Received: 17 July 2018 | Revised: 13 October 2018 | Accepted: 23 October 2018

DOI: 10.1111/mec.14937

ORIGINAL ARTICLE

WILEY MOLECULAR ECOLOGY

The role of parasite dispersal in shaping a host–parasite system at multiple evolutionary scales

Andrew D. Sweet | Kevin P. Johnson

Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, Champaign, Illinois

Correspondence
Andrew D. Sweet, Department of Entomology, Purdue University, West Lafayette, IN.
Email: sweet19@purdue.edu

Funding information
National Science Foundation, Division of Environmental Biology, Grant/Award Number: DEB-1239788 and DEB-1342604 ; UIUC Graduate College Dissertation Travel Grant; American Ornithological Society Student Research Award

Abstract

Parasite dispersal can shape host–parasite interactions at both deep and shallow timescales. One approach to understanding the effects of dispersal is to study parasite lineages that differ in dispersal capability but are from the same group of hosts. In this study, we compared phylogenetic and population genetic patterns of wing and body lice from ground-doves. Wing lice are more capable of dispersal than body lice. We sequenced full genomes of individual lice for multiple representatives of several wing and body louse species. From these data, we assembled genes for phylogenetic analysis and called SNPs for population genetic analysis. At the phylogenetic level, body lice showed more codivergence with their hosts than did wing lice. However, both wing and body lice exhibited some phylogenetic congruence with their hosts. Within species, body lice showed more population genetic structure than wing lice, although both types of lice showed some structure according to biogeography. Body lice also had significantly lower heterozygosity than wing lice, suggesting more inbreeding. Our results demonstrate that dispersal can shape a host–parasite system across evolutionary time, but also that other factors (e.g., host association and biogeography) can have varying degrees of influence on different groups of parasites and at different evolutionary scales.

KEYWORDS
avian lice, coevolution, doves, phylogenomics, population genomics

1 | INTRODUCTION

Dispersal, the movement of individuals away from their place of birth, is a fundamental ecological process. Although less well-studied than dispersal of free-living organisms, previous research has indicated that parasite dispersal can shape the nature of host–parasite interactions at both population (micro) and species-level (macro) scales (Criscione, 2008; McCoy, Boulinier, Chardine, Danchin, & Michalakis, 1999; McCoy, Boulinier, Tirard, & Michalakis, 2003; Poulin, 2007; Poulin, Krasnov, & Mouillot, 2011; Price, 1980; Stefka, Hoeck, Keller, & Smith, 2011). Parasites that are able to disperse effectively often have little population structure among different host populations or species (Dybdahl & Lively, 1996; Kochzius et al., 2009; McCoy, Boulinier, & Tirard, 2005). Dispersal can also facilitate parasite lineages in switching between different host species over evolutionary time (Clayton, Bush, & Johnson, 2004; Hoberg & Brooks, 2008; Page & Charleston, 1998).

Despite its importance, dispersal is not the only factor that can shape a host–parasite system. For example, host diversification, host ecology, host specificity and biogeography can all potentially drive host–parasite evolution in some systems (Barrett, Thrall, Burdon, & Linde, 2008; Martinu, Hypsa, & Stefka, 2018; Vinarski, Korallo, Krasnov, Shenbrot, & Poulin, 2007; Weckstein, 2004; Whiteman, Kimball, & Parker, 2007). Although there are many studies focused on these topics at either the microevolutionary or macroevolutionary scale (Criscione, Poulin, & Blouin, 2005; Cruaud & Rasplus, 2016; de Vienne et al., 2013), few studies have examined the effects of dispersal on both micro- and macroevolutionary patterns simultaneously

in the same host–parasite system (Bell, Calhoun, Hoberg, Demboski, & Cook, 2016; du Toit, Vuuren, Matthee, & Matthee, 2013; Huyse, Poulin, & Théron, 2005). Ideally, such an approach would compare "ecological replicate" parasites, that is, different lineages of parasites with similar life histories that are associated with the same group of hosts, but have some ecological variable (e.g., dispersal ability) that differs among the parasites (Clayton & Johnson, 2003; Marussich & Machado, 2007; Weiblen & Bush, 2002). Because hosts commonly harbour multiple types of similar parasites, there are many potential examples of ecologically replicate systems, including figs and fig-wasps (Marussich & Machado, 2007; Weiblen & Bush, 2002), parasitoid wasps (Hackett-Jones, Cobbold, & White, 2009), avian malarial parasites (Ricklefs, Fallon, & Bermingham, 2004) and helminth worms of mammals (Bordes & Morand, 2009). This framework can also be extended beyond host–parasite relationships to systems such as endosymbiotic bacteria of insects (Moran & Baumann, 2000) or plant–herbivore interactions (Ehrlich & Raven, 1964).

One model ecological replicate system comprises the wing and body lice (Insecta: Phthiraptera) of pigeons and doves (Aves: Columbidae) (Clayton & Johnson, 2003; Clayton, Bush, & Johnson, 2016; Johnson & Clayton, 2004). Both louse "ecomorphs" spend their entire life cycle on the host and consume downy feathers (Nelson & Murray, 1971). However, the two ecomorphs from pigeon and doves are not closely related (Johnson, Reed, Hammond Parker, Kim, & Clayton, 2007; Johnson, Shreve, & Smith, 2012; Johnson, Weckstein, Meyer, & Clayton, 2011), and they use different strategies to avoid host preening. Wing lice have an elongated body morphology that allows them to insert themselves between barbs in wing and tail feathers, whereas body lice burrow into the downy feathers close to the host's body to avoid being removed (Clayton, Lee, Tompkins, & Brodie, 1999). Importantly, the two ecomorphs of lice also differ in their dispersal abilities. Both are primarily transmitted vertically (from parent to offspring) or horizontally by direct contact (e.g., mating) (Clayton & Tompkins, 1994; Rothschild & Clay, 1952). However, wing lice can also use winged hippoboscid flies to disperse between host individuals or host species, a behaviour known as phoresy (Bartlow, Villa, Thompson, & Bush, 2016; Harbison, Bush, Malenke, & Clayton, 2008; Harbison, Jacobsen, & Clayton, 2009; Keirans, 1975). Hippoboscid flies are generalist blood-feeding parasites, with single fly species often recorded from multiple genera of pigeons and doves (Maa, 1969). Several individual wing lice can grasp to a single fly with their legs and mandibles and can then be transported by the fly to another host individual, perhaps resulting in the establishment of a new louse population. Although there is a record of body lice attached to hippoboscid flies in the wild (Couch, 1962), phoresy appears to be extremely rare in this ecomorph. Body lice have short legs that inhibit them from grasping to the flies. In an experimental study comparing the phoretic ability of wing and body lice from captive pigeons, no body lice were found attached to hippoboscid flies, whereas wing lice were attached to several flies (Harbison & Clayton, 2011).

The difference in dispersal ability between wing and body lice appears to have considerable effects over evolutionary time. Clayton and Johnson (2003) showed that wing lice have little cospeciation with their hosts and high levels of host switching compared to body lice from the same host species. Focusing within a louse species, Johnson, Williams, Drown, Adams, and Clayton (2002) and DiBlasi et al. (2018) demonstrated that wing lice have less population genetic structure than body lice. To build on this work, an ideal approach would integrate both phylogenetic and population genetic patterns for the same louse taxa, thus simultaneously providing macro- and microevolutionary perspectives of the pigeon and dove louse system. Sampling is also an important consideration for such a comparison. First, phylogenetic comparisons should utilize comprehensive taxonomic representation from a subset of taxa. A host or parasite phylogeny that is missing key lineages can result in misleading cophylogenetic patterns (Paterson, Wallis, Wallis, & Gray, 2000; Sweet, Boyd, & Johnson, 2016). Similarly, phenomena such as clade-limited host switching can produce seemingly congruent host and parasite phylogenies at broader (e.g., family-wide) taxonomic scales (Demastes et al., 2012; Jackson, Machado, Robbins, & Herre, 2008; Sorenson, Balakrishnan, & Payne, 2004). Second, sampling many genetic markers, rather than a single gene or set of a few genes, provides more power for phylogenetic and population genetic analyses (Delsuc, Brinkmann, & Philippe, 2005; Luikart, England, Tallmon, Jordan, & Taberlet, 2003). Whole genomic sequence data can be particularly useful, as it is possible to obtain markers for both levels of analysis from the same underlying data source (Cutter, 2013).

Here, we focus on the wing and body lice of small-bodied New World ground-doves, a monophyletic group of 17 dove species distributed from the southern United States to southern South America (Gibbs, Cox, & Cox, 2001; Pereira, Johnson, Clayton, & Baker, 2007; Sweet & Johnson, 2015). There are three described species of both wing (genus *Columbicola*) and body lice (genus *Physconelloides*) on this host group, although there are likely additional cryptic species (Price, Hellenthal, Palma, Johnson, & Clayton, 2003; Sweet & Johnson, 2016; Sweet et al., 2018). Both types of lice also form monophyletic groups within their respective genera (Johnson et al., 2007, 2011), which makes interpretation of evolutionary history straightforward. Obtaining genomic-level data is very feasible for these lice, as recently published genomic studies on avian lice have established pipelines for assembling data appropriate for both phylogenetic and population genetic analysis (Allen et al., 2017; Boyd et al., 2017; Sweet et al., 2018).

Over macroevolutionary timescales, we focus on two types of patterns in ground-dove lice: phylogenetic congruence and the relative timing of divergence between species. If dispersal is a major driver of host–parasite evolution, then we expect body lice to show more phylogenetic congruence and cospeciation with their hosts than do wing lice (Brooks & McLennan, 1991; Clayton & Johnson, 2003). Similarly, dispersal can influence the rate at which lineages of parasites diverge once two host lineages have speciated. If dispersal between host species is highly limited, as is the case for body lice, then we would expect these louse lineages to diverge and speciate at the same time as their host lineages

(Hafner & Page, 1995; Page, 1993). However, if dispersal between host species is less limited, then there may be a time lag between divergence and speciation of host lineages compared to their associated parasite lineages (Banks & Paterson, 2005; Hafner et al., 1994; Light & Hafner, 2007). Although this might be difficult to detect directly, we can predict that for an equivalent divergence event (i.e., two daughter lineages of wing and body lice on sister species of hosts), wing lice may show less overall genetic divergence than body lice, because their divergence is more likely to lag behind that of their hosts (Vogwill, Fenton, & Brockhurst, 2008). It may also be the case that host speciation strongly influences diversification of both parasite ecomorphs, irrespective of dispersal differences. If measures of phylogenetic congruence are correlated between wing and body lice from the same host species, this could indicate that host diversification influences wing and body lice in similar ways.

On an ecological (microevolutionary) timescale, comparative population structure and genetic diversity (heterozygosity) are informative for assessing the role of dispersal in host–parasite evolution. Parasite populations could be structured across several scales—for example, among host species or among biogeographic regions (Falk & Perkins, 2013; McCoy, Boulinier, Tirard, & Michalakis, 2001; Nieberding et al., 2008; Stefka et al., 2011; Sweet & Johnson, 2016). Because dispersal is local, we predict that differences in dispersal between wing and body lice should manifest themselves as population structure between host species but not necessarily as structure between biogeographic regions. Host dispersal itself is likely to be the strongest factor allowing lice to disperse between biogeographic regions, because lice are intimately tied to their hosts. In this case, host dispersal should affect parasite dispersal in similar ways between wing and body lice. In particular, we predict that body lice should show more population genetic structure among host species than wing lice (Johnson et al., 2002), but not necessarily more population structure among biogeographic regions. Dispersal may also contribute to genetic structure between louse populations (infrapopulations) on different host individuals of the same host species (DiBlasi et al., 2018; Koop, DeMatteo, Parker, & Whiteman, 2014). In this case, because dispersal is likely to be more limited for body lice, their infrapopulations are more likely to be highly inbred (Nadler, 1995). Thus, we predict that body lice will show lower levels of heterozygosity.

In this study, we address the question of whether the impacts of dispersal differences can be observed at both macro- and microevolutionary timescales by comparing phylogenomic and population genomic patterns between wing and body lice sampled from across the diversity of small New World ground-doves. To estimate these patterns, we use genome sequence data from multiple individuals of each wing and body louse species. These data include assemblies of over 1,000 nuclear genes and tens of thousands of single nucleotide polymorphisms (SNPs) called from these same genes. The results provide important insights into how dispersal shapes host–parasite interactions, and ultimately how ecological mechanisms link to evolutionary patterns.

2 | MATERIALS AND METHODS

2.1 | Sampling

Samples of wing (*Columbicola*) and body (*Physconelloides*) lice were collected from ground-doves in the field using pyrethrin powder dusting or fumigation methods as outlined in Clayton and Drown (2001). All collected specimens were immediately placed in 95% ethanol and stored long-term at −80°C. Each louse was then photographed as a voucher. Individual lice were then ground up in a 1.5-ml tube, and genomic DNA (gDNA) was extracted using reagents and a modified protocol of the Qiagen QIAamp DNA Micro Kit (Qiagen, Valencia, CA, USA). Our modification extended the duration of the incubation step to 48 hr, instead of the recommended 1–3 hr. The extractions were then quantified with a Qubit 3.0 Fluorometer (Invitrogen, Carlsbad, CA, USA) using the manufacturer's recommended protocols and reagents.

2.2 | Library preparation and sequencing

Total gDNA was fragmented on a Covaris M220 Focused-ultrasonicator (Covaris, Woburn, MA, USA) targeting a mean fragment size of 400 nt. The fragmented gDNA of each specimen was then constructed into a library for paired-end Illumina whole genome shotgun sequencing using a Hyper Library Preparation Kit (Kapa Biosystems, Wilmington, MA, USA). A 10-nt barcode was adapted to each library so that up to 16 individual libraries could be pooled and sequenced on a single Illumina lane (two lanes in total). The libraries were sequenced with the HISEQ4000 v1 sequencing kit for 151 cycles on an Illumina HiSeq4000 instrument. The sequencing resulted in 150-bp paired-end reads in fastq files generated in BCL2FASTQ v2.17.1.14. All library preparation and sequencing were carried out at the Roy J. Carver Biotechnology Center (University of Illinois, Urbana, IL, USA). We deposited the raw reads for 31 newly sequenced wing louse samples on the NCBI SRA database (accession SRP116697; BioProject PRJNA400795). We obtained additional raw genomic read data from NCBI's SRA database for five in-group (SRR3161921-SRR3161923, SRR3161930-SRR3161931) and four out-group *Columbicola* taxa (*C. columbae*: SRR3161917, *C. gracilicapitis*: SRR3161913, *C. macrourae*: SRR3161953, *C. veigasimoni*: SRR3161919) (Boyd et al., 2017). We also obtained raw sequence reads for 34 body louse individuals (*Physconelloides*) from the SRA database (SRP076185) (Sweet et al., 2018). These data represent all described ground-dove wing and body louse species, several potential cryptic species and most host species and biogeographic areas (Supporting Information Table S1).

We ran several quality control measures on the raw Illumina data. First, we removed duplicate read pairs using the fastqSplitDups script (https://github.com/McIntyre-Lab/mcscript and https://github.com/McIntyre-Lab/mclib). We then removed the Illumina sequencing adapters with FASTX_CLIPPER v0.014 from the FASTX-Toolkit (http://hannonlab.cshl.edu/fastx_toolkit). Finally, we removed the first 5 nt of the 5' ends of reads using FASTX_TRIMMER v0.014 and removed the 3' ends of reads until reaching a base with a phred score

≥28 using FASTQ_QUALITY_TRIMMER v0.014. Following quality control, we removed any reads less than 75 nt and analysed the cleaned libraries with FASTQC v0.11.5 (Babraham Bioinformatics) to check for additional errors.

2.3 | Sequence assembly

To assemble nuclear loci from genomic reads, we used an approach similar to the one detailed in Sweet et al. (2018), which maps lower coverage, multiplexed genomic data to reference loci from a closely related taxon. For our reference set of nuclear loci for wing lice, we used 1,039 exons of *Columbicola drowni* generated in Boyd et al. (2017) (raw data: SRR3161922). This data set was assembled de novo in aTRAM (Allen, Huang, Cronk, & Johnson, 2015) using orthologous protein-coding genes from the human body louse genome (*Pediculus humanus humanus*; Kirkness et al., 2010) as a set of target sequences. We mapped our newly generated *Columbicola* reads and the reads obtained from GenBank to the *C. drowni* references using BOWTIE2 (Langmead & Salzberg, 2012). We then created VCF files for each sample using SAMtools and BCFTOOLS (Li et al., 2009) and filtered out sites according to sequencing depth (<5 or >150) and quality (phred scores <28) using SAMTOOLS and the GENOME ANALYSIS TOOLKIT v3.7 (GATK; McKenna et al., 2010). The entire read mapping pipeline is detailed at https://github.com/adsweet/louse_genomes.git. For body lice, nuclear data were obtained using the same pipeline and software parameters, except that 1,095 loci from *P. emersoni* were used as the references for mapping.

In addition to the nuclear exons, we used aTRAM to assemble mitochondrial genes for ground-dove lice. To generate a set of target genes for wing lice, we mapped cleaned Illumina reads from *C. passerinae* (SRA accession SRR3161930) to annotated mitochondrial protein-coding genes of *Campanulotes compar* (pigeon body louse; GenBank accession AY968672) in GENEIOUS v8.1.2 (Biomatter, Ltd., Auckland, NZ). Our preliminary analyses indicated the *Campanulotes compar* mitochondrial genes were too divergent from *Columbicola* to be useful as target genes in aTRAM. Based on the mapping, we identified the *Columbicola* mitochondrial genes, extracted these regions and translated the sequences to amino acids. We used these protein sequences as our target set in aTRAM. We ran aTRAM for a single iteration using ABySS (Simpson et al., 2009) for de novo assembly. We also used one of several library fractions (1.5%, 4.7%, 15.6%, 50% or 100%), and for each library chose the minimum fraction that had uniform coverage above 20×. Because *Campanulotes compar* is more closely related to *Physconelloides*, we were able to obtain mitochondrial sequences of *Physconelloides* that were assembled in aTRAM using *Campanulotes compar* target sequences.

2.4 | Calling SNPs in widespread lice

To compare population structure between wing and body lice across multiple host species, we focused on the most widespread (i.e., least host-specific) species of wing and body lice. For wing lice, we called SNPs jointly for *C. passerinae* with GATK following the "Best Practices" guide (Van der Auwera et al., 2013; https://software.broadinstitute.org/gatk/best-practices/). We used *C. drowni* loci as a reference and filtered out SNP calls with QD (quality by depth) <2.0, FS (Fisher strand test)>60.0, MQ (mapping quality) <40.0 and MQRankSum (mapping quality rank sum test) <−12.5. SNPs were called for body lice with the same approach using *P. emersoni* as the reference.

2.5 | Phylogenetic estimation

We applied similar approaches for estimating phylogenetic relationships in both wing and body lice. First, we aligned each nuclear locus in MAFFT (--auto; Katoh, Misawa, Kuma, & Miyata, 2002) and removed columns with only ambiguous sequences ("N"). We concatenated all alignments using SEQUENCEMATRIX (Vaidya, Lohman, & Meier, 2011) and tested for optimal partitioning schemes and substitution models with the rcluster search in PARTITIONFINDER v2.1.1 (Lanfear, Calcott, Kainer, Mayer, & Stamatakis, 2014; Lanfear, Frandsen, Wright, Senfeld, & Calcott, 2017). We selected optimal partitions based on the Akaike information criterion (AIC; Akaike, 1974). From the partitioned concatenated alignment, we estimated the best likelihood tree and 250 rapid bootstrap replicates in RAXML v8.1.3 (Stamatakis, 2006). We also estimated phylogenies using coalescent-based methods, which account for discrepancies between gene and species trees due to Incomplete Lineage Sorting. For these analyses, we first estimated gene trees in RAXML with a GTR +Γ substitution model for each gene alignment. We then summarize the gene trees in ASTRAL v4.10.6 with local posteriori probability branch support (Mirarab & Warnow, 2015; Sayyari & Mirarab, 2016).

We also estimated mitochondrial phylogenies from the assembled mitochondrial genes. As with the nuclear data, we aligned the mitochondrial genes in MAFFT, tested for optimal partitioning and model schemes based on the AIC in PartitionFinder and estimated a phylogeny from the concatenated alignment with 250 rapid bootstrap replicates in RAXML.

We also used the mitochondrial data to estimate the number of operational taxonomic units (OTUs). First, we used the COI alignment in the web version of the automatic barcode discovery method (ABGD; http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html; Puillandre, Lambert, Brouillet, & Achaz, 2012), which tests for interspecific boundaries based on the distribution of genetic distances from a barcode gene. We used default parameters (P_{min} – 0.001, P_{max} = 0.1, Steps = 10, Relative gap width = 1.5, Bins = 20) and three distance models (uncorrected, Jukes-Cantor, and Kimura) for our ABGD analysis. We also tested for OTUs using the Bayesian General Mixed Yule Coalescent Model (bGMYC; Reid & Carstens, 2012). Because this method requires ultrametric trees, we estimated trees with our concatenated mitochondrial alignment in BEAST v2.4.4 (Bouckaert et al., 2014) on the CIPRES SCIENCE GATEWAY (Miller, Pfeiffer, & Schwartz, 2010). We set the alignment partitions and substitution models in accordance with the RAXML analysis, used a Yule tree prior, default substitution priors and a strict molecular clock. We ran the MCMC for 50 million generations, sampling every 10,000

generations and discarding the first 10% of MCMC samples as a burn-in based on ESS values viewed in TRACER v1.5 (http://tree.bio.ed.ac.uk/software/tracer/). We then randomly selected 100 trees from the post burn-in distribution of trees and used these for our bGMYC analysis. For all 100 trees, we ran bGMYC for 20,000 generations, with a burn-in of 10,000, thinning = 10 and a conspecific probability cut-off ≥0.05.

2.6 | Cophylogenetic patterns in ground-dove lice

We tested for phylogenetic congruence between the putative louse species trees (trimmed to one representative per OTU) and the small New World ground-dove phylogeny from Sweet and Johnson (2015). First, we used the distance-based methods ParaFit (Legendre, Desdevises, & Bazin, 2002) and PACo (Balbuena, Míguez-Lozano, & Blasco-Costa, 2013). We converted the host and parasite trees to patristic distance matrices and ran ParaFit for 100,000 iterations in the R package APE (Paradis, Claude, & Strimmer, 2004), using the Cailliez correction for negative eigenvalues and testing for the contribution of individual links with both ParaFit link tests (ParaFitLink1 [PF1] and ParaFitLink2 [PF2]). We corrected the resulting *p*-values for the individual link tests with the Benjamini–Hochberg correction (Benjamini & Hochberg, 1995). For PACo, we used the same patristic distance matrices and ran 1,000 iterations in the PACo R package (Hutchinson, Cagua, Balbuena, Stouffer, & Poisot, 2017). We also used the jackknife approach in PACo to calculate the squared residual values for each host–parasite association. Second, we tested for specific "coevolutionary events" between ground-doves and their wing lice using the event-based method JANE v4 (Conow, Fielder, Ovadia, & Libeskind-Hadas, 2010). We set generations to 500 and population size to 1,000 for the Genetic Algorithm and randomized the tip associations 999 times to test for the statistical significance of our optimal score.

To test for a correlation between the cophylogenetic patterns of ground-dove wing and body lice, we compared the PACo residuals, PF1 and PF2 values associated with each host species. We did not include information for wing lice from *Metriopelia aymara* or *Columbina picui*, because there were no body lice associated with those host species. We used average values for host species with multiple louse associations. For all three metrics, we used the Spearman's rank coefficient in R to test for a correlation between wing and body lice.

2.7 | Comparing divergence rates

Two pairs of sister species, *C. drowni* and *C. gymnopeliae* (wing lice) and *P. emersoni* and *P. robbinsi* (body lice), are associated with the same two host species (*M. ceciliae* and *M. melanoptera*), and both pairs likely codiverged with their hosts. This implies both louse species pairs diverged in response to the same host speciation event, and comparing their genetic distances can provide an estimate of relative divergence rates between the two groups of lice. For each aligned nuclear gene, we calculated the uncorrected genetic distances between each species pair in APE. We used data from one representative of each species: *C. drowni* and *C. gymnopeliae* sequenced by Boyd et al. (2017) and the higher-coverage *P. emersoni* and *P. robbinsi* from Sweet et al. (2018). We excluded genes not present in both wing and body louse data sets. Based on our initial assessment of the distribution of distances, we also removed 11 genes with outlier distances (higher than 5%) in either wing or body lice. After these filtering steps, we were able to calculate distances for 1,006 genes. We also used a chi-square test to compare the proportion of total differences across all aligned genes between the two pairs of wing and body louse sister species.

We also calculated the uncorrected distances between mitochondrial sequences in each species pair. Although we treated the mitochondrial data as a single locus (i.e., we calculated distances from concatenated gene alignments), we used only the 6 mitochondrial genes available for both wing and body lice. However, rather than use single representatives of each species, we compared distances among all samples of each species pair (three samples of *C. drowni* and *C. gymnopeliae*; 4 samples of *P. emersoni* and *P. robbinsi*).

2.8 | Population genomic analysis

We assessed the population structure of widespread louse species using STRUCTURE, discriminant analysis of principal components (DAPC) and principal component analysis (PCA). Our approach followed the analysis of the body louse *P. eurysema* in Sweet et al. (2018). For STRUCTURE analyses, we randomly selected one SNP per assembled gene, which ensures that individual SNPs are unlinked. For wing lice, we ran STRUCTURE 20 times on these subsets of SNPs with 50,000 MCMC iterations and 25,000 burn-in iterations for $K = 2–8$. We then used the ΔK method (Evanno, Regnaut, & Goudet, 2005) in STRUCTURE HARVESTER v0.6.94 (Earl & VonHoldt, 2012) to determine the optimal number of clusters. We summarized all STRUCTURE runs in CLUMPP v1.1.2 (Jakobsson & Rosenberg, 2007) and visualized the results by constructing plots with DISTRUCT v1.1 (Rosenberg, 2004). We also ran STRUCTURE analyses for two possible cryptic wing louse taxa (*C. passerinae* 1 and *C. passerinae* 2) identified in previous phylogenetic studies of the genus (Johnson et al., 2007; Sweet et al., 2016). We once again randomly selected SNPs and ran STRUCTURE as detailed above. We performed DAPC in the R package ADEGENET (Jombart, 2008) using all SNPs for *C. passerinae* (25 clusters retained and default parameters for find.clusters(); five principle components and two discriminant functions retained, default parameters for dapc()). For PCA, we subsampled SNPs for the cryptic taxa *C. passerinae* 1 and *C. passerinae* 2 using VCFTOOLS v0.1.14 (Danecek et al., 2011) and analysed them separately in ADEGENET. Finally, we tested for population genetic structure in *P. eurysema* 3, *C. passerinae* 1 and *C. passerinae* 2 using analysis of molecular variance (AMOVA) in GENODIVE v2.0b27 (Meirmans & Van Tienderen, 2004). For each taxon, we used two different population schemes: one based on host species and the other based on biogeographic region. For each of these schemes, we ran the AMOVA in GENODIVE with 999 permutations.

Heterozygosity can be a useful measure of host specificity and the effect of ecological dynamics (e.g., dispersal) on parasite populations. We estimated heterozygosity for wing and body louse individuals using two approaches. First, we estimated the scaled population mutation rate (θ), an indicator of heterozygosity, for individuals using MLRHO v2.9, which uses a maximum-likelihood approach to estimate population parameters for diploid individuals (Haubold, Pfaffelhuber, & Lynch, 2010). We converted pileup files generated from Samtools to "profile" files and formatted these for MLRHO using the auxiliary software for the program (available at http://guanine.evolbio.mpg.de/mlRho/). For each individual, we ran mlRho with maximum distance (-M) set to 0. Second, we calculated the standardized individual heterozygosity (Coltman, Pilkington, Smith, & Pemberton, 1999) by dividing the number of heterozygous sites by the number of called sites for each sample. We used the standardized heterozygosity to account for missing data.

3 | RESULTS

3.1 | Sequencing and assembly

Paired-end Illumina sequencing of 31 *Columbicola* specimens yielded an average ~44.9 million raw reads per specimen (Supporting Information Table S1). After clean-up steps, there were on average ~33.4 million reads per specimen, which translates to an average predicted sequencing depth of ~25× per specimen (based on a 200 Mbp genome size). Including the nine additional samples from GenBank (five out-group taxa and four previously sequenced in-group samples), an average of 1,036 genes per library mapped against the *C. drowni* reference (1,039 genes targeted). For body lice, we obtained an average of 1,055 genes per library mapped against the *P. emersoni* reference.

For wing lice, we assembled seven mitochondrial protein-coding genes for most samples (CO1, CO2, CO3, Cytb, ND1, ND3 and ND5), using an average library fraction of 57.1%. The other targeted mitochondrial protein-coding genes (ATP6, ATP8, ND2, ND4, ND4L and ND6) assembled for none or only a few samples, and so we excluded those genes from downstream analyses. For the 7 "successful" genes, aTRAM assembled data for all 40 samples in all but one gene (ND5), which assembled for 38 samples. By comparison, we obtained 10 body louse mitochondrial genes (all but ATP8, ND3 and ND6) assembled with aTRAM using an average library fraction of 15.7%.

The GATK pipeline called 25,952 SNPs for *C. passerinae* after filtering. This included 15,225 SNPs for *C. passerinae* 1 and 14,456 SNPs for *C. passerinae* 2. Selecting one random SNP per gene for STRUCTURE analyses resulted in 773 SNPs for *C. passerinae*, 635 SNPs for *C. passerinae* 1 and 636 SNPs for *C. passerinae* 2. We obtained 56,232 SNPs from *P. eurysema*, including 880–908 SNPs for STRUCTURE.

3.2 | Phylogenetic analysis

The concatenated nuclear alignment for wing lice was 1,104,066 bp long, only 3.8% of which consisted of gaps or ambiguous characters

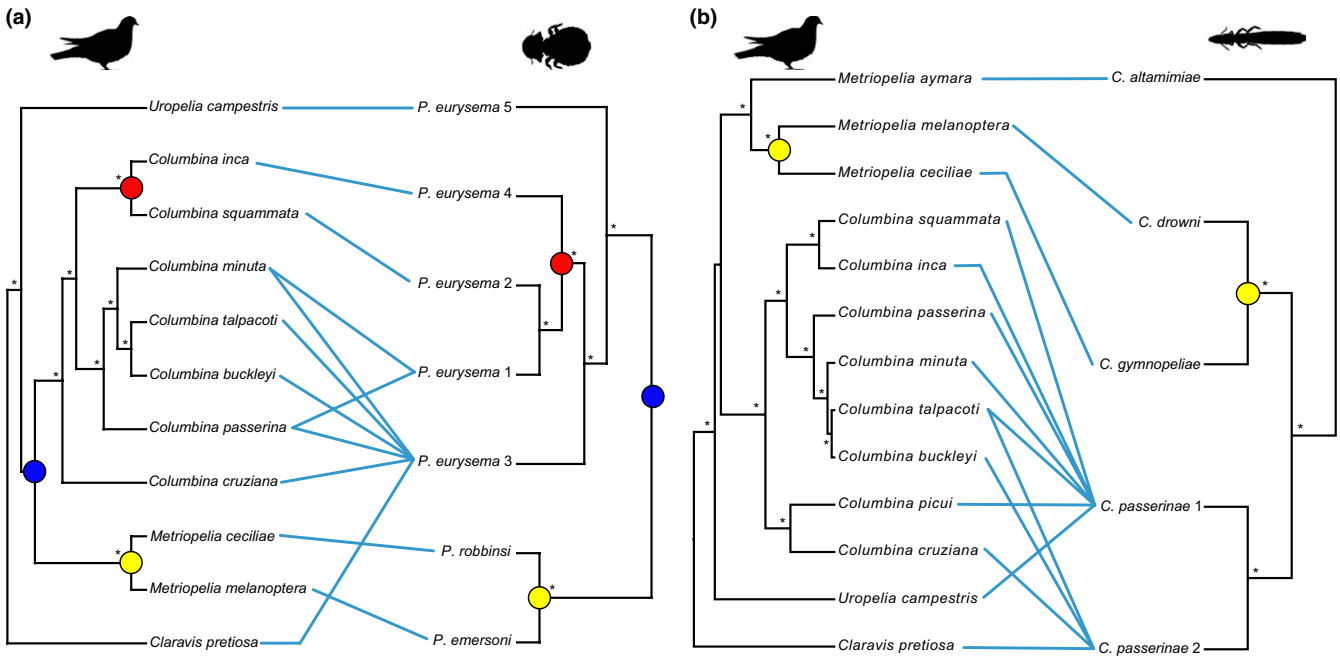

FIGURE 1 Tanglegrams comparing the phylogeny of New World ground-doves to the phylogenies of their (a) body lice (*Physconelloides*) and (b) wing lice (*Columbicola*). The ground-dove phylogeny is to the left, and the louse phylogenies are to the right. The wing louse phylogeny is from this study, the body louse phylogeny is adapted from Sweet et al. (2018), and the ground-dove phylogeny is adapted from Sweet and Johnson (2015). Blue lines between the phylogenies indicate associated taxa. Asterisks indicate well-supported branches (>75% bootstrap support). In the louse phylogenies, all relationships have 100% bootstrap support. Circles over nodes indicate cospeciation events recovered from Jane4 reconciliation analyses

(missing data). The best partitioning scheme of the concatenated alignment estimated in PARTITIONFINDER consisted of 345 subsets. The resulting phylogeny from RAXML was very well supported. All OTUs received 100% bootstrap (BS) support, and many of the branches within OTUs received high support (>75% BS). The species-level relationships agreed with other phylogenetic assessments of this group (Johnson et al., 2007; Sweet & Johnson, 2016). *Columbicola altamimiae* (ex *Metriopelia aymara*) was sister to the rest of the in-group, and *C. gymnopeliae* (ex *M. ceciliae*) and *C. drowni* (ex *M. melanoptera*) were sister to *C. passerinae* (Figure 1, Supporting Information Figure S1). The coalescent phylogenies estimated from individual gene trees in ASTRAL were also well supported and largely agreed with the concatenated phylogeny (Supporting Information Figure S2). In the ASTRAL phylogeny, all species-level relationships received 100% local posterior probability support and were identical to the concatenated phylogeny. Finally, the concatenated mitochondrial alignment was 5,535 bp long and contained 13.4% missing data. The resulting mt phylogeny also exhibited well-supported species relationships in agreement with the nuclear phylogenies (Supporting Information Figure S3). The only topological differences among the concatenated, coalescent and mitochondrial phylogenies were all within species. Concatenated and coalescent phylogenetic estimates of body lice, based on 1,553,983 nuclear bp and 9,121 mitochondrial bp, also produced consistent, well-supported hypotheses. *Physconelloides emersoni* and *P. robbinsi* were recovered as sister to *P. eurysema*.

The OTU assessments indicated there are five in-group species of wing lice. In the ABGD analysis based on the COI alignment, all distances models supported five distinct taxa. Likewise, the bGMYC analysis based on 100 mitochondrial trees sampled from a posterior distribution supported five taxa at the 0.05 conspecific cut-off. The supported taxa include the three species that parasitize *Metriopelia* doves (*C. altamimiae*, *C. drowni* and *C. gymnopeliae*) and two species within *C. passerinae* ("*C. passerinae* 1" and "*C. passerinae* 2"). The presence of two possible cryptic species within *C. passerinae* supports the results of previous work (Johnson et al., 2007). By comparison, assessments of body lice recovered five potentially cryptic OTUs within *P. eurysema* (7 total OTUs). The average uncorrected mitochondrial distances among potentially cryptic OTUs were 12.0% in wing lice and 18.9% in body lice.

3.3 | Cophylogenetic analysis

Both ParaFit (ParaFitGlobal = 1.97, $p = 0.005$) and PACo ($m^2 = 0.078$, $p = 0.003$) indicated the ground-dove and wing louse phylogenies were significantly congruent overall. However, none of the individual links were significant in the ParaFit test (Supporting Information Table S2). The Jane reconciliation recovered a single cospeciation event between ground-doves and their wing lice (between *M. melanoptera*/*M. ceceiliae* and their lice), along with two duplications, no host switches, 10 losses and eight failures to diverge (Figure 1, Supporting Information Figure S3). This least-costly solution was significantly lower than with randomized associations (observed cost = 27, mean randomized cost = 35.42, $p = 0.03$). Ground-doves and their body lice also had significantly congruent phylogenies, but there were more cospeciation events (3) and significant individual associations (2) than in the wing louse system.

Comparisons of cophylogenetic analyses in ground-dove wing and body lice produced varied results. When only considering host species present in both data sets (the wing louse data set includes two more host species than the body louse data set), PACo residual values between wing and body louse links were not significantly different (Mann–Whitney $U = 57$, $p = 0.847$; Table 1), but they were positively correlated ($\rho = 0.71$, $p = 0.019$; Figure 2). Notably, lice from *Metriopelia* had low residual values in both wing and body lice, whereas lice from *Claravis pretiosa* had high residual values in both groups of lice. Lower residuals indicate a greater contribution to phylogenetic congruence. One the other hand, metrics from ParaFit were not correlated between wing and body louse links (PF1: $\rho = 0.45$, $p = 0.17$; Supporting Information Figure S4a and PF2: $\rho = 0.59$,

TABLE 1 Comparison of cophylogenetic measures for New World ground-dove wing and body lice. Included are the residuals from PACo, and the ParaFitLink1 and ParaFitLink2 statistics from ParaFit. Average values are reported for host species with multiple wing or body louse associations

Host	Wing residuals	Body residuals	Wing PF1	Wing PF2	Body PF1	Body PF2
Claravis pretiosa	0.138	0.147	−1.33E-06	−4.05E-04	−1.39E-05	−4.37E-03
Columbina buckleyi	0.070	0.062	1.17E-06	3.57E-04	1.34E-05	4.21E-03
Columbina cruziana	0.069	0.075	3.21E-07	9.78E-05	3.43E-06	1.07E-03
Columbina inca	0.050	0.032	1.57E-06	4.78E-04	8.11E-06	2.54E-03
Columbina minuta	0.046	0.061	1.81E-06	5.51E-04	1.13E-05	3.54E-03
Columbina passerina	0.039	0.057	1.61E-06	4.90E-04	9.92E-06	3.11E-03
Columbina squammata	0.049	0.034	1.56E-06	4.75E-04	8.46E-06	2.65E-03
Columbina talpacoti	0.058	0.062	1.49E-06	4.54E-04	1.35E-05	4.23E-03
Metriopelia ceciliae	0.014	0.042	3.49E-06	1.06E-03	2.80E-05	8.77E-03
Metriopelia melanoptera	0.019	0.046	2.91E-06	8.88E-04	2.58E-05	8.07E-03
Uropelia campestris	0.149	0.066	−2.04E-06	−6.22E-04	1.85E-05	5.79E-03

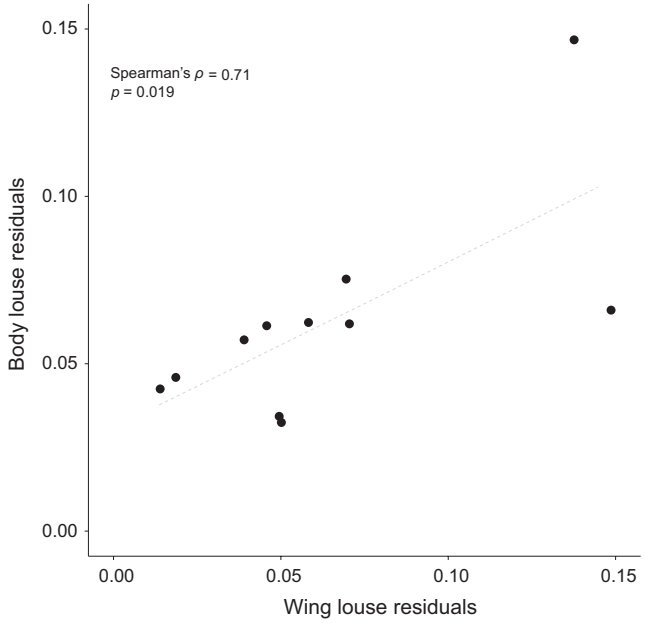

FIGURE 2 Correlation of New World ground-dove wing and body louse residuals from a PACo analysis. Points indicate host species. For hosts with multiple wing or body louse associations, the points represent mean residual values. A regression line is provided merely to indicate trend

p = 0.057; Supporting Information Figure S4b). In the ParaFit analysis, body louse links also had significantly higher PF1 and PF2 values than wing louse links (PF1: Mann–Whitney U = 12, p = 0.001; PF2: Mann–Whitney U = 11, p-value = 0.001; Table 1). Unlike PACo residuals, higher PF1 and PF2 values indicate a greater contribution to overall congruence between host and parasite phylogenies.

3.4 | Comparative genetic distances between wing and body lice

Uncorrected distance values from the 1,007 nuclear genes were higher for *P. emersoni* and *P. robbinsi* (body lice; median = 0.007) than for *C. drowni* and *C. gymnopeliae* (wing lice; median = 0.005) (Mann–Whitney U = 1,537,100, p < 0.001). The body lice also had a higher proportion (0.008) of differences across all genes compared to the wing lice (0.006) (χ^2 = 249.49, p < 0.001). The opposite pattern was true of the mitochondrial distances: Wing lice (median = 0.173) had higher distances than body lice (median = 0.146) (Mann–Whitney U = 0, p < 0.001).

3.5 | Population genomic patterns

STRUCTURE and DAPC analyses for the wing louse *C. passerinae* indicated K = 2 as the optimal number of clusters. The patterns of these two subsets correspond with the two OTUs recovered from ABGD and bGMYC (Supporting Information Figure S6). Further STRUCTURE analysis on the two OTUs recovered an optimal K = 2 for *C. passerinae* 1 and K = 5 for *C. passerinae* 2. However, neither of these results suggested significant patterns of structure within these two OTUs (Supporting Information Figure S7). DAPC indicated there are two clusters within *C. passerinae* 1 (Supporting Information Figure S8). These patterns roughly correspond to biogeographic areas, which is further highlighted in the PCA (Figure 3a). AMOVA results indicated significant structure when taxa were classified into populations according to either host species (F_S = 0.036, p = 0.01) or geographic region (F_{ST} = 0.057, p = 0.001). DAPC did not recover any structure in *C. passerinae* 2, and although the PCA indicated there is some structure in the group, there are no clear patterns associated with either host species or biogeography as in other ground-dove louse taxa (Figure 3b). AMOVA also did not indicate structure at the level of either host species (F_{ST} = 0.011, p = 0.136) or geography (F_{ST} = 0.012, p = 0.119). By comparison, the body louse species *P. eurysema* had an optimal K = 3, but with more structure evident at higher values of K. Within the widespread OTU *P. eurysema* 3, some lice clustered according to host species and others according to biogeography (Figure 3c). AMOVA results also indicated significant structure at both of these levels (host species: F_{ST} = 0.197, p = 0.001; biogeography: F_{ST} = 0.055, p = 0.027).

In assessments of heterozygosity in wing and body lice, estimates of standardized individual heterozygosity (ratio of heterozygous sites to total genotyped sites) and θ (estimated from mlRho) were comparable (Spearman's ρ = 0.58, p = 1.48e^{-7}; Supporting Information Table S3). Therefore, comparative tests using the two metrics gave similar results, and here, we report the results from the θ metric. Overall, wing lice had higher θ values than body lice (Mann–Whitney U = 275.5, p < 0.001; inset of Figure 4). However, this pattern is driven by differences between specialist lice (i.e., lice that are only associated with a single host species). Wing and body louse specialists have significantly different θ values (Mann–Whitney U = 0, p < 0.001), whereas wing and body louse generalists have θ values that are not significantly different (Mann–Whitney U = 235, p = 0.220; Figure 4). Separately, wing louse specialists had higher θ than wing louse generalists (Mann–Whitney U = 20, p < 0.001), whereas the opposite pattern was apparent in body lice; body louse generalists had higher θ than body louse specialists (Mann–Whitney U = 211.5, p = 0.004).

4 | DISCUSSION

Phylogenomic and population genomic comparisons of "ecological replicate" lice from ground-doves demonstrate the influence of an ecological process (dispersal) in shaping host–parasite coevolutionary patterns at both micro- and macroevolutionary scales. As we predicted, when compared to body lice, wing lice have less codivergence with their hosts and lower host specificity. Wing lice also did not show any obvious population structure according to host species, whereas some body lice did show this pattern. Finally, the most widespread (i.e., occurring on the most host species and over a broad geographic range) wing louse OTUs (*C. passerinae* 1 and 2) overall had less population structure than the most widespread body louse OTU

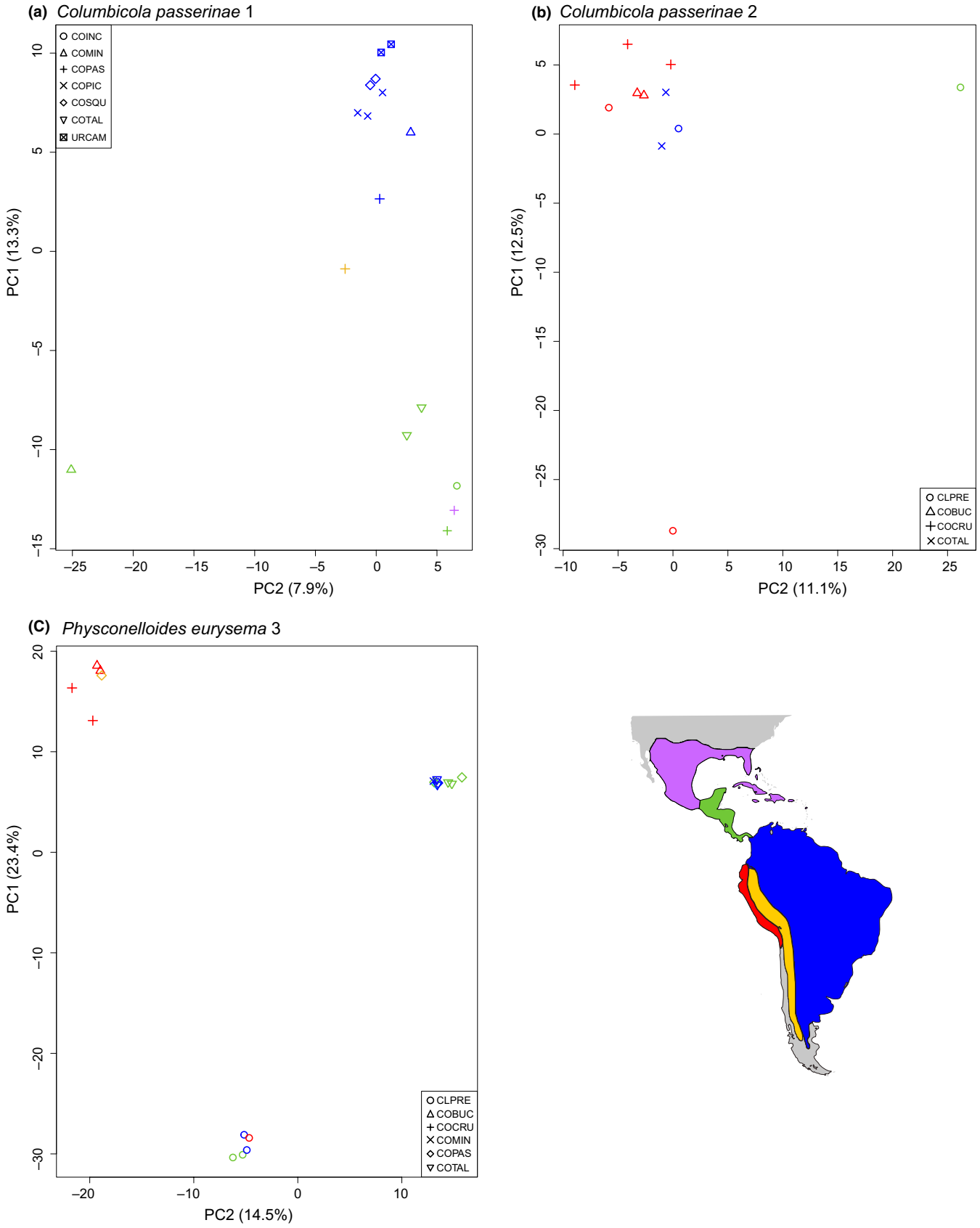

FIGURE 3 Principal component analysis (PCA) plots from SNP data of the ground-dove louse taxa (a) *Columbicola passerinae* 1, (b) *C. passerinae* 2 and (c) *Physconelloides eurysema* 3 (adapted from Sweet et al., 2018). The points represent individual lice; they are coloured according to biogeographic regions (see inset map) and shaped according to host species. The host species key shows the first two letters of the genus and first three letters of the species (e.g., Coinc = *Columbina inca*)

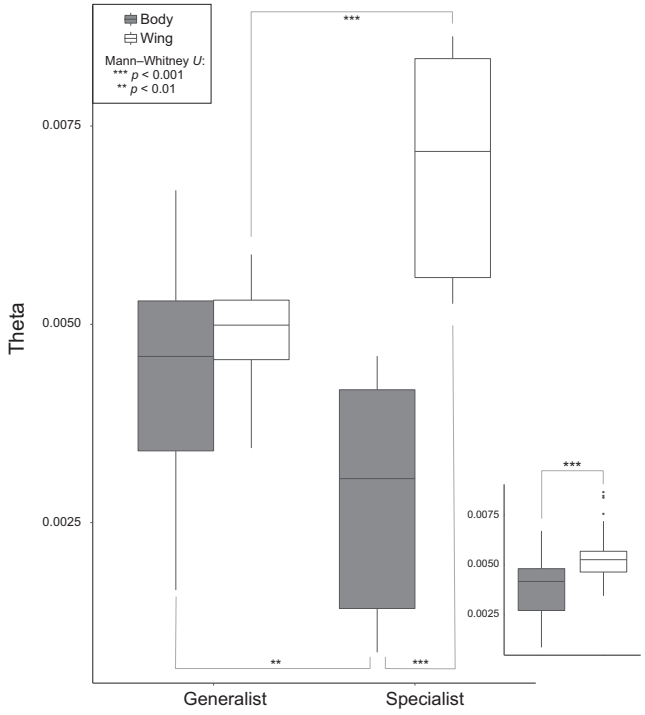

FIGURE 4 Box plots of θ (theta) estimated from individual New World ground-dove wing and body louse genomes. The inset plot (bottom right) shows the overall values of θ for wing (white) and body (grey) lice. The main figure shows the values of generalist (associated with multiple host species) and specialist (associated with a single host species) lice. Significantly different distributions are indicated with asterisks

(*P. eurysema* 3). Taken together, these findings suggest that parasite dispersal can be a primary driving force in host–parasite coevolution. Parasite dispersal has also been identified as an impactful factor for shaping other host–parasite systems (e.g., mites, Engelbrecht, Matthee, Toit, and Matthee (2016); trematodes, Lively (1999); ticks, McCoy et al. (2003)). In the dove louse system, lice that cannot use hippoboscid flies for dispersal (i.e., body lice) can become isolated on a particular host species, leading to rapid population divergence and ultimately cospeciation with the host (Clayton & Johnson, 2003; Harbison & Clayton, 2011).

Nevertheless, dispersal alone cannot account for all cophylogenetic patterns. In ground-dove lice, dispersal and host diversification interact to shape host–parasite interactions. Both wing and body louse phylogenies were significantly congruent with the host phylogeny, and both had at least one reconstructed cospeciation event. Although the lice (especially wing lice) can disperse to other host species, both types of lice still have a strong association with their hosts and display some patterns of host specificity. Lice cannot survive for long off the host, and they spend their entire life cycle on the host (Marshall, 1981; Tompkins & Clayton, 1999). In theory, this type of host–parasite relationship should result in at least some phylogenetic congruence (Fahrenholz, 1913; Eichler, 1948), which is what we observe here. It is also noteworthy that measures of congruence for individual host–parasite associations were positively correlated between wing and body lice (Figure 2). This further suggests host species are a key factor in promoting phylogenetic congruence, regardless of ecological differences between the two types of lice. Of course, neither louse system shows perfect phylogenetic congruence with hosts, and there is considerable variation between the two groups of lice. However, lice associated with *Metriopelia* ground-doves stand out as having consistent patterns of congruence. Both wing and body lice have a cospeciation event with these birds, and both are host-specific. Ecological barriers—notably the geographical and altitudinal differences among different species of *Metriopelia* and between *Metriopelia* and lowland ground-dove species—could inhibit host switching and over time lead to phylogenetic congruence in both types of lice.

We also predicted that for shared divergence events, wing lice may exhibit delayed divergence, as compared to body lice, because they can more readily disperse among host species during the early stages of their divergence. Because they cannot effectively use hippoboscid flies for dispersal, body louse populations are expected to become isolated rapidly among diverging host lineages, whereas wing lice would be better able to retain some level of gene flow after an initial split. We therefore expected to see a higher genetic divergence between body louse species pairs compared to a pair of wing louse species that diverged with the same pair of host species. Comparing the shared cospeciation event among *Metriopelia* doves and wing and body lice (Figure 1), this is exactly the pattern we see in the nuclear genes, with body lice showing more genetic divergence than wing lice across all loci. Surprisingly, the mitochondrial data show the opposite pattern; wing lice have a higher divergence between the same pair of host taxa than do body lice. This pattern could be related to the different architectures of the mitochondrial genomes. Body lice have a single mitochondrial chromosome, whereas wing lice likely have several mitochondrial "mini-chromosomes" (Cameron, Yoshizawa, Mizukoshi, Whiting, & Johnson, 2011; Covacin, Shao, Cameron, & Barker, 2006). This uncommon architecture in wing louse mitochondrial genomes might enable the lice to withstand higher mutation rates in the mitochondria (S. Cameron, personal communication). Alternatively, the mini-chromosomes may actually cause increases in mutation rates, because of increased speed or frequency of replication. It could also be that the mutation rate differs for nuclear loci in the opposite direction, but there would be no known mechanism for this. In either case, comparisons of relative nuclear and mitochondrial divergence rates across different groups of lice appear to be a potentially rich field for further investigation.

Like host speciation, biogeography also plays an important role in shaping the phylogenetic and population divergence outcomes between lice and ground-doves, although it appears to affect wing and body lice differently. Wing lice show biogeographic structure at the phylogenetic level, but do not exhibit a similar structure within species. Conversely, body lice do not have biogeographic structure at the phylogenetic level, but they do within a widespread species (see also Sweet et al, 2018). This pattern suggests that body louse population structure can be shaped by biogeography, but that lineages sort according to host species over time. The underlying mechanism

driving these patterns could still be dispersal differences (Weckstein, 2004). Because wing lice can more readily switch among sympatric host species, speciation may be driven by geographic events rather than host speciation. However, it is also possible that host and/or hippoboscid fly dispersal is responsible for the biogeographic patterns. Further phylogeographic analysis of lice, flies and doves is needed to rigorously address these hypotheses.

Dispersal also appears to have consequences at the population level, particularly as it relates to genetic diversity and inbreeding. Measures of heterozygosity in wing and body lice generally reflect the difference in dispersal ability. Overall, wing lice had higher levels of heterozygosity than body lice, which suggest that wing lice are more outbred. The ability of wing lice to disperse between different host individuals provides an opportunity for multiple populations to maintain gene flow. Because body lice have more limited opportunities for dispersal, they can become isolated on a host population or individual, thus leading to lower heterozygosity and more inbred louse populations (DiBlasi et al., 2018; Koop et al., 2014; Nadler, 1995). However, when examining patterns in heterozygosity in more detail, the overall pattern seems to be driven by differences in heterozygosity for host specialists (i.e., species of lice associated with a single host species). Whereas wing louse specialists had much higher heterozygosity than body louse specialists, heterozygosity levels of wing and body louse generalists were not significantly different. Not all body lice are strictly host-specific (i.e., there are some body louse species associated with multiple host species), and these body louse species appear to have gene flow on the same magnitude as some wing louse species, suggesting that body lice can disperse through modes other than phoresis. Many of the hosts parasitized by generalist body lice have overlapping geographic ranges and form mixed foraging flocks, so it is possible body lice are transferred through host contact or proximity (e.g., direct contact, shared dust baths, shared nest sites) (Clayton, 1991; Clayton & Tompkins, 1994; Clayton et al., 2016). Because wing and body louse generalists have similar levels of heterozygosity, perhaps interspecific dispersal via host contact occurs with similar frequency in both types of lice.

A more puzzling result is the higher heterozygosity of specialist wing lice compared to generalist wing lice (Barrett et al., 2008). This pattern may exist because wing lice are more able to disperse among individuals of a single host species than they are among multiple host species. In cases where multiple host species co-occur, it may be that the overall dispersal rate in wing lice is lower than in cases where a single host species occurs alone. Another similar possibility is related to the number of new louse infrapopulations founded by phoresis versus those founded by parent–offspring transmission. Infestation prevalence of lice on doves (i.e., the fraction of host individuals with parasites) is often much less than 50%, suggesting there are many opportunities for founding of new infrapopulations (i.e., establishment of a louse population on an individual bird that previously did not have lice) (Clayton et al., 2004; Price et al., 2003). In the case of host specialists, a high proportion of the new infrapopulations would be founded by direct contact between male and female birds or through parent–offspring transmission at the nest. These transmission (dispersal) events would often involve greater numbers of founding individual lice than would those founder events initiated through phoresis, which typically involve a very small number of lice (Harbison & Clayton, 2011). For host generalist wing lice, there would likely be many founder events originating from phoresis, resulting in more population bottlenecks and thus leading to lower heterozygosity compared to host specialists.

Additional insight comes from the population genetic variation of the lice on *Metriopelia* doves, the most geographically isolated of all of the ground-doves. All *Metriopelia* doves live at high elevations (usually >2,000 m.) in the Andes and are well-separated from closely related lowland ground-dove species (Gibbs et al., 2001). Some *Metriopelia* dove species are also separated from one another, by either geographical or altitudinal differences (e.g., some species are at higher elevations). The lice on these birds have large differences in estimates of θ, with wing lice having much larger values than body lice. It could be that without other host species in close proximity, wing lice avoid inbreeding by having a relatively high dispersal rate among conspecific host individuals, as compared to a mixed flock situation where some dispersal is within and some is between host species.

Variation in host population size could explain the differences in heterozygosity between wing and body louse specialists, if the pattern of specialization varies between the two groups (Hesse & Buckling, 2016). If wing louse specialists are associated with dove species with high population sizes, whereas body louse specialists are associated with hosts with relatively small populations, then higher heterozygosity could be maintained in wing lice as compared to body lice. However, some wing and body louse specialists share two host species (*Metriopelia melanoptera* and *M. ceciliae*) in common, so differences in host population size could not be a factor in this case. Overall heterozygosity could also be a reflection of louse population sizes (Nei, Maruyama, & Chakraborty, 1975). Wing lice are often more prevalent and have higher abundance than body lice, which could explain the observed patterns of heterozygosity (Clayton et al., 2016; Harbison & Clayton, 2011). However, wing and body louse generalists have similar estimates of heterozygosity, and any relative differences in population size should have a similar effect on the heterozygosity of those taxa. It also seems plausible that generalist lice should have higher heterozygosity than specialist lice just because they could have higher overall population sizes by occurring on more host species. Indeed, in body lice, generalists have significantly higher heterozygosity than specialists. However, wing lice show the opposite pattern: Specialists have significantly higher heterozygosity than generalists, so overall population size does not appear to be the most likely explanation for the variation in heterozygosity among specialist and generalist wing and body lice.

In summary, we use comparative phylogenetic and population genetic approaches in a single system to demonstrate that parasite dispersal shapes host–parasite coevolutionary patterns at multiple scales. However, host-related factors and biogeography can also be important for shaping patterns across evolutionary history and can having varying effects at different evolutionary scales and for

different groups of parasites. This complexity is consistent with previous studies that identify a variety of factors driving population or phylogenetic patterns in a host–parasite system (e.g., host social structure and mites, van Schaik, Kerth, Bruyndonckx, and Christe (2014); host movement and nematodes, Blouin, Yowell, Courtney, and Dame (1995)). The results from our study have important implications for understanding parasite movement and host switching, while also helping to further clarify how ecological processes (e.g., dispersal, host association) connect to evolutionary patterns in host–parasite systems (Clayton & Johnson, 2003).

ACKNOWLEDGEMENTS

We are grateful for the following individuals who provided louse samples or assisted in collecting efforts: Vitor de Q. Piacentini, Michel P. Valim, Robert E. Wilson, Jose L. Rivera-Parra, Edith Montalvo, Edison Auqui, Angelo Capparella, Dale H. Clayton, Kevin G. McCracken, Robert Faucett, Jeff DaCosta, Peggy Guttan-Mayerma, John Klicka, Matthew Miller and Garth Spellman. We are also thankful for Alvaro Hernandez and Chris Wright at the Roy J. Carver Biotechnology Center (University of Illinois) for assisting with genome library prep and sequencing, and for Jeff Haas and the University of Illinois Life Science Biocomputing Support Team for maintaining servers and software. We thank Graham Stone and three anonymous reviewers for helping to improve the paper. This study was supported by a UIUC Graduate College Dissertation Travel Grant and American Ornithological Society Student Research Award to A.D.S., and National Science Foundation (USA) grants DEB-1239788 and DEB-1342604 to K.P.J.

AUTHOR CONTRIBUTIONS

A.D.S. and K.P.J. designed the research, A.D.S. collected and analysed the data, and A.D.S. and K.P.J. wrote the paper.

DATA ACCESSIBILITY

Raw sequence data generated for this study are available from the NCBI SRA database under Accession no SRP116697 (BioProject 400795). Relevant data for phylogenetic and population genetic analyses are available on Dryad at https://doi.org/doi:10.5061/dryad.gr36743.

ORCID


Andrew D. Sweet https://orcid.org/0000-0003-2765-7021

REFERENCES

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions*, *19*, 716–723.

Allen, J. M., Boyd, B., Nguyen, N. P., Vachaspati, P., Warnow, T., Huang, D., … Johnson, K. P. (2017). Phylogenomics from whole genome sequences using aTRAM. *Systematic Biology*, *66*, 786–798. https://doi.org/10.1093/sysbio/syw105

Allen, J. M., Huang, D. I., Cronk, Q. C., & Johnson, K. P. (2015). aTRAM-automated target restricted assembly method: a fast method for assembling loci across divergent taxa from next-generation sequencing data. *BMC Bioinformatics*, *16*, 98.

Balbuena, J. A., Míguez-Lozano, R., & Blasco-Costa, I. (2013). PACo: A novel Procrustes application to cophylogenetic analysis. *PLoS ONE*, *8*, e61048. https://doi.org/10.1371/journal.pone.0061048

Banks, J. C., & Paterson, A. M. (2005). Multi-host parasite species in cophylogenetic studies. *International Journal for Parasitology*, *35*, 741–746. https://doi.org/10.1016/j.ijpara.2005.03.003

Barrett, L. G., Thrall, P. H., Burdon, J. J., & Linde, C. C. (2008). Life history determines genetic structure and evolutionary potential of host–parasite interactions. *Trends in Ecology & Evolution*, *23*, 678–685. https://doi.org/10.1016/j.tree.2008.06.017

Bartlow, A. M., Villa, S. M., Thompson, M. W., & Bush, S. E. (2016). Walk or ride? Phoretic behaviour of amblyceran and ischnoceran lice. *International Journal for Parasitology*, *46*, 221–227. https://doi.org/10.1016/j.ijpara.2016.01.003

Bell, K. C., Calhoun, K. L., Hoberg, E. P., Demboski, J. R., & Cook, J. A. (2016). Temporal and spatial mosaics: Deep host association and shallow geographic drivers shape genetic structure in a widespread pinworm, *Rauschtineria eutamii* (Nematoda: Oxyuridae). *Biological Journal of the Linnean Society*, *119*, 397–413.

Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society. Series B*, *57*, 289–300.

Blouin, M. S., Yowell, C. A., Courtney, C. H., & Dame, J. B. (1995). Host movement and genetic structure of populations of parasitic nematodes. *Genetics*, *141*, 1007–1014.

Bordes, F., & Morand, S. (2009). Coevolution between multiple helminth infestations and basal immune investment in mammals: Cumulative effects of polyparasitism? *Parasitology Research*, *106*, 33–37. https://doi.org/10.1007/s00436-009-1623-6

Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., … Drummond, A. J. (2014). BEAST 2: A software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, *10*, e1003537. https://doi.org/10.1371/journal.pcbi.1003537

Boyd, B. M., Allen, J. M., Nguyen, N., Sweet, A. D., Warnow, T., Shapiro, M. D., … Johnson, K. P. (2017). Phylogenomics using target-restricted assembly resolves intra-generic relationships of parasitic lice (Phthiraptera: *Columbicola*). *Systematic Biology*, *66*, 896–911.

Brooks, D. R., & McLennan, D. A. (1991). *Phylogeny, ecology, and behavior: A research program in comparative biology*. Chicago, IL: The University of Chicago Press.

Cameron, S. L., Yoshizawa, K., Mizukoshi, A., Whiting, M. F., & Johnson, K. P. (2011). Mitochondrial genome deletions and minicircles are common in lice (Insecta: Phthiraptera). *BMC Genomics*, *12*, 394. https://doi.org/10.1186/1471-2164-12-394

Clayton, D. H. (1991). Coevolution of avian grooming and ectoparasite avoidance. In J. E. Loye, & M. Zuk (Eds.), *Bird-parasite interactions: Ecology, evolution, and behavior*. Oxford: Oxford University Press.

Clayton, D. H., Bush, S. E., & Johnson, K. P. (2004). Ecology of congruence: Past meets present. *Systematic Biology*, *53*, 165–173. https://doi.org/10.1080/10635150490265102

Clayton, D. H., Bush, S. E., & Johnson, K. P. (2016). *Coevolution of life on hosts: Integrating ecology and history*. Chicago, IL: The University of Chicago Press.

Clayton, D. H., & Drown, D. M. (2001). Critical evaluation of five methods for quantifying chewing lice (Insecta: Phthiraptera). *Journal of Parasitology*, *87*, 1291–1300. https://doi.org/10.1645/0022-3395(2001)087[1291:CEOFMF]2.0.CO;2

Clayton, D. H., & Johnson, K. P. (2003). Linking coevolutionary history to ecological process: Doves and lice. *Evolution*, *57*, 2335–2341. https://doi.org/10.1111/j.0014-3820.2003.tb00245.x

Clayton, D. H., Lee, P. L. M., Tompkins, D. M., & Brodie, E. D. (1999). Reciprocal natural selection on host–parasite phenotypes. *The American Naturalist*, *154*, 261–270.

Clayton, D. H., & Tompkins, D. M. (1994). Ectoparasite virulence is linked to mode of transmission. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *256*, 211–217.

Coltman, D. W., Pilkington, J. G., Smith, J. A., & Pemberton, J. M. (1999). Parasite-mediated selection against inbred soay sheep in a free-living, island population. *Evolution*, *53*, 1259–1267. https://doi.org/10.2307/2640828

Conow, C., Fielder, D., Ovadia, Y., & Libeskind-Hadas, R. (2010). Jane: A new tool for the cophylogeny reconstruction problem. *Algorithms for Molecular Biology*, *5*, 16. https://doi.org/10.1186/1748-7188-5-16

Couch, A. B. (1962). Phoretic mallophagans from hippoboscids of mourning doves *Zenaidura macroura*. *The Journal of Parasitology*, *48*, 497. https://doi.org/10.2307/3275230

Covacin, C., Shao, R., Cameron, S., & Barker, S. C. (2006). Extraordinary number of gene rearrangements in the mitochondrial genomes of lice (Phthiraptera: Insecta). *Insect Molecular Biology*, *15*, 63–68. https://doi.org/10.1111/j.1365-2583.2005.00608.x

Criscione, C. D. (2008). Parasite co-structure: Broad and local scale approaches. *Parasite*, *15*, 439–443. https://doi.org/10.1051/parasite/2008153439

Criscione, C. D., Poulin, R., & Blouin, M. S. (2005). Molecular ecology of parasites: Elucidating ecological and microevolutionary processes. *Molecular Ecology*, *14*, 2247–2257. https://doi.org/10.1111/j.1365-294X.2005.02587.x

Cruaud, A., & Rasplus, J.-Y. (2016). Testing cospeciation through large-scale cophylogenetic studies. *Current Opinion in Insect Science*, *18*, 53–59. https://doi.org/10.1016/j.cois.2016.10.004

Cutter, A. D. (2013). Integrating phylogenetics, phylogeography and population genetics through genomes and evolutionary theory. *Molecular Phylogenetics and Evolution*, *69*, 1172–1185. https://doi.org/10.1016/j.ympev.2013.06.006

Danecek, P., Auton, A., Abecasis, G., Albers, C. A., Banks, E., DePristo, M. A., … Durbin, R. & 1000 Genomes Project Analysis Groups. (2011). The variant call format and VCFtools. *Bioinformatics*, *27*, 2156–2158. https://doi.org/10.1093/bioinformatics/btr330

de Vienne, D. M., Refrégier, G., López-Villavicencio, M., Tellier, A., Hood, M. E., & Giraud, T. (2013). Cospeciation vs host-shift speciation: Methods for testing, evidence from natural associations and relation to coevolution. *New Phytologist*, *198*, 347–385. https://doi.org/10.1111/nph.12150

Delsuc, F., Brinkmann, H., & Philippe, H. (2005). Phylogenomics and the reconstruction of the tree of life. *Nature Reviews Genetics*, *6*, 361–375. https://doi.org/10.1038/nrg1603

Demastes, J. W., Spradling, T. A., Hafner, M. S., Spies, G. R., Hafner, D. J., & Light, J. E. (2012). Cophylogeny on a Fine Scale: *Geomydoecus* chewing lice and their pocket gopher hosts, *Pappogeomys bulleri*. *Journal of Parasitology*, *98*, 262–270. https://doi.org/10.1645/GE-2904.1

DiBlasi, E., Johnson, K. P., Stringham, S. A., Hansen, A. N., Beach, A. B., Clayton, D. H., & Bush, S. E. (2018). Phoretic dispersal influences parasite population genetic structure. *Molecular Ecology*, *27*, 2770–2779. https://doi.org/10.1111/mec.14719

du Toit, N., Van Vuuren, B. J., Matthee, S., & Matthee, C. A. (2013). Biogeography and host-related factors trump parasite life history: Limited congruence among the genetic structures of specific ectoparasitic lice and their rodent hosts. *Molecular Ecology*, *22*, 5185–5204. https://doi.org/10.1111/mec.12459

Dybdahl, M. F., & Lively, C. M. (1996). The geography of coevolution: Comparative population structures for a snail and its trematode parasite. *Evolution*, *50*, 2264–2275.

Earl, D. A., & VonHoldt, B. M. (2012). STRUCTURE HARVESTER: A website and program for visualizing STRUCTURE output and implementing the Evanno method. *Conservation Genetics Resources*, *4*, 359–361. https://doi.org/10.1007/s12686-011-9548-7

Ehrlich, P. R., & Raven, P. H. (1964). Butterflies and plants: A study in coevolution. *Evolution*, *18*, 586–608. https://doi.org/10.1111/j.1558-5646.1964.tb01674.x

Eichler, W. D. (1948). Some rules in ectoparasitism. *The Annals and Magazine of Natural History*, *1*, 588–598.

Engelbrecht, A., Matthee, S., Du Toit, N., & Matthee, C. A. (2016). Limited dispersal in an ectoparasitic mite, *Laelaps giganteus*, contributes to significant phylogeographic congruence with the rodent host, *Rhabdomy*. *Molecular Ecology*, *25*, 1006–1021.

Evanno, G., Regnaut, S., & Goudet, J. (2005). Detecting the number of clusters of individuals using the software STRUCTURE: A simulation study. *Molecular Ecology*, *14*, 2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Fahrenholz, H. (1913). Ectoparasiten und abstammungslehre. *Zoologischer Anzeiger*, *41*, 371–374.

Falk, B. G., & Perkins, S. L. (2013). Host specificity shapes population structure of pinworm parasites in Caribbean reptiles. *Molecular Ecology*, *22*, 4576–4590. https://doi.org/10.1111/mec.12410

Gibbs, D. E., Cox, E., & Cox, J. (2001). *Pigeons and doves: A guide to the pigeons and doves of the world*. Sussex, UK: Pica Press.

Hackett-Jones, E., Cobbold, C., & White, A. (2009). Coexistence of multiple parasitoids on a single host due to differences in parasitoid phenology. *Theoretical Ecology*, *2*, 19–31. https://doi.org/10.1007/s12080-008-0025-1

Hafner, M. S., & Page, R. D. (1995). Molecular phylogenies and host–parasite cospeciation: Gophers and lice as a model system. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *349*, 77–83. https://doi.org/10.1098/rstb.1995.0093

Hafner, M. S., Sudman, P. D., Villablanca, F. X., Spradling, T. A., Demastes, J. W., & Nadler, S. A. (1994). Disparate rates of molecular evolution in cospeciating hosts and parasites. *Science*, *265*, 1087–1090. https://doi.org/10.1126/science.8066445

Harbison, C. W., Bush, S. E., Malenke, J. R., & Clayton, D. H. (2008). Comparative transmission dynamics of competing parasite species. *Ecology*, *89*, 3186–3194. https://doi.org/10.1890/07-1745.1

Harbison, C. W., & Clayton, D. H. (2011). Community interactions govern host-switching with implications for host–parasite coevolutionary history. *Proceedings of the National Academy of Sciences of the United States of America*, *108*, 9525–9529. https://doi.org/10.1073/pnas.1102129108

Harbison, C. W., Jacobsen, M. V., & Clayton, D. H. (2009). A hitchhiker's guide to parasite transmission: The phoretic behaviour of feather lice. *International Journal for Parasitology*, *39*, 569–575. https://doi.org/10.1016/j.ijpara.2008.09.014

Haubold, B., Pfaffelhuber, P., & Lynch, M. (2010). mlRho - a program for estimating the population mutation and recombination rates from shotgun-sequenced diploid genomes. *Molecular Ecology*, *19*, 277–284. https://doi.org/10.1111/j.1365-294X.2009.04482.x

Hesse, E., & Buckling, A. (2016). Host population bottlenecks drive parasite extinction during antagonistic coevolution. *Evolution*, *70*, 235–240. https://doi.org/10.1111/evo.12837

Hoberg, E. P., & Brooks, D. R. (2008). A macroevolutionary mosaic: Episodic host-switching, geographical colonization and diversification in complex host–parasite systems. *Journal of Biogeography*, *35*, 1533–1550. https://doi.org/10.1111/j.1365-2699.2008.01951.x

Hutchinson, M. C., Cagua, E. F., Balbuena, J. A., Stouffer, D. B., & Poisot, T. (2017). paco: Implementing Procrustean Approach to Cophylogeny in R. *Methods in Ecology and Evolution*, *8*, 932–940. https://doi.org/10.1111/2041-210X.12736

Huyse, T., Poulin, R., & Théron, A. (2005). Speciation in parasites: A population genetics approach. *Trends in Parasitology*, *21*, 469–475. https://doi.org/10.1016/j.pt.2005.08.009

Jackson, A. P., Machado, C. A., Robbins, N., & Herre, E. A. (2008). Multilocus phylogenetic analysis of neotropical figs does not support cospeciation with the pollinators: The importance of systematic scale in fig/wasp cophylogenetic studies. *Symbiosis*, *45*, 16.

Jakobsson, M., & Rosenberg, N. A. (2007). CLUMPP: A cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. *Bioinformatics*, *23*, 1801–1806. https://doi.org/10.1093/bioinformatics/btm233

Johnson, K. P., & Clayton, D. H. (2004). Untangling coevolutionary history. *Systematic Biology*, *53*, 92–94. https://doi.org/10.1080/10635150490264824

Johnson, K. P., Reed, D. L., Hammond Parker, S. L., Kim, D., & Clayton, D. H. (2007). Phylogenetic analysis of nuclear and mitochondrial genes supports species groups for *Columbicola* (Insecta: Phthiraptera). *Molecular Phylogenetics and Evolution*, *45*, 506–518. https://doi.org/10.1016/j.ympev.2007.07.005

Johnson, K. P., Shreve, S. M., & Smith, V. S. (2012). Repeated adaptive divergence in microhabitat specialization in avian feather lice. *BMC Biology*, *10*, 52.

Johnson, K. P., Weckstein, J. D., Meyer, M. J., & Clayton, D. H. (2011). There and back again: Switching between host orders by avian body lice (Ischnocera: Goniodidae). *Biological Journal of the Linnean Society*, *102*, 614–625. https://doi.org/10.1111/j.1095-8312.2010.01612.x

Johnson, K. P., Williams, B. L., Drown, D. M., Adams, R. J., & Clayton, D. H. (2002). The population genetics of host specificity: Genetic differentiation in dove lice (Insecta: Phthiraptera). *Molecular Ecology*, *11*, 25–38. https://doi.org/10.1046/j.0962-1083.2001.01412.x

Jombart, T. (2008). adegenet: A R package for the multivariate analysis of genetic markers. *Bioinformatics*, *24*, 1403–1405. https://doi.org/10.1093/bioinformatics/btn129

Katoh, K., Misawa, K., Kuma, K. I., & Miyata, T. (2002). MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research*, *30*, 3059–3066.

Keirans, J. E. (1975). A review of the phoretic relationship between Mallophaga (Phthiraptera: Insecta) and Hippoboscidae (Diptera: Insecta). *Journal of Medical Entomology*, *12*, 71–76. https://doi.org/10.1093/jmedent/12.1.71

Kirkness, E. F., Haas, B. J., Sun, W., Braig, H. R., Perotti, M. A., Clark, J. M., … Pittendrigh, B. R. (2010). Genome sequences of the human body louse and its primary endosymbiont provide insights into the permanent parasitic lifestyle. *Proceedings of the National Academy of Sciences of the United States of America*, *107*, 12168–12173. https://doi.org/10.1073/pnas.1003379107

Kochzius, M., Seidel, C., Hauschild, J., Kirchhoff, S., Mester, P., Meyer-Wachsmuth, I., … Timm, J. (2009). Genetic population structures of the blue starfish *Linckia laevigata* and its gastropod ectoparasite *Thyca crystallina*. *Marine Ecology Progress Series*, *396*, 211–219. https://doi.org/10.3354/meps08281

Koop, J. A., DeMatteo, K. E., Parker, P. G., & Whiteman, N. K. (2014). Birds are islands for parasites. *Biology Letters*, *10*, 20140255. https://doi.org/10.1098/rsbl.2014.0255

Lanfear, R., Calcott, B., Kainer, D., Mayer, C., & Stamatakis, A. (2014). Selecting optimal partitioning schemes for phylogenomic datasets. *BMC Evolutionary Biology*, *14*, 82. https://doi.org/10.1186/1471-2148-14-82

Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T., & Calcott, B. (2017). PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, *34*, 772–773.

Langmead, B., & Salzberg, S. L. (2012). Fast gapped-read alignment with Bowtie 2. *Nature Methods*, *9*, 357–359. https://doi.org/10.1038/nmeth.1923

Legendre, P., Desdevises, Y., & Bazin, E. (2002). A statistical test for host – parasite coevolution. *Systematic Biology*, *51*, 217–234. https://doi.org/10.1080/10635150252899734

Li, H., Handsaker, B., Wysoker, A., Fennell, T., Ruan, J., Homer, N., … Durbin, R. (2009). The sequence alignment/map format and SAMtools. *Bioinformatics*, *25*, 2078–2079. https://doi.org/10.1093/bioinformatics/btp352

Light, J. E., & Hafner, M. S. (2007). Cophylogeny and disparate rates of evolution in sympatric lineages of chewing lice on pocket gophers. *Molecular Phylogenetics and Evolution*, *45*, 997–1013. https://doi.org/10.1016/j.ympev.2007.09.001

Lively, C. M. (1999). Migration, virulence, and the geographic mosaic of adaptation by parasites. *The American Naturalist*, *153*, S34–S47. https://doi.org/10.1086/303210

Luikart, G., England, P. R., Tallmon, D., Jordan, S., & Taberlet, P. (2003). The power and promise of population genomics: From genotyping to genome typing. *Nature Reviews Genetics*, *4*, 981–994. https://doi.org/10.1038/nrg1226

Maa, T. C. (1969). A revised checklist and concise host index of Hippoboscidae (Diptera). *Pacific Insects Monograph*, *20*, 261–299.

Martinu, J., Hypsa, V., & Stefka, J. (2018). Host specificity driving genetic structure and diversity in ectoparasite populations: Coevolutionary patterns in *Apodemus* mice and their lice. *Ecology and Evolution*, *8*, 10008-10022 1–15. https://doi.org/10.1002/ece3.4424

Marshall, A. G. (1981). *The ecology of ectoparasitic insects*. London, UK: Academic Press.

Marussich, W. A., & Machado, C. A. (2007). Host-specificity and coevolution among pollinating and nonpollinating New World fig wasps. *Molecular Ecology*, *16*, 1925–1946. https://doi.org/10.1111/j.1365-294X.2007.03278.x

McCoy, K. D., Boulinier, T., Chardine, J. W., Danchin, E., & Michalakis, Y. (1999). Dispersal and Distribution of the Tick *Ixodes uriae* within and among seabird host populations: The need for a population genetic approach. *The Journal of Parasitology*, *85*, 196–202. https://doi.org/10.2307/3285619

McCoy, K. D., Boulinier, T., & Tirard, C. (2005). Comparative host–parasite population structures: Disentangling prospecting and dispersal in the black-legged kittiwake *Rissa tridactyla*. *Molecular Ecology*, *14*, 2825–2838. https://doi.org/10.1111/j.1365-294X.2005.02631.x

McCoy, K. D., Boulinier, T., Tirard, C., & Michalakis, Y. (2001). Host specificity of a generalist parasite: Genetic evidence of sympatric host races in the seabird tick *Ixodes uriae*. *Journal of Evolutionary Biology*, *14*, 395–405. https://doi.org/10.1046/j.1420-9101.2001.00290.x

McCoy, K. D., Boulinier, T., Tirard, C., & Michalakis, Y. (2003). Host-dependent genetic structure of parasite populations: Differential dispersal of seabird tick host races. *Evolution*, *57*, 288–296. https://doi.org/10.1111/j.0014-3820.2003.tb00263.x

McKenna, A., Hanna, M., Banks, E., Sivachenko, A., Cibulskis, K., Kernytsky, A., … DePristo, M. A. (2010). The Genome Analysis Toolkit: a MapReduce framework for analyzing next-generation DNA sequencing data. *Genome research*, *20*(9), 1297–303. https://doi.org/10.1101/gr.107524.110

Meirmans, P. G., & Van Tienderen, P. H. (2004). GENOTYPE and GENODIVE: Two programs for the analysis of genetic diversity of asexual organisms. *Molecular Ecology Resources*, *4*, 792–794.

Miller, M. A., Pfeiffer, W., & Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE) (pp. 1–8). New Orleans, LA.

Mirarab, S., & Warnow, T. (2015). ASTRAL-II: Coalescent-based species tree estimation with many hundreds of taxa and thousands of genes. *Bioinformatics*, *31*, i44–i52. https://doi.org/10.1093/bioinformatics/btv234

Moran, N. A., & Baumann, P. (2000). Bacterial endosymbionts in animals. *Current Opinions in Microbiology*, *3*, 270–275. https://doi.org/10.1016/S1369-5274(00)00088-6

Nadler, S. (1995). Microevolution and the genetic structure of parasite populations. *The Journal of Parasitology*, *81*, 395–403. https://doi.org/10.2307/3283821

Nei, M., Maruyama, T., & Chakraborty, R. (1975). The bottleneck effect and genetic variability in populations. *Evolution*, *29*, 1–10. https://doi.org/10.1111/j.1558-5646.1975.tb00807.x

Nelson, B. C., & Murray, M. D. (1971). The distribution of Mallophaga on the domestic pigeon (*Columba livia*). *International Journal for Parasitology*, *1*, 21–29. https://doi.org/10.1016/0020-7519(71)90042-7

Nieberding, C. M., Durette-Desset, M.-C., Vanderpoorten, A., Casanova, J. C., Ribas, A., Deffontaine, V., … Michaux, S. R. (2008). Geography and host biogeography matter for understanding the phylogeography of a parasite. *Molecular Phylogenetics and Evolution*, *47*, 538–554. https://doi.org/10.1016/j.ympev.2008.01.028

Page, R. D. M. (1993). Parasites, phylogeny and cospeciation. *International Journal for Parasitology*, *23*, 499–506. https://doi.org/10.1016/0020-7519(93)90039-2

Page, R. D. M., & Charleston, M. A. (1998). Trees within trees: Phylogeny and historical associations. *Trends in Ecology and Evolution*, *13*, 356–359. https://doi.org/10.1016/S0169-5347(98)01438-4

Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics*, *20*, 289–290. https://doi.org/10.1093/bioinformatics/btg412

Paterson, A. M., Wallis, G. P., Wallis, L. J., & Gray, R. D. (2000). Seabird and louse coevolution: Complex histories revealed by 12S rRNA sequences and reconciliation analyses. *Systematic Biology*, *49*, 383–399. https://doi.org/10.1080/10635159950127303

Pereira, S. L., Johnson, K. P., Clayton, D. H., & Baker, A. J. (2007). Mitochondrial and nuclear DNA sequences support a Cretaceous origin of Columbiformes and a dispersal-driven radiation in the Paleocene. *Systematic Biology*, *56*, 656–672.

Poulin, R. (2007). Are there general laws in parasite ecology? *Parasitology*, *134*, 763–776. https://doi.org/10.1017/S0031182006002150

Poulin, R., Krasnov, B. R., & Mouillot, D. (2011). Host specificity in phylogenetic and geographic space. *Trends in Parasitology*, *27*, 355–361. https://doi.org/10.1016/j.pt.2011.05.003

Price, P. W. (1980). *Evolutionary biology of parasites*. Princeton, NJ: Princeton University Press.

Price, R. D., Hellenthal, R. A., Palma, R. L., Johnson, K. P., & Clayton, D. H. (2003). *The chewing lice: World checklist and biological overview*. Champaign, IL: Illinois Natural History Survey.

Puillandre, N., Lambert, A., Brouillet, S., & Achaz, G. (2012). ABGD, Automatic Barcode Gap Discovery for primary species delimitation. *Molecular Ecology*, *21*, 1864–1877. https://doi.org/10.1111/j.1365-294X.2011.05239.x

Reid, N. M., & Carstens, B. C. (2012). Phylogenetic estimation error can decrease the accuracy of species delimitation: A Bayesian implementation of the general mixed Yule-coalescent model. *BMC Evolutionary Biology*, *12*, 196. https://doi.org/10.1186/1471-2148-12-196

Ricklefs, R. E., Fallon, S. M., & Bermingham, E. (2004). Evolutionary relationships, cospeciation, and host switching in avian malaria parasites. *Systematics Biology*, *53*, 111–119. https://doi.org/10.1080/10635150490264987

Rosenberg, N. A. (2004). DISTRUCT: A program for the graphical display of population structure. *Molecular Ecology Notes*, *4*, 137–138. https://doi.org/10.1046/j.1471-8286.2003.00566.x

Rothschild, M., & Clay, T. (1952). *Fleas, flukes, and cuckoos: A study of bird parasites*, 3rd ed. London, UK: Collins.

Sayyari, E., & Mirarab, S. (2016). Fast coalescent-based computation of local branch support from quartet frequencies. *Molecular Biology and Evolution*, *33*, 1654–1668. https://doi.org/10.1093/molbev/msw079

Simpson, J. T., Wong, K., Jackman, S. D., Schein, J. E., Jones, S. J. M., & Birol, I. (2009). ABySS: A parallel assembler for short read sequence data. *Genome Research*, *19*, 1117–1123. https://doi.org/10.1101/gr.089532.108

Sorenson, M. D., Balakrishnan, C. N., & Payne, R. B. (2004). Clade-limited colonization in brood parasitic finches (*Vidua* spp.). *Systematic Biology*, *53*, 140–153. https://doi.org/10.1080/10635150490265021

Stamatakis, A. (2006). RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, *22*, 2688–2690. https://doi.org/10.1093/bioinformatics/btl446

Stefka, J., Hoeck, P. E., Keller, L. F., & Smith, V. S. (2011). A hitchhikers guide to the Galapagos: Co-phylogeography of Galapagos mockingbirds and their parasites. *BMC Evolutionary Biology*, *11*, 284.

Sweet, A. D., Boy, B. M., Allen, J. M., Villa, S. M., Valim, M. P., Rivera-Parra, J. L., … Johnson, K. P. (2018). Integrating phylogenomic and population genomic patterns in avian lice provides a more complete picture of parasite evolution. *Evolution*, *72*, 95–112. https://doi.org/10.1111/evo.13386

Sweet, A. D., Boyd, B. M., & Johnson, K. P. (2016). Cophylogenetic patterns are uncorrelated between two lineages of parasites on the same hosts. *Biological Journal of the Linnean Society*, *118*, 813–828. https://doi.org/10.1111/bij.12771

Sweet, A. D., & Johnson, K. P. (2015). Patterns of diversification in small New World ground doves are consistent with major geologic events. *The Auk*, *132*, 300–312. https://doi.org/10.1642/AUK-14-193.1

Sweet, A. D., & Johnson, K. P. (2016). Cophylogenetic analysis of New World ground-doves (Aves: Columbidae) and their parasitic wing lice (Insecta: Phthiraptera: *Columbicola*). *Molecular Phylogenetics and Evolution*, *103*, 122–132. https://doi.org/10.1016/j.ympev.2016.07.018

Tompkins, D. M., & Clayton, D. H. (1999). Host resources govern the specificity of swiftlet lice: Size matters. *Journal of Animal Ecology*, *68*, 489–500. https://doi.org/10.1046/j.1365-2656.1999.00297.x

Vaidya, G., Lohman, D. J., & Meier, R. (2011). SequenceMatrix: Concatenation software for the fast assembly of multi-gene datasets with character set and codon information. *Cladistics*, *27*, 171–180. https://doi.org/10.1111/j.1096-0031.2010.00329.x

Van der Auwera, G. A., Carneiro, M. O., Hartl, C., Poplin, R., Del Angel, G., Levy-Moonshine, A., … DePristo, M. A. (2013). From FastQ data to high confidence variant calls: The Genome Analysis Toolkit best practices pipeline. *Current Protocols in Bioinformatics*, *43*, 11.10.1–33.

Van Schaik, J., Kerth, G., Bruyndonckx, N., & Christe, P. (2014). The effect of host social system on parasite population genetic structure: Comparative population genetics of two ectoparasitic mites and their bat hosts. *BMC Evolutionary Biology*, *14*, 18.

Vinarski, M. V., Korallo, N. P., Krasnov, B. R., Shenbrot, G. I., & Poulin, R. (2007). Decay of similarity of gamasid mite assemblages parasitic on Palaearctic small mammals: Geographic distance, host-species composition or environment. *Journal of Biogeography*, *34*, 1691–1700. https://doi.org/10.1111/j.1365-2699.2007.01735.x

Vogwill, T., Fenton, A., & Brockhurst, M. A. (2008). The impact of parasite dispersal on antagonistic host–parasite coevolution. *Journal of Evolutionary Biology*, *21*, 1252–1258. https://doi.org/10.1111/j.1420-9101.2008.01574.x

Weckstein, J. D. (2004). Biogeography explains cophylogenetic patterns in toucan chewing lice. *Systematic Biology*, *53*, 154–164. https://doi.org/10.1080/10635150490265085

Weiblen, G. D., & Bush, G. L. (2002). Speciation in fig pollinators and parasites. *Molecular Ecology*, *11*, 1573–1578. https://doi.org/10.1046/j.1365-294X.2002.01529.x

Whiteman, N. K., Kimball, R. T., & Parker, P. G. (2007). Co-phylogeography and comparative population genetics of the threatened Galápagos hawk and three ectoparasite species: Ecology shapes population histories within parasite communities. *Molecular Ecology*, *16*, 4759–4773. https://doi.org/10.1111/j.1365-294X.2007.03512.x

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Sweet AD, Johnson KP. The role of parasite dispersal in shaping a host–parasite system at multiple evolutionary scales. *Mol Ecol*. 2018;27:5104–5119. https://doi.org/10.1111/mec.14937