Hafner et al., 1994), EF1-For3 and EF1-Cho-10 for EF-1α (Danforth and Ji, 1998), BR50-181L and BR50-621R for HYP, BR62-295L and BR62-429R for DIPP, and BR69-190F and BR69-432R for TMEDE6 (Sweet et al., 2014). Segments were amplified with GoTaq (Promega, Madison, WI, USA), NEB 5X Master Mix (New England Biolabs, Ipswich, MA, USA) or Platinum taq (Invitrogen, Carlsbad, CA, USA) kits according to reaction and annealing temperature protocols outlined in Bush et al. (2016) and Sweet et al. (2014). PCR products were confirmed on a 2% agarose gel, and purified using Qiagen PCR Purifications kits or ExoSAP-IT according to standard protocols (Affymetrix, Inc., Santa Clara, CA, USA). We sequenced purified PCR products using an ABI Prism BigDye Terminator kit, with fragments run on an AB 3730× capillary sequencer (Applied Biosystems, Foster City, CA, USA). Geneious v.8.1.2 (Biomatter Ltd., Auckland, NZ) or Sequencher v.5.1 were used to manually resolve complementary chromatograms and remove primer sequences. We also downloaded existing GenBank sequence data for *Cox1* and EF-1α generated from Bush et al. (2015, 2016). In total, our data set contained 380 *Brueelia*-complex louse samples and 30 outgroup louse samples.

2.2. Phylogenetic analysis

We aligned each locus individually in Geneious v.8.1.2 using default gap parameters in the MAFFT plugin (Katoh et al., 2002), and because all loci were protein-coding we verified that each locus was within the reading frame. A highly variable intron region was removed from DIPP, and only the exon regions in the alignment were used. All five alignments were concatenated into a single data matrix in Geneious. We only included samples that had both *Cox1* and EF-1α data to ensure the data matrix was complete for at least two loci.

Using the concatenated alignment, we used corrected Akaike Information Criterion (AICc; Sugiura, 1978) to test for optimal partitioning schemes and substitution models in PartitionFinder v.1.1.1 (Lanfear et al., 2012) with a greedy search algorithm and linked branch lengths. We ran the programmed search only through substitution models implemented in MrBayes, and treated each gene as a potential partition.

To estimate a phylogeny for the lice, a partitioned Bayesian analysis was run with MrBayes v.3.2.6 (Ronquist and Huelsenbeck, 2003) on the CIPRES Scientific Gateway (Miller et al., 2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees, in: Proceedings of the Gateway Computing Environments Workshop (GCE). New Orleans, LA, USA). We ran two Markov Chain Monte Carlo (MCMC) runs of four chains and 45 million generations, sampling every 1000 generations. The resulting .p files were viewed in Tracer v.1.5 (http://tree.bio.ed.ac.uk/software/tracer/) to assess parameter convergence based on Effective Sample Size (ESS) values, and topological convergence was assessed by analysing tree (.t) files in the R (https://www.r-project.org/) package RWTY (Warren et al., 2017). Based on these assessments we discarded the first 50% of generations as a burn-in, and summarised the tree distributions with an MCC tree using the –mcct option in the DendropPy programme SumTrees (https://github.com/jeetsukumaran/DendroPy). We viewed all resulting tree files in Figtree v.1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/), and rooted the trees on *Chelopistes* sp. ex. *Ortalis canicollis* (Chaco Chachalaca louse) and *Oxylipeurus chiniri* ex. *Ortalis vetula* (Plain Chachalaca louse).

2.3. OTU analysis

For cophylogenetic studies at the species level, it is important to objectively assess the appropriate number of OTUs in a data set. This is especially important for studies involving parasitic lice, because lice (and parasites in general) often harbour cryptic taxonomic diversity. To address this issue, we used a Bayesian general mixed Yule-coalescent (bGMYC) model to test for OTUs (Reid and Carstens, 2012). Because this method requires ultrametric trees from a single locus, we ran BEAST v.1.8.2 on the *Cox1* alignment (Drummond et al., 2012). BEAST was run for 100 million MCMC generations, sampling every 10,000 generations. We ran the MCMC with a Yule process tree prior under an uncorrelated lognormal relaxed clock and a GTR + I + Γ substitution model with uniform substitution priors. All other priors were set as defaults. The resulting .log file was viewed in Tracer and based on this assessment the first 10% of generations were discarded as burn-in. For bGMYC, we sampled 100 random trees from the post-burnin posterior distribution of trees from the BEAST analysis. All 100 trees were rooted as in the concatenated topologies, and then the outgroup taxa were removed from each tree. Using this distribution of trees as input, we ran bGMYC using the APE and bGMYC packages in R (Paradis et al., 2004). We tested for appropriate parameter values by running bGMYC with the single.phy function with several different parameter sets, and checked convergence with parameter likelihood plots. Based on these assessments we ran bGMYC on the distribution of trees for 20,000 MCMC generations, discarding the first 50% (10,000) as burn-in, and with thinning set to 10. A conservative conspecific probability cutoff of ≥0.95 was chosen, meaning that taxa clustering together with a posterior probability of ≥0.95 were considered conspecific.

2.4. Cophylogenetic analysis

We conducted the cophylogenetic analysis using the distance-based method ParaFit in APE (Legendre et al., 2002). ParaFit takes a host tree, parasite tree and association matrix as input, and tests for random associations between the host and parasite trees. Significant ParaFit results indicate overall phylogenetic congruence between the two groups of organisms. ParaFit also tests for the contribution of each host–parasite association (link) to global (i.e. overall) congruence. A significant value for a particular host–parasite association indicates that the link is a congruent evolutionary association. More specifically, a significant value means that the contribution of that particular association to the overall congruence is higher than under randomly permutated associations. For the parasite phylogeny in our ParaFit analysis, we used the MCC tree from the post-burnin posterior distribution of trees from the MrBayes analysis. We collapsed conspecific tips in the MCC tree based on the bGMYC analysis and removed outgroup taxa with the "drop.tip" command in *ape*. For the host tree, we downloaded 100 trees including all host taxa from the "Hackett All Species" source on birdtree.org (Hackett et al., 2008; Jetz et al., 2012), rooting all trees on *Gallus gallus* (Red Junglefowl). From this distribution of trees, we obtained an MCC tree with SumTrees and removed the outgroup taxon. The host and parasite trees were converted into patristic distance matrices using the "cophenetic" function in *ape*, and the patristic distance matrices were sorted according to the host–parasite association matrix.

We ran ParaFit for 999 permutations, using the Cailliez correction for negative eigenvalues, and tested for the contribution of individual host–parasite links with the ParaFitLink1 and ParaFitLink2 tests. Because the individual link tests are multiple tests, we corrected the individual link test statistics using the Benjamini and Hochberg (1995) correction for false discovery rate using the "p.adjust" command in R. Finally, since many of the internal parasite nodes were poorly supported, we ran ParaFit on a distribution of 100 random post-burnin *Brueelia*-complex Bayesian trees (with conspecific tips collapsed based on the bGMYC analysis) and the 100 host trees from Jetz et al. (2012). Using these trees as input, we ran ParaFit 100 times using a custom R script, and tested the global statistic for each run. We then summarised the results of the 100 runs to get a sense for how consistent the ParaFit results were across this distribution of parasite and host trees. All ParaFit R code is available at https://github.com/adsweet/cophylogenetic_analyses.

2.5. Trait correlation

We examined the correlations between various host, parasite and biogeographic variables, and individual link statistics (host–parasite associations). For each correlation test, we classified link statistics for each host–parasite association as either significant or not. A host–parasite association was considered significant if its corrected *P* value was $\leq$0.05 under the ParaFitLink1 individual link test. We only used the ParaFitLink1 results because this statistic is more appropriate for host–parasite systems where a given species of parasite may occur on multiple host species (Legendre et al., 2002; Pérez-Escobar et al., 2015). We tested for correlations by including all factors in a logistic regression analysis. To test for the optimal independent variables to include in the model, we used the step procedure ("stepAIC") in the MASS R package (Venables and Ripley, 2002) and choose the best model based on the AIC. A logistic regression was then run using the variables identified in the best model.

In the logistic regression model, we included host, louse and biogeographic traits as independent variables. First, host morphological traits might influence phylogenetic congruence. Specifically, we investigated host body size and two plumage patterns: (i) sexual dichromatism and (ii) general colour pattern. For host body size, we used mean body mass data from Dunning (1993) and del Hoyo et al. (1992–2013). For sexual dichromatism, we classified bird species as monomorphic (males and females with visibly similar plumage patterns) or dimorphic (males and females with visibly different plumage patterns). Within species of birds that were monomorphic, we classified plumage patterns as follows: species that were largely one colour were considered solid, species with plumage that is largely two colours were considered bicoloured, and species with large patches of three or more colours of plumage were coded as multicoloured. One author (S.E. Bush) conducted all classifications using illustrations in del Hoyo et al. (1992–2013), blind to the results of the cophylogenetic analyses. We also included an aspect of louse morphology in the model, specifically louse ecomorph. Each link was categorised as including either a head, wing, body, or generalist ecomorph louse, based on a morphological examination of representative specimens from each louse OTU. These were classified by one of the authors (D.R. Gustafsson), blind to the results of the cophylogenetic analysis. Finally, we included biogeographic region in the model. We categorised lice as belonging to one of six biogeographic regions according to Bush et al. (2016): Nearctic, Australia, Indo-Malayan, Afrotropical, Palearctic or Neotropical. Because songbirds are globally distributed, this level of biogeographic delimitation is appropriate for testing general biogeographical patterns in their lice. Furthermore, we expected a relationship between cophylogenetic associations and biogeography because Bush et al. (2016) found significant phylogenetic signal for these biogeographic areas when mapped onto their *Brueelia*-complex phylogeny.

3. Results

3.1. Phylogenetic inference

For this study, we sequenced lice in the *Brueelia*-complex from 68 avian host families, 163 host genera and 258 host species. All samples had sequence data for *Cox1* and EF-1α, an additional 103 samples had sequence data for HYP (70.4% missing data), 133 samples had data for TMEDE6 (67.5% missing data), and 85 samples had data for DIPP (75.6% missing data). We obtained sequence data for outgroup lice from 18 different host families (Supplementary Table S1). Novel sequence data are available from GenBank with accession numbers KY619306–KY619672. Using these sequence data, we produced an alignment for each locus including 385 bp for COI (243 variable sites, 219 parsimony-informative sites), 347 bp for EF-1α (152 variable sites, 127 parsimony-informative sites), 388 bp for HYP (264 variable sites, 209 parsimony-informative sites), 145 bp for DIPP without the intron region (94 variable sites, 51 parsimony-informative sites), and 261 bp for TMEDE6 (127 variable sites, 93 parsimony-informative sites). The final concatenated alignment with additional GenBank data included 378 taxa and was 1,526 bp in length. PartitionFinder indicated the optimal partitioning scheme was three separate partitions for *Cox1*, HYP and DIPP, and a combined partition for EF-1α and TMEDE6. AICc indicated the best substitution models were a GTR + I + Γ model for *Cox1*, GTR + I + Γ for HYP, K80 + Γ for DIPP, and SYM + I + Γ for TMEDE6/EF-1α.

Tracer indicated ESS values were >200 for parameter values from the MrBayes MCMC chains, and RWTY indicated an average standard deviation of split frequencies <0.01 post-burnin. These results suggest that the chains converged to stationarity. Based on the MrBayes analysis, 46% of nodes from the MCC tree received posterior probability (PP) support $\geq$0.95, 30% of nodes received PP support of 1.0, and 33% of nodes received support $\leq$0.5 PP (Supplementary Fig. S1). The MrBayes tree from Bush et al. (2016) had a similar distribution of support values, with 44% of nodes receiving $\geq$0.95 PP, 28% of nodes with support of 1.0 PP, and 31% of nodes with support $\leq$0.5. However, the tree generated from this current study provided generally greater support for backbone nodes.

3.2. Cophylogenetic analysis

The bGMYC OTU analysis with a 0.95 conspecific probability cut-off indicated 174 distinct ingroup taxonomic units out of 348 total ingroup samples. This is considerably more OTUs than identified by the Bush et al. (2016) bGMYC analysis (114 OTUs), even accounting for additional samples included in our data set. However, our result is similar to their 5% delimitation cut-off (166 OTUs). Accounting for louse OTUs associated with multiple host species and host species associated with multiple louse OTUs, our final comparative data set included 283 host–parasite links. The ParaFit analysis indicated global congruence between the MCC phylogenies of *Brueelia*-complex lice and their hosts (ParaFit Global = 1,204,852, $P = 0.0001$). All ParaFitGlobal tests on the distribution of 100 parasite and host trees were also significant ($\alpha = 0.05$). Of the 283 host–parasite links, the ParaFit individual link tests indicated 141 (49.8%) significantly contributed to the global congruence after correcting for multiple tests with the Benjamini-Hochberg false discovery rate ($\alpha = 0.05$; Fig. 1, Supplementary Table S2). The ParaFitLink1 and ParaFitLink2 tests gave similar *P* values for each link.

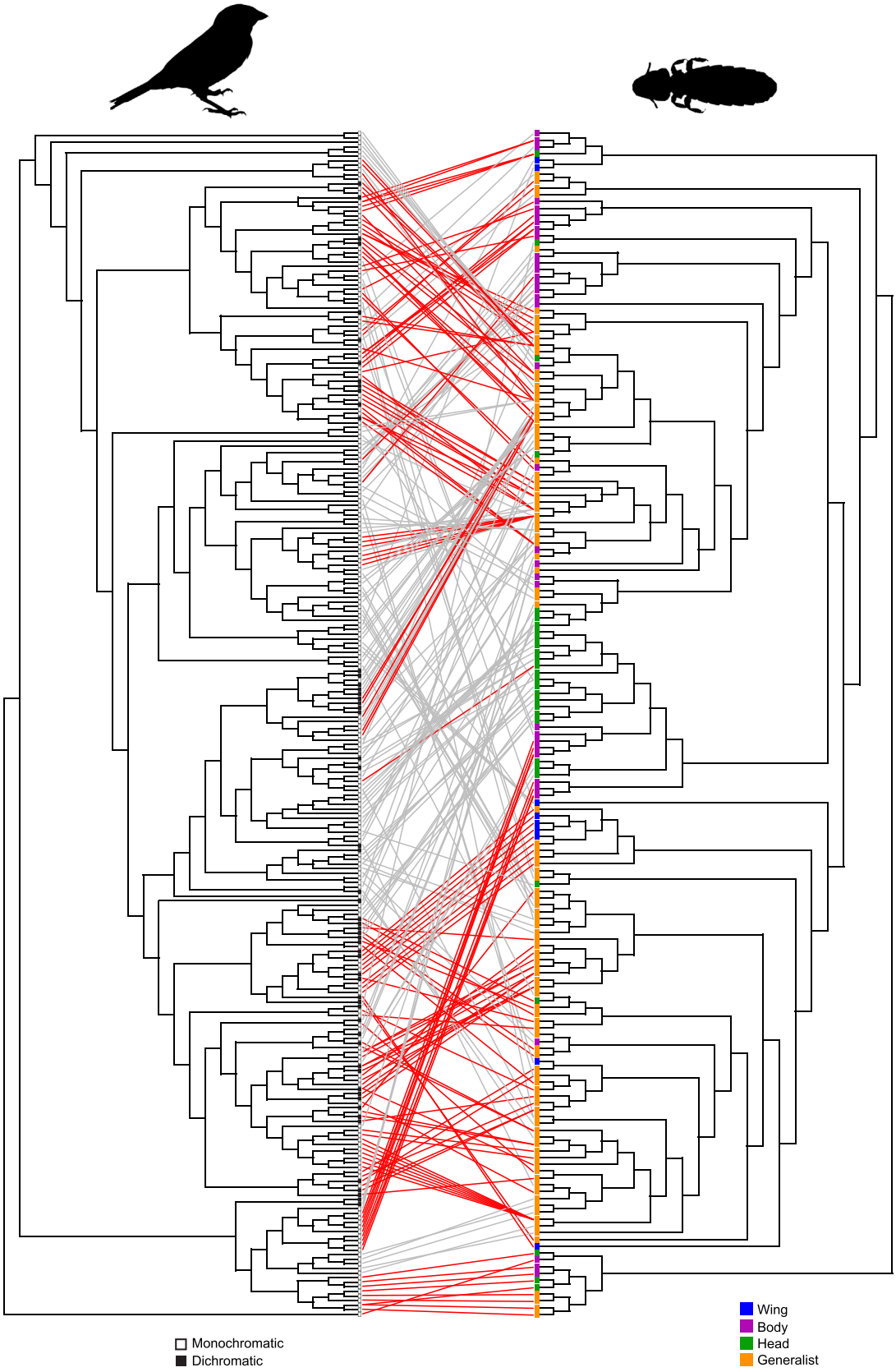

Fig. 1. Tanglegram showing the associations between *Brueelia*-complex lice and their avian hosts. The louse phylogeny is a cladogram of the Maximum Clade Credibility summary tree from a MrBayes analysis with tips collapsed into operational taxonomic units, and the bird tree is a cladogram of the Maximum Clade Credibility tree summarised from a distribution of trees downloaded from birdtree.org. Boxes at the tips are coloured according to ecomorph for the lice and sexual dichromatism for the birds. Lines between tips indicate associated taxa, with red lines indicating significant links according to the ParaFitLink1 test after correction. The two phylogenies have been rotated to minimise crossing lines.

3.3. Traits correlated with significant links

The step AIC procedure indicated that ecomorph ($P = 0.02$) and sexual dichromatism ($P = 0.0003$) were the best factors to include in the generalised linear model describing patterns of congruent host–parasite associations. The other factors (biogeography, body mass and host colour pattern) were not recovered as optimal factors. A logistic regression model with the optimal factors indicated the louse head ecomorph was significantly associated with incongruent associations, and that host sexual dichromatism was significantly associated with congruent associations (Table 1).

4. Discussion

In this study, we generated a new molecular phylogenetic tree for avian feather lice in the *Brueelia*-complex, based on four nuclear loci and one mitochondrial locus. This tree was significantly congruent with a tree for their avian hosts. However, the degree of congruence varied dramatically across the tree, with some host–parasite associations contributing significantly to the overall congruence and others not contributing to overall congruence (Fig. 1). To further understand this variability, we used a novel approach to examine the relationship of host–parasite associations ("links") with various factors including host morphology, parasite morphology and biogeography. The results of such a large-scale cophylogenetic meta-analysis provided important insights into the evolutionary dynamics of the *Brueelia*-complex system, and this approach will likely be useful for other host–parasite systems.

Several aspects of host morphology may be extremely important in limiting the ability of lice to switch between host species. One feature that has been demonstrated to play an important role in bird-louse interactions is host body size (Tompkins and Clayton, 1999; Bush and Clayton, 2006; Tryjanowski et al., 2007). Given that the hosts of lice in the *Brueelia*-complex vary dramatically in body size, we expected to find sufficient variation to detect an effect if it exists. However, we found no evidence for an effect of host body size on whether a particular host–parasite association contributes to overall congruence between host and parasite trees. This may be because lice are more likely to become extinct on smaller birds, whereas they are more likely to successfully switch hosts between larger avian hosts (Rozsa, 1997). Both scenarios would erode congruence between host and parasite trees. However, these scenarios operate in opposite directions, and thus if the two scenarios were relatively similar in magnitude, they would prevent any correlation between host body size and phylogenetic congruence. It is also possible that larger or smaller body size per se is not the relevant factor. Instead, similarity in body sizes amongst sympatric hosts may be the more important underlying factor. For example, Clayton et al. (2003) showed that dove lice occurring on multiple host species tended to occur on hosts more similar in size than expected by chance, irrespective of whether the hosts were large or small. In this respect, lice on large and small hosts might contribute equally to overall congruence between host and parasite trees, and this is what we found. However, our study cannot address the role of relative differences in size, as was hypothesised by Clayton et al. (2003).

Table 1
Results from a logistic regression analysis including louse ecomorph and host sexual dichromatism as independent variables. The dependent variable is significant association according to the corrected ParaFitLink1 test (significant/not significant).

		Odds ratio (95% CI)	*P*
Ecomorph			
	Body (reference)	1.15 (0.63–2.14)	0.66
	Generalist	1.04 (0.76–1.43)	0.82
	Head	0.21 (0.09–0.45)	0.0001[a]
	Wing	0.63 (1.14–3.81)	0.44
Sexually dimorphic		2.06 (1.14–3.81)	0.02[a]

CI, confidence interval.
[a] Significant at $\alpha = 0.05$.

A second major feature of host morphology that may influence host switching is a match between host and parasite colouration. Comparative evidence indicates that the colouration of lice matches that of their avian hosts, presumably as a form of camouflage to avoid preening (Bush et al., 2010). The ability of lice to avoid preening may be compromised on host species where males and females are differently coloured, or on host plumage that is not uniformly coloured. We examined how several different host plumage patterns related to phylogenetic congruence, and found that bird species with strikingly distinct sexually dimorphic plumage were significantly associated with congruent links. However, other patterns of plumage colouration were not significantly associated with congruent links.

Initially, we were surprised that lice associated with dimorphic host species were most commonly associated with congruent links. One might expect that lice parasitizing dimorphic hosts would be capable of parasitizing host species of many different colours, and thus could switch between host species. However, most dimorphic bird species have brightly coloured males and dull-coloured females. In contrast, many monomorphic bird species have dull colouration in both sexes, and these colours are similar across related host species (Mayr, 1942; Peterson, 1996). Thus, lice might switch between and parasitise many monomorphic host species because they are similarly coloured. For example, *Catharus* thrushes are both cryptic and monomorphic, and all the host associations with *Catharus* thrushes were non-significant links. In contrast, amongst strikingly dimorphic species, male colouration patterns often differ dramatically amongst related bird species, perhaps limiting the ability of lice to switch hosts. Under this scenario, dull-coloured females should have higher louse prevalence than their brightly-coloured male counterparts. Future comparative work focused on louse prevalence amongst different sexes for mono- and dimorphic bird species could address this hypothesis. The observation that other host plumage patterns are not significantly associated with congruent links indicates that lice are not more likely to co-diversify with birds of one particular plumage colour type. Additional studies are needed to determine whether differences in plumage colouration amongst related or sympatric hosts influence the ability of lice to switch between hosts.

Aspects of parasite ecology and morphology may also influence congruence between host and parasite trees. We examined how the ecomorphology of lice in the *Brueelia*-complex relates to phylogenetic congruence, and we found that different ecomorphs were not randomly distributed amongst congruent parts of the trees. In particular, head louse morphology was significantly correlated with incongruent associations. Amongst the lice on pigeons and doves, wing lice are phoretic and body lice are not, and this difference in phoretic dispersal is consistent with the cophylogenetic pattern differences observed between pigeons and their feather lice (Clayton et al., 2016). Some lice in the *Brueelia*-complex are phoretic (Bartlow et al., 2016), but the pattern of phoresis amongst different ecomorphs is more complex than that exhibited amongst lice on pigeons and doves. In the *Brueelia*-complex the different ecomorphs have evolved repeatedly, and lice in the genera *Bizarrifrons*, *Buerelius*, *Meropoecus* and *Sturnidoecus* appear to be head lice (Bush et al., 2016). Of these genera, phoresis is known to occur amongst *Sturnidoecus* spp. Phoresis may also occur amongst the other head lice listed above, but our understanding of phoresis in the *Brueelia*-complex is largely based on a small number of observational records. If head lice are more likely to engage in phoresis than other louse ecomorphs, then head lice may move

more frequently between host species and this could explain why head lice are more likely to be associated with non-congruent links. However, within the *Brueelia*-complex, phoresis is also known to occur amongst generalist lice (Bartlow et al., 2016; Bush et al., 2016), and our analysis indicated that generalist lice are more likely to be associated with congruent links. Ultimately, phoresis should be more rigorously explored as a factor that may drive phylogenetic incongruence. At present, however, this analysis cannot be conducted because there is insufficient information about the phoretic abilities of most louse species. There are also other possible modes of host-switching that could be explored such as hosts sharing nest holes or dust baths (Timm, 1983; Clayton et al., 2016).

Another explanation of the association between head louse morphology and non-congruent links is that head lice escape from preening by specialising on a region of the bird that hosts cannot preen. By altogether avoiding preening, this releases head lice from preening-imposed selection for cryptic colouration (Bush et al., 2010; Valim and Weckstein, 2012). Moreover, by specialising on an area of the host's body that cannot be preened, head lice could more easily parasitise a greater diversity of host species, which could allow these lice to either behave as host generalists or successfully host switch over macroevolutionary timescales. Another factor that may be important is that head lice infest a much smaller microhabitat (the head) than the other louse ecomorphs, and may therefore have lower population sizes (lower intensity) on an individual host. Small populations are at an increased risk of extinction (sorting events), which erodes phylogenetic congruence.

We chose the distance-based approach ParaFit to assess the relationship between patterns of host–parasite phylogenetic congruence and various biological factors. At present, ParaFit is the best method to use for this approach because it tests both overall congruence between two phylogenies and the contributions of individual host–parasite associations to the overall congruence. Although a significant association does not signify cospeciation, it does imply the overall congruence would be worse without that particular association. Whereas event-based cophylogenetic methods explicitly test for cospeciation, host-switching, etc. (e.g. Jane; Conow et al., 2010), these methods do not easily scale computationally to very large phylogenies needed to provide statistical power for the type of analysis used in this study. Furthermore, by focusing on individual host–parasite associations, we characterised aspects of those particular host or parasite species for inclusion in the statistical model (e.g. sexual dichromatism). Event-based methods (such as Jane) identify nodes or branches in trees associated with particular cophylogenetic events, but it is not immediately clear how to categorise those nodes with respect to host and parasite features. At a minimum, one would need to consider the ancestral states of each feature in any analysis.

We found that host–parasite congruence was significantly associated with sexual dichromatism in host plumage and with louse ecomorphology. Specifically, lice on species of birds with strikingly distinct sexually dimorphic plumage were more likely to have congruent host–parasite associations. Conversely, head lice were more likely to have incongruent associations with their hosts. We found no correlation between significant host–parasite associations and host body size, plumage patterns or biogeography. However, there is the potential for phylogenetic non-independence of the relevant host and parasite traits. Therefore, it is important to note that our results must be interpreted as potential correlation, and not as causation. Overall, this study reveals that host and parasite morphology may influence the degree of congruence between host and parasite evolutionary trees. Our study also points to traits that appear to be important over macroevolutionary time. Determining the mechanistic basis of these relationships will require further experimental and comparative studies.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.ijpara.2018.01.007.

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