Title: Long-distance dispersal of pigeons and doves generated new ecological opportunities for host-switching and adaptive radiation by their parasites.

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Abstract

Adaptive radiation is an important mechanism of organismal diversification, and can be triggered by new ecological opportunities. Although poorly studied in this regard, parasites present an ideal system to study adaptive radiations because of their close associations with host species. Both experimental and comparative studies suggest that the ectoparasitic wing lice of pigeons and doves have undergone an adaptive radiation, resulting in differences in both body size and overall coloration. Here we show that long-distance dispersal by dove hosts was important for parasite diversification, providing new ecological opportunities for parasites to speciate by host-switching. We further show that these new opportunities for host-switching decreased over time, and cospeciation became the more dominant mode of parasite speciation. Taken together, our results suggest that host dispersal, followed by host-switching, provided novel ecological opportunities that facilitated adaptive radiation by parasites.

Keywords: Phylogenomics, cospeciation, Columbidae, ectoparasite, lice

Introduction

Adaptive radiations have profoundly influenced the development of evolutionary theory [1,2]. An adaptive radiation occurs when speciation is triggered by new ecological opportunities [1,3]. Classic examples of adaptive radiation involve the evolution of diverse morphological features, such as bill shape in Galapagos finches [4] and Hawaiian honeycreepers [5], body shape in Caribbean anole lizards [6], mouthparts and body shape in African rift lake cichlid fishes [7], and growth habit in Hawaiian silversword plants [8]. These notable radiations occurred in isolated habitats, such as volcanic islands or recently formed lakes, in which a newly colonizing lineage diversified into multiple lineages in response to new ecological opportunities [1,3].

Relatively few studies of adaptive radiation have focused on animal parasites, despite the fact that they represent much of the world's biodiversity [9]. There is great potential for adaptive radiation by parasites, especially when a parasite lineage can switch to a novel host lineage that was not previously colonized. In particular, when a parasite species colonizes a previously un-infested host lineage (analogous to a free-living species dispersing to an uninhabited island or lake), the parasite may subsequently switch among the species in that host lineage, resulting in parasite diversification [9]. This, in short, is an example of adaptive radiation of parasites across host "islands".

Two recent studies identified the ecological mechanisms of adaptive speciation within a group of animal parasites [10,11], the wing lice (Insecta: Phthiraptera: *Columbicola*) of pigeons and doves (hereafter doves; Aves: Columbiformes). Wing lice are permanent ectoparasites that pass all stages of their life cycle on the body of the host, feeding on downy feathers and escaping from host preening by inserting between the feather barbs in the wing [9]. In these lice, both size and color are correlated with that of their hosts [10,12,13]. Recent experimental studies demonstrated the adaptive basis of size and color [10,11]. Wing lice (*Columbicola columbae*) transferred to pigeon breeds that differ dramatically in size (simulating host-switching), rapidly evolved differences in size within a few generations [11]. Size was an adaptation to escape host-preening defense [11,12]. Changes in body size triggered reproductive isolation, a precursor to speciation, due to a mismatch between male and female body sizes that limited copulation [11]. Through similar transfer experiments, louse coloration was shown to be an adaptation for crypsis, such that lice transferred to white pigeon breeds became lighter and those to dark breeds became darker [10]. Again, this adaptation was selected by host preening defense, as birds more readily removed lice that did not match host coloration [10]. Together, these experiments demonstrated the adaptive basis of morphological variation across this clade of parasites and recreated the diversity of size and color phenotypes observed across known wing louse species [10,13]. Moreover, these studies show how parasites can potentially rapidly and dramatically diversify when presented with novel ecological conditions.

Given that the adaptive mechanisms underpinning reproductive isolation have been identified through experimental work emulating host-switching [10,11], we went beyond these studies to focus on the ecological opportunities for host-switching that serve as a foundation for adaptive radiations in parasites. Host dispersal and contact between host species have been recognized as having the potential to increase parasite diversity [14-16]. Here we specifically focused on the role host dispersal plays in bringing parasite lineages into contact with novel host species with which they did not previously overlap in geographic range. We then evaluated whether this novel range overlap provided new opportunities for host-switching by identifying host dispersal events that preceded parasite speciation through host-switching [17]. If host-switching was facilitated by host sympatry, two possibilities exist: first, resident parasites may have switched to newly arriving hosts; reciprocally, parasites on the newly arriving hosts may have switched to resident hosts [18,19]. By comparing the dove and wing louse trees, we identified the direction of host-switching by parasites following host dispersal.

While ecological opportunity is essential for the occurrence of adaptive radiations, these opportunities are finite and radiating lineages will ultimately saturate open niche space [20-23]. Thus, in an adaptive radiation, the predominant mode of speciation should change over time. In host-parasite systems, parasite speciation events can be categorized as having resulted from 1) host-switching, which involves dispersal to and establishment on a host species on which a parasite did not previously occur, or 2) cospeciation, which is the simultaneous divergence of host and parasite lineages [9]. Using cophylogenetic reconstruction and time-calibrated trees of doves and their wing lice, we classified louse speciation events as resulting from either host-switching or cospeciation. Finally, we compared the relative timing of these two events. Specifically, we evaluated whether the age of dove wing louse speciation events triggered by host-switching tend to be older than speciation events triggered by cospeciation. This pattern might be predicted if host lineages become more fully colonized by a parasite lineage over time, eventually filling up open niches and reducing ecological opportunity. Taken together, these analyses provide a framework to evaluate the phylogenetic and biogeographic underpinnings of adaptive radiation in host-parasite systems, by focusing on new ecological opportunities generated by long-distance host dispersal and the relative timing of host-switching and cospeciation events.

Methods

A total of 61 species of doves were used for whole genome sequencing. These species were selected to include dove species that host the parasitic wing lice in the phylogenomic tree described by Boyd et al. [24]. Genomic DNA was extracted from dove tissues and sequenced on the Illumina

HiSeq platform. Protein-coding genes were identified from the *Columba livia* reference genome using the MAKER pipeline [25,26]. We then identified single-copy orthologous genes in the genome of *C. livia* and all Sauropsida available in OrthoDB v8 [27]. We then removed candidate within-clade paralogs (supplementary methods). Sequence reads from each library were mapped to the remaining *C. livia* orthologs using Bowtie2 (v2.3.4.1) [28]. Final gene sequences for all 61 dove species were generated by taking the consensus base at each position [29] and clustered into orthologous gene sets.

We used two methods to infer the evolutionary relationships of dove species. Ortholog sets were aligned as translated amino acid sequences using UPP (v2.0) [30] and back translated to nucleotide sequences. RAxML (v8.2.9) [31] was used to estimate individual gene trees under the GTR+Γ models and 100 bootstrap replicates. ASTRAL-II (v4.9.9) [32], a coalescence-based analysis, was used to estimate a species tree from the maximum likelihood (ML) gene trees. Next, we sought to estimate the dove phylogeny from all of the sequence data simultaneously. We generated a concatenated alignment including all sequence data to estimate the ML tree based on this supermatrix. For each gene tree, the GTR+Γ parameters were estimated for each codon position, and k-means clustering was applied to these codon rate parameters to create a partition for the alignment. An ML tree was estimated from the partitioned alignment using RAxML under GTR+Γ models. A total of 100 bootstrap replicate trees were computed to infer support.

MCMCTree, implemented in PAML (v4.9) [33], was then used to estimate the timing of dove and wing louse speciation events. We identified six dove fossils suitable as minimum age internal calibration points (table S1). A maximum constraint was added to the root in order to estimate global DNA substitution rates. Two different analyses were conducted to accommodate two different root constraints (table S1). The oldest fossil in the tree, *Arenicolumba*, is a biogeographic anomaly (fossil described from New World, but closely allied species found in Old World) [34], so each analysis was done both with and without this fossil calibration. Likewise, wing louse species divergence times were estimated in millions of years using the ML tree described by Boyd et al. [24]. Nine internal calibration points were used based on terminal cospeciation events, in which terminal sister species of lice were associated with terminal sister species of hosts (table S1). The age ranges of these internal calibration points were based on the 95% confidence intervals of the estimated dates of these nodes in host trees. Maximum constraints were added to the root and to estimate global DNA substitution rates (table S1). We conducted four analyses in total using all possible combinations of two different maximum constraints and two different sets of internal calibration points (based on different estimates of the timing of cospeciation given the two different host trees). In both dove and louse trees, branch lengths were estimated using baseml and then divergence times were estimated under a GTR+Γ model with Markov chain Monte Carlo (MCMC) approximation and an independent rates model. We determined that node age estimates converged between identical runs using Tracer (v1.7.1) [35]. Additionally, a time-calibrated tree was then used to estimate the ancestral species ranges of doves using BioGeoBEARS (v1.1.1) [36] under the optimal model of DIVA-like+J.

JANE (v4) [37] was used to identify host-parasite cospeciation events and speciation following host-switching by comparing host and parasite phylogenies. In total, three comparisons were conducted. First, we compared louse and host trees disregarding node ages. Second, we compared louse and host trees while binning speciation events within three different time intervals based on node age. The three intervals were based on a review of Gondwanan biotic interchange (66-45, 45-30, and 30-0 mya) [38]. Time-constrained comparisons were conducted with one louse time-tree and both available host time-trees (additional comparisons were not needed, given the time intervals used, because the node age category assignments were identical). In all comparisons, nodes in the louse tree with less than 75% bootstrap support were collapsed to reflect ambiguity around species relationships. Using the BioGeoBEARS reconstruction, we identified lineages in the tree that were inferred to have colonized one biogeographic region from another. By combining the results from JANE and BioGeoBEARS, we evaluated whether dove lineages moving from one region to another 1) acquired lice from a dove lineage already in that region, or 2) carried lice to a new region where they switched to dove lineages already in the region. We also categorized each speciation event (i.e. node) in the louse tree as the result of: 1) host-switching or 2) cospeciation. Using the estimated dates for each of these events, we plotted the relative ratio of cospeciation and host-switching events to overall speciation events and the generation of parasite diversity over time.

Results

We identified 6,363 single-copy orthologs from which to infer the phylogenetic relationships of 61 dove species. Simultaneous analysis of a supermatrix (11,103,960 bases) produced a well-supported tree (100% bootstrap support for 62 of 63 nodes; figure S1) that was largely in agreement with a coalescence-based species tree (0.99-1 posterior probability for 60 of 63 nodes; figure S2). Species divergence times were estimated using two different sets of root maximum constraints, and these analyses suggest that doves began to diversify around 51 or 60 mya depending on root age calibration (figures 1, S3-S4). Removing a biogeographically unusual and comparatively old fossil from the genus *Arenicolumba* resulted in node ages that were only slightly younger (45 or 55 mya), indicating that this fossil did not have a dramatic impact on the results. Species divergence time estimates for wing lice showed diversification began around either 15 or 24 mya depending on root age calibration (figures S5-S8). Both dove and wing louse trees were structured by geographic region, and ancestral area reconstruction suggested Australasia + New World was the ancestral range of doves. The earliest divergence splits the dove tree into two clades, one with an Australasian origin (Raphinae) and the other with a New World origin (Claravinae + Columbinae; figure 1). During the Neogene, members of the Australasian clade went on to colonize Eurasia and Africa, while members of the New World clade went on to colonize Australasia, Eurasia, and Africa.

An initial comparison of the dove and wing louse trees, without considering the timing of speciation events, suggests that the lice had an ancestral host among the Australasian dove clade (table S2). When the timing of louse speciation events is constrained by time intervals informed by habitat connectivity (wing louse diversification beginning at 15 or 24 mya), the analysis again supported a single geographic origin of wing lice. However, the ancestral host of wing lice is unclear, with four possible origins: one in Australasia, two in the New World, and one in Africa (figures S9-S11, table S2). Comparisons of dove and louse trees identified 32 cospeciation events and 28 host-switching events (figure 2; table S2). The overall proportion of cumulative wing louse speciation events attributable to cospeciation increased over time (figures 3, S12). The median age of louse speciation events due to cospeciation was significantly younger than those due to host-switching (Wilcoxon Signed Rank test $P = 0.021$). A comparison of host and parasite trees without consideration of time constraints found additional cospeciation events (table S2). However, based on divergence times obtained from the host tree, these additional events would have occurred prior to our estimates for the onset of louse diversification, and thus are incompatible with the time calibrated host and parasite trees. Examining dove clades that are inferred to have colonized new biogeographic regions through long-distance dispersal, we observed two patterns: 1) doves acquiring lice from native hosts following dispersal and colonization of a new region (3 cases) and 2) a dove bringing lice to new region through dispersal, which then switch to a native host in that region (1 case). Three examples of doves acquiring lice from native hosts after colonizing a new region include *Columba* species, which had a New World origin and acquired parasites after colonizing Africa; *Turtur* species, which had an Australasian origin and acquired lice after colonizing Africa; and *Macropygia* + *Reinwardtoena* species, which had a New World origin and acquired lice upon colonizing Australasia. An example of doves bringing lice to new region include lice carried from Africa to Australasia by dispersing *Columba* species, where the lice then switched to the genus *Chalcophaps* (figures S9-S11).

Discussion

In this study, we explored new ecological opportunities provided by host dispersal for adaptive radiation in parasites. Specifically, we used phylogenomic datasets derived from whole genome sequence reads for both dove hosts and their wing louse parasites to reconstruct the biogeographic context and timing of host-switching events. We found that long-distance dispersal by doves, in multiple cases, was followed by a host-switching event of their lice to a novel host lineage with which that louse lineage now had geographic overlap. In addition, over the course of wing louse diversification, we found that the contribution of host-switching to parasite speciation declined over time, relative to cospeciation. These results indicate that hosts without a lineage of parasites initially presented a new ecological opportunity for adaptive radiation by their parasites.

Focusing specifically on the evolutionary history of the avian hosts, our phylogenomic results show that early dove diversification was shaped by continental drift and occurred prior to the diversification of extant wing louse species groups. Modern dove species diversity is highest in the southern hemisphere, with centers of dove diversity found in Australasia, Asia, South America, and central Africa [39]. Our analyses point to a subset of these areas, specifically South America and Australasia, as the ancestral range of doves. Doves began to diversify just after the K-Pg boundary, when Australia and South America were connected via Antarctica. The Australia-Antarctica-South American land bridge had a near tropical climate during this period [40], which could have supported a diverse assemblage of early dove species across the region and allowed them to move among these continents [38,41]. Australia broke away from Antarctica at 49-50 mya [42], followed by South America at 39 mya [43]. The timing of this separation corresponds to initial divergence of dove lineages, with one lineage remaining in the New World and the other in Australasia.

Following the geologic breakup of the ancestral range of doves, further diversification was shaped by long-distance dispersal. The separation of Australia and South America from Antarctica marks the start of a period when doves could have used Antarctica as a stepping-stone in dispersal between Australia and South America. We found evidence of one such event, with cuckoo-doves

(*Macropygia+Reinwardtoena*) moving from the New World to Australasia at this time. The establishment of circumpolar ocean currents around Antarctica 33-34 mya [44] substantially cooled the region [45] and would have prevented further use of this region as a stepping-stone between Australia and the New World [38]. During this later period of dispersal, we see evidence of the movement of green doves (*Treron*), emerald doves (*Chalcophaps*), and wood doves (*Turtur*) from Australasia to Eurasia and Africa. We also see evidence of movement from the New World to the Old World by a clade of rock (*Columba*) and collared (*Streptopelia*) doves (this lineage colonized Africa, Eurasia, and Australasia).

While doves began to diversify shortly after the K-Pg boundary, wing louse speciation was delayed relative to host speciation and appears to have been facilitated by host-switching following host dispersal. It appears that a single wing louse lineage was isolated within a single geographical region prior to diversification. Wing louse diversification began at 15 or 24 mya, with lice colonizing multiple continents. The timing of wing louse diversification corresponds with the later period of host dispersal. Thus, host dispersal appears to have provided ecological opportunity for host-switching by wing lice. In particular, our phylogenetic reconstructions indicate that resident wing lice switched to newly arriving dove lineages. We also see evidence of the reverse pattern, i.e., wing lice on newly arriving host lineages switched to resident doves.

Host-switching allowed wing lice to establish on new host clades, leading to parasite radiation. However, our data show that parasite speciation events triggered by host-switching events are significantly older than host-parasite cospeciation events, highlighting the relative importance of dispersal followed by host-switching early in wing louse diversification. However, as new host groups became infested, our data indicate that host-switching became less frequent, suggesting that congeneric competition [46] may have diminished ecological opportunities of wing louse speciation by interfering with host-switching and establishment. A key finding from this work, was not that speciation is diminished following loss of ecological opportunity, but that cospeciation became a relatively more common mode of divergence. This shift was detectable by classifying the mechanism of speciation (host-switching versus cospeciation) relative to time.

Our results suggest that long-distance dispersal and colonization of new biogeographic regions by host species is important for the initial diversification of parasites and that parasites may take advantage of new ecological opportunities on novel host species. Our results further suggest that long-distance dispersal by host species can shape parasite diversity over evolutionary timescales, providing new opportunities for adaptive radiation by parasites. We observed parallels between our study system and another host-parasite system, lice that parasitize humans. There is evidence that: 1) modern humans acquired head lice from extinct hominids following dispersal and colonization of Eurasia [47], 2) humans carried head lice with them as they colonized the New World via Beringia [48,49], and 3) human lice switched to New World primates after humans colonized the New World [50]. These events mirror the evolutionary patterns of wing lice and their hosts and suggest these processes may be important for parasite diversification more broadly. Additional studies examining the consequences of long-distance host dispersal on parasite speciation and adaptive radiation are needed across a variety of parasites. The results of such studies may have broad relevance to the biology of invasive species and species conservation [18,19].

Ethics

Research on animals was conducted under University of Illinois, Champaign, Illinois IACUC protocols 10119, 13121, and 15212.

Data accessibility

Data are available from Figshare 10.6084/m9.figshare.12730337 and raw sequence data are available from the Short Read Archive https://www.ncbi.nlm.nih.gov/sra and are organized under BioProject PRJNA318048.

Competing interests

We declare we have no competing interests.

Author contributions

Study design (BMB, KPJ, DHC, SEB, MDS), sample procurement (KPJ, SEB, DHC), genome annotation (MDS), identified single-copy orthologs (RMW, BMB), designed and implemented ortholog assembly method (BMB, KPJ), ML and ASTRAL tree construction (NPN), fossil evaluation and MCMCtree doves (JMA), MCMCtree lice (KPJ, BMB), comparative analysis (KBV, BMB, ADS), biogeographic analysis (BMB), manuscript preparation (BMB, NPN, JMA, RMW, KBV, ADS, DHC, SEB, MDS, KPJ).

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Figures and tables

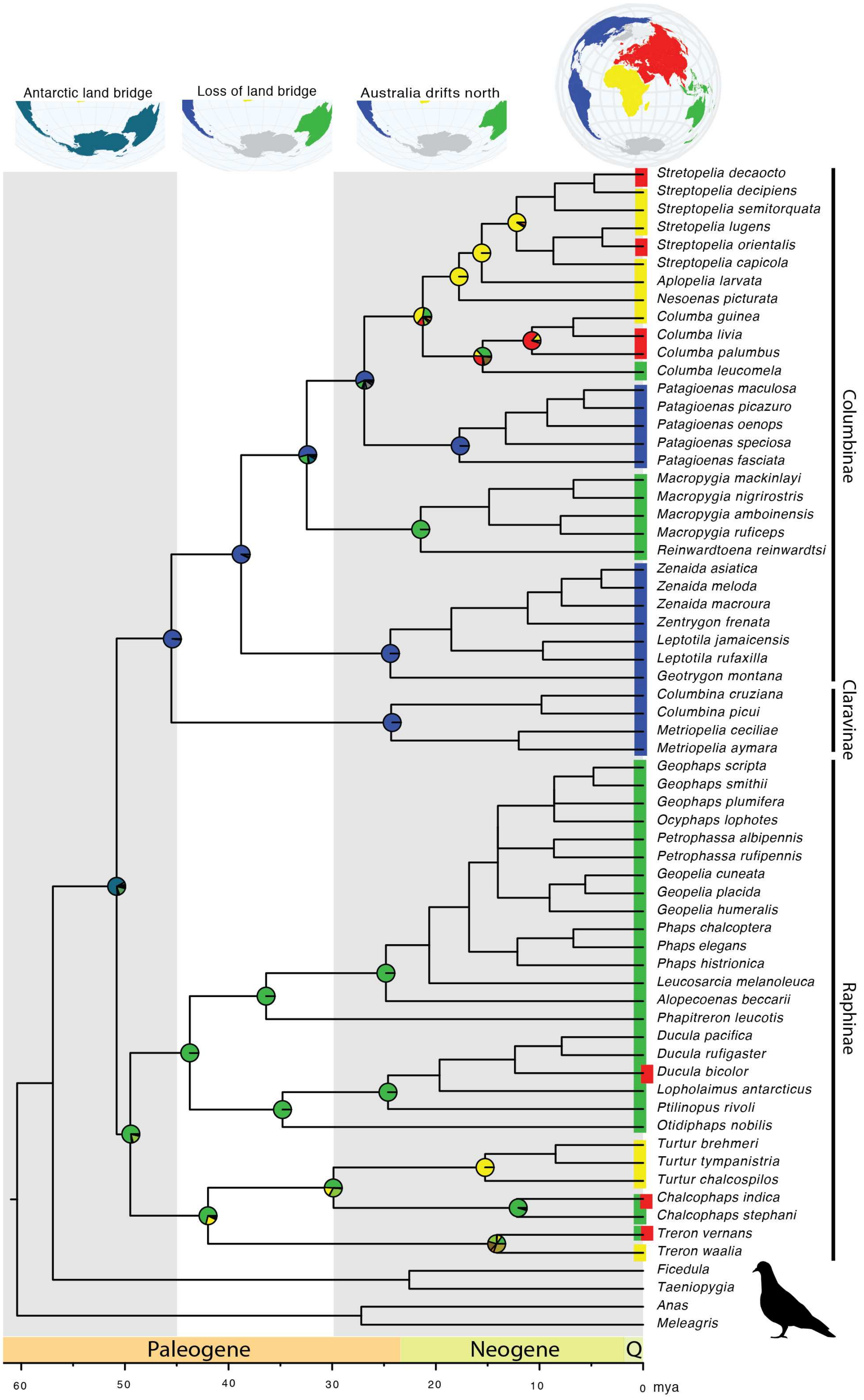
Antarctic land bridge
Loss of land bridge
Australia drifts north
Stretopelia decaocto
Streptopelia decipiens
Streptopelia semitorquata
Stretopelia lugens
Streptopelia orientalis
Streptopelia capicola
Aplopelia larvata
Nesoenas picturata
Columba guinea
Columba livia
Columba palumbus
Columba leucomela
Patagioenas maculosa
Patagioenas picazuro
Patagioenas oenops
Patagioenas speciosa
Patagioenas fasciata
Macropygia mackinlayi
Macropygia nigrirostris
Macropygia amboinensis
Macropygia ruficeps
Reinwardtoena reinwardtsi
Zenaida asiatica
Zenaida meloda
Zenaida macroura
Zentrygon frenata
Leptotila jamaicensis
Leptotila rufaxilla
Geotrygon montana
Columbina cruziana
Columbina picui
Metriopelia ceciliae
Metriopelia aymara
Geophaps scripta
Geophaps smithii
Geophaps plumifera
Ocyphaps lophotes
Petrophassa albipennis
Petrophassa rufipennis
Geopelia cuneata
Geopelia placida
Geopelia humeralis
Phaps chalcoptera
Phaps elegans
Phaps histrionica
Leucosarcia melanoleuca
Alopecoenas beccarii
Phapitreron leucotis
Ducula pacifica
Ducula rufigaster
Ducula bicolor
Lopholaimus antarcticus
Ptilinopus rivoli
Otidiphaps nobilis
Turtur brehmeri
Turtur tympanistria
Turtur chalcospilos
Chalcophaps indica
Chalcophaps stephani
Treron vernans
Treron waalia
Ficedula
Taeniopygia
Anas
Meleagris
Columbinae
Claravinae
Raphinae
Paleogene
Neogene
Q
60
50
40
30
20
10
0 mya

Figure 1. Time calibrated phylogeny of doves based on sequences of 6,363 nuclear single-copy orthologs. Scale bar at base of figure represents age in millions of years ago and geographic periods are designated above scale bar. Gray and white columns represent time intervals significant to biotic interchange across the Australia-Antarctica-South American land bridge and subsequent loss of habitat connectivity used to inform host-parasite phylogeny comparisons (66-45, 45-30, and 30-0 mya). Colors at tree tips represent modern geographic ranges of pigeon and dove species and circles at nodes represent estimated ancestral ranges corresponding with the globe at the top of the tree. Blue-green color in basal circle represents an ancestral range combining Australia and South America, corresponding to the Australia-Antarctica-South American land bridge illustrated at top of the figure. World maps created using rnaturalearth (https://github.com/ropensci/rnaturalearth).

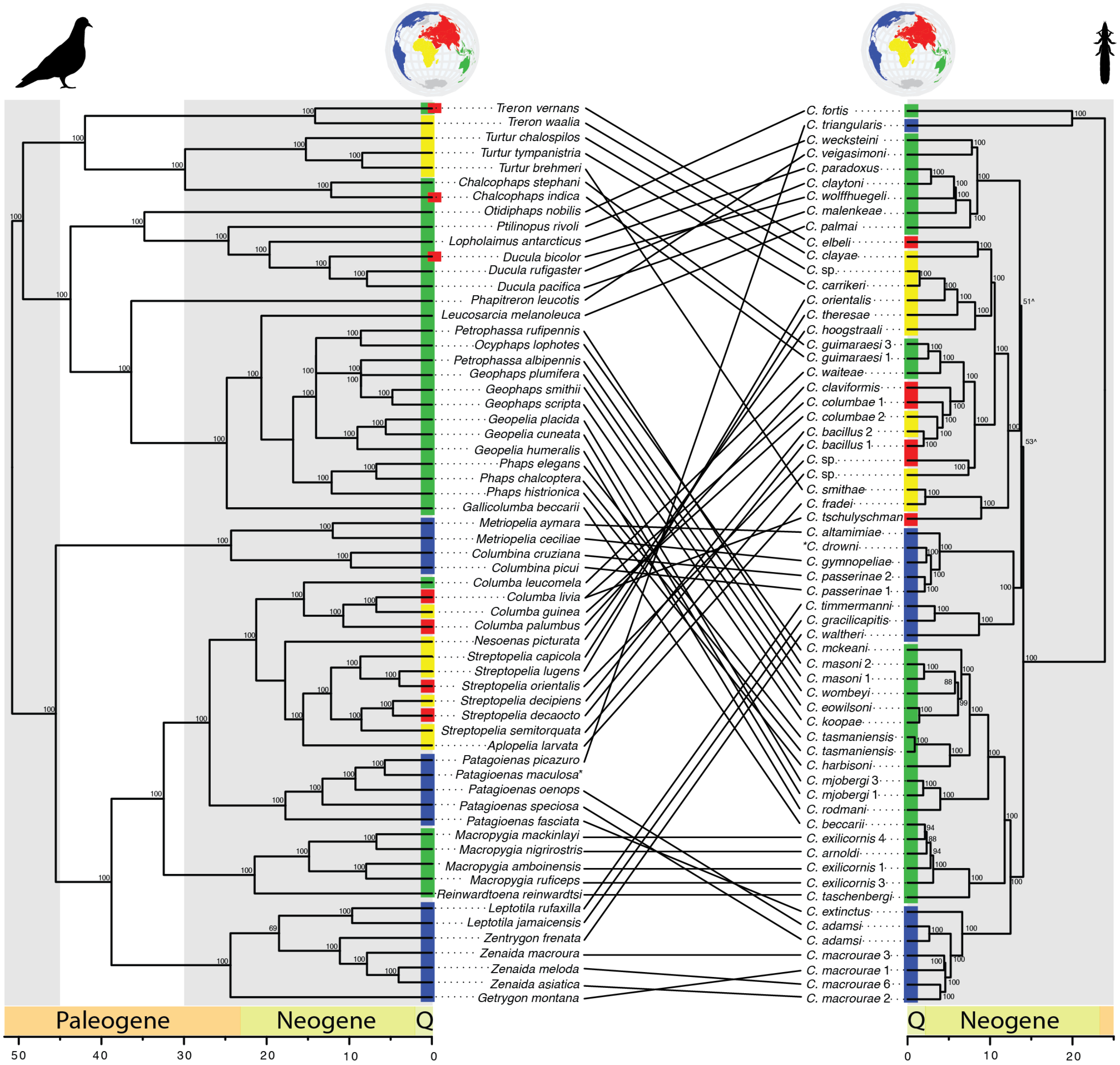

Figure 2. Time calibrated phylogeny of doves based on sequences of 6,363 nuclear single-copy orthologs (left) and their parasitic wing lice based on sequences of 977 single-copy orthologs

(right). Links between tree tips represent host-parasite associations. Conventions as in figure 1. * indicates taxa removed for comparative analysis. ^ indicates nodes collapsed in parasite tree for comparative analysis. World maps created using rnaturalearth (https://github.com/ropensci/rnaturalearth).

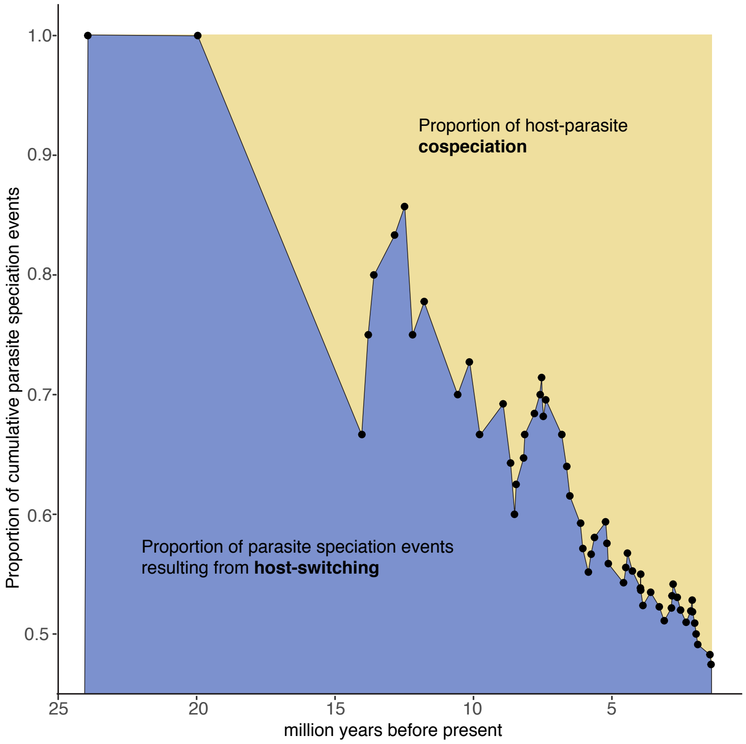

Figure 3. Proportion of cumulative host-parasite cospeciation events and parasite speciation events resulting from host-switching over time. Data based on cophylogenetic reconstructions of doves and wing lice that assumes an Australasian origin of parasitic wing lice with speciation events constrained by three time periods that correspond with host dispersal between geographical regions described in figure 1. Wing louse speciation event ages based on phylogenetic results described in figure S12.