Review article

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Phylogenomics and comparative genomic perspective on the avian radiation

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Abstract

Adaptive radiation is a pivotal driver of macroevolution, substantially contributing to the diversity of life by promoting rapid phenotypic and ecological adaptations. In birds, neoavian species account for over 95% of modern avian diversity, emerging from an explosive radiation event near the Cretaceous–Palaeogene boundary. In this Review, we explore the current challenges in resolving the avian tree of life and examine the key drivers of their radiation. We discuss the emerging consensus from phylogenomic studies using whole-genome data to illuminate the early diversification of Neoaves. Additionally, we discuss how the radiation of birds has influenced their diversity, emphasizing the interconnected macroevolution of phenotypic traits and genomic characteristics. Finally, we discuss the multiple impacts of climate change on bird populations, highlighting how evolutionary history informs and enhances our understanding of avian resilience to environmental change. This Review underscores the critical importance of integrating genomic data with trait-based analysis to explore unresolved questions pertaining to the adaptive radiation of birds, and sets the stage for future research on how contemporary ecological pressures might continue to shape avian diversity.

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Review article

Introduction

Taxonomic groups vary substantially in metrics of evolutionary diversity, such as species number, trait diversity or population density. Those groups with unusually high diversity attract additional attention from researchers studying evolutionary biology, driven by a desire to understand the mechanisms beneath this macroevolutionary pattern. This phenomenon is often caused by adaptive radiation, defined as the rapid divergence of an ancestral lineage into multiple species that adapted to a wide variety of ecological niches[1–6]. Adaptive radiation has long been regarded as the primary mechanism underlying Darwin's principle of divergence for highly diverse clades[7–9]. Unlike natural selection, which optimizes the fitness of a given population, adaptive radiation results in the emergence of multiple species with distinct traits and ecological adaptation strategies. Iconic examples of adaptive radiation include Darwin's finches on the Galápagos islands[10], Hawaiian honeycreepers[11], Caribbean *Anolis* lizards[12], and the cichlid fishes of the African Great lakes[13]. Explosive adaptive radiations have occurred not only in these contemporary lineages, but also at various ancient timepoints, leading to the rise of many major taxonomic groups and contributing to the origin of the spectacular diversity of life on Earth. The most famous examples of adaptive radiation in deep time include the Cambrian explosion[14], the radiation of angiosperms[15], the diversification of insects[16], and the evolutionary radiation of placental mammals and birds following the extinction of the non-avian dinosaurs at the end of the Cretaceous period[17].

Birds are one of the most species-rich groups among vertebrates, consisting of three major groups: Palaeognathae (comprising ratites and tinamous), Galloanserae (which includes land- and water-fowl) and Neoaves (all remaining modern birds). The International Ornithological Committee (IOC) World Bird List[18] indicates that there are 11,250 recorded species. The macroevolutionary history of birds is characterized by multiple adaptive radiations that have generated their remarkable morphological, ecological and taxonomic diversity. The crown avian lineage emerged from theropod dinosaurs during the Jurassic period, approximately 165 to 150 million years ago[19], and is characterized by the development of key innovations, including pennaceous feathers, pneumatized skeletal elements and powered flight. These adaptations contributed to early bird diversification and colonization of diverse ecological niches throughout the Jurassic and Cretaceous periods[19–21]. The Cretaceous–Palaeogene (K–Pg) mass extinction event extirpated non-avian dinosaurs and several major stem-avian lineages, such as the toothed Hesperornithes, the Ichthyornithes and the diverse Enantiornithes clade[22], and the Ambiortiformes[23]. However, members of the crown group of modern birds survived this extinction event and underwent explosive diversification, particularly within Neoaves. This diversification culminated in a remarkably diverse clade comprising approximately 95% of all extant avian species. The timing of the diversification of Neoaves relative to the K–Pg extinction event remains contentious, with competing phylogenomic analyses and fossil evidence suggesting either a pre-K–Pg radiation or a post-extinction adaptive radiation[17,24–30]. Timing aside, both molecular and palaeontological data indicate that nearly all major lineages of Neoaves experienced rapid cladogenesis within a remarkably short temporal window[17,27,28,30]. The radiation poses major phylogenetic challenges, particularly regarding the resolution of early branches of the neoavian clade[31–35]. Despite advances in phylogenomic methods and the increasing availability of molecular data, many early-branching relationships within Neoaves remain poorly resolved. Resolving the relationships of these early branches is hindered by incomplete lineage sorting (ILS), high levels of homoplasy and the methodological challenges of reconstructing ancient rapid radiations[34–36]. However, these challenges are not exclusive to the earliest branches of Neoaves itself. The hyperdiverse Order Passeriformes (>6,000 species) represents another instance of rapid cladogenesis within Neoaves, characterized by multiple bursts of diversification that have similarly confounded efforts to resolve phylogenetic relationships, particularly among the oscine passerines[37].

Despite extensive research over the past century, key questions persist about the process of adaptive radiation in birds and its role in the evolution of modern bird diversity. The intrinsic and extrinsic factors driving this radiation remain debated, and the contribution of these drivers to the remarkable phenotypic and ecological diversity seen in birds today. This uncertainty is further compounded by challenges in resolving the early branches of the avian phylogeny, cementing the early diversification of Neoaves as one of the most complex and unresolved puzzles in evolutionary biology. The availability of large-scale avian genomic data and comparative studies offer potential insights for clarifying the intricate relationships within avian phylogeny[30,38]. Moreover, the combination of genomic insights with ecological and phenotypic data provides a powerful framework for understanding how the avian radiation has shaped modern bird diversity[39–42].

In this Review, we explore the current state of knowledge around the avian radiation by summarizing phylogenetic debates emerging from recent phylogenomic studies and discussing the causes behind the persistent challenges in seeking resolution. We discuss the key ecological and intrinsic factors that might have driven the avian radiation and assess how these factors have influenced the evolution of bird genomes and phenotypes. Additionally, we discuss how the evolutionary history of birds provides valuable insights into the effect of climate change on avian species and their predictive potential. Finally, we propose key future research directions within avian evolutionary biology.

Phylogenomic insights into avian radiation

Phylogenetic trees illustrate evolutionary relationships among species, detailing their evolution via common ancestors. However, they also serve as essential tools for understanding trait evolution, testing evolutionary hypotheses and informing conservation efforts. Despite intensive efforts over the past century to resolve the phylogeny of modern birds using morphological or limited molecular data[43–45], the high-level avian phylogenetic tree remains poorly resolved, particularly concerning the relationship among the orders comprising Neoaves. In the past two decades, the establishment of large-scale phylogenomic studies has sparked renewed enthusiasm for tackling this challenge, generating unprecedented amounts of genomic data that could illuminate the early diversification of birds[31,33,46–49].

The earliest attempt to construct higher-level avian systematics used 19 loci (totalling around 32 kb) from 169 species, amplified using polymerase chain reaction (PCR)[48]. This foundational work established a well-supported phylogenetic framework among the three major groups (Palaeognathae, Galloanserae and Neoaves) and strong support for some branches within Neoaves such as Telluraves (also known as landbirds).

The development and application of advanced genomic methods such as target capture (for conserved regions of the genome, including ultra-conserved elements[50] or conserved coding regions[51]), and high-throughput sequencing technology has contributed to researchers' understanding of systematics in many taxa, including birds[31,52–54]. In the years following its development, target capture was swiftly

Review article

used in studies of bird phylogeny to resolve relationships at multiple taxonomic levels, from phylogeny within specific genera[55–57], across families[58–61], and within deeper evolution trees across avian orders[62,63]. Target capture has also been instrumental in clarifying the relationship of deep branches of the Neoaves clade, observed in the Prum tree[33] of 198 bird species representing all major avian lineages, based on 259 loci (mostly exons) and a total of around 0.4 million base pair alignable sequences[33].

In 2014, the Avian Phylogenomics Consortium conducted the first phylogenomic analyses by combining data from coding regions, introns and ultra-conserved elements (into a total evidence nucleotide tree (TENT)) encompassing 41.8 million sequences across 48 species, with at least one species representing each order of Neoaves[34] (herein referred to as the Jarvis TENT). Several other efforts with specific data types have also been conducted over the past couple of decades, often producing contrasting results[26,36,64]. The Avian Phylogenomics Consortium developed into the Bird Genome 10K project (B10K) with the aim of generating draft genomes for a broad sample of birds, and ideally for all extant species[65]. Subsequently, the largest phylogenomic effort so far was released by the B10K consortium in 2024, reporting a new family tree including 363 species covering 218 taxonomic families (92% of total recorded avian families) based on 63,430 loci spanning about 63 Mb from intergenic regions[30]. This tree, referred to here as the Stiller tree, resolved the majority of the uncertainties with 98.1% of nodes supported by full posterior probabilities and 100% bootstrap support, providing a solid taxon-rich backbone tree for future studies. Furthermore, the tree revealed several recalcitrant deep relationships and pervasive incongruence, both with previous trees and among individual gene trees[30].

These intensive efforts over the past several decades reveal marked conflicts among analyses, most concerning the deep branching of the Neoaves, such as the sequence of radiation and the interrelationships among the major groups within Neoaves. Here, we use the Stiller tree[30], comprising the most comprehensive dataset and the greatest resolution of most nodes, as a framework within which to discuss agreements and differences at the superorder level with topologies proposed by other studies (Fig. 1; detailed comparisons among some of previous trees have been reviewed elsewhere[35,66–68]). The combination of the Jarvis TENT and Prum trees suggest that early Neoaves rapidly diversified into at least ten major clades[68], including seven superordinal clades, often referred to as the 'magnificent seven', and three orphan orders (shorebirds, cranes and hoatzin). These orphan orders are not placed in any of the superorders, although the two trees revealed differences in the sequence of diversification among the major clades. The controversy surrounding the deep branching relationship of Neoaves is reflected in two further analyses within the past few years. Each of these analyses used different types of genomic data: genome-wide data based on untranslated regions (UTRs)[49], and genomic region data totalling over 20 Mb comprised of coding sequences, conserved non-exonic elements, introns and intergenic sequences[26]. The Stiller tree[30] resolved Neoaves into four major clades: Mirandornithes, grouping grebes and flamingos; Columbaves, which includes Columbimorphae (doves, sandgrouse and mesites) and Otidimorphae (cuckoos, bustards and turacos); Telluraves, the higher landbirds including Afroaves and Australaves; and a new superordinal clade Elementaves, including the remaining orders, containing Opisthocomiformes (the monotypic hoatzin), Aequornithes (pelicans, tubenoses, penguins and loons), Phaethontimorphae (kagu, sunbittern and tropicbirds), Strisores (nightbirds, swifts and hummingbirds), and Cursorimorphae (shorebirds and cranes).

The Telluraves superorder has been well supported using various datasets[30,33,34,48,49] (Table 1). The Columbimorphae and Otidimorphae formed a monophyletic group named Columbaves, supported by the Stiller[30], Prum[33], Kuhl[49] and Wu trees[26], despite showing different interrelationships within this clade. However, the two groups were split in the Jarvis TENT, with Columbimorphae forming a monophyletic group with Mirandornithes, which appeared as the earliest diverging clade from the early Neoaves. In both the Stiller and Kuhl trees, the Mirandornithes form an independent lineage as the sister to other Neoaves, but by contrast, the Prum tree and Wu tree placed the Mirandornithes within the Aequorlitornithes (waterbirds). Notably, several analyses identify non-monophyletic relationships for several traditionally recognized superorders or orders (Fig. 1), because their species were split into different orders (for example, the former Gruiformes), or the whole group was nested within other orders (for example, the Ciconiiformes, which was merged with the Pelecaniformes).

Despite the resolution of many nodes of the bird phylogeny improving with years of continual data collection, some branches remain contentious. Different types of data input can result in substantial conflicts between species trees and different hypotheses of topology, with protein-coding data deviating the most from other types, such as ultra-conserved elements, introns and intergenic regions[30,33,34]. These deviations might be attributed to the characteristics of protein-coding data, which often contain less efficient phylogenetic signals than other types (including ultra-conserved elements, introns and intergenic regions) and are influenced by lineage-specific natural selection. Furthermore, the data quantity can have a substantial impact on the level of support in phylogenetic inference; the increased numbers of loci generally produce more consistent trees with stronger support. This trend can be observed across all data types except for coding sequences[30,34,68,69].

With sufficient data, 97% of the clades reported by the Stiller tree can be consistently recovered, although the required data amounts vary among clades, leaving ten clades challenging to resolve, including the two nodes uniting the Strisores with the Phaethoquornithes and the Opisthocomiformes with the Cursorimorphae within the Elementaves, as well as the node joining the Apterygiformes and the Casuariiformes within the Palaeognathae. Even with the substantial data available, the proportion of gene trees supporting alternative topologies could not be reduced efficiently. Most of these challenging nodes are associated with short branches following the K–Pg boundary. For instance, the Accipitriformes and the Strigiformes were grouped together as the sister to the remaining Afroaves in the main tree, but alternative placements for these two nodes and the Coliiformes (mousebirds) was supported by 30% of subsets of examined gene trees[36]. Additionally, although Opisthocomiformes was considered as a monotypic clade within the Elementaves, the hard polytomy hypothesis involving Opisthocomiformes and other clades within this group cannot be rejected. The difficulty in resolving these complex nodes, even with abundant data, suggests that certain biological processes might be challenging to model in phylogenetic analyses, representing major ongoing challenges in the phylogenomic era.

Challenges for the avian tree of life

The ongoing debates surrounding avian phylogeny are complicated by intricate evolutionary processes during the rapid avian radiation and are further confounded by the uses of different datasets and analytical methods. The impact of these technical issues on the avian phylogeny
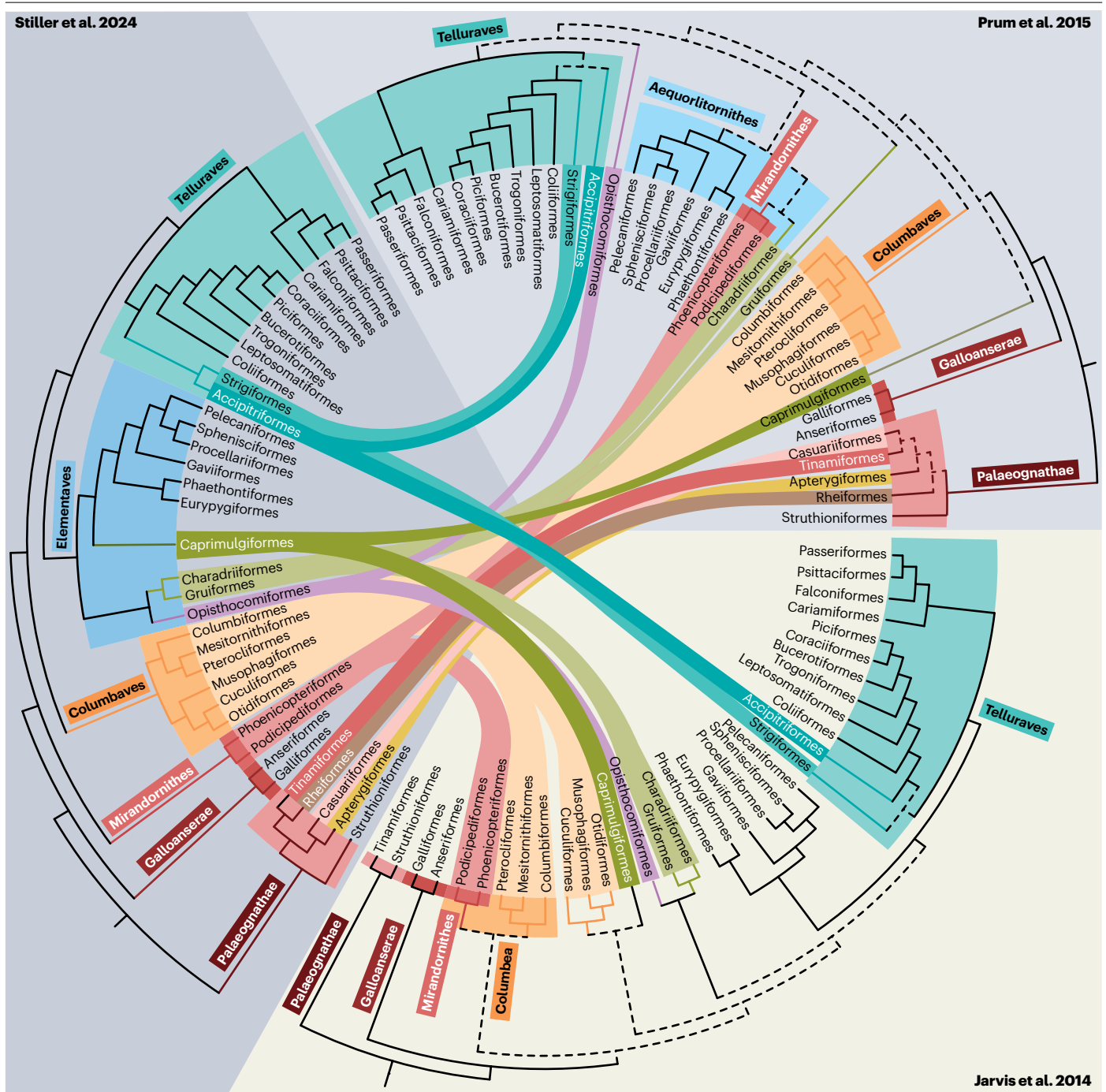
Review article

Fig. 1 | Phylogenomic incongruence in the avian tree. Three major avian phylogenomic studies illustrate variable relationships in major avian groups. The Stiller family tree classified the Neoaves into four major clades: the Mirandornithes (coral), the Columbaves (orange), the Elementaves (blue) and the Telluraves (turquoise)[30]. The order-level backbone tree derived from this classification is compared to the order-level trees from two other phylogenomics studies, the Jarvis TENT tree[34], and the Prum conserved loci tree[33]. Dashed branches indicate incongruent nodes between the Stiller tree and the other trees. Coloured bands highlight the discordant lineages between Stiller tree and the other trees.

has been thoroughly discussed in previous reviews[35,68–70]. Here we focus on some of the most profound biological reasons contributing to phylogenetic uncertainty in the bird group.

Most of the remaining challenging nodes, like the base of Elementaves and the divergence of the Columbaves, Elementaves and Telluraves, have short internal branches, which is a hallmark of rapid

Review article

and successive branching events that occur during radiation. Neoaves emerged at around the K–Pg boundary about 66 million years ago, radiated into the major clades of modern birds within just one to two million years[30,71] and consequently has short divergence times among descendent lineages. Consequently, lineage sorting in some genomic regions might not have been completed, so ancestral polymorphisms could be randomly retained in the descendent lineages — a phenomenon called ILS[33,36,72,73]. Under ILS, alleles fail to coalesce with closely related species following the speciation process and instead align with more distantly related species sharing the same ancient genotypes (Fig. 2a). Thus, the genealogical processes in some genomic regions do not match with the species phylogeny under ILS. This phenomenon is particularly apparent when ancient populations are large and the interval time between speciation events is short[74,75].

The effects of ILS can be detected in some nodes in avian phylogenetic trees, which exhibited an equal frequency of two alternative topologies that are incongruent with the species trees[32,34,36]. However, there are further signals that can be indicative of ILS, particularly following rapid radiation. Detection of homoplasy-free rare genomic changes, such as insertions and deletions (indels), insertion events of retrotransposed elements and nuclear mitochondrial DNA (NUMT) insertions, can reveal the stochastic presence of these homoplasy-free signals across descendent lineages. These signals have been identified as accompanying the neoavian radiation[33,34,36,48,76]. For instance, in both the Stiller tree and the Jarvis TENT, mousebirds (Coliiformes) were placed as the sister to the rest of the Coraciimorphae[30,34]. However, the phylogeny reconstructed by the presence or absence of insertions of transposable elements (TEs) exhibited a mixture of all six possible

alternative topologies within the Telluraves[36]. Indels distribution patterns also showed high levels of incongruence at those short and deep nodes, particularly on the two branches joining mousebirds and owls, which exhibited the highest levels of indel incongruence, consistent with the TE distribution patterns[34,36]. We note that the percentage of incongruent indels in each node can be predicted by its internal branch length[36]. In summary, it is evident that a relatively large amount of ILS had occurred near the base of Neoaves.

Although ILS has occurred pervasively alongside the rapid diversification process, and can be detected in almost all of the difficult-to-resolve deep nodes in bird phylogeny, ILS alone cannot fully explain the challenges in resolving the avian radiation. For example, the relationship between the Mirandornithes and the Columbimorphae poses a particular challenge. Although the Mirandornithes had previously been combined with the Columbimorphae[48,77], the Stiller tree alternatively proposes Mirandornithes to be an earliest monophyletic group of Neoaves (Fig. 2b). Comparison along the genome discovered two long genomic blocks with a total length of 21 Mb on chromosome 4 provided consistently strong support for the combination of the Mirandornithes with the Columbimorphae[34]. This long supergene cluster might be derived from an ancestral rearrangement and followed by an ILS event such that the rearranged genomic blocks were selectively reserved in the Mirandornithes and Columbimorphae (Fig. 2b). Such events are rare, but the rapid diversification of birds often involved other evolutionary events such as hybridization among descendants from the adaptive radiation. Owing to short divergence times, introgressive hybridization could occur among closely related species occupying overlapping ecological niches. The genetic introgression introduced

Table 1 | Summary of former super clades that are no longer used or remain controversial

| Former clade	Advocated by	Composition	Location in Stiller tree, 2024
Metaves	Fain & Houde (2004); ref. 305	Phoenicopteridae and Podicipedidae	Mirandornithes
		Columbidae, Mesitornithidae and Pteroclidae	Columbaves
		Caprimulgidae, Apodidae, Trochilidae, Aegothelidae and Podargidae	Strisores (Elementaves)
		Opisthocomidae	Opisthocomiformes (Elementaves)
		Phaethontidae	Phaethontiformes (Elementaves)
		Eurypygae (sunbittern and kagu)	Eurypygiformes (Elementaves)
Coronaves	Fain & Houde (2004); ref. 305	Pelecanae (waterbirds, waders and cuckoos)	Split into Columbaves and Elementaves
		Charadriae (shorebirds, alcids, skuas and gulls)	Charadriiformes
		Passerae (higher landbirds)	Telluraves
Columbea	Jarvis et al. (2014); ref. 34	Phoenicoptermorphae (Phoenicopteriformes and Podicipediformes)	Phoenicoptermorphae (Mirandornithes)
		Columbimorphae (Pterocliformes, Mesitornithiformes and Columbiformes)	Merged into Columbaves
Passerea	Jarvis et al. (2014); ref. 34	Otidimorphae (Musophagiformes, Otidiformes and Cuculiformes)	Merged into Columbaves
		Caprimulgimorphae (Caprimulgiformes)	Merged into Elementaves
		Opisthocomiformes, Cursorimorphae (Gruiformes and Charadriiformes), Phaethontimorphae (Phaethontiformes and Eurypygiformes) and core waterbirds (Gaviiformes, Sphenisciformes, Procellariiformes and Pelecaniformes)	Merged into Elementaves
		Core landbirds (Telluraves: Accipitriformes, Strigiformes, Coliiformes, Leptosomatiformes, Trogoniformes, Bucerotiformes, Coraciiformes, Piciformes, Cariamiformes, Falconiformes, Psittaciformes and Passeriformes)	Kept the same as Telluraves
Basal landbirds	Kuhl et al. (2021); ref. 49	Pterocliformes, Mesitornithiformes, Columbiformes, Cuculiformes, Musophagiformes and Otidiformes	Merged into Columbaves
		Caprimulgiformes, Opisthocomiformes, Charadriiformes and Gruiformes	Merged into Elementaves
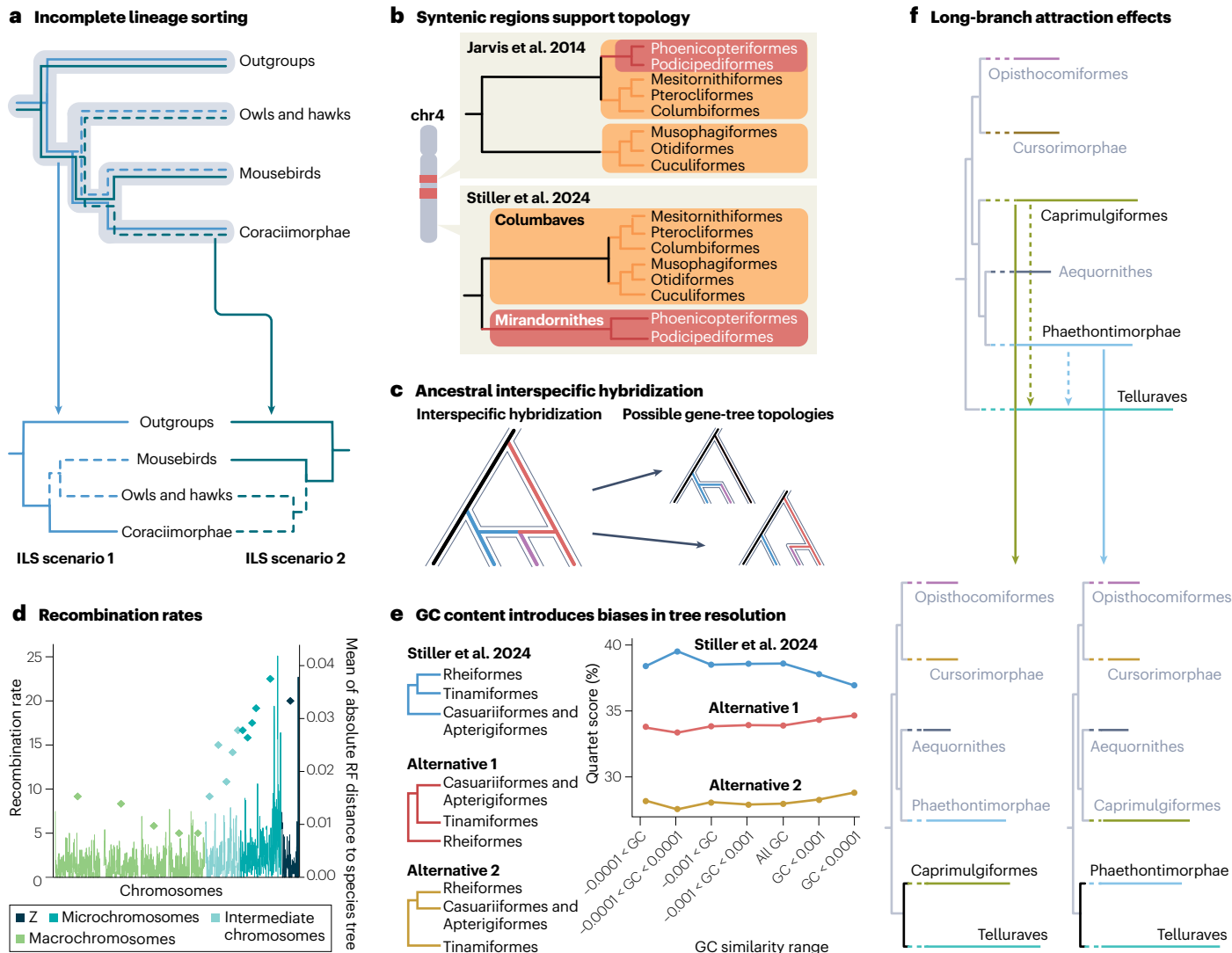
Fig. 2 | Evolutionary scenarios that contribute to gene trees and species tree conflicts. a, Incomplete lineage sorting (ILS) leads to discrepancies between the gene trees and species tree related to the mousebird[30,36]. The grey background represents the species tree, and the blue and black lines represent two alternative topologies caused by ILS. **b**, Two long genomic syntenic regions on chromosome 4 uniformly supported the topology in the Jarvis TENT tree[34] for the Columbea, which is different from other genomic regions supporting the topology in the Stiller tree[72]. **c**, A hypothetical schematic of ancestral interspecific hybridization, which accelerates diversification and can also contribute to gene-tree and species-tree discordance[78]. Coloured lines represent different gene flows, and the purple line highlights the hybridization event. **d**, Avian microchromosomes exhibited elevated recombination rates, which

correlate with incongruences between the gene trees and the species trees. Colours indicate different chromosomes. Lines represent the recombination rates and diamonds represent the mean of the absolute Robinson–Foulds (RF) distances to the species tree. **e**, GC content — the percentage of guanine (G) and cytosine (C) nucleotides — similarity influences the supporting Quartet scores of three alternative topologies of Palaeognathae, introducing systematic biases in tree resolution. Coloured lines correspond to three different topologies. **f**, Long-branch attraction effects in avian phylogeny are exemplified in clades such as the Caprimulgiformes and the Phaethontimorphae. These clades are wrongly grouped together with Telluraves owing to the long-branch length in these three lineages[30]. Species tree (top) and two alternative topologies influenced by long-branch attraction (bottom). Data in parts **d** and **e** are from ref. 30.

by interspecies hybridization would enable the rapid generation of adaptive trait combinations that could enhance adaptability and further accelerate diversification[78] (Fig. 2c). Such a syngameon hybridization mechanism has been reported in the rapid radiation of *Heliconius* butterflies and cichlid fishes[79,80].

The existence of complex gene introgression in birds during the rapid radiation has also been increasingly demonstrated[30,77,81].

For instance, a coalescent phylogeny of 63,000 intergenic data groups hawks (Accipitriformes) and owls (Strigiformes) as sister to the remaining Afroaves[30]. However, the associated concatenated analyses supported an alternative topology, placing Accipitriformes as a monotypic sister clade to the remaining Afroaves. The quartet frequency was indistinguishable for these two topologies, but the quartet support of the third topology was much lower[30], contradicting the expectation of

Review article

the ILS scenario that the two alternative topologies should have equal quartet frequency. A possible explanation is that an ancestral hybridization event between hawks and other Afroaves lineages might have happened during the short period of diversification. However, detecting such an ancient hybridization signal with the currently available methods is challenging, owing to the weak signal. Nevertheless, such ancient hybridization events have been successfully recovered between families of species-rich clades like the Passeriformes, Sphenisciformes, Charadriiformes, Galliformes and Anseriformes[81–84], thus contributing to understanding of phylogenetic incongruence within these orders.

The variation of some genomic features among loci can also contribute to gene-tree incongruence, for example, recombination between alleles in the population. The simplest model of coalescence assumes no recombination within loci but complete recombination between loci. Therefore, failure to recognize recombination between loci can result in incongruence between gene trees and the true species tree[85]. Because coalescence-based species-tree inference treats each gene tree independently, recombination could contribute to the uncertainty in the estimated species tree[86,87]. Additionally, recombination introduces heterogeneity that might affect the branch-length estimation and interaction with other aspects in the speciation history, such as population size, given that the recombination rate increases linearly with the effective population size of the ancestors[88]. The rate of coalescence is proportional to the square of the number of ancestors[89], so genomic regions with higher recombination rates tend to have higher rates of gene-tree and species-tree incongruence[30,77,90]. Even when using only intergenic regions[30,68,91] (intended to avoid the higher risk of recombination offered by long protein-coding genes), a general pattern of high recombination rates can be observed in regions such as avian micro-chromosomes, contributing to phylogenetic incongruence (Fig. 2d). This trend is confounded with the variation of guanine+cytosine (GC) content in the genome. For example, Rheiformes was placed as a sister to Tinamiformes in the Stiller tree[30]. Rheiformes and Tinamiformes both have more genomic regions with higher GC content than other taxa in Palaeognathae (Fig. 2e). By removing loci with higher GC similarity, the support for placing rheas in a sister group to that of tinamous was reduced. This finding implies that an alternative placement of rheas in a sister group to that of kiwis and emus is also plausible when considering ILS[30].

Heterogeneity in evolutionary rates among lineages contribute to the long-branch attraction effect, in which distantly related taxa with longer branches are incorrectly grouped together owing to misleading similarities, resulting in an inaccurate phylogenetic reconstruction[92,93]. Such effects can also be introduced by factors such as convergent evolution, inadequate model, insufficient data and sampling bias[68]. Inevitably, some taxonomic groups have very few species, especially the orphan bird orders (the Eurypygiformes, Phaethontiformes and Opisthocomiformes, among others)[68], which are more prone to long-branch attraction effects. Consider the Phaethontimorphae, for instance, whose phylogenetic positioning has been controversial because it differs according to the type of genomic data that is used[33,36,72]. Analyses with large amounts of intergenic data showed three possible topologies, with Phaethontimorphae + Aequornithes scoring a slightly better quartet score but higher global bootstrap support than the other two. The partial support of the remaining two topologies might be explained by long-branch attraction, as Phaethontimorphae exhibited a longer root-to-tip distance relative to Aequornithes but greater similarity to Telluraves. Telluraves also had a longer average branch length than the rest of Elementaves[30], except

for Caprimulgiformes, which had also been attracted to Telluraves (Fig. 2f). Overall, all these examples demonstrate the complicated evolutionary events that have occurred within and alongside the avian rapid radiation. Understanding the factors behind these ongoing challenges in the bird phylogeny will help us to address complex branches elsewhere on the tree of life.

Drivers of the avian radiation

Another key aspect of adaptive radiation is the diversification of descendent lineages from common ancestors that have adapted to a wide range of distinct ecological niches. Exploring the drivers behind rapid diversification is fundamental to understanding adaptive radiation. In this section, we explore the mechanistic hypotheses, biological and non-biological factors driving the avian adaptive radiation.

Mechanistic hypotheses

Ecological opportunity has historically been proposed as a prerequisite for rapid radiation, pertaining to four key factors: the emergence of new resources, the extinction of dominant species, the colonization of unexploited areas and the evolution of traits that facilitate the utilization of resources in novel ways[1]. Ecological opportunity has since been highlighted as central to understanding how and when adaptive radiation occurs[94], and has been used to explain several radiation events[95–98]. Nevertheless, the precise timing and mechanisms that facilitated the Neoaves radiation remain debated[99,100].

The K–Pg mass extinction has been linked to the Chicxulub asteroid impact and the Deccan Traps volcanic eruption[101–105], which initiated a sequence of events that led to the extinction of all dominant non-avian dinosaurs, including most Mesozoic birds such as the Enantiornithes[22], Ichthyornithes and Hesperornithes. Only a few lineages survived the event, some of which eventually led to modern birds[23]. The mass survival hypothesis (Fig. 3a), proposed in the late 1990s, posits that several major clades of modern neoavian birds originated prior to the K–Pg boundary and survived through the mass extinction[24]. By contrast, the big bang hypothesis (Fig. 3b), proposed in 1995, argues that neoavian diversification occurred post-K–Pg, on the basis of more extensive Mesozoic bird fossil evidence[17,27].

Both the mass survival and big bang hypotheses emphasize the major role of the K–Pg boundary in avian radiation, with the central debate focusing on whether the rapid diversification occurred before or after the mass extinction. The mass survival hypothesis, drawing on support from limited mitochondrial DNA, fewer species and several fossil records of modern neoavians, suggests that the diversification of birds dates back to approximately 100 million years ago[24,26,106]. This conclusion could be influenced by the limited sampling of modern birds[24,26], fragmented fossils[24] and incomplete mitochondrial data[24,106]. The rise of modern birds has been linked to the concurrent diversification of flowering plants during the late Cretaceous, based on coding sequence. This link implies that some avian lineages might have diversified prior to the K–Pg boundary[26]. By contrast, extensive fossil sampling supports the big bang hypothesis, suggesting that modern avian species diversified after the K–Pg boundary[17,27] (Fig. 3b). Evidence from 1,000 clock-like genomic loci and about 150 fossil calibration points suggests that the neoavian ancestor began differentiating before the K–Pg mass extinction, with all neoavian orders originating within a short period after the K–Pg boundary[28]. Genomic scale phylogenomic analyses with extensive fossil calibration further reinforcing the hypothesis that most, if not
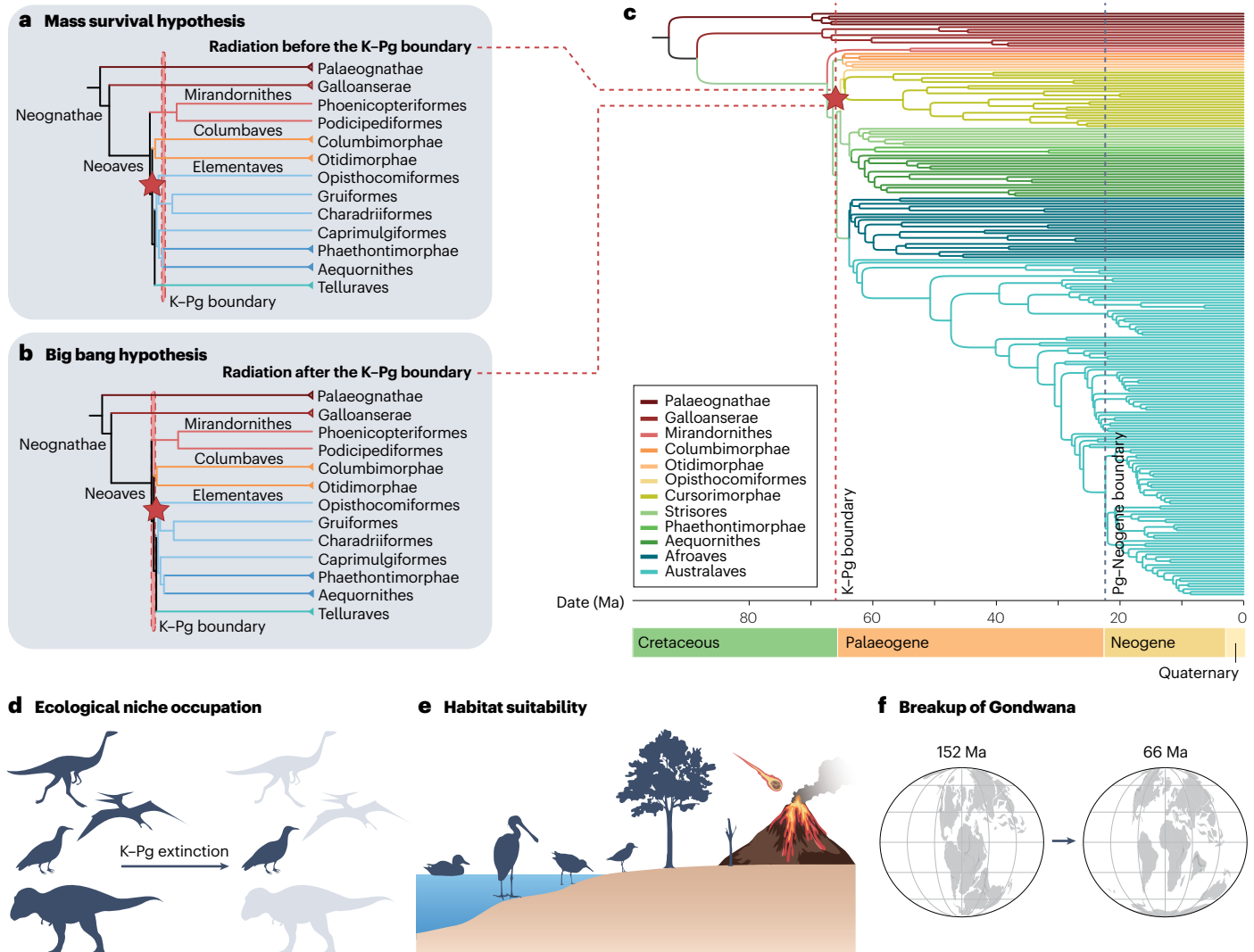
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Fig. 3 | Radiation hypotheses and ecological factors associated with the evolution of avian life history traits. a, The mass survival hypothesis of avian radiation, following ref. 24, posits that modern birds radiated (star) before the Cretaceous–Palaeogene (K–Pg) boundary (dashed line) and subsequently survived the K–Pg mass extinction event. **b**, The big bang hypothesis of avian radiation, following refs. 17,27, posits that modern birds underwent a rapid diversification (star) immediately following the K–Pg boundary (dashed line). **c**, Phylogenetic relationships and estimated divergence times for 218 bird species, providing a comprehensive perspective on avian diversification across families. Each branch represents a distinct bird family, and the colours indicate major clades, following ref. 30. **d**, Following the K–Pg mass extinction event, ecological niches previously occupied by non-avian dinosaurs and other reptiles, such as pterosaurs, became available for avian occupation. **e**, Near-freshwater environments provided refuge for surviving avian lineages following the K–Pg mass extinction event[114]. **f**, The progressive continental isolation resulting from the breakup of Gondwana, which promoted geographic and ecological separation, facilitated the avian radiation. Ma, million years ago. Data in part **c** are taken from ref. 30. Data in part **f** are taken from the GPlates Web Service using the GOLONKA PlateModel.

all, neoavian divergences except Mirandornithes and Columbaves emerged after the K–Pg boundary[30] (Fig. 3c). These findings underscore the indisputable role of ecological opportunity in the rapid radiation of modern birds.

Ecological impacts

The K–Pg mass extinction event eliminated three-quarters of Earth's plant and animal species – including all known non-avian dinosaurs and most other large-weight tetrapods (except turtles and crocodilians, and other surviving archosaurs). This event opened up numerous ecological niches and eased competitive and predatory pressures on surviving species[23,107,108], enabling birds to diversify and flourish in the absence of these dominant groups[23] (Fig. 3d). Consistent with the ecological release hypothesis, the earliest divergences of Neoaves probably occurred prior to the K–Pg boundary, with most of the divergences of Neoaves postdating the boundary[28]. Further evidence indicates that nearly all the divergences on the order level had occurred within 10 million years[30]. These results, taken together with some previous

studies, demonstrate the effect of ecological opportunities following mass extinction on the bird radiation[23,107,108].

The catastrophic events at the end of the Cretaceous period triggered a global environmental collapse, drastically altering the planet's climate and causing widespread disasters such as acid rain, earthquakes, tsunamis and wildfires[29,109,110]. Marine environments experienced severe disruption, including changes in the carbon cycle and widespread anoxia that led to extinctions of many taxa[111–113]. However, freshwater and near-freshwater environments appear to have been relatively shielded from these drastic changes[114,115], as evidenced by the lower extinction rates in freshwater tetrapods, like amphibians and turtles, across the K–Pg boundary compared to marine tetrapods[116,117]. By contrast, non-avian dinosaurs living in terrestrial and marine environments were unable to survive these stresses and ultimately went extinct. Although the specific lifestyle of the neoavian ancestors remains a mystery, the freshwater birds (Mirandornithes) are recovered as the earliest branching group of Neoaves[30,49]. This placement suggests that adaptation or dispersal to freshwater ecosystems probably played a part in the early diversification of Neoaves[114] (Fig. 3e). Although some early birds thrived in aquatic or freshwater environments during the Late Cretaceous[118], such as the Hesperornithes and the Ichthyornithes, they did not survive into the Palaeogene. This could be because of their inability to adapt to the drastic environmental changes occurring around the K–Pg boundary. Some fossil taxa recorded from the Late Cretaceous have been assigned to Neornithes, which exhibited morphological characteristics similar to those of transitional shorebirds, such as similar post-cranial skeleton with thick knees (like *Burhinus*) and long-legged shorebird-like body[119,120], and are assumed to be the mostly basal taxa of higher waterbirds[17,121]. This adaptation enabled them to exploit a range of ecological niches left vacant following the mass extinction event, from freshwater to near-freshwater environments, bringing reduced predation pressures and benefits from the resilience of near-freshwater ecosystems. Consequently, this niche expansion created a pathway for rapid avian radiation, allowing birds to diversify to fill varied unoccupied ecological roles. The fossil evidence supports this inference, indicating that several modern neornithine groups emerged within approximately the first 10 million years following the end-Cretaceous extinction[122].

Reproductive isolation is pivotal in speciation because it prevents gene flow between populations, thereby enabling them to diverge genetically and evolve into distinct species over time[123]. This process can arise through various pre-mating mechanisms, including geographical barriers, behavioural differences, and temporal asynchronies in mating period, as well as post-mating mechanisms such as gametic incompatibility, and hybrid sterility or breakdown[124,125]. The ecological differentiation of birds following the end-Cretaceous mass extinction probably reduced competition for resources and enabled the emergence of specialized traits that might have contributed to reproductive incompatibilities[108,126]. The establishment of geographical barriers between habitats will have further separated populations and limited the gene flow between them. Some hypotheses suggest that the ongoing breakup of the Gondwana supercontinent (Fig. 3f), beginning in the Late Jurassic and continuing through the Cretaceous, might have facilitated the early diversification of Neoaves[127,128]. The establishment of geographical barriers caused by the breakup of the Gondwana supercontinent created isolated environments[129,130] that might have further fostered rapid adaptive radiation in birds, through a mechanism similar to that leading to the rapid adaptive radiation for the birds on modern-day islands[131,132]. Molecular dating suggests that

most of the derived orders of Neoaves emerged after the K–Pg boundary around 66 million years ago[30], during the final stages of Gondwana's breakup[133]. As such, the influence of continental dispersal is likely to be localized to the earlier branches of the avian diversification, and had little or no influence on more derived branches such as Psittaiformes and Passeriformes[122]. This early influence will have shaped broader biogeographic patterns and created isolated environments that fostered the divergence of ancestral lineages, which later colonized and adapted to various continental landmasses[128,134]. The ancestor of Neoaves probably originated in West Gondwana (comprising modern-day South America and Antarctica) and dispersed from South America either via North America into the Old World or through Antarctica to Australia and Zealandia around the K–Pg boundary, facilitating the subsequent neoavian radiation[28].

Genomic and intrinsic factors

In addition to ecological opportunity, the occurrence and scale of adaptive radiation also depends on evolvability, defined as the capacity for an ancestral population to generate heritable phenotypic variation upon which natural selection can act. Evolvability enables lineages to adapt to diverse ecological niches, thereby increasing the likelihood of speciation events within a given clade[96,135]. Intrinsically, the evolvability of clades can be improved via the acquisition of key genomic or phenotypic innovations that allow lineages to exploit new adaptive zones[136–138]. However, the emergence of key innovations alone does not necessarily directly trigger immediate diversification[137,139–141]. Rather, many key features associated with clade radiation often evolve from the repurposing of pre-existing traits under novel selective pressures through phenotypic exaptation[96,142,143]. These evolutionary lags can be observed in the long geological time interval between the emergence of a novel trait and the onset of phenotypic diversification[144,145]. For instance, the transition of vertebrates from aquatic to terrestrial environments required a series of biological innovations, especially the capacity to breathe air and possess flexible limbs. Comparative genomics indicate that these traits, once regarded as innovations of terrestrial tetrapods, were already present in bichirs – early-branching bony fishes that emerged around 453 million years ago – long before the first vertebrates appeared on land around 375 million years ago[146]. Similarly, many morphological advantages observed in birds arose from traits related to flight or rapid dispersal, which appeared well before the diversification of modern birds[147–149]. A classic example is the evolution of powered flight in modern birds, involving the exaptation of feathers. Feathers themselves can be traced back to theropod dinosaurs, and were believed to have evolved for purposes such as insulation, display and thermoregulation rather than flight[150,151]. Over time, feathers gradually acquired aerodynamic function, eventually enabling lift generation and powered flight in early avian ancestors like *Archaeopteryx*, which dates back approximately 150 million years ago[19].

The evolution of birds from their theropod dinosaur ancestor required multiple substantial changes in body plan, with many of the derived features pertaining to powered flight[152–154]. One of the most striking is the miniaturization of body size, observed in birds when compared to their bulky dinosaur ancestors[155] (Fig. 4a). This reduction in body size continued throughout modern bird evolution, especially during the radiation of Neoaves[30]. Reduced body size can confer various selective advantages like reduced resource requirements such as food[156], faster sexual maturation[157] and higher survival rates in mass extinction events[158]. Together, these factors might enhance the evolutionary potential of bird morphology[29,159,160].
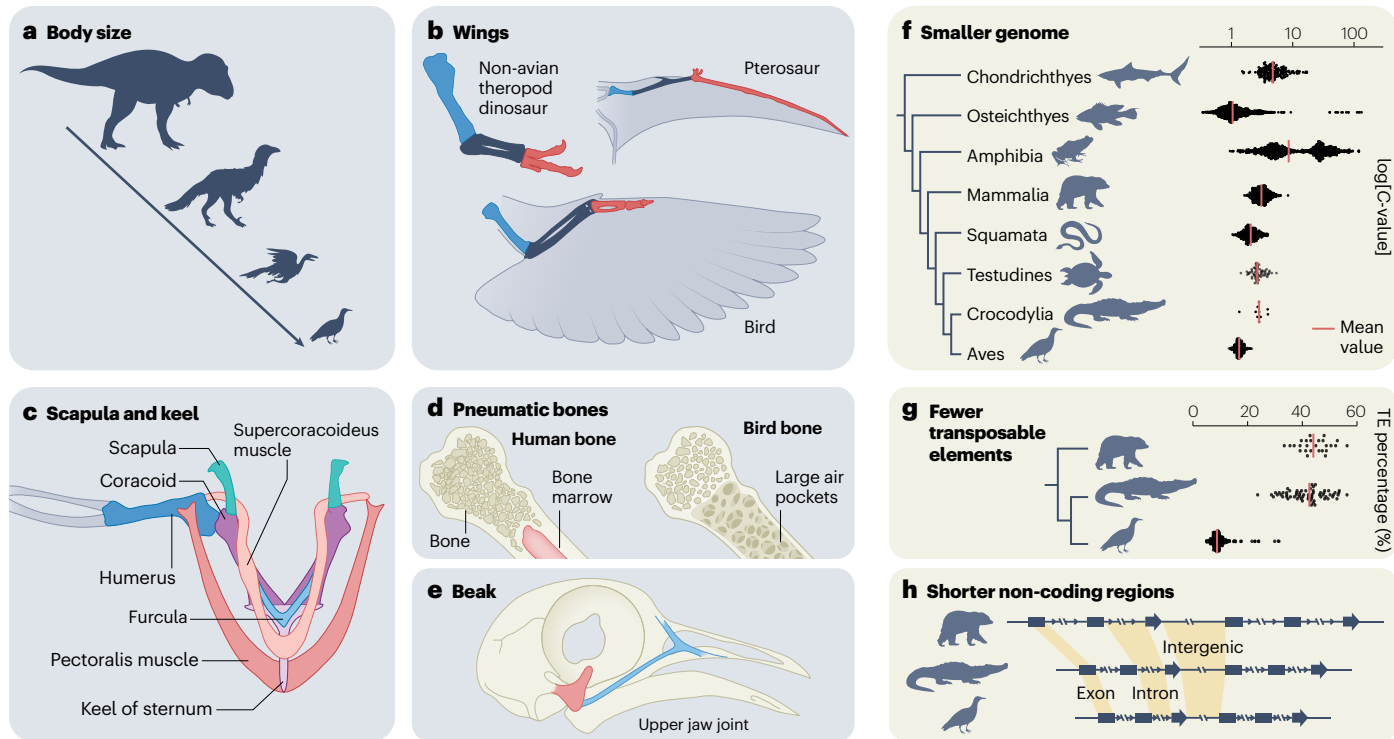
Fig. 4 | Morphological and genomic innovations contributing to the avian radiation. a, Body size generally reduced during the evolutionary transition from dinosaurs to birds, with lower body mass helping to enable avian flight[154,166]. **b**, The fusion of phalanx bones in bird wings, a characteristic that distinguishes birds from other flying vertebrates like non-avian theropod dinosaurs and pterosaurs. This fused structure provides greater opportunity for feather attachment, enhancing wing structural properties and flight efficiency[164,306]. **c**, Large pectoralis and supercoracoideus muscle attachment sites on the keel facilitate lift generation for powered flight. The orientation of the scapula enables a large range of wing movement and supports high wingbeat frequency in birds[165,307]. **d**, Pneumatic bones in birds, compared with denser human bones, reduce gravitational force constraints for flight[154,166]. **e**, The upper jaw joint of the beak provides flexible jaw movement[166,173,174], enabling the evolution of various beak morphologies adapted to a diverse range of feeding behaviours. **f**, Birds have some of the smallest mean genome sizes among amniotes, which minimizes cellular energy demands and supports higher metabolic rates essential for flight. The *C*-value is the amount of DNA in the haploid genome of an organism. Lines represent mean values. **g**, Birds have a reduced proportion of transposable elements (TEs) in their genome compared to other amniotes. Lines represent the mean values. **h**, Bird genomes generally have shorter non-coding regions when compared to genomes from mammals and reptiles, contributing to a more compact and efficient genetic structure. Data in part **f** are taken from the Animal Genome Size Database. Data in part **g** are from refs. 38,308. Data in part **h** are from ref. 184.

Size miniaturization was accompanied by changes in modular integration of skeletal proportions and increased evolutionary variability in wing skeleton proportions across birds, highlighting the impact of body-size changes on other morphological traits[157]. A distinct morphological change in wing skeletal structure during the transition from the ancestral dinosaurian body shape to that of avialan was the drastic elongation of the forelimb. This change is hypothesized to have occurred near the origin of Avialae (meaning bird wings)[161], a clade of dinosaurs that includes modern birds and their closest relatives, such as *Archaeopteryx*, which is thought to be the first recorded avialan[162]. This innovation coincided with a slowdown in evolutionary rate in stem avialan lineages, suggesting that elongated forelimbs were subject to strong evolutionary constraint owing to its adaptations for flight[163]. Forelimb elongation also involved the fusion of the phalanges, enabling the attachment of a greater number of feathers for the wings[164] (Fig. 4b).

Several other traits evolved in protobirds that might also have supported the capacity for flight. For example, in modern birds, greater mobility of the scapula and the keel, formed by breastbone fusion, enhanced wing-movement amplitude[165] (Fig. 4c). Additionally, the presence of lightweight pneumatic bones reduces the gravitational potential that must be exceeded to achieve powered flight[154,166] (Fig. 4d). Furthermore, the loss of teeth and the development of beak-like structure in bird ancestors contributed to a streamlined skull, aiding in flight efficiency[167].

Palaeognathae birds, such as ostriches, have immobile fused upper beaks, which was historically suggested to be a trait inherited from avian ancestors[168]. This hypothesis implied that the mobile joints in the pterygoid bone evolved later in Neognathae, allowing the upper beak to move freely up and down independently of the head[168–171]. However, the discovery of the Neognathae-like mobile joint in *Janavis* fossils[172], an extinct toothed avialan closely related to the common ancestor of all modern birds, implies that the jointed upper beak is a more ancestral trait than first thought[166,173,174] (Fig. 4e). The flexible upper beak might provide some advantages by enhancing biting forces, facilitating the gathering of diverse foods such as seeds and nuts[175], and collecting materials for nest-building[176]. By contrast, the fused pterygoids in the upper beak of palaeognathous birds restrict beak function[177]. Cranial kinesis has been proposed to contribute to the

Review article

survival capacity and adaptive radiation observed in Neognathae[178,179], facilitating varied beak adaptations associated with dietary and foraging diversification[180–182]. Examples include the hooked beak of eagles for tearing flesh, the chisel beak of woodpeckers for drilling into wood to extract insects, and the curved beak of the pied avocet for sweeping through shallow water to capture aquatic invertebrates, in contrast to the lower functional diversity in Palaeognathae[183].

Alongside morphological innovations, avian genomes exhibit distinctive characteristics compared to other vertebrates, probably contributing to their extraordinary evolutionary radiation[184]. One of the most notable features is their relatively smaller and more stable genome size compared to other terrestrial vertebrates, at approximately one gigabyte[184–186] (Fig. 4f). Although the reduction of the genome size has also been observed in other reptilian species, implying that such change might not be directly linked to the evolution of flight in birds, it is reasonable to hypothesize that the streamlined genome size could optimize metabolic processes and increase efficient cellular functions. This in turn could optimize energy conservation during powered flight[187,188].

The compact genome size in birds appears to have arisen through several mechanisms, including the resistance of TE insertion[189–191] (Fig. 4g), and reduction of intronic regions[184,192] (Fig. 4h). TEs, one of the key drivers of genome size and complexity evolution, are highly abundant in other terrestrial vertebrates, but have been maintained at low proportions in most bird species (on average 9%), except the Piciformes (range from 13% to 32%) and a few Bucerotiformes birds (22% in scimitarbill and 18% in hoopoe)[184]. In addition to selection for energy conservation, the removal of TEs and inhibition of their activity helps to maintain genomic integrity and to reduce genetic load by minimizing the risk of mutations arising from their mobilization. Consequently, bird genomes have maintained highly conserved gene syntenic structure for over 100 million years[184], facilitating the coordinated expression of functional related genes and enhancing developmental efficiency and responses to environmental stimuli[193,194]. Furthermore, ancestors to modern birds have experienced large-scale segmental deletions spanning thousands of functional genes, producing a major impact on trait evolution in modern birds[186]. These include several genes related to dentin and enamel, essential components of the key genetic machinery for tooth formation, which were lost in the common ancestor of all modern birds[195]. The loss of teeth is likely to have reduced morphological constraints on the beak, facilitating the development of the rhamphotheca on the premaxilla and anterior mandible[196,197]. This opportunity in turn contributed to the development of complex beak structure, enabling birds to explore diverse feeding strategies, such as granivory, nectarivory and filter-feeding and to adapt to a wide range of ecological niches[198–200].

The evolution of the ZW sex chromosome system represents another distinct genomic feature of birds that differentiates them from their dinosaur ancestors and other closely related reptiles. Other reptiles exhibit diverse sex determination systems, including genetic sex determination and environmental sex determination, in which an embryo's sex depends on temperature or other environmental factors during incubation[201,202]. The ZW sex chromosome evolved in the common ancestor of modern birds and is maintained in all extant species, providing a stable genetic mechanism for sex determination that is not reliant on external factors. This system enables bird populations to adapt to changing environmental conditions and social structure[203] without compromising on population sex ratios. Additionally, the ZW sex chromosome system also promotes genetic diversity via genetic recombination during meiosis, and facilitates the evolution of sexual dimorphism traits, which can enhance reproductive success through mating selection[204]. Thanks to these selective advantages, the ZW chromosome system has been conserved across bird lineages since its emergence. Overall, genomic changes in bird ancestors have shaped the evolution and development of unique avian traits, establishing the genetic foundation for their subsequent diversification.
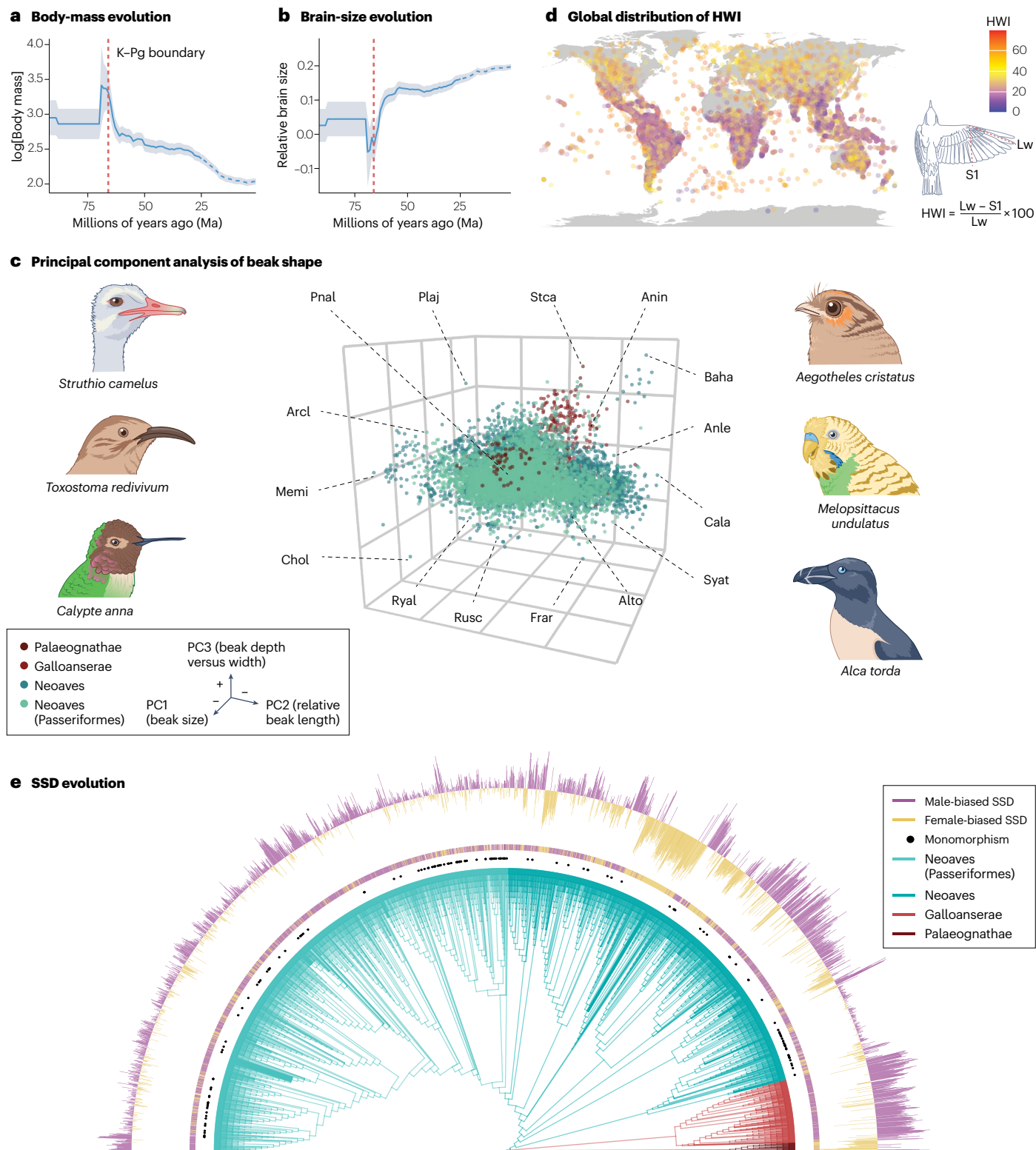
Adaptive radiation shapes bird morphology

Modern birds exhibit an extraordinary diversity of morphological traits, showcasing substantial variations in traits such as body mass, brain size, wing structure, sexual dimorphism and beak morphology. These traits are intricately linked to the diverse ecological niches that birds occupy, including those of herbivores, predators, scavengers, seed dispersers and pollinators[205–208]. The evolutionary trajectory of the avian radiation suggests that the K–Pg mass extinction event not only catalysed a rapid and substantial diversification of bird species but also influenced life-history traits such as developmental mode, adult body mass and metabolic patterns[42].

Rapid radiation can be modelled as a burst of species diversification during the initial phase of adaptive radiation, where newly emerged species quickly occupy the ecological space left vacant by a mass extinction[1]. Furthermore, there exists a general positive correlation between the rates of speciation and morphological evolution at broad macroevolutionary scales[141,209,210]. Thus, it is predictable to also observe such tempo and mode patterns in the macroevolution of morphological traits. Variation in body mass is one of the most vital morphological factors in how birds adapt to a wide range of ecological niches[211]. Concurrent with the avian radiation, the body mass of avian species shows a rapid reduction near the K–Pg boundary followed by a more gradual long-term reduction until the present day[30] (Fig. 5a). This long-term reduction in body mass was accompanied by a sharp increase in relative brain size near the K–Pg event, which stabilized following the avian radiation event (Fig. 5b). Furthermore, phylogenetic analyses of three-dimensional bill morphology across over 2,000 bird species revealed that major morphological shifts occurred near the base of the avian radiation, followed by relatively constrained divergence within sub-clades, consistent with modelling expectations[211].

These short bursts of rapid evolution driven by niche availability were accompanied by unevenly distributed phenotypic disparity among lineages and ecological zones. Phylogenetic analyses consistently identify heterogeneity in rates of phenotypic evolution between bird groups[42,212,213]. Understanding how rapid radiation contributes to phenotypic disparity and the principles underlying this disparity forms a central question in macroevolutionary study. Broad sampling of skeletal elements across species identifies early establishment patterns of diversification in the avian head and forelimb near the K–Pg boundary[214], suggesting that morphological adaptation of these structures was crucial for the colonization of new ecological niches. By contrast, some other elements, like the hindlimb and pectoral girdle, did not show an early establishment pattern of diversification[165,215], suggesting that not all anatomical features evolved concurrently or in response to ecological change. Furthermore, waterbird subclades present much higher disparity in body proportions and a broader exploration of morphospace compared to landbirds[214], indicative of a more extensive adaptive radiation to exploit a variety of ecological niches in aquatic environments during early radiation. Similar disparity patterns can be observed in the shape of the bird's beak, which strongly

a **Body-mass evolution**

b **Brain-size evolution**

d **Global distribution of HWI**

$$HWI = \frac{Lw - S1}{Lw} \times 100$$

c **Principal component analysis of beak shape**

Struthio camelus

Toxostoma redivivum

Calypte anna

Aegotheles cristatus

Melopsittacus undulatus

Alca torda

- Palaeognathae
- Galloanserae
- Neoaves
- Neoaves (Passeriformes)

PC3 (beak depth versus width)

PC1 (beak size)

PC2 (relative beak length)

e **SSD evolution**

- Male-biased SSD
- Female-biased SSD
- Monomorphism
- Neoaves (Passeriformes)
- Neoaves
- Galloanserae
- Palaeognathae

correlates with dietary habits and varies according to feeding strategies and dietary needs[208,216]. The Neoaves exhibit a greater diversity in beak shape compared to the Palaeognathae and Galloanserae (Fig. 5c), with certain lineages displaying highly specialized forms, like the elongated beaks of hummingbirds for nectar feeding and the robust beaks of woodpeckers adapted for boring in wood and specialized foraging behaviours[217,218]. This disparity among avian clades further suggests that variation in spatial and climatic heterogeneity, along with localized

Review article

selection pressures among different ecosystems, probably has a crucial role in shaping morphological diversity.

Wing shape is also an important trait in the adaptive radiation of birds. The interplay of ecological factors, evolutionary pressures and behavioural adaptations during periods of rapid radiation has resulted in the remarkable diversity of wing shapes observed in modern birds[219,220]. Wing shape can be quantified in several ways, one of which is the hand-wing index (HWI), which is used to model a bird's wing shape (rounded versus pointed)[221], and can predict flight efficiency and dispersal capabilities[221,222]. For example, flightless bird lineages like ratites exhibit the lowest HWI, whereas highly dispersive clades such as shorebirds and swifts tend to have high HWI values[223]. HWI values vary among bird lineages and across geographic distributions (Fig. 5d). Species with a higher HWI are often characterized by migratory tendencies, lower territoriality and a preference for habitats with large temperature fluctuations during the breeding season; these traits collectively enhance dispersal capabilities, which have a crucial role in influencing the potential for speciation within specific geographic regions. The ability to migrate and occupy diverse environments enables species to exploit various resources and adapt to different selective pressures, driving diversification. In regions that present distinct ecological opportunities, such as oceanic islands with varied ecological niches across elevation gradients (for example the Hawaiian archipelago or the Galapagos Islands), or during periods of major environmental upheaval (like the K–Pg boundary event), species with higher HWI would have greater ability to colonize and adapt to available niches[222], potentially promoting adaptive radiation[224,225]. Under stable environmental conditions, extremely reduced dispersal would limit colonization of new areas and gene flow between populations. Conversely, very high dispersal abilities could homogenize populations and prevent speciation. An intermediate level of dispersal ability might therefore optimize the balance between colonization opportunity and population isolation necessary for diversification[226–229]. Thus, HWI represents a key trait influencing both dispersal and the subsequent evolutionary pathways that lead to increased biodiversity through adaptive radiation[223].

Morphological diversity in birds has also been influenced by sexual selection, which is a major driver for the evolution of traits that enhance reproductive success and affect ecological interactions[230,231]. Sexual selection often results in pronounced sexual dimorphism, with males and females displaying distinct morphological traits that serve as signals in mate choice and social competition. Such traits can rapidly diverge, leading to reproductive isolation and facilitating speciation

during an adaptive radiation[232,233]. Over 96% of 4,761 investigated bird species display sexual size dimorphism (SSD), with the majority of orders predominantly exhibiting male-biased SSD, indicating pervasive male-biased sexual selection[234] (Fig. 5e). Of notable interest when exploring SSD are the Passeriformes. The body mass of both sexes in the Passeriformes has further decreased in conjunction with their rapid radiation following the split from other Neoaves groups[234] (Fig. 5e), but the evolutionary rate of changes in body mass in females has been higher than in males within this order. These patterns suggest that both fecundity selection (mediated by female–female competition) and male-bias sexual selection (favouring larger males) contribute to the evolution of SSD in the Passeriformes[234]. Furthermore, consistent with the hypothesis that sexual selection can drive speciation, the prevalence of male-biased sexual selection through SSD is positively correlated with speciation rates within the Passeriformes[235].

Colour ornamentation is another classical trait under strong sexual selection in birds, as evidenced by numerous striking examples of sexual dichromatism in species with highly polygynous mating systems[236,237]. Although sexual selection is the strongest predictor of plumage dichromatism in the Passeriformes, the elaboration of sexual ornamentation is closely linked to variations in other morphological, social and life-history traits[238,239]. For instance, tropical species or species with relatively larger body sizes are found to display more elaborate ornaments. This association probably exists because ornamental traits are often employed in competitive interaction for non-sexual resources[232,240]. Consequently, the interplay between sexual selection and other natural selection might have jointly influenced trait diversity during the rapid radiation of birds.

Avian radiation and genomic diversity

The level of genomic diversity among modern birds is a testament to their evolutionary resilience and adaptability. Although bird genomes are generally compact and conserved compared to other vertebrates[185,186], many genomic features exhibit striking diversity among different bird lineages. This variability can manifest in several ways, such as karyotype structure, gene contents, regulatory elements, TEs and mutation rate. Germline mutation rates display over 40-fold variation among bird species, ranging from 9.79×10^{-10} mutations per site per generation in the snowy owl to 3.98×10^{-8} mutations per site per generation in Darwin's rhea[241]. Furthermore, mutation rate across generations is strongly correlated with substitution rates across species in birds[241]. Lineage-specific variations in substitution rate are positively correlated with species richness per order[184] (Fig. 6a), suggesting that

Review article

a Substitution rates and species richness
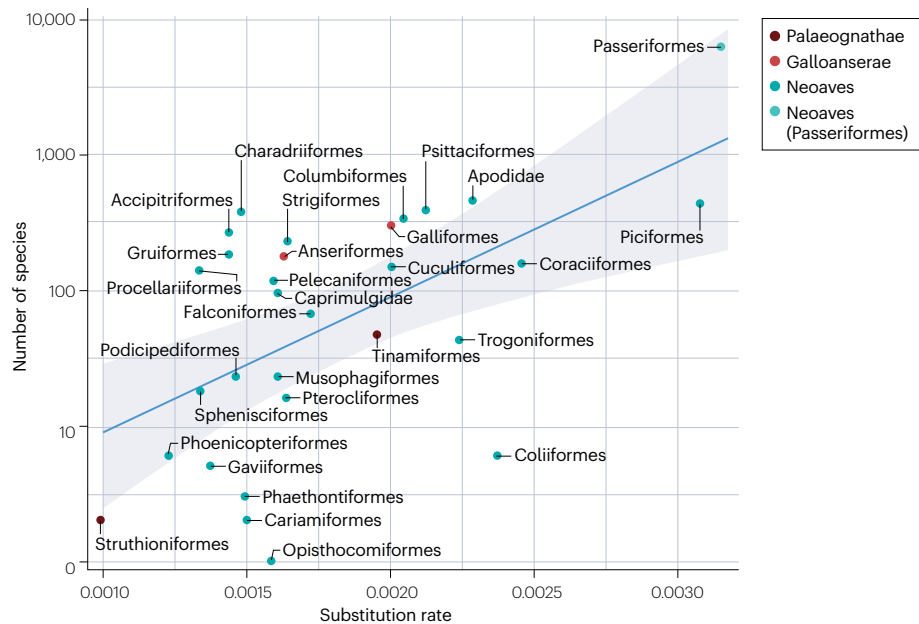
b Sex chromosome evolutionary strata

c Lineage-specific sequences among orders

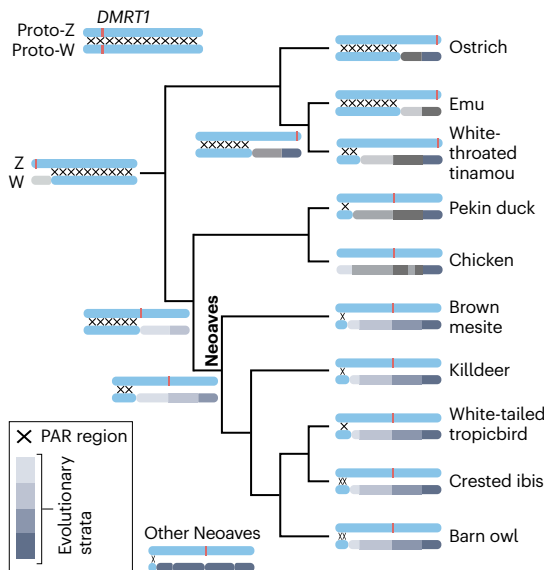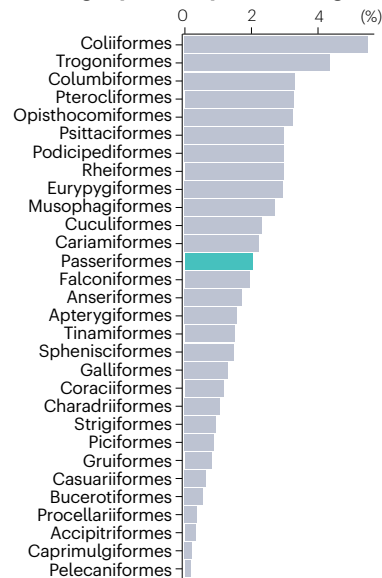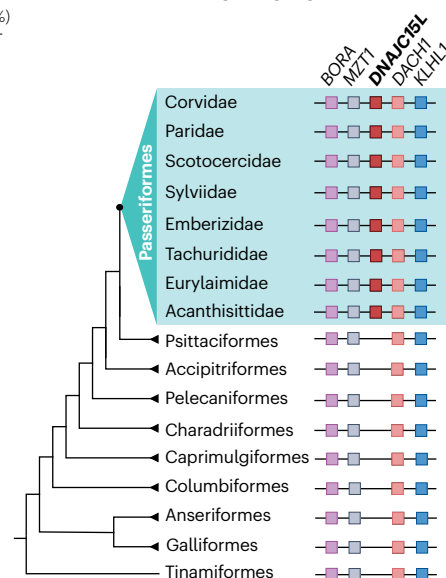## d Conserved synteny in passeriformes

Fig. 6 | Trends in avian genomic evolution. a, Relationship between base substitution rate per million years and species richness at the ordinal level. The solid line represents the correlative trend and shading indicates the 95% confidence interval. **b**, Evolutionary strata of avian sex chromosomes, illustrating diversification across bird lineages. The blue shading indicates the recombining regions in the Z or W chromosome. The black hatching denotes the homologous recombination between proto-sex chromosomes at pseudoautosome regions (PAR). Grey bars represent degenerate regions in W chromosomes. **c**, Lineage-specific sequence percentages highlight the proportion of unique genomic features present in each major bird order. **d**, The *DNAJC15L* sequence is conserved in Passeriformes and shows highly conserved synteny with neighbouring genes across the clade when compared to other bird groups. Data in part **a** are from ref. 184. Part **b** adapted with permission from ref. 258, American Association for the Advancement of Science. Data in parts **c** and **d** are from ref. 38.

microevolutionary processes at the molecular level have profound effects on long-term macroevolutionary patterns.

Most bird genomes contain nine or ten pairs of macrochromosomes and 28–34 pairs of microchromosomes, which are defined according to their size[242,243]. Macrochromosome counts are highly conserved across

species, whereas the number of microchromosomes varies across avian taxa. For instance, the chicken (*Gallus gallus*, Galliformes) and zebra finch (*Taeniopygia guttata*, Passeriformes) both possess 33 pairs of microsomes[244,245], raptors from the Accipitridae (Accipitriformes) have the lowest microchromosome counts (ranging from 2 to 12)

and the Coraciiformes have the highest microchromosomes counts (exceeding 100)[246]. Bird microchromosomes are distinguished by their high gene density, high GC content and increased recombination rate[30,247]. Despite their small size, accounting for only 25% of the bird genome, microchromosomes encode approximately 50% of genes, thus strongly influencing avian evolution[248]. Microchromosomes themselves are highly conserved, showing a one-to-one orthology even among distantly related bird species. However, gain and loss of microchromosomes through fusion and fission has been observed in many lineages, representing major interchromosomal changes during avian diversification[247,249,250]. Almost all bird genomes also have a pair of female heterogametic sex chromosomes (ZZ in males and ZW in females), which originated from an ancestral autosome[251,252]. The traditional view on sex-chromosome evolution holds that the sex-specific W and Y chromosomes have usually lost most of their genes owing to recombination suppression with their ancient homologs, the Z and X chromosomes, resulting in the gradual reduction of W and Y chromosomes, as is observed in chicken and human[252,253]. However, karyotyping analyses across 200 bird species have revealed substantial variation in the length of W chromosomes, even among closely related species, indicating that the evolutionary dynamics of these chromosomes might be more complex than previously assumed[254]. Palaeognathae species, like ostrich and emu, maintain long pseudoautosome regions (PARs) spanning two-thirds of their Z chromosome, and the Z chromosomes largely resemble their ancestral state[255–258] (Fig. 6b). By contrast, different Neognathae lineages exhibit substantial variation in PAR length, probably owing to lineage-specific recombination suppression events that vary by emergence time and the genomic regions involved. Surprisingly, some species of Neoaves have retained a substantial number of functional genes within the non-recombining regions of their W chromosomes[258], potentially under sexual selection[259]. Finally, fusion of the Z/W chromosomes and autosomes has been identified in many bird species, resulting in neo-sex chromosomes[249,250,260–263]. This process offers an alternative evolutionary trajectory that contributes to the rich gene contents found in the W chromosomes of these species, thereby enhancing the diversity of sex chromosomes among avian lineages.

The inter-species variation in genome size among birds is associated with the metabolic demands of powered flight. Species such as hummingbirds with the highest metabolic rates tend to have smaller genomes, whereas the flightless ratite species are among those exhibiting larger genome sizes[184,188,264]. Nevertheless, the increased genome size in ratite does not appear to be related to the lineage-specific gains of DNA; instead, the flightless species in ratites generally exhibit notable lower rates of genomic deletion and maintain more ancient TEs than flying birds[192]. Consistently across the Neoaves there is a negative correlation between DNA deletion rate and body mass[265], supporting the hypothesized link between metabolic rate and genomic size reduction[187]. Some of these DNA losses might be adaptive and functionally relevant, especially when they occur in protein-coding gene regions. For instance, all extant penguin species have lost the genes encoding taste receptors for umami, sweet and bitter tastants, resulting in a substantial reduction in the sense of taste in modern penguins[82,266].

The frequency of lineage-specific DNA gains does not correlate with flight capability; however, it varies substantially across lineages (Fig. 6c), ranging from 0.2% to 5.5%[38]. These DNA gains can arise through gene duplication. For example, *DNAJC15L* is a gene specific to the Passeriformes, derived from retrotransposition, which has maintained highly conserved synteny with neighbouring genes across the Passeriformes since its emergence (Fig. 6d). The dynamics of TEs also contributes to genome-size variation across bird species. Recurrent activity of young TEs in certain avian lineages has led to differences in TE contents among birds, with the downy woodpecker exhibiting the highest abundance of TEs making up over 22% of the genome[38]. Almost all amniote genomes contain endogenous retroviral sequences, which are the remnants of ancestral invasion of reverse-transcribing single-stranded RNA viruses with long terminal repeats (LTRs). These endogenous retroviral sequences are often deleted through unequal homologous recombination, leaving solitary long terminal repeats (solo-LTRs)[191]. Birds have an unusually high rate of solo-LTRs compared to other amniotes, suggesting strong evolutionary pressure to remove endogenous retroviral sequences during avian evolution. However, Passerida species, within Passeriformes, have experienced recurrent invasion of ERVK, an endogenous retrovirus family that also invaded several other animal lineages during the Palaeogene–Neogene transition period at around 22.4 million years ago. The accumulation of ERVK solo-LTRs appears to accompany the speciation events of this parvorder, indicative of high ERVK activity and an ongoing expansion of these solo-LTRs throughout the diversification of these Passeriformes over the past 22 million years[191]. Some of these solo-LTRs have been co-opted as *cis*-regulatory elements controlling the temporal and spatial expression patterns of host genes, suggesting that the expansion of ERVKs might have introduced novel genomic materials contributing to adaptive evolution of the host species[191].

Trait evolution and climate adaptation

Climate change is a critical driver of evolutionary processes, influencing species adaptation, distribution and interactions, and can lead to extinction by imposing selective pressures on reproduction, survival, growth and dispersal[267,268]. The past 50 years feature the most dramatic climate change in recorded history[269], which, alongside habitat destruction and species exploitation, has contributed to a 58% decline in vertebrate populations and placed over a quarter of surveyed species at risk of extinction[270,271]. This signals the urgent threat of the sixth mass extinction, which could disrupt essential ecosystems and biodiversity worldwide. Importantly, the ways in which species cope with or are affected by climate change can vary substantially, even among closely related or sympatric species, owing to differences in their biological traits and ecological roles[272,273]. For instance, smaller species tend to be more tolerant of climate change than larger species, particularly under warming conditions, owing to the reduced metabolic cost and nutrient demands associated with small body size[274–277]. This finding aligns with evolutionary trends in body mass during the avian radiation, as well as fossil records showing that many marine and terrestrial organisms shrank during previous warming periods[278–280]. Body mass is central to understanding trait–trait interactions because of its role in explaining variations in other biological traits and ecological processes, such as metabolic rate, lifespan, reproduction and territory range[281–284]. In the case of birds, specific traits such as beak shape or feeding behaviour also have crucial roles in determining how species respond to environmental pressures[285] (Fig. 7a). This process is exemplified by the adaptive radiation of Darwin's finches, which underwent dramatic diversification in beak form and function to exploit various feeding niches[286,287]. Moreover, species with larger population size or greater genetic diversity are often more resilient and capable of adjusting their life-history traits (Fig. 7a) to survive in new environmental contexts[288]. Given the complex and multifaceted nature of species' response to climate change, a comprehensive
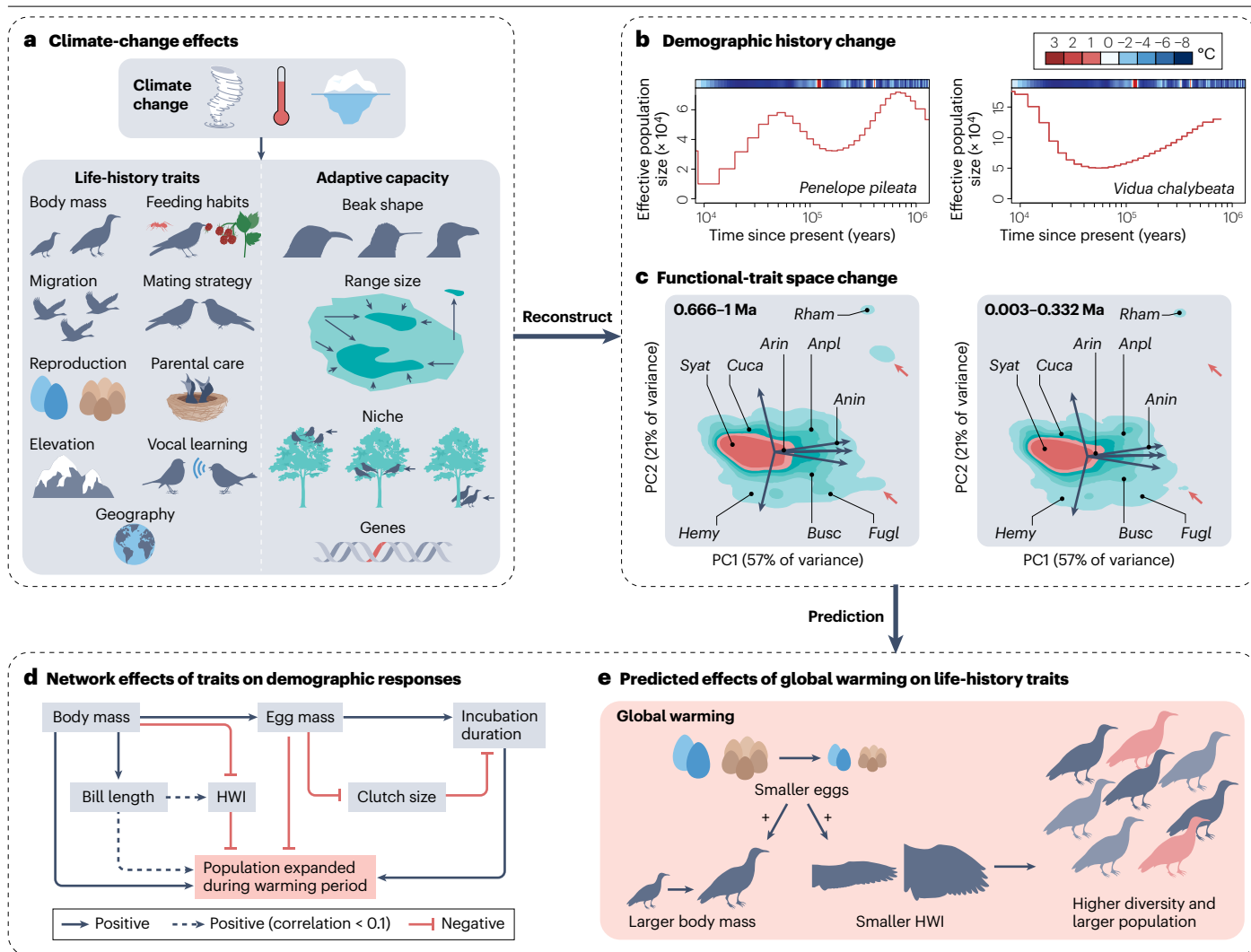
Review article

Fig. 7 | Lineage-specific responses to climate change can aid in predicting avian demographic sensitivity. a, Climate change effects influence avian life-history traits and adaptive capacity. **b**, Demographic history change of *Penelope pileata* (white-crested guan, left) and *Vidua chalybeata* (village indigobird, right) over the past million years, exemplifying two distinct patterns of avian population dynamics. The coloured bar represents the global temperature (°C) changes over time. Ma, million years ago. **c**, Principal components (PC) analysis of change in functional-trait space occupation of bird species over the past million years. Contour lines represent the density of species in the defined space and the arrows depict peripheral regions of functional space that have eroded over time. Anpl, *Anas platyrhynchos*; Anin, *Anser indicus*; Arin, *Arenaria interpres*; Busc, *Bubo scandiacus*; Cuca, *Cuculus canorus*; Fugl, *Fulmarus glacialis*; Hemy, *Hemiprocne mystacea*; Rham, *Rhea americana*; Syat, *Sylvia atricapilla*. **d**, Network effects of key morphological and life-history traits on demographic responses to climate warming. During climate-warming scenarios, *Numida meleagris* (helmeted guineafowl) — a large-bodied bird species with relatively small eggs and rounded wings — exhibits demographic increases, whereas *Limosa lapponica* (bar-tailed godwit) — a small-bodied bird species with large eggs and slender wings — exhibits demographic decreases. **e**, Life-history trait relationships to climate effects, such as global warming, can be used to predict future demographic change. HWI, hand-wing index. Data in part **b** are from refs. 39,309. Part **c** adapted with permission from ref. 290, PNAS. Part **d** adapted from ref. 39, Springer Nature Limited.

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understanding of trait evolution and interactions could provide valuable insights to inform effective conservation strategies to protect vulnerable species.

The full genome not only captures the current genetic diversity of a species but also reflects its demographic history. By modelling the coalescent events across diploid genomes as a Markov process, the pairwise sequentially Markovian coalescent (PSMC) method estimates changes in population size over time based on the distribution pattern of genetic diversity[289]. This approach enables the reconstruction of a population's historical dynamic, including bottlenecks or expansions, over the past million years in conjunction with climatic events, such as ice ages or global temperature fluctuations (Fig. 7b). Integrating data on life-history traits with historical demographic changes can elucidate how functional-trait space and trait-interaction networks have evolved in response to past climate shifts[290] (Fig. 7c), and can predict how these response

Review article

mechanisms could function under current and future climate conditions[291]. Demographic histories across avian families indicate that longer incubation duration and larger clutch sizes are associated with increased effective population size (N_e) during periods of climate warming[39] (Fig. 7d). By contrast, shorter incubation duration, lower HWI and longer bill lengths correlate with increased N_e during climate cooling[39]. Furthermore, phylogenetic path analyses of trait interactions and climate responses demonstrate that species exhibiting a combination of larger body masses, lower HWI and smaller egg masses were more likely to adapt to climate warming[39] (Fig. 7e). Given that greater body mass exerts a positive effect on egg mass and a negative correlation with HWI[39], it is likely that the positive effect of body mass is counterbalanced by the associated increase in egg mass or decrease in HWI. This example emphasizes the complex trade-offs among reproductive, survival, growth and dispersal traits in the context of evolutionary responses to climate change. Such trait-network influences on long-term demographic responses to climate change largely align with the contemporary global distributions of bird species: those in tropical latitudes generally exhibit longer incubation durations and longer bills, but smaller clutch sizes, smaller eggs, lower HWIs and reduced body mass[39]. Understanding the intricate relationships between life-history traits and demographic responses not only enhances our comprehension of species adaptations to past climate changes but also provides critical insights for predicting future resilience in the face of ongoing environmental shifts.

Summary and future directions

Rapid radiation promotes the formation of biodiversity by facilitating the accelerated diversification of species in response to ecological opportunities and environmental changes. This process not only enhances species richness but also boosts genetic and functional diversity within brief geological time windows, representing the most dramatic bursts of speciation and adaptation. The diversification of Neoaves near the K–Pg boundary is a seminal example of rapid radiation, leading to the rise of 95% of extant bird species. This event has been extensively studied over the past century, offering insight into the patterns and mechanisms of rapid radiation. However, temporal bursts of diversification generate several unresolved questions that hinder complete understanding of the detailed course of the radiation process and its driving forces. The rapid pace of speciation and the complex patterns of evolutionary divergence within the Neoaves clade have made it difficult to reconstruct the deep-branching relationship and precise timing of the radiation. Furthermore, disentangling the relative contributions of various potential drivers (such as environmental changes, the emergence of key adaptations, and ecological opportunities) remains an active area of research. Unravelling the complex interplay of these factors that facilitated the dramatic bursts of diversification within this bird group continues to be an important goal for evolutionary biologists.

Phylogenomics is a swiftly progressing field that offers promising approaches to unravelling the complex puzzles of rapid radiation processes and mechanisms. Indeed, the accumulation of additional

Glossary

Avialan
Any member of the clade Avialae, which includes all modern birds and their most immediate extinct relatives among non-avian dinosaurs; the term has been extensively used in studies of Mesozoic avian evolution.

Coalesce
The process by which alleles merge into a single ancestral lineage when traced backwards in evolutionary time.

Crown group
A crown group is a monophyletic clade that contains the most recent common ancestor of all extant members, and all of that ancestor's descendants.

Exaptation
The evolutionary process by which a trait that originally evolved for one function is subsequently co-opted for a different purpose; exaptations differ from adaptations in that the latter are directly shaped by natural selection for their current role.

Loci
A locus refers to a specific, defined position on a chromosome, typically corresponding to a gene or other functional DNA element.

Phalanges
The bones that constitute the digits of the limbs — specifically, the fingers in the forelimbs (wings) and the toes in the hindlimbs (feet) of vertebrates, including birds.

Polytomy
A condition in a phylogenetic tree in which a single node gives rise to three or more lineages, indicating either simultaneous divergence or unresolved evolutionary relationships.

Protobirds
Also referred to as stem birds, this term denotes transitional forms in the evolutionary continuum from non-avian theropod dinosaurs to crown-group birds; it has been frequently used in palaeontological literature to describe early avialan-grade taxa.

Rhamphotheca
The keratinous sheath covering the bony structure of a bird's beak.

Syngameon
A group of closely related taxa that frequently engage in natural hybridization and lack complete reproductive isolation; the concept has been applied to various avian groups exhibiting reticulate evolution and gene flow across species boundaries.

Syntenic structure
The conserved order and orientation of genes or genomic segments on chromosomes, either across different species or within duplicated regions of the same genome; syntenic relationships provide insight into chromosomal evolution, genome rearrangements and deep homology.

Target capture
A targeted DNA enrichment technique designed to isolate and sequence specific genomic regions of interest; it enables the retrieval of relatively long DNA fragments — often up to tens of thousands of base pairs — for downstream analyses such as phylogenomics or comparative genomics.

Transposable elements
(TEs). Mobile genetic elements capable of changing their position within the genome.

Review article

phonetically informative data has resolved many of the previous polytomies attributed to rapid species diversification within the Neoaves. However, several nodes remain recalcitrant to resolution even with whole-genome data, owing to a mix of factors including long-branch attraction, ILS[33,36,72] or ancient hybridization events[78]. It has been argued that the basal branching pattern of Neoaves could represent a hard polytomy that cannot be fully resolved with a bifurcating tree because of near-simultaneous speciation at the base of this major avian clade[35,75,292,293]. To exclude this possibility, it is essential to incorporate full genome data from additional species to evaluate the robustness of published phylogenomic trees[26,30,33,34,49]. The Bird Genome 10K Consortium is expected to complete the genus-phase programme within the next few years and will release thousands of genomes covering most of the recorded genera, which will be a valuable resource with which to rigorously assess the stability and accuracy of topologies. Additionally, comparing long-reads based on chromosome-level genome assemblies across lineages could help researchers to investigate gene synteny breaks and genomic structures — variations that are less prone to reversion than the single-nucleotide variations, which can easily revert and lead to misleading similarities, or homoplasy. These new data will undoubtedly continue to provide fresh insights into the sequencing process of rapid radiation. To efficiently manage and optimize the use of this unprecedented volume of data, encompassing millions of loci across thousands of genomes, new analytical algorithms are urgently needed to tackle the formidable computational challenges ahead.

The comparative genomic studies of birds have provided crucial insights not only into the conserved features shared by all modern birds but also into the radiation and adaptations of specific lineages, such as Darwin's finches[294,295], munias[296] and penguins[82]. These contemporary species radiations offer ideal time frames within which to detect hybridization events or gene introgression during the early stages of speciation, which is challenging to investigate in the ancient radiation of Neoaves. With an increasing number of genomes available for denser taxon sampling, we anticipate that comparative genomics analyses across different clades will help to identify any taxa-specific genomic components present in each clade, as defined by the phylogenetic tree. Such comparative genomic studies across bird lineages can reveal genetic diversity patterns accompanying macroevolutionary processes, offering opportunities to test macroevolutionary hypotheses at the molecular level. Given that speciation involves descent with modification through various factors like mutations, genetic drift and natural selection, one could argue that macroevolution is fundamentally an extension of microevolution[297–300]. However, palaeontologists and other macroevolutionary biologists have highlighted several macroevolutionary phenomena that indicate discontinuities between macroevolution and microevolution[136,301–304]. For example, rapid radiation can result in differential success among clades and lead to morphological disparities. Therefore, it is intriguing to evaluate the extent to which genetic diversity at different hierarchical levels can explain macroevolutionary patterns, such as the non-random origination of evolutionary novelties and morphological disparities. An integrative approach combining genomic, morphological, developmental and palaeoenvironmental data will help to reveal the genetic basis of macroevolutionary changes and enhance our understanding of the driving mechanisms behind the radiation process and other macroevolutionary patterns that arise from the rapid radiation.

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G.Z. contributed substantially to discussion of content. All authors wrote the article and reviewed and/or edited the manuscript before submission.

Competing interests

The authors declare no competing interests.

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