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

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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.

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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. Overall, the results from this study represent an important step towards understanding the factors driving hybridization, and have major implications for coevolutionary biology.

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.

Comparisons of 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

59 comparing the impact of dispersal differences on other aspects of biology, such as population
60 structure and codivergence (Clayton and Johnson 2003; Johnson and Clayton 2004; Clayton et
61 al. 2015; DiBlasi et al. 2018; Sweet and Johnson 2018). Specifically, this is an excellent system
62 in which to assess the effect of differences in dispersal capabilities on levels of introgression
63 because both of these two lineages of feather lice: 1) significantly differ in their dispersal ability
64 (Harbison et al. 2008, 2009; Bartlow et al. 2016), 2) co-occur across the diversity of pigeons and
65 doves, 3) present highly comparable temporal patterns of diversification, specifically, both
66 lineages originated on the common ancestor of *Metriopelia* doves (11.3-14.9 mya) and have a
67 correlated pattern of codiversification within the same group of hosts (including a shared
68 cospeciation event which occurred within the *Metriopelia* genus 5.2-7.4 mya; Sweet and Johnson
69 2015, 2018), 3) and have the same basic life history and diet (Clayton et al. 2015; Sweet and
70 Johnson 2015, 2018). Both wing and body lice disperse vertically between parents and offspring
71 in the nest. However, wing lice can also attach to and hitchhike on hippoboscid flies to disperse
72 "phoretically" between host individuals or host species (Harbison et al. 2008, 2009; Bartlow et
73 al. 2016). Indeed, this hitch-hiking dispersal mechanism profoundly influences their degree of
74 population structure and cophylogenetic history (Clayton and Johnson 2003; Sweet et al. 2017b;
75 DiBlasi et al. 2018; Sweet and Johnson 2018). In addition, wing lice have a higher rate of host-
76 switching (Clayton and Johnson 2003; Clayton et al. 2015; Sweet et al. 2017b) (i.e., successful
77 colonization of new host species) and of straggling (Whiteman et al. 2004) (i.e., dispersal to new
78 host species without reproduction on that new host).

79 To compare differences in the extent of introgression between wing and body lice, we
80 used whole-genome data from 71 louse individuals belonging to five taxa of wing lice
81 (*Columbicola*) and seven taxa of body lice (*Physconelloides*) that occur across the same host

species and have highly comparable patterns of diversification (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).

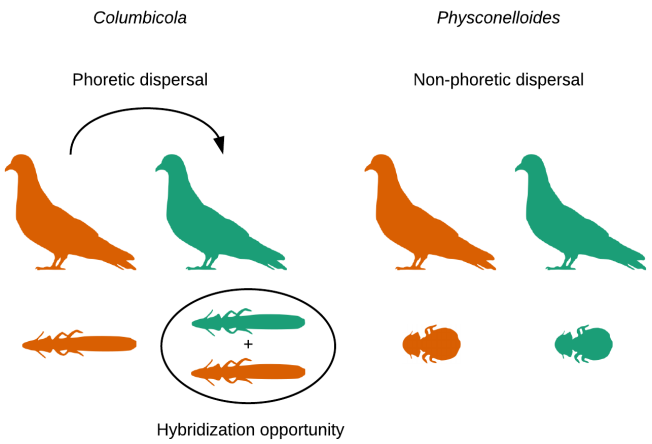


Figure 1. Diagram depicting the ecological replicate system and the hypothesis of this study. Wing lice (*Columbicola*) have higher dispersal abilities than body lice (*Physconelloides*), and thus higher odds of encountering individuals of a different louse sp.

Materials and Methods

Data

We studied 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). All raw sequence data used were available from previous studies (Boyd BM, et al. 2017; Sweet et al. 2017a; Sweet and Johnson 2018) and represent all described New World ground-dove wing and body louse species–most host species in this group–including lice samples across multiple biogeographic areas within species of hosts

98 (Sweet and Johnson 2018; Supplementary Table S2). Illumina genome sequence data pre-
99 processing included several steps (Sweet and Johnson 2018). First, we discarded duplicate read
100 pairs using the fastqSplitDups script (https://github.com/McIntyre-Lab/mcscriptand
101 https://github.com/McIntyre-Lab/mclib). We then eliminated the Illumina sequencing adapters
102 with Fastx_clipper v0.014 from the FASTX-Toolkit (http://hannonlab.cshl.edu/fastx_toolkit).
103 Also, we removed the first 5 nt from the 5' ends of reads using Fastx_trimmer v0.014 and
104 trimmed bases from the 3' ends of reads until reaching a base with a phred score ≥28 (which is
105 equivalent to a base call accuracy higher than 99.8 %) using Fastq_quality_trimmer v0.014.
106 Finally, we removed any reads less than 75 nt and analyzed the cleaned libraries with Fastqc
107 v0.11.5 to check for additional errors. We assembled nuclear loci in aTRAM following previous
108 studies (Allen et al. 2015; Boyd BM, et al. 2017; Sweet and Johnson 2018). In particular, we
109 mapped modest coverage (25-60X), multiplexed genomic data to reference loci from a closely
110 related taxon. For our reference set of nuclear loci for wing lice, we used 1,039 exons of
111 *Columbicola drowni* (Boyd BM, et al. 2017) (raw data: SRR3161922). This data set was
112 assembled de novo (Allen et al. 2015) using orthologous protein-coding genes from the human
113 body louse genome (*Pediculus humanus humanus* (Kirkness et al. 2010) as a set of target
114 sequences. We mapped *Columbicola* reads to the *C. drowni* references using Bowtie2
115 (Langmead and Salzberg 2012). For body lice, we obtained nuclear data using the same pipeline
116 and software parameters, except that we used 1,095 loci from *Physconelloides emersoni* as the
117 reference for mapping. To generate the input ultrametric gene trees for Phylonet v3.6.8 (Than et
118 al. 2008; Yu and Nakhleh 2015; Wen et al. 2018), we first aligned each nuclear locus in MAFFT
119 (Katoh 2002)(--auto) and removed columns with only ambiguous sequences ("N"). Then, we
120 estimated gene trees in RAxML v8.1.3 (Stamatakis 2006) with a GTR + Γ substitution model for

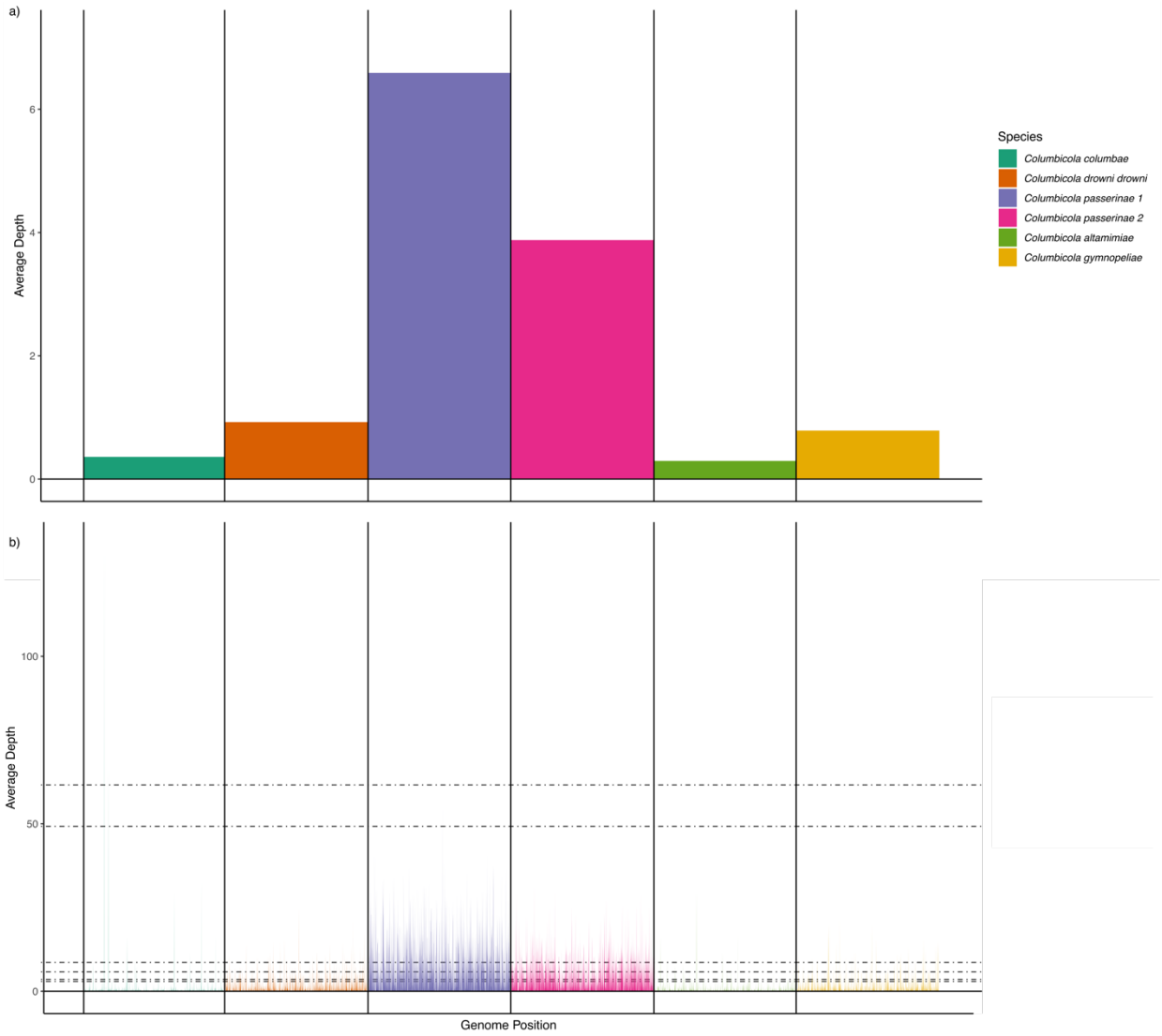
121 each gene alignment. Finally, we made trees ultrametric using the nnls method in the
122 force.ultrametric function within the "phytools" R package (Revell 2011).

123 Quantifying introgression

124 We used two different approaches to quantify differences in the extent of introgression (i.e.,
125 ancient plus recent) between the two louse genera. We employed methods suitable to detect
126 introgression between species and between individuals from the same species (i.e., we did not
127 employ methods aimed to detect differences at the population level, e.g., TreeMix; Pickrell and
128 Pritchard 2012). First, we used sppIDer (Langdon et al. 2018) to quantify the genomic
129 contributions of different louse species in an individual louse genome (Fig. 2). We built our
130 reference for each genus using all the nuclear loci from a single individual per species. For the
131 reference, we selected those individuals for which we assembled the highest number of genes for
132 each genus. We estimated the extent of introgression as the sum of the mean coverages of reads
133 mapped from all the species excluding the focal louse species, divided by the mean coverage of
134 the focal louse species (Fig. 2). Note that these mean coverage values are calculated using only

135 those reads that mapped with a mapping quality (MQ) > 3 (Li et al. 2009; Langdon et al. 2018;

136 Figs. S1-S12).



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

142

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

144 sorting (ILS) (i.e., reticulations in this method can be attributed to hybridization events), using a

145 maximum pseudo-likelihood framework with PhyloNet 3.6.1 (Than et al. 2008; Yu and Nakhleh

146 2015; Wen et al. 2018). We trimmed the unrooted gene trees to the same individuals used as
147 reference taxa in sppIDer, and performed eleven independent analyses with a differing maximum
148 number of reticulation nodes (i.e., from zero to ten). We conducted ten runs per analysis. We
149 then selected the optimal network for each genus based on AIC values.

150 Statistics and reproducibility

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

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

171 **Results**

172 Both approaches revealed highly concordant results: higher levels of introgression among
173 species of wing lice compared to body lice. In particular, using a read-mapping based method,
174 the genomic signature of introgression was significantly higher in wing louse species than in
175 body louse species (GLM with the mean values of the simulations; F = 21.0705, df = 69, P =
176 2.367 x 10^{-5}, R^2=0.58; Fig. 3, Supplementary Table S1, Figs. S1-S12). Contrary to this effect,
177 one body louse individual (included in the GLMs) exhibited the highest level of introgression
178 (Fig. 3, Figs. S1-S12). However, the other individual from the same taxon, inhabiting the same
179 host species and collected in the same geographic region, did not show these elevated levels of
180 introgression (Supplementary Table S2, Figs. S1-S12).

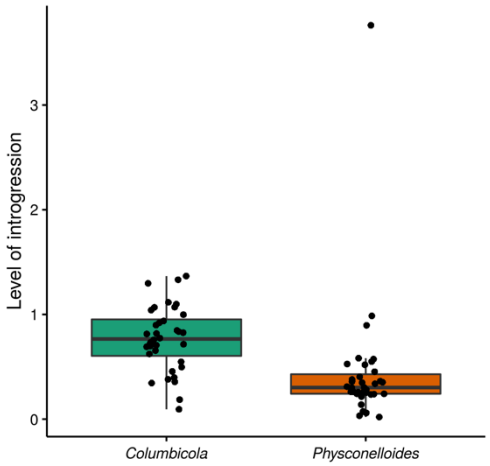

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Figure 3. Boxplot showing the differences in levels of introgression between wing (green) and body (orange) lice. Level of introgression represents the sum of the mean coverage of reads mapped from all the species excluding the focal louse species, 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).

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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).

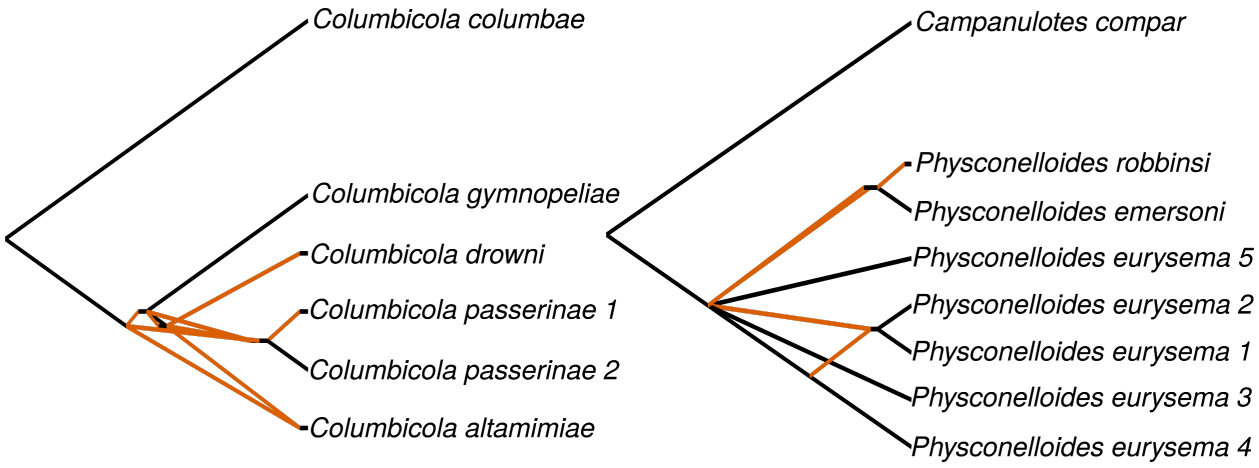

Figure 4. Optimal phylogenetic networks of feather lice genera. Orange branches depict reticulations: seven in *Columbicola* and four in *Physconelloides*. Note that though visually overlapped, every reticulation in this figure involves at least two taxa (extant or extinct). See the raw unedited networks (Figs. S13-S14) for more details on specific reticulations.

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

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

217 In this vein, a careful examination of the introgression history of these taxa (and
218 symbionts as a whole) is needed to better understand the patterns of introgression that we found.
219 Questions such as how much introgression can be expected or how the introgressed regions are
220 retained in parasite/symbiont genomes across time, among many others, require further attention
221 and will certainly have a strong impact in coevolutionary biology theory. For instance, in this
222 study, the levels of introgression detected by the sppIDer analyses (i.e., the magnitude but not the
223 comparative pattern) may be unrealistic. It may be that some fraction of the level of introgression
224 detected by sppIDer may be due to ILS, and not introgression. However, both louse genera are

225 expected to have relatively similar rates of ILS (if any), and our PhyloNet analysis, which does
226 control for ILS, showed highly congruent results. On the other hand, sppIDer can detect
227 introgression from species that are not included in the reference data (and, in those cases, the
228 reads map to the closest taxon available in the reference, and thus could artificially increase the
229 level of introgression from a given species; Langdon et al. 2018). Accordingly, the levels of
230 introgression detected by sppIDer in certain species could be an aggregate of introgression
231 events from more than one species. Indeed, our PhyloNet analysis supports this scenario, with
232 several reticulations from ghost lineages and species (Figs. S13-S14), although in this system we
233 have nearly complete sampling of host taxa and are missing few, if any, extant species.

234 Overall, the results from this study represent an important step towards understanding the
235 factors driving hybridization, because most previous studies focus on the presence/absence of
236 hybridization and the evolutionary consequences of hybridization (Arnold 2015; Folk et al. 2018;
237 Taylor and Larson 2019). Further research is needed to understand the factors shaping the
238 frequency of hybridization and to ascertain their influence across different scales (e.g., from
239 ancient to recent hybridization events).

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