A Study Based On Distributions and Evolution of Avian Diversity Through Space And Time

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ABSTRACT

After the extinction of the nonavian dinosaurs and pterosaurs at the Cretaceous-Paleogene boundary, the previous 65 million years have seen the evolution and diversification of most contemporary orders of birds. Significant rate increases in several clades across the entire phylogeny drove the overall acceleration of bird diversification beginning around 50 million years ago. There appears to be no evidence of a slowing in the pace of diversification overall, suggesting that diversity equilibrium has not yet been reached. Breeding bird populations can be found on every continent, and birds have adapted to virtually every ecosystem. Species range from narrow-range endemics confined to a single island in the ocean or to a specific environment within a relatively limited region of land to near cosmopolitan species that reproduce on nearly all continents. The greatest variety of birds can be found in the tropics, close to the equator, and gradually declines as one move toward the poles, as is the case with most groups. The latitudinal diversity gradient is a trend that may be affected by both evolutionary and ecological factors, but there is no one mechanism that can be used to explain it. Speciation, extinction, and dispersal are the three main causes of biodiversity in a region. The process of speciation begins with the gradual increase in genetic differences between populations and ends when they become reproductively isolated from one another. During this time, populations become geographically isolated from one another, a process known as allopatric speciation. Evolution of reproductive isolation without geographic separation, or sympatric speciation, looks uncommon in birds, as does speciation with ongoing gene flow between populations, or parapatric speciation. For a long time, vicariance evolution has been used to explain the strikingly similar distribution patterns of many bird families across the Southern Hemisphere. An example of vicariance would be the separation of a species' range due to a mountain range being raised or a new ocean being formed as a result of tectonic plate movement. Allopatric speciation in various clades should be encouraged by the appearance of these barriers, leading to consistent biogeographic patterns.

However, some subsequent research have shown inconsistencies between sequences of geological events and phylogenetic patterns, suggesting that the phylogenetic theories used in the previous studies are outdated. Therefore, the current distribution patterns of several avian taxa can be explained only by past dispersal events, often spanning great distances and oceans.

It's possible that changes in the environment won't cause all bird species to diversify at the same rate at the same time. An older bird lineage likely has more time to populate an area outside a barrier. As a result, there is a better chance that organisms may move across the barrier, leading to increased diversity on both sides. The rate at which genetic variations accrue between populations is also predicted to be larger for bird groups with weaker dispersion skills than for lineages with better dispersal capability. Thus, the ecological features of various avian lineages, their environment, and the age of a given lineage all interact to produce diversification patterns. A variety of biotic and abiotic variables constrain the distributions of birds across the globe. In addition to being a necessary precursor to speciation, species range expansion also affects the density of coexisting species and, by extension, the dynamics of biodiversity change through time and space.

KEYWORDS

Avian diversity · Avian distribution · Allopatric speciation · Parapatric speciation · Sympatric speciation

SPATIOTEMPORAL DIVERSIFICATION OF MODERN BIRDS

Modern birds, Neornithes, are the only surviving lineage of dinosaurs, creating a well-supported monophyletic lineage), despite their lack of resemblance to Tyrannosaurus or Stegosaurus. Palaeognathae, which includes the ratites and tinamous, diverged from the remaining lineages within Neornithes, which are collectively referred to as Neognathae (Fig. 8.1). There is a division among the latter between the Galloanseres, which include all land- and waterfowl, and the Neoaves, which include all other living birds. Both morphological and molecular evidence (see, for example, Cracraft 2001, Hackett et al. 2008, Jarvis et al. , Livezey and Zusi 2007, Mayr 2011, and Prum et al. 2010) provide strong support for these deep evolutionary

links among current birds. Including gulls, herons, hummingbirds, owls, parrots, penguins, pelicans, raptors, and songbirds, the clade of Neoaves contains the vast majority of living bird species. Despite utilizing genome-wide molecular data (Jarvis et al. ; Prum et al.), the evolutionary connections of the several basic lineages within Neoaves remain disputed and have not been definitively established.
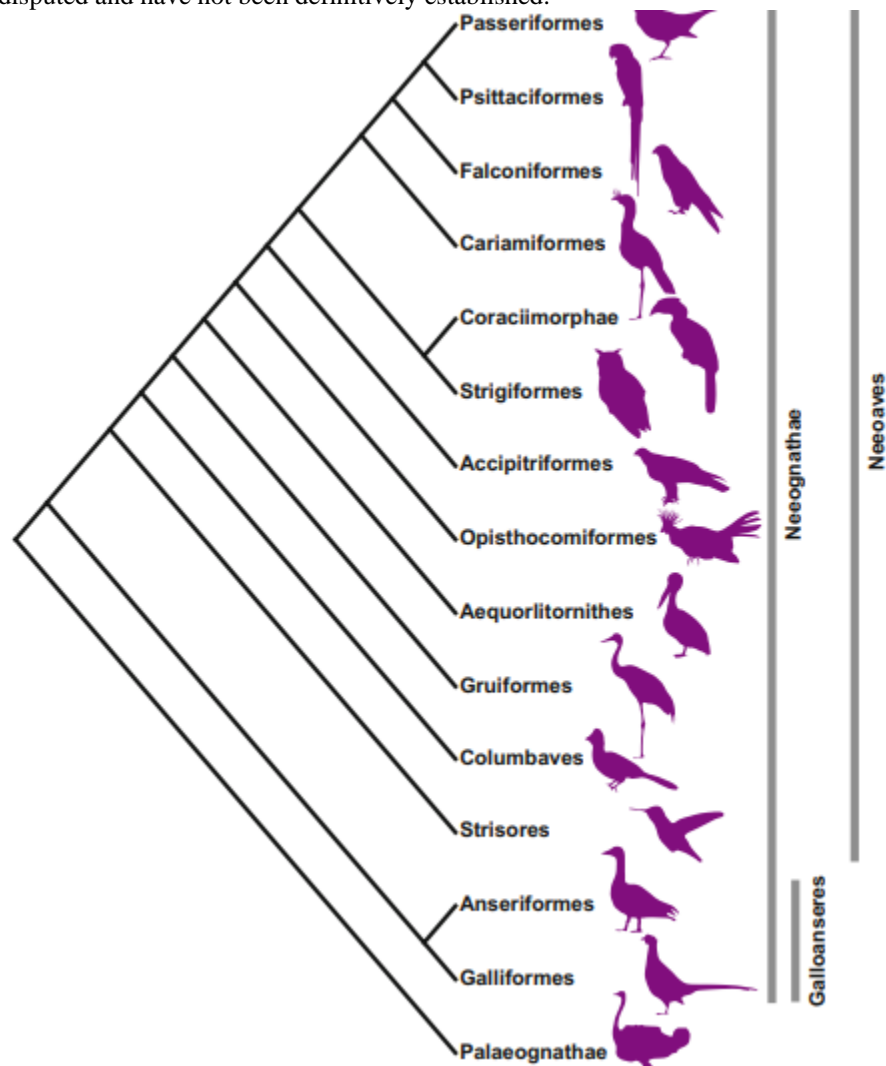

Fig. 8.1 Cladogram illustrating the phylogenetic relationships of the major clades of modern birds (Neornithes) redrawn and modified after Prum et al.

The Cretaceous extinction, caused by the asteroid strike at Chicxulub, Mexico, was one of the three greatest in the Phanerozoic (the last 541 million years; Alroy, 2008). Pterosaurs, ammonites, and rudists, among other groups of dinosaurs, went extinct as a result (Schulte et al., 2010). However, this is highly improbable due to the fossil record showing that the earliest birds similar to Neornithines arose around 80-85 Ma in the late Cretaceous and resembled Palaeognathae . Only in the Maastrichtian (72.1-66.0 Ma) do we have definitive fossil evidence for the presence of Neognathae . This lends credence to the idea that the ecological window created by the extinction of nonavian dinosaurs and pterosaurs at the K-Pg boundary led to rapid diversification. As a result, modern birds quickly expanded into the previously unoccupied ecological niche. It is still not clear why the Neornithes were the only dinosaur family to survive the mass extinction that occurred at the end of the Cretaceous period.

Changes in rates of progression typically appear to be linked to seminal innovations or ecological window of opportunity. Furthermore, Jetz et al. (2012) discovered that latitudinal differences do not drive geographical variation in diversification rates; rather, hemispheric differences drive these rates, with the Western Hemisphere having higher rates than the Eastern Hemisphere and the Northern and Southern Hemispheres showing no overall difference.

It's possible that density-dependence effects on diversification are to blame for the fact that some ancient radiations originated in Australia or Africa.

GLOBAL DISTRIBUTION AND DIVERSITY PATTERNS

Birds can be found practically wherever on Earth, as they have evolved to thrive in a wide variety of environments and can now reproduce on every continent. However, there is no such thing as a truly global bird species, one that can be found on every continent. The Peregrine Falcon Falco peregrinus is one example of a truly global species; it breeds on every continent bar Antarctica. The Osprey Pandion haliaetus is another; it breeds on five continents and visits a sixth, South America, as a nonbreeding visitor. In addition, throughout their annual migration cycles, some long-distance migrants and pelagic birds traverse greater portions of the earth. Narrow endemics, on the other hand, can only be found on a single island in the ocean or in a very specific ecosystem within a very small region of the world. Sombre Rock Chats, Oenanthe dubia, are one such species that has likely become confined to a tiny location in Ethiopia's Upper Awash Valley, where it dwells exclusively on rocky slopes with some grass and plants (Collar and Sharpe. Hawaiian honeycreepers and white-eyes are two well-known examples of the different oceanic island endemic passerine species that have extremely limited ranges and extremely small populations. Early naturalists attempted to categorize the world into regions based on similarities or differences in their flora and fauna, presciently realizing that species are not distributed at random. One of the primary goals of biogeography (Kreft and Jetz, 2010) is to create such regionalizations. The first global regionalization using bird distributions was reported in 1858 by British naturalist P.L. Sclater. A.R. Wallace (1867) extended this classification to the mammals of the world. Surprisingly, this original zoogeographic regionalization is still widely used, despite the fact that several modifications have been published (e.g., Ficetola et al.; Holt et al. ; Kreft and Jetz 2010; Vilhena and Antonelli) that incorporate not only up-to-date species distribution information but also phylogenetic data in some cases and use different criteria for the delimitation of regions (Fig. 8.2). Nearctic, Neotropical, Palearctic, Afrotropical, Oriental, and Australasian are the six main biogeographic zones of the Earth. The number of endemic families is highest in the Neotropical region (42), followed by Australasia (38), Africa (27), Asia (10), Europe (5), and the Middle East (1) (Winkler et al.,).

Fig. 8.2 Image of the world with the six primary biogeographic zones as defined by WWF superimposed on it (adapted from https://en.wikipedia.org/wiki/Biogeographic_realm). An revised biogeographic regionalization of amphibians, non-pelagic birds, and terrestrial mammals based on an integration of worldwide distribution data and evolutionary relationships. As updated by Holt et al.

The accuracy of these estimates is highly reliant on the taxonomic approach taken. More than 600 species have been documented in just a few square kilometers in Peru and Ecuador (Bass et al., 2010; Greenberg, making the Neotropics the most species-diverse region on Earth (Newton, 2003). The Neotropics are

also home to many of the world's most important centers of bird diversity. Orme et al. (2005) found nine places on Earth with exceptionally high species diversity, or "hotspots," defined as the top 2.5% most diverse grid cells at a resolution of 1 x 1 kilometers. The Andes, Amazon Basin, Guiana Highlands, Atlantic coastal forests, Mato Grosso Plateau, Panama, and Costa Rica highlands are just some of the Neotropical hotspots; the other three are in the Afrotropics (Western Great Rift Valley, Eastern Great Rift Valley), and the Oriental region (Himalaya). Except for the Amazon, all hotspots are found in the tropics and are linked to mountainous areas that remained forested even throughout the last glacial maximum. Although mountains only make up around 1/8 of the world's landmass (not counting Antarctica), they are home to about a third of the world's terrestrial species (Antonelli, . The largest variety of birds can be found in the tropics, close to the equator, but it gradually declines as one travels to the poles. One of the most prevalent global trends in biology is the so-called "latitudinal diversity gradient" (Jablonski et al., It may have multiple causes and be difficult to attribute to a specific process. This gradient has been attributed to ecological mechanisms, evolutionary mechanisms, and historical mechanisms (Mittelbach et al., 2007; Pulido-Santacruz and Weir, . The carrying capacity of a given ecosystem's species should decrease with increasing latitude if the first hypothesis is correct. Different rates of speciation, extinction, and immigration are predicted to occur at different latitudes based on evolutionary hypotheses, but older ecosystems are thought to be more diverse on the basis of historical hypotheses that emphasize the age of ecosystems and the time available for species accumulation.

GEOGRAPHY OF SPECIATION

The processes of speciation, extinction, and colonization largely determine the overall diversity of species in a region. The latter entails a species' spread to a new location and the subsequent development of a reproductive population there (Bellemain & Ricklefs, 2008). The process of speciation progresses from the gradual accumulation of genetically based divergence between populations to the last stage of the process, reproductive isolation. Reproductive isolation can occur through a variety of methods, and different species ideas emphasize different points along this speciation continuum (Chapter 2). Speciation can be studied from many vantage points. One looks at the causes of reproductive isolation (Chapter 11), while the other examines speciation in a geographical setting (Price 2008; Rundle and Nosil 2005). Allopatric speciation refers to the process by which two or more genetically distinct populations become geographically separated and cannot interbreed (Coyne and Orr, 2004) and this is supported by the fact that the vast majority of bird speciation events involve at least some periods of allopatry with no gene flow. Parapatric speciation (Coyne & Orr, 2004) refers to the process by which two geographically separated populations can become reproductively isolated from each other despite continued gene flow at least at the beginning of their divergence. Parapatric speciation can take three distinct forms, as described by Price (2008). Within a clinal speciation scenario, population divergence could happen along an environmental gradient as a result of adaptation to local environmental conditions. The populations at each end of a continuous distribution area can diverge from one another over time due to isolation, while those in the middle can still interact genetically. According to the island model of speciation, genetic exchange between populations continues to some degree despite physical separation. When immigrants (and their progeny) have low reproductive success or when migration between neighboring populations is restricted, reproductive isolation can develop (Price, 2008). Distance-based speciation models like the ring species model are a subset of this process. As a population expands across a barrier, gene flow may be maintained between neighboring populations while decreasing between more distant ones. When the two populations finally meet after spreading over the barrier, they may have achieved reproductive isolation from each other due to the rising divergence between them (cf. Coyne and Orr 2004; Mayr 1942). The Greenish Warbler (Phylloscopus trochiloides) species complex is one example of an avian group where such a mechanism may have contributed to the observed variety (Irwin et al., 2005). With five recognized taxa and an extra, isolated one in the Caucasus, its distribution is a ring around the Tibetan Plateau (Fig. 8.3) (Alcaide et al. ; Irwin et al. 2001, 2005). The species viridanus and plumbeitarsus diverge most noticeably in morphology, song, and cry north of the Tibetan Plateau. Unlike the other populations, which show a genetic gradient around the ring, these forms show genome-wide differentiation. However, reproductive isolation is not total in the northern contact zone, and secondary contact after divergence in allopatry is the sole explanation for a genomic split in the Southwest (Alcaide et al. Therefore, temperature change during the past 1–2 million years may account for the (repeated) phases of allopatry along the ringlike distribution, rather than speciation by distance alone. It is true that secondary contact zones with ongoing gene flow make it hard to tell apart speciation in a ring from other types of speciation. There is a lot of evidence that birds engage in hybridization in secondary contact zones after allopatry (Aliabadian et al., 2005; Weir and Price, 2011) (Chapter 10), and this sort of hybridization may be hard to tell apart from parapatric divergence in most cases. Reproductive isolation occurs in the situation of sympatric speciation without the need for physical separation of populations. Mathematical models (Gavrilets, and empirical investigations (Savolainen et al., 2006; Sorenson et al., 2003) have shown that this model of speciation is possible under specific, albeit realistic, biological conditions, despite decades of disagreement.

However, this phenomenon appears to be extremely unusual, and just a few of similar episodes in birds can likely be considered to have occurred in sympatry. Importantly, an allopatric stage cannot play a role in the divergence of two modern, sympatric sister species. That is to say, sympatric speciation is required, because geographical separation can never have been the cause of the first split. Birds of the genus Vidua in Africa are one of the most convincing cases of sympatric speciation (Sorenson et al., 2003). Specifically, waxbills, munias, and allies (Estrildidae) are brood parasites on the nests of other songbirds throughout Western and Southern Africa. Male indigobirds, sometimes known as foster dads, are taught their songs by members of the host species. Balakrishnan and Sorenson (2006) found that females give mating preferences to men who sang like their foster parents.
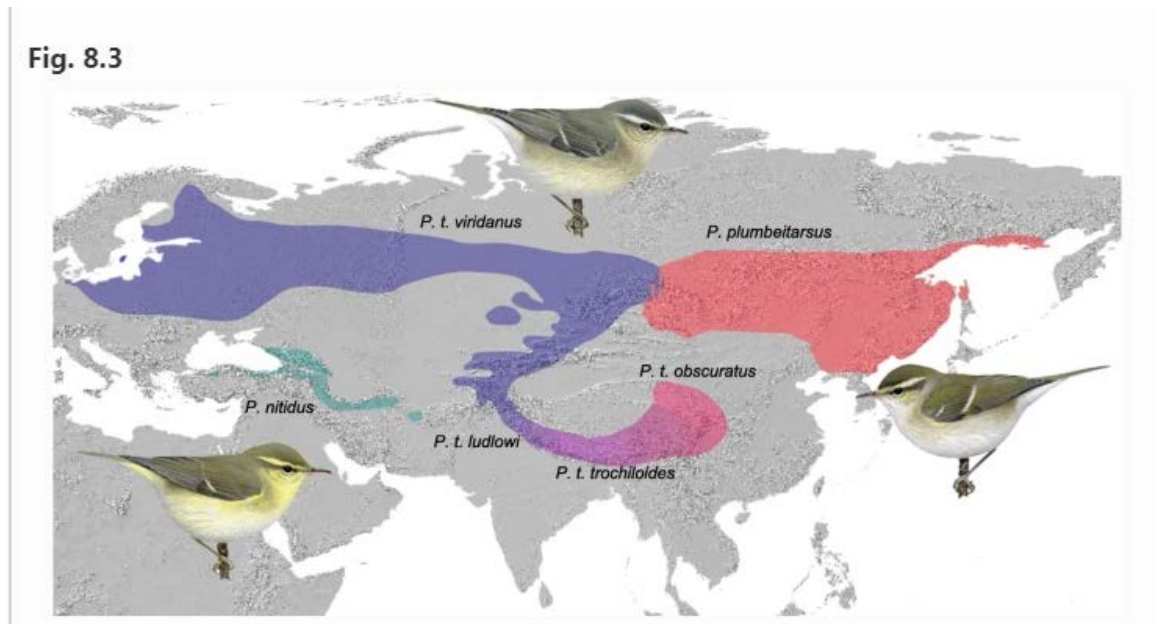
Fig. 8.3

Phylloscopus trochiloides, often known as the Greenish Warbler, has a wide range and a number of subspecies (shown in Fig. 8.3). There are currently five described taxa, with a sixth isolated in the Caucasus, forming a ring around the Tibetan Plateau. North of the Tibetan Plateau, viridanus and plumbeitarsus diverge most noticeably in terms of morphology, song, and call. Modifications were made to distribution ranges based on data from BirdLife International and the Handbook of the World's Birds. Del Hoyo et al.'s avian illustrations were used with their kind permission.

VICARIANCE VS. DISPERSAL AND THE DYNAMICS OF RANGE EVOLUTION IN BIRDS

Each bird species has a limited distribution, or range, that corresponds to a specific ecosystem or climate. Although species ranges vary greatly (as shown above), there are several groups that exhibit remarkably similar patterns of distribution. Historical biogeography has traditionally been dominated by the concept of vicariance, which has been invoked for a long time to explain such large-scale biogeographic patterns in many groups of birds. The term "vicariance" refers to the separation of a species' geographic range as a result of geological processes such mountain uplift or ocean formation as continents move (tectonic rifting) (de Queiroz 2005; Lomolino et al. 2010). It was hypothesized that such historical events could trigger synchronous allopatric speciation events, resulting in biogeographically consistent distributions across many clades (cf. Halas et al., 2005; Upchurch, 2008). Several groups of organisms, including birds, have distinct distributions in the Southern Hemisphere, and this has been attributed to vicariant evolution, which was thought to have been caused by the breakup of the supercontinent Gondwana from c. 160-30 Ma (e.g. Cracraft 2001; Hedges et al. 1996; Upchurch 2008). Modern-day Antarctica, Australia, the Indian subcontinent, Madagascar, and South America were all a part of this ancient Southern Hemisphere supercontinent.However, in the last decade, dated molecular phylogenetic theories have become more widely available, making it possible to directly examine whether the timing and location of phylogenetic branching events are consistent with theorized drivers of vicariance such the breakup of Gondwana. Integrating ancient DNA evidence from extinct elephant birds and moas into a phylogenetic framework (Mitchell et al., 2014) indicated a disagreement with the connections anticipated by vicariance through the Gondwana separation (Fig. 8.4). Taxa within these families have distributions that are broken up by topographical features including the Andes, the Amazon River, and the Isthmus of Panama. There was no evidence of a unified response to changes in the landscape because no taxa studied diverged at the same

time across the several barriers considered. The boundaries were more like a porous matrix inside a landscape that was organized regionally. The age of the respective lineage was shown to be significantly linked with diversity. This suggested that lineages that had been present in a landscape for a longer length of time had more opportunities to spread over barriers and hence to differentiate as a result. Lineage diversity was also significantly impacted by ecological factors. Less mobile lineages living in the understory of tropical forests were far more numerous and varied than those living in the forest's upper levels. Alternatively, genetic divergence appears to have accumulated at a faster pace among lineages with limited dispersal capabilities. Overall, the ecological features of the various lineages, their environment, and the age of a given lineage all interact to produce diversification patterns in these Neotropical avian lineages, with landscape changes only acting as a secondary impact. The importance of dispersal as a main driver of allopatric speciation in birds is highlighted by this finding (Smith et al.. Birds' ability to disperse has been shown to have a positive effect on the rate at which sister lineages reach sympatric ranges after speciation in spatial segregation (Pigot and Tobias, As a result, dispersion plays a crucial role in determining the spatial and temporal composition of species communities. However, the dynamics of range expansions and the ability to colonize new areas are constrained by more than just physical constraints, time, and dispersal ability in birds. Climate, habitat limits, feeding and nesting sites, predators, parasites and infections, and competition are just some of the biotic and abiotic elements that limit geographic ranges (see also Chapters 9 and 12). Winter temperatures may be a major factor in limiting bird ranges at higher latitudes, whereas competition may play a larger role in the tropics (Newton, 2003). Interspecific competition is hard to detect in field investigations and not easily testable in controlled trials (Greenberg, , hence the relative role of biotic variables in limiting species ranges is debatable (Pigot, Tobias, . However, phylogenies in conjunction with ecological data can be used to investigate whether or not competition plays a role in restricting species' distributions. Consistent with this, we found that species pairs that differ in ecomorphology in relation to resource utilization and foraging strategy experienced increased transition rates to sympatry. Species diversity increases in Eastern Himalayan songbird communities due in part to biotic interactions. Since the available niche space has been filled due to competing biotic interactions, it appears that this is a limiting factor in biodiversity (Price et al.).
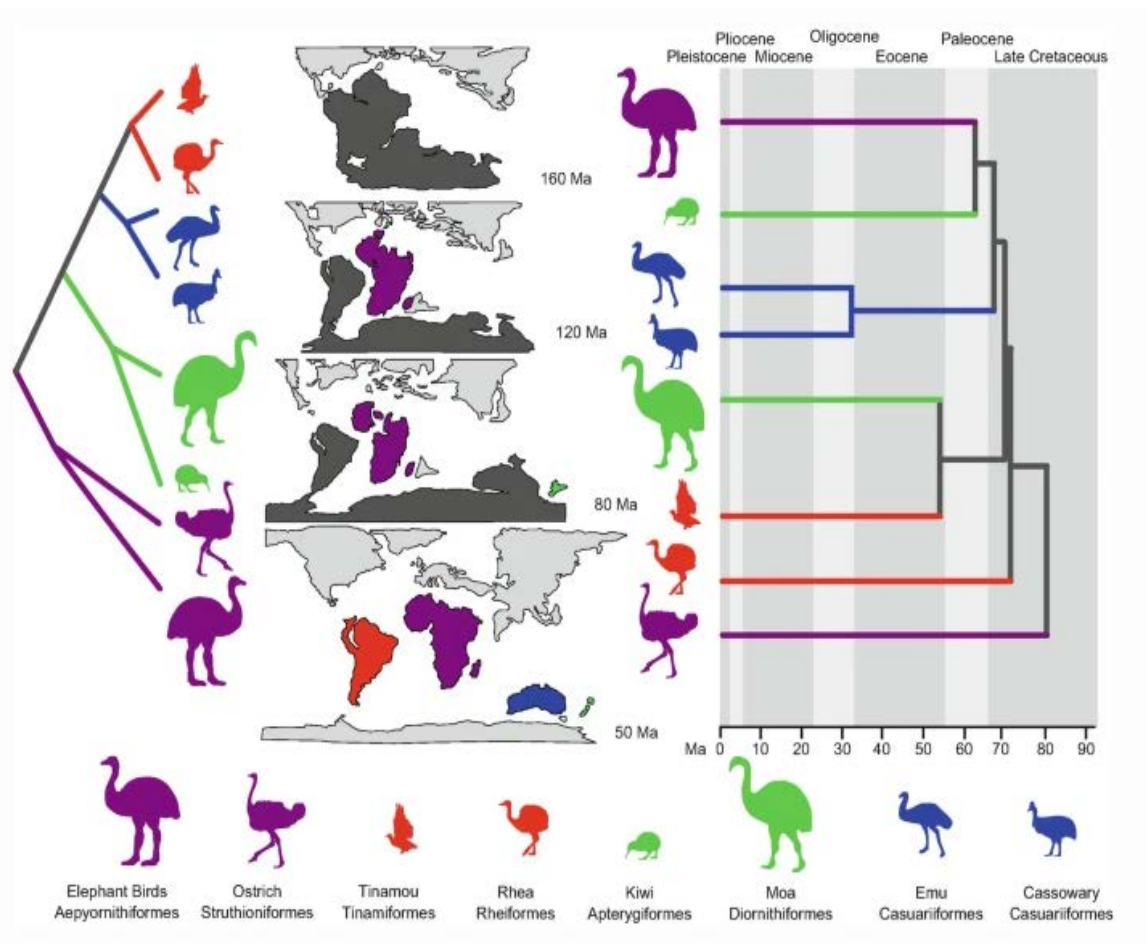
Fig. 8.4 The diversification of the ratites (Palaeognathae) was long supposed to have been influenced by the split of Gondwana and hence served as a textbook example of vicariant evolution. The cladogram on the left displays the expected evolutionary relationships of ratites under this scenario, while the middle depicts the breakup of Gondwana during the last 160 million years and illustrates the relative position of the continents. Adapted with AAAS approval from the original by Mitchell et al. Redrawn with permission from Elsevier, on the right, is the most up-to-date time-calibrated phylogenetic hypothesis of ratites based on genomic and morphological data. It's clear that the Gondwana separation disrupted the ties envisaged by vicariance. Moreover, the tinamous' position as the moas' closest cousins implied that the ability to fly independently must have been lost in several lineages.

CONCLUSION

The largest variety of birds can be found in the tropics, close to the equator, but it gradually declines as one travels to the poles. One of the most prevalent global trends in biology is the so-called "latitudinal diversity gradient."

The current global patterns of biodiversity are the product of processes that work over geography and time, necessitating an approach that takes these two scales into account simultaneously. We now have a better grasp on the rate and pattern of diversification thanks to molecular time trees, which have also uncovered some astonishing adaptive radiations across the tree of life. But joint phylogenetic and geographical sampling being too small has restricted generalization. Therefore, it is uncertain how common rapid radiations are and how much their locations matter to the overall patterns of biodiversity across the globe. We offer the first fully dated phylogeny of all 9,993 bird species, a group that has been extensively investigated due to the diversity of the adaptations among its members. From roughly 50 million years ago to the present, we observe that the diversification rate of birds has increased dramatically. Songbirds and other young and predominantly temperate radiations, such as waterfowl, gulls, and woodpeckers, are to blame for this quickening. It is noteworthy that species characterized by extremely rapid historical rates of diversification are spread out over the bird family tree and the globe. The largest disparities in diversification rates are hemispheric rather than latitudinal, with a disproportionate number of species from recent rapid radiations concentrated in bird assemblages in Asia, North America, and southern South America. An all-encompassing geographical and taxonomic approach is demonstrated by the contribution of quickly radiating lineages to temporal diversification dynamics and spatial distributions of species diversity. It is possible that the adaptive zone into which modern birds have expanded since the Cretaceous still offers prospects for diversification, despite the fact that individual clades may show signs of slowing down.

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