Title: Comparing rates of introgression in parasitic feather lice with differing dispersal capabilities

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Running title: Dispersal and introgression rate.

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Data availability: All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Supplementary Materials: Supplementary data are available at GitHub (https://jorge-dona.github.io/Comparing-rates-of-introgression-in-parasitic-feather-lice-with-differing-dispersal-capabilities/supplementary.html) and at Figshare (DOI: 10.6084/m9.figshare.9176204). Individual gene trees are available at Figshare (DOI: 10.6084/m9.figshare.9176204).

Abstract: Organisms vary in their dispersal abilities, and these differences can have important biological consequences, such as impacting the likelihood of hybridization events. However, there is still much to learn about the factors influencing hybridization, and specifically how dispersal ability affects the opportunities for hybridization. Here, using the ecological replicate system of dove wing and body lice (Insecta: Phthiraptera), we show that species with higher dispersal abilities exhibited increased genomic signatures of introgression. Specifically, we found a higher proportion of introgressed genomic reads and more reticulated phylogenetic networks in wing lice, the louse group with higher dispersal abilities. Our results are consistent with the hypothesis that differences in dispersal ability might drive the extent of introgression through hybridization.

Introduction

Dispersal is the permanent movement of organisms away from their place of origin. It is a fundamental process in biology with significant implications at multiple scales of organization (Barton 1992; Clobert et al. 2001; Nathan 2001; Matthysen 2012), including the reproduction of individuals, the composition of populations and communities, and the geographical distribution of species (Clobert et al. 2001, 2012).

Organisms differ in their dispersal abilities, and these differences have an impact on their biology, such as on the distributional range of a species or gene flow between populations (Bohonak 1999). For example, organisms with lower dispersal abilities tend to have smaller distributional ranges and populations that are genetically more structured (Bohonak 1999; Dawson et al. 2014; DiBlasi et al. 2018).

Dispersal ability might also affect the opportunities for hybridization between species because the rates at which individuals encounter different species are likely to be higher in organisms with higher dispersal capabilities. Indeed, recent evidence supports this prediction by demonstrating that range expansion is associated with the extent of introgression (Currat et al. 2008; Nussberger et al. 2018). Similarly, dispersal differences explain more than 30% of the variation in the width of hybrid zones across animals (McEntee et al. 2018). However, overall there is still much to learn about the factors influencing hybridization (Randler 2006; Arnold 2015; Taylor and Larson 2019), and, in particular, the influence of dispersal ability on the rate of hybridization remains understudied.

Testing for the effect of dispersal on hybridization should ideally hold constant most factors other than dispersal. The ecological replicate system of wing and body lice (Insecta: Phthiraptera) of pigeons and doves (Aves: Columbidae) has proven to be an ideal system for

comparing the impact of dispersal differences on other aspects of biology, such as population structure and codivergence (Clayton and Johnson 2003; Johnson and Clayton 2004; Clayton et al. 2015; DiBlasi et al. 2018; Sweet and Johnson 2018). Specifically, this is an excellent system in which to assess the effect of differences in dispersal capabilities on levels of introgression because both of these lineages of feather lice: 1) significantly differ in their dispersal ability (Harbison et al. 2008, 2009; Bartlow et al. 2016), 2) co-occur across the diversity of pigeons and doves, and 3) have the same basic life history and diet (Clayton et al. 2015; Sweet and Johnson 2015, 2018). Both wing and body lice disperse vertically between parents and offspring in the nest. However, wing lice can also attach to and hitchhike on hippoboscid flies to disperse "phoretically" between host individuals or host species (Harbison et al. 2008, 2009; Bartlow et al. 2016). Indeed, this hitch-hiking dispersal mechanism profoundly influences their degree of population structure and cophylogenetic history (Clayton and Johnson 2003; Sweet et al. 2017b; DiBlasi et al. 2018; Sweet and Johnson 2018). In addition, wing lice have a higher rate of host-switching (Clayton and Johnson 2003; Clayton et al. 2015; Sweet et al. 2017b) (i.e., successful colonization of new host species) and of straggling (Whiteman et al. 2004) (i.e., dispersal to new host species without reproduction on that new host).

To compare differences in the extent of introgression between wing and body lice, we used whole-genome data from 71 louse individuals belonging to five species of wing lice (*Columbicola*) and seven species of body lice (*Physconelloides*) that occur across the same suite of host species and have highly comparable patterns of diversification (Sweet and Johnson 2015, 2018). Specifically, both lineages within these two groups of lice that are the focus of this study originated on the common ancestor of *Metriopelia* doves (11.3-14.9 mya) and have a correlated pattern of codiversification within the same group of hosts (including a shared cospeciation event

which occurred within the *Metriopelia* genus 5.2-7.4 mya; Sweet and Johnson 2015, 2018). We predicted that wing lice, which have higher dispersal abilities and thus higher odds of encountering individuals of a different louse species on the same host, should show more extensive evidence of introgression (Fig. 1).

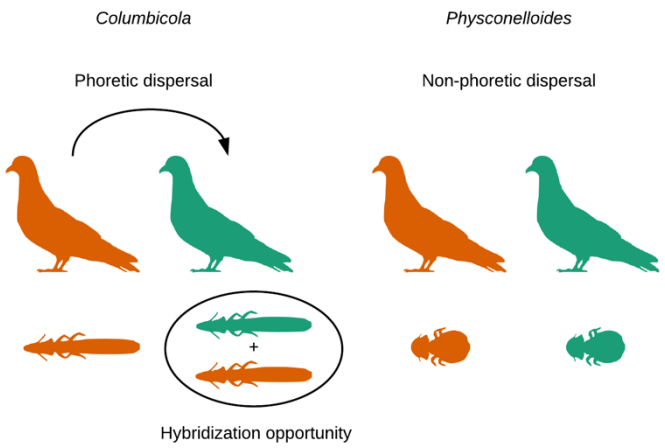


Figure 1. Diagram depicting the ecological replicate system and the hypothesis of this study. Wing lice (*Columbicola*) have higher dispersal abilities than body lice (*Physconelloides*), and thus higher odds of encountering individuals of a different louse sp.

Materials and Methods

Data

We analyzed Illumina whole genome sequence data (150 or 160bp paired-end reads) from 71 louse individuals belonging to five and seven taxa of *Columbicola* and *Physconelloides*, respectively (Supplementary Table S2) hosted by the monophyletic clade of small New World ground doves. This paper's taxonomic classification of lice is based on Sweet and Johnson (2018) species delimitation analyses. In particular, they found most *Columbicola* OTUs matched known species, and some *Physconelloides* OTUs were yet to be formally described as species

100 (and are named here following Sweet & Johnson, 2018). All raw sequence data used were
101 available from previous studies (Boyd et al. 2017; Sweet et al. 2017a; Sweet and Johnson 2018)
102 and represent all described New World ground-dove wing and body louse species (sampled from
103 most host species in this group) including lice samples across multiple biogeographic areas
104 within species of hosts (Sweet and Johnson 2018; Supplementary Table S2). Illumina genome
105 sequence data pre-processing included several steps (Sweet and Johnson 2018). First, we
106 discarded duplicate read pairs using the fastqSplitDups script (https://github.com/McIntyre-
107 Lab/mcscriptand https://github.com/McIntyre-Lab/mclib). We then eliminated the Illumina
108 sequencing adapters with Fastx_clipper v0.014 from the FASTX-Toolkit
109 (http://hannonlab.cshl.edu/fastx_toolkit). Also, we removed the first 5 nt from the 5' ends of
110 reads using Fastx_trimmer v0.014 and trimmed bases from the 3' ends of reads until reaching a
111 base with a phred score ≥28 (which is equivalent to a base call accuracy higher than 99.8 %)
112 using Fastq_quality_trimmer v0.014. Finally, we removed any reads less than 75 nt and analyzed
113 the cleaned libraries with Fastqc v0.11.5 to check for additional errors. We assembled nuclear
114 loci in aTRAM following previous studies (Allen et al. 2015; Boyd et al. 2017; Sweet and
115 Johnson 2018). In particular, we mapped modest coverage (25-60X), multiplexed genomic data
116 to reference loci from a closely related taxon. For our reference set of nuclear loci for wing lice,
117 we used 1,039 exons of *Columbicola drowni* (Boyd et al. 2017) (raw data: SRR3161922). This
118 data set was assembled de novo (Allen et al. 2015) using orthologous protein-coding genes from
119 the human body louse genome (*Pediculus humanus humanus* (Kirkness et al. 2010) as a set of
120 target sequences. We mapped *Columbicola* reads to the *C. drowni* references using Bowtie2
121 (Langmead and Salzberg 2012). For body lice, we obtained nuclear data using the same pipeline
122 and software parameters, except that we used 1,095 loci from *Physconelloides emersoni* as the

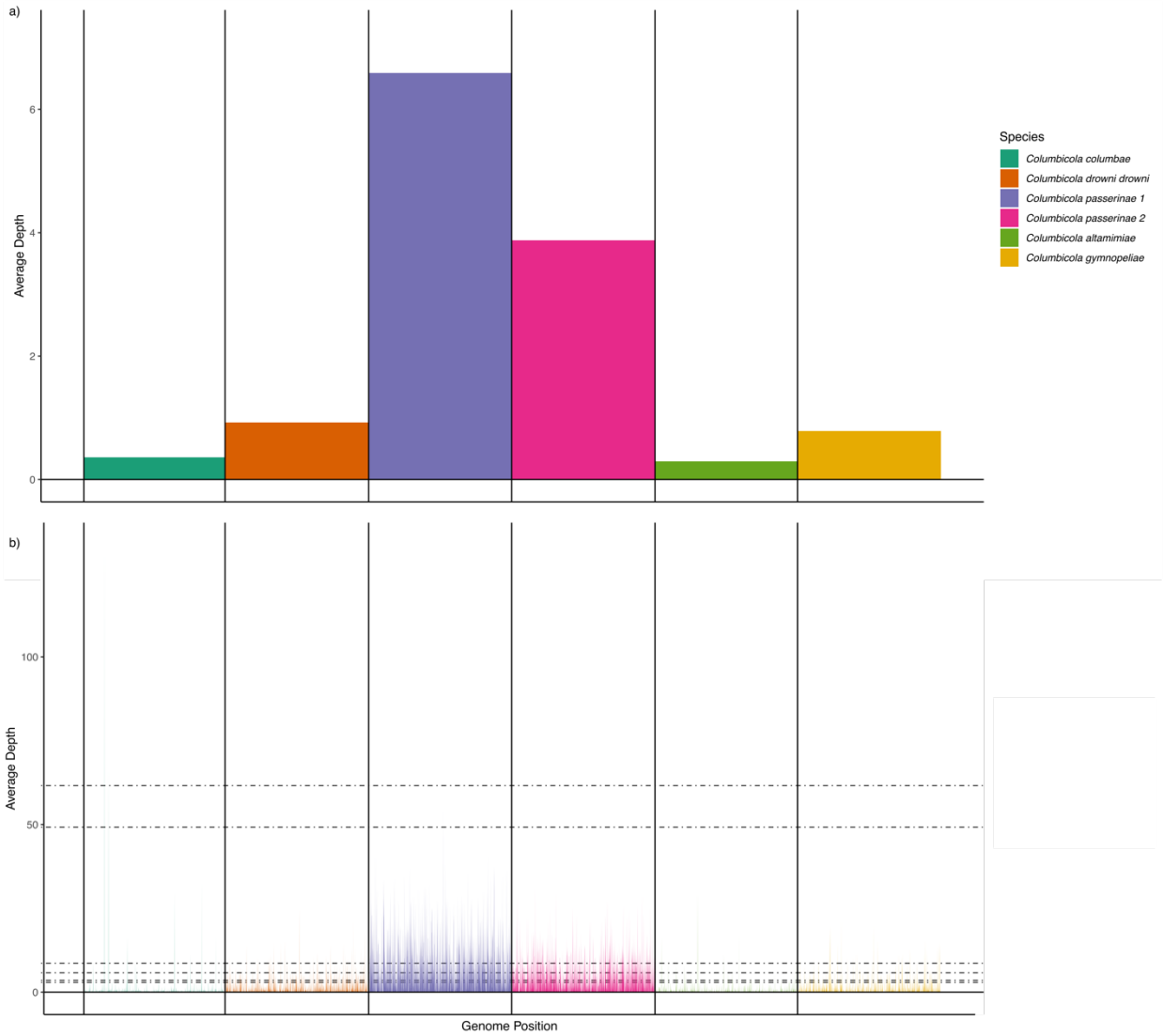
123 reference for mapping. To generate the input ultrametric gene trees for Phylonet v3.6.8 (Than et
124 al. 2008; Yu and Nakhleh 2015; Wen et al. 2018), we first aligned each nuclear locus in MAFFT
125 (Katoh 2002) (--auto) and removed columns with only ambiguous sequences ("N"). Then, we
126 estimated gene trees in RAxML v8.1.3 (Stamatakis 2006) with a GTR + Γ substitution model for
127 each gene alignment. Finally, we made trees ultrametric using the nnls method in the
128 force.ultrametric function within the "phytools" R package (Revell 2011).

129 Quantifying introgression

130 We used two different approaches to quantify differences in the extent of introgression (i.e.,
131 ancient plus recent) between the two louse genera. We employed methods suitable to detect
132 introgression between species and between individuals from the same species (i.e., we did not
133 employ methods aimed to detect differences at the population level, e.g., TreeMix; Pickrell and
134 Pritchard 2012). First, we used sppIDer (Langdon et al. 2018) to quantify the genomic
135 contributions of different louse species in an individual louse genome (Fig. 2). We built our
136 reference for each genus using all the nuclear loci from a single individual per species. For the
137 reference, we selected those individuals for which we assembled the highest number of genes for
138 each genus. We estimated the extent of introgression as the sum of the mean coverages of reads
139 mapped from all the species excluding the focal louse species, divided by the mean coverage of
140 the focal louse species (Fig. 2). Note that these mean coverage values are calculated using only
141 those reads that mapped with a mapping quality (MQ) > 3 (Li et al. 2009; Langdon et al. 2018;
142 Figs. S1-S12). Plots of coverage across the genomes suggested that reads mapping to other
143 species were not artificial mappings (e.g., high coverage mappings to short repetitive regions;

144 Figs. S1-S12). In addition, we used SPAdes v3.12.0 (default parameters) to perform a de-novo

145 assembly of the putatively introgressed reads detected by sppIDer).



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147 **Figure 2**. Illustrative example of sppIDer results with an individual of *Columbicola passerinae* 1 (Cosp.Copas.11.7.2016.8).
148 Panel a) shows the average mean coverages of reads mapping to every species (i.e., the values that were used for the calculations
149 of introgression levels), and panel b) shows the mean coverages of reads mapping to each species across the whole set of loci.
150 These and additional visualizations of all the individuals can be found in the supplementary material (Figs. S1-S12).

151

152 Second, we quantified introgression at the species level, while accounting for incomplete lineage

153 sorting (ILS) using a maximum pseudo-likelihood framework with PhyloNet 3.6.1 (Than et al.

154 2008; Yu and Nakhleh 2015; Wen et al. 2018). Reticulations in this method can be attributed to

155 hybridization events. We trimmed the unrooted gene trees to the same individuals used as
156 reference taxa in sppIDer, and performed eleven independent analyses with a differing maximum
157 number of reticulation nodes (i.e., from zero to ten). We conducted ten runs per analysis. We
158 then selected the optimal network for each genus based on AIC values.

159 Statistics and reproducibility

160 We compared the sppIDer results using generalized linear models (GLMs). We used a Gaussian
161 distribution of errors and an identity link function. We performed one GLM for each simulation
162 iteration using the glm function of the "stats" R package (R Core Team 2013). The extent of
163 introgression for each louse genus was the dependent variable, the genus identity was the
164 independent variable, and we accounted for the introgression differences between louse species
165 including louse identity as a fixed factor. We confirmed assumptions underlying GLMs by
166 testing the normality of regression residuals for normality against a Q-Q plot. We also
167 considered the possibility that some of the reads mapping to other species were technical
168 contaminations, i.e., due to index-swapping (Carlsen et al. 2012; Esling et al. 2015; Schnell et al.
169 2015; Sinha et al. 2017). Previous studies have found that the misassignment of reads generally
170 ranges from 1 to 9% (Carlsen et al. 2012; Esling et al. 2015; Schnell et al. 2015; Sinha et al.
171 2017). Thus, to account for possible contaminants, we wrote a simulation in R that randomly
172 subtracted 9% (Carlsen et al. 2012; Esling et al. 2015; Schnell et al. 2015; Sinha et al. 2017)
173 from the mean coverage value of a particular sample (i.e., we subtracted a random proportion of
174 the mean coverage value for each sample until reaching 9%). We ran 100 iterations of the
175 simulation and ran a GLM for each iteration (Table S1). Finally, we used the χ^2 test to compare
176 the number of species in pairwise comparisons of each genus with the number of reticulations
177 found in each optimal phylogenetic network. Because we had an *a priori* prediction that

178 *Physconelloides* should exhibit less evidence of reticulation than *Columbicola*, we used a one-
179 tailed test; however, we also report the results of the two-tailed test equivalent.

180 **Results**

181 Both approaches revealed highly concordant results: higher levels of introgression among
182 species of wing lice compared to body lice. In particular, using a read-mapping based method,
183 the genomic signature of introgression was significantly higher in wing louse species than in
184 body louse species (GLM with the mean values of the simulations; F = 21.0705, df = 69, P =
185 2.367×10^{-5}, R^2=0.58; Fig. 3, Supplementary Table S1, Figs. S1-S12). The contigs assembled
186 from reads mapping to the non-focal species were in the size range of the loci used as reference
187 (mean max contig length= 1214 bp; mean contig length=292 bp; Table S3). Even though wing
188 lice showed more evidence for introgression, one body louse individual (included in the GLMs)
189 exhibited the highest level of introgression (Fig. 3, Figs. S1-S12). However, the other individual
190 from the same taxon, inhabiting the same host species and collected in the same geographic
191 region, did not show these elevated levels of introgression (Supplementary Table S2, Figs. S1-
192 S12).

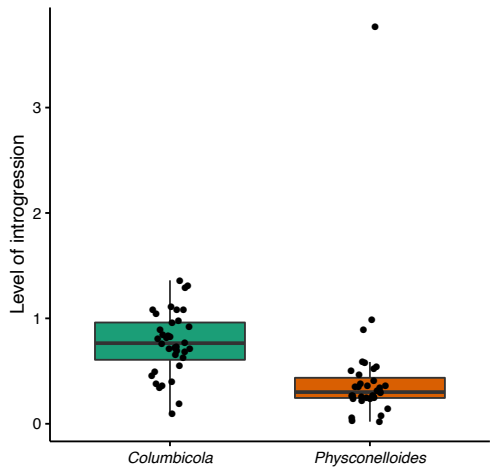

Figure 3. Boxplot showing the differences in levels of introgression between wing (green) and body (orange) lice. Level of introgression represents the sum of the mean coverage of reads mapped from all the species excluding the focal louse species, divided by the mean coverage of the focal louse species (see Methods). Black dots show the levels of introgression (i.e., resulting from the equation) for each individual sample (horizontally jittered values).

Secondly, in a phylogenetic network framework, the optimal networks of wing lice were more reticulated than those of body lice even though the number of taxa included in the networks was lower (seven reticulations in *Columbicola* vs. four in *Physconelloides*, Fig. 4). Accordingly, the number of reticulations given the number of potential combinations under a one-tailed test was significantly higher in *Columbicola* (One-sided: χ^2= 3.8132; df=1; *P*= 0.03; CI=0.03–1), and the p-value was still near 0.05 with a two-tailed test (Two-sided: χ^2= 3.8132; df=1; *P*= 0.05; CI=-0.01–0.66). Also, the specific lineages involved in the reticulations were generally congruent with signatures of introgression from the read-mapping based approach (Fig. S1-S12).

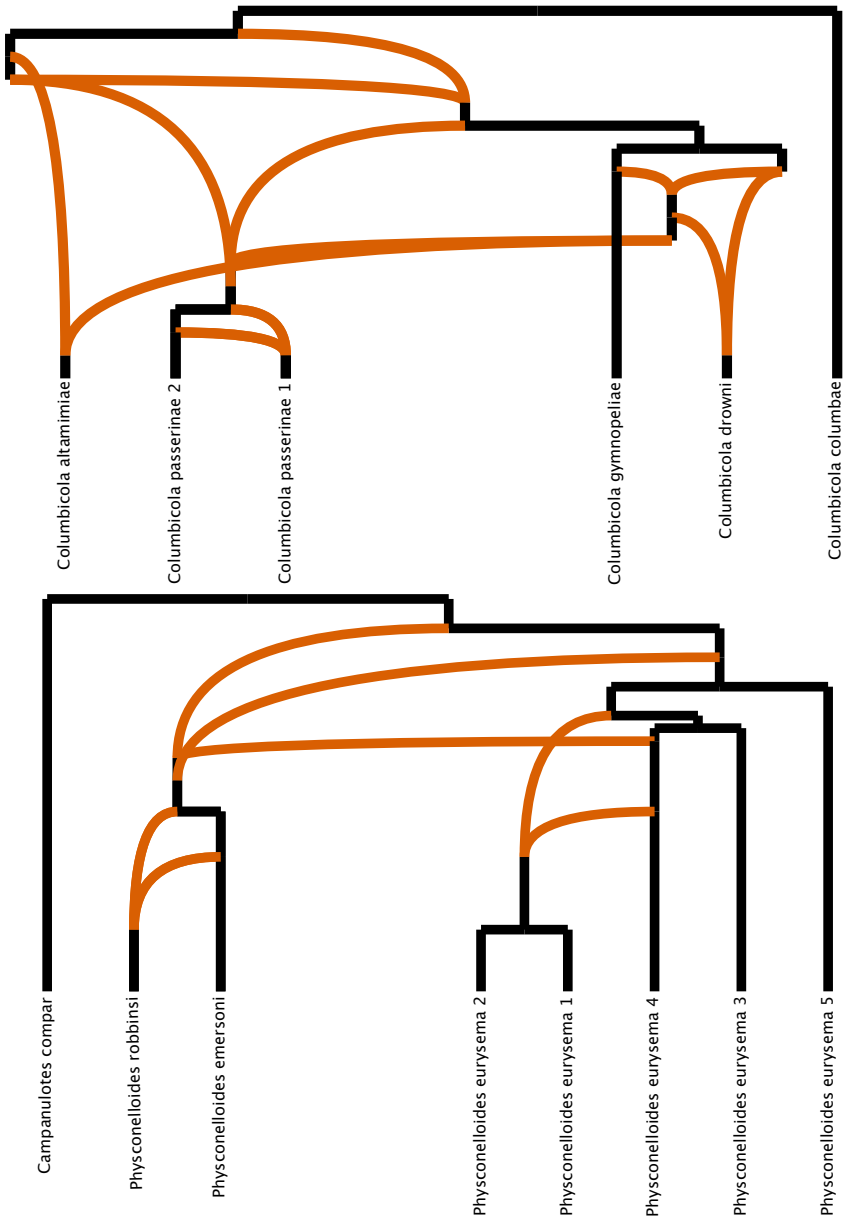

Figure 4. Optimal phylogenetic networks of feather lice genera. Orange branches depict reticulations: seven in *Columbicola* and four in *Physconelloides*.

Discussion

Estimates of introgression in two groups of ectoparasites that differ in their dispersal abilities, wing and body lice of doves, indicate that the lineage with higher dispersal ability (wing lice) shows more evidence of introgression. This evidence from wing and body louse genomes is

213 consistent with the hypothesis that dispersal differences might drive differences in the level of
214 introgression in this system of parasites. Admittedly, there may be some unknown factor, other
215 than dispersal, differing between these two groups of lice that causes the difference in the level
216 of introgression, but prior work on these groups of parasites points to dispersal as a crucial factor
217 underlying many of the ecological and evolutionary patterns in these parasites. Further research
218 on other taxa is needed to confirm the generality of these findings. This work is among the first
219 studies of introgression in a host-symbiont system (Detwiler and Criscione 2010). Notably,
220 recent studies have found that straggling and host-switching are relatively common processes in
221 host-symbiont systems (De Vienne et al. 2013; Bourguignon et al. 2018; Nylin et al. 2018; Doña
222 et al. 2019). Our study suggests that in a straggling/host-switching scenario, hybridization can
223 provide further genetic variation with important ecological and evolutionary consequences (e.g.,
224 facilitating adaptation to current hosts or facilitating the colonization of new ones) (Barton
225 2018). Indeed, we may have found a potential recent hybridization event (i.e., the
226 *Physconelloides* individual showing the highest level of introgression), though this requires
227 further study to rule out methodological issues (e.g., wet-lab contamination).

228 In this vein, a careful examination of the introgression history of these taxa (and
229 symbionts as a whole) is needed to better understand the patterns of introgression that we found.
230 Questions such as how much introgression can be expected or how the introgressed regions are
231 retained in parasite/symbiont genomes across time, among many others, require further attention.
232 For instance, in this study, the levels of introgression detected by the sppIDer analyses (i.e., the
233 magnitude but not the comparative pattern) may be unrealistic. It may be that some fraction of
234 the level of introgression detected by sppIDer may be due to ILS, and not introgression.
235 However, both louse genera are expected to have relatively similar rates of ILS (if any). It is also

236 possible that taxon age and interspecific divergence might affect introgression rates.
237 Nevertheless, Sweet and Johnson (2018) compared the degree of genetic divergence of two pairs
238 of species of both genera that inhabits the same host species and share a cospeciation event. In
239 this case of taxa of the same age, the pair of *Columbicola* species had lower interspecific genetic
240 distances than *Physconelloides*. This could be as a result of mutation rate differences between the
241 two genera. However, this could also be due to higher gene flow among host infrapopulations
242 due to higher dispersal capabilities of wing lice. The same pattern can be found overall across the
243 species studied here, i.e., on average, lower uncorrected interspecific genetic distances among
244 *Columbicola* than among *Physconelloides* species, though the range of the interspecific distances
245 does overlap (Table S4). Thus, if present, ILS could potentially be more prevalent in
246 *Columbicola* species (Pamilo & Nei, 1988; Maddison, 1997). The PhyloNet analysis, however,
247 does control for ILS, and showed highly congruent results. In addition, some individual gene
248 trees exhibit signatures suggestive of introgression with highly similar sequences shared by some
249 individuals of different species and much less likely to be a consequence of ILS (Figs. S13-S14).
250 Overall, the species of *Columbicola* and *Physconelloides* are from the same group of hosts and
251 thus are overall comparatively similar in levels of divergence, so it seems unlikely that these
252 small differences are driving the results.

253 Another caveat is that sppIDer can detect introgression from species that are not included
254 in the reference data. In those cases, the reads may map to the closest taxon available in the
255 reference set, and thus could artificially increase the level of introgression from a given species;
256 Langdon et al. 2018). Accordingly, the levels of introgression detected by sppIDer in certain
257 species could be an aggregate of introgression events from more than one species. Indeed, our
258 PhyloNet analysis supports this scenario, with several reticulations from ghost lineages and

species (Fig. 4). However, in this system we have nearly complete sampling of host taxa and are missing few, if any, extant species making this concern less likely.

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