

**Interactions of climate, migration and life history traits in the
evolutionary history of birds**

**A klíma, a vonulás és az életmenet-jellegek kölcsönhatása madarak
evolúciójában**

Egyetemi doktori (PhD) értekezés

Nagy Jenő

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Prof. Dr. Varga Zoltán

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Interactions of climate, migration and life history traits in the evolutionary history of birds

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Preface

When I was a child, I wanted to become computer scientist for a long time. Although I am interested in computer sciences, I managed to learn biology quickly, and further, due to my visual impairment, I finally choose to learn biology in secondary school.

Later, as I progressed in my studies at the Univeristy of Debrecen, it soon became clear that my primary interest lies in animals, out of other fields of life sciences. This is not surprising, because my attention has always been directed to birds and mammals since we got our first dog when I was very young. As a result, I first became an ecologist, then a zoologist.

Although I chose biology, as a consequence of the twist of fate, I got close to informatics during my researches. This motivated me to deepen my knowledge in mathematics to acquire a better understanding of the formulae behind the approaches I am using. Thus, after I qualified as a teacher of biology, I studied mathematics. Hence, I successfully became a teacher of mathematics, parallelly to my ongoing doctoral programme.

Meanwhile, my interest focused on the evolution of life history and behaviour traits in birds, especially on historical biogeographic patterns and the origin of migration in several groups. The present dissertation is the result of the efforts I invested into research during the past eight years, since I have begun to prepare my first thesis at bachelor level at the Department of Evolutionary Zoology and Human Biology.

My related findings in the studies on raptors and passerines indicate novel insights into the biogeography and evolution of these groups, and also regarding to migratory behaviour and its related factors with significant implications for conservation aspects.

Előszó

Amikor gyerek voltam, hosszú ideig informatikus szerettem volna lenni. Azóta is érdeklődöm a számítástechnikai tudományok iránt, azonban a biológiát is nagyon könnyen tanultam, nem mellesleg veleszületett szembetegségem miatt úgy döntöttem, hogy középiskolában a biológiatanulás útjára lépek.

Később, ahogy a Debreceni Egyetemen folytatott tanulmányaim előrehaladtak, hamar kiderült, hogy leginkább az állatvilág érdekel az élettudományok megannyi területe közül. Ez nem meglepő, hiszen figyelmem mindig is a madarak és emlősök felé irányult, amióta nagyon fiatalon megkaptam első kutyámat. Végeredményként, előbb ökológus, majd zoológus képesítést szereztem.

Annak ellenére, hogy a biológiát választottam, a sors különös fintora következtében mégis közel kerültem az informatikához kutatásaim során. Ez tovább motivált matematikai tudásom elmélyítésére, hogy megérthessem azokat az „egyenleteket”, melyek a mindennap használt módszerek mögött rejlenek. Ezért, miután már biológiatanári végzettségem is megszereztem, elkezdtem matematikát tanulni. A folyamatban lévő doktori programom mellett sikeresen elvégeztem a matematikatanári szakot is.

Mindeközben érdeklődési köröm egyre inkább a madarak életmenet-jellegeinek és viselkedésének evolúciója irányába fordult, különös tekintettel az egyes csoportok biogeográfiai mintázataira és a vonulás kialakulására. Jelen doktori értekezés annak a hosszú munkának az eredménye, melyet az elmúlt nyolc évben fektettem be kutatásaimba, mióta az első szakdolgozatommal kapcsolatos feladatokat megkaptam az Evolúciós Állattani és Humánbiológiai Tanszéken, mint alapképzésben részt vevő hallgató.

A ragadozó és énekes madarak tanulmányozása során olyan eredményeket sikerült kimutatnom, melyek több szempontból is újak eme csoportok biogeográfiáját és evolúcióját illetően, ideértve a vonulási viselkedéssel és az azzal összefüggő tényezőkkel kapcsolatos megállapításokat, amelyek akár természetvédelmi szempontból is alkalmazhatóak lehetnek.

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1. Introduction

Historical events have always been in the focus of mankind's interest: from fundamental questions such as 'where did humans originate from' to personal issues such as 'who was my great-grandfather'. Nations were born and buried because of the knowledge or indeed, the ignorance of true history that could strengthen or weaken societies. Motivated by this curiosity, the desire for knowledge led to turn interest to science.

History and religion are inseparable in many nations' culture. In this respect, birds have always been a miraculous group of animals that people admired due to their mysterious behaviour, magnificent appearance or surprising intelligence. For example, birds in Celtic mythology represent knowledge, speech and prowess, and often associated with the message or the messenger (Noodén 1992) in the form of eagle, owl, starling, blackbird, raven and crow, even included in archaic Japanese stories. The Romans believed in the messenger role of birds which carried the messages of gods in the form of augurs, priests whom were deeply respected (Green 2009). Furthermore, many raptors represent national and ethnic symbols: e.g. "golden kite" in Japan, "turul" (considered as the saker falcon *Falco cherrug*) in Hungary, "golden-winged eagle" in Mongolia, representing strength, law of living in harmony with nature, hope and origin (Waida 1978). Crows, eagles and hummingbirds also played fundamental roles in tales of American native Indians (Du Bois 1904). The Egyptians often depicted their gods as birds, including falcons, hawks, vultures, and herons (March 1898, Buhl 1947). The cattle egret (*Bubulcus ibis*) known as the Egyptian "Bennu" may have been the inspiration for the Greeks' mysterious "Phoenix" bird. The Greeks, beyond religion, tried to scientifically describe the world around them. For instance, Aristotle described that migratory birds hibernate or simply hide during winter periods. As already seen from these examples, imaginations and scientific explanations have already been born in relation to bird migration (e.g. Heather 1939, Bairlein 2008, Somveille et al. 2015).

This chapter aims to review the main changes in Earth's history to provide background for my main findings on biogeography and its consequences for the evolutionary origin of migration in birds.

1.1. Historical biogeography and its consequences in the evolution of birds

Species have some regularities in distributions which allows the distinction of biogeographic realms. However, as these patterns are continuously changing, they have not remained constant during the geological history of Earth. The movements of tectonic plates have inevitably driven the changes e.g. in the ratio of terrestrial/marine surfaces, composition of the atmosphere, and consequently in climatic zonality, including cyclic changes of orbital factors. The biosphere, the subject of our main interest here, inseparably depends on the lithospheric crust system, but is divided into separate components. These plates are drifting and more or less correspond to the main biogeographic realms, however, they cannot be limited within the boundaries of continents.

In the next three subsections, I summarise the major geo-biospheric changes that drove the main climatic processes, after a brief overview of the past, focusing on the Tertiary in terms of forming the current biogeographic division of the animal kingdom, especially for birds.

1.1.1. Historical changes of the geo-biosphere

Tectonic movements and orogenic events played a fundamental role during the history of Earth, thus in the formation of nowadays geographical surface and climatic zonality. In the Late Carboniferous and Permian, all terrestrial surfaces on the globe had started to converge. Laurentia (including North America, Scotland, Ireland, Greenland) merged with Gondwana (South America, Africa, Arabia, Madagascar, India, Australia, Antarctica), and the formation of the supercontinent of Pangea was completed by the Triassic and Early Jurassic (Scotese and McKerrow 1990, Condie 1997, Scotese 2004).

The re-segmentation of Pangea started during the Late Jurassic. Nevertheless, the movements of the recent continents suggest the formation of a new supercontinent in the far future.

Around 140-120 million years ago (Mya), the North Atlantic began to open up (Condie 1997, Scotese 2004). By that time, the rest of Gondwana detached from South America/Africa and the latter two completely separated in the Late Cretaceous. Australia was split from Antarctica, and Madagascar also separated from India and almost reached its current position around 100-80 Mya (Scotese 2004). India collided with the southern parts of Eurasia during the Eocene, and the formation of the Alpine-Himalayan collisional orogeny process started (Condie 1997, Cawood et al. 2009). Africa also merged with Eurasia via Arabia, during the Oligocene, whilst the Panama land bridge came into existence connecting North and South America. Hence, the continents had almost occupied their present positions. The uplift of the Eastern Cordilleras and the Andes, along the southern end of the Cordilleran accretionary orogen events, also occurred during the Miocene (Gregory-Wodzicki 2000, Hooghiemstra and Van der Hammen 2004, Barke and Lamb 2006).

The geo-biospheric events in the Tertiary played a significant role in the evolution and radiation of Neognathae, resulting both major barriers and corridors for organisms, also in recent times. India collided with Asia approximately 65-34 Mya, initiating the uplift of the Himalaya and Tibetan Plateau (Molnar et al. 2010, Najman et al. 2010, DeCelles et al. 2014, Zhang et al. 2018 and their references, but see also Zheng et al. 2000 for an alternative hypothesis). The elevation range of the area significantly increased 8 Mya, during the Late Miocene (Harrison et al. 1992, Molnar et al. 1993, Zhisheng et al. 2001) that formed barriers between the southern and northern part of Asia and induced radical climatic changes as described in the next subsection.

Compared to other continents, the climate and biome zonality of Africa changed the most dramatically during the Cenozoic, driven by important geotectonical changes. The development of North African basins started in the Paleozoic-Mesozoic (Coward and Ries 2003) and the Atlas belt significantly changed during the Cenozoic (see also Piqué et al. 2002 for a comprehensive review). During the Early Miocene (20-18 Mya), Africa

merged with Asia via the Arabian Peninsula (Sanders and Miller 2002). However, the Ethiopian Plateau already began to uplift during the Oligocene, almost simultaneously with the emergence of the eastern branch of the East African Rift System during the Eocene-Oligocene (Chorowicz 2005, Sepulchre et al. 2006). The western part of the rift system began to develop around 12-10 Mya with major uplifts between 5-2 Mya, forming a long north-south area bordered by chains of ridge. Furthermore, the South African Karoo Plateau started to uplift during the Early Pliocene (Sepulchre et al. 2006).

Other important event in the geological history is represented by the South American orogeny. Although the elevation of the West Indies started around 35-33 Mya, the islands just occupied their almost-present locations after the Middle Miocene (Hedges 1996, Iturralde-Vinent and MacPhee 1999, Ricklefs and Bermingham 2008). After the migration of the Caribbean Plate between Yucatan and South America, and the narrowing of that corridor, the Nazca Plate collided with South America. The uplift of the Eastern Cordillera and Central Andes occurred between 10-3 Mya (Gregory-Wodzicki 2000, Hooghiemstra and Van der Hammen 2004, Barke and Lamb 2006, Cawood et al. 2009), whilst the complete closure of the Panama isthmus finished during the Pliocene (see discussions of the estimated time intervals in e.g. Rea et al. 1998, Iturralde-Vinent and MacPhee 1999, Mercer and Roth 2003, Bonnefille 2010 and the references therein).

Besides the southern connection of North America, representing its northern link to Eurasia, an important biogeographical component – the Beringian land bridge and strait is also discussed. Its significance lies in the simultaneous connection of land masses and the separation of marine regions or vice versa, multiple times during the history (Hopkins 1959). The time of an early opening of the Bering Strait is thought to take place between 7.4-4.8 Mya, based on fossils of molluscs (Marincovich and Gladenkov 1999, but 4.3-3.1 Mya in some of the references therein), however the land bridge remained accessible for the migration of humans and animals until 11,000 years ago due to lower sea level (Hopkins 1959, Elias et al. 1996).

All of these geographical changes had significant effects on the past and present-day climate on Earth and consequently the recent composition of biogeographic realms will be discussed in the next two subsections.

1.1.2. Climatic consequences of geo-biospheric changes

In the following subsection I provide an overview of those climatic changes that played important roles in the biogeography of birds. These effects are classified into three categories: (1) orbital cycles, (2) tectonic movements, (3) and biotic factors, which are strongly interacted with each other, thus I prefer to summarise them following the above geographical division. In general, after the Paleocene-Eocene thermal maximum, the Earth's climate cooled during the Oligocene, when the Antarctic ice shield began to extend, but fluctuated including a warmer interval during the Middle Miocene and the Pleistocene (Zachos et al. 2001, Ravelo et al. 2004). The development of Antarctic and North Polar inland ice shields resulted in decreased sea level compared to the previous times (Haq et al. 1987, Müller et al. 2008). Although the current climatic changes are characterised by more extreme conditions, our present day climate is part of a long-term colder period.

The uplift of the Himalayas and the Tibetan Plateau caused significant changes in the climate of Eurasia beginning during the Late Miocene or even earlier (Harrison et al. 1992, Kutzbach et al. 1993, Molnar et al. 1993, Dupont-Nivet et al. 2008). The elevating region had increasingly captured the wet air streams from the ocean which facilitated the emergence of the monsoon system, whilst the central and inner part of Asia became increasingly arid (Rea et al. 1998, Zhisheng et al. 2001, Molnar et al. 2010, Zhang et al. 2018). The two monsoon cycles are different in timing and location. The South Asian monsoon includes the tropical monsoon of India, the Indochina Peninsula, and the South China Sea and brings large amounts of precipitation in summer, whereas the East Asian monsoon as a subtropical monsoon, affects the climate of China, the Korean Peninsula, Japan, and Mongolia with dry winter and rainy spring/summer (see Molnar et al. 2010, Zhang et al. 2018 for detailed review). These

changes are connected to the expansion of grassland vegetation and the restriction of forests during the Late Miocene (Harrison et al. 1992, Molnar et al. 2010), and furthermore to the glaciation of the Tibetan Plateau and the cooling of the Northern Hemisphere (Molnar et al. 1993, Rea et al. 1998, Zhisheng et al. 2001, Dupont-Nivet et al. 2008).

The first savanna/grassland formations appeared during the Late Miocene in Africa (Bobe and Behrensmeyer 2004, Bonnefille 2010). The cooling climate and aridisation of North Africa led to the emergence of the Sahara and the shift of forested and grassy/arid climatic zones by the Plio-Pleistocene, becoming similar to present conditions (deMenocal 2004, Hernández Fernánde and Vrba 2006). This phenomenon could be considered as a unique biospheric change different from the history of any other continent.

Furthermore, the Andes in South America forms the only significant barrier to atmospheric circulations in the Southern Hemisphere (Gregory-Wodzicki 2000). The mountains extending in a north-south direction blocked the moist air currents from Amazonia, and alongside the cooling climate from the Miocene the west coastal region of the continent became thus more arid. The uplift of the Andes also resulted in the backward flow of the Amazonas, which river plays a fundamental role in the biogeography of South America, and it is heading toward the Atlantic in present days (Sacek 2014).

Due to the cooling climate, aridisation and the formation of grasslands were typical in North America (Flower and Kennett 1994). However, the Beringian region and Alaska had warmer climate compared to the rest of the Arctic (Ruddiman and Kutzbach 1989), but the vegetation of the land bridge remained mostly tundra also during the Pleistocene (Hopkins 1959).

These global climatic changes and the appearance of new vegetation types during the Miocene fundamentally modified the former biogeographic realms and facilitated the radiation of birds and other animals associated with different adaptations to open grassy biomes.

1.1.3. Recent biogeographical regionalisation

The distribution of animals has been classified applying several different approaches during the last two centuries. To date, the actuality of traditional divisions is challenged by some modern approaches which generates debate in numerous questions.

The original geographic division classified the ranges of animals into six major regions: Palearctic, Nearctic, Ethiopian, Neotropical, Oriental, and Australian (Wallace 1876). According to the taxonomic summary in the books of Wallace, the above regions are characterised by endemic families of birds (Table 1). Barely a century later, these regions were refined, while keeping the main biogeographical classification such as Eastern and Western Palearctic, Nearctic, Afrotropical, Neotropical, Indomalayan, Australian, Oceanian, and Antarctic regions (Udvardy 1975).

Furthermore, a phylogenetical revision is also available based on vertebrates (Holt et al. 2012), which was debated, especially considering its methodology (Kreft and Jetz 2013). Nonetheless, I provide here a brief summary of this approach and suggestions. Using distributional and phylogenetic data on amphibians, birds, and mammals, the following evolutionarily unique regions can be distinguished: Palearctic, Nearctic, Afrotropical, Saharo-Arabian, Madagascan, Neotropical, Panamanian, Oriental, Sino-Japanese, Australian, and Oceanian. Their phylogenetic measurements of diversity and the amount of endemic species and families of birds (see Table 1) clearly support Australia and South America as being biodiversity hotspots, the regions that were separated from other continents in significant time intervals.

Table 1. Bird families endemic to the Wallacean biogeographic regions as defined in Wallace's time. The Palearctic region forms an exception because none of the bird families is exclusively typical for this region (Wallace 1876).

Regions	Sub-regions	Bird families
Ethiopian		
	Madagascar	Paictidae (a family of pittas in Wallace's time) Leptosomidae (family with a single species: Leptosomus discolor)
	African mainland	Musophagidae (turacos) Coliidae (mousebirds) Irrisoridae (insectivorous birds allied to the hoopoes, corresponding family cannot be found) Serpentariidae (secretarybird)
Neotropical		
	Neotropical region (mainland and islands)	Cotingidae (cotingas)
	Neotropical region except Chile	Coerebidae (bananaquits)
	Brazil and Mexico	Oxyrhamphidae (considered to be Oxyruncus cristatus, part of Tityridae) Pipridae (manakins) Formicariidae (formicarids) Rhamphastidae (toucans, Ramphastidae) Bucconidae (puffbirds) Galbulidae (jacamars) Momotidae (motmots) Cracidae (guans, chachalacas, curassows) Aramidae (family with a single species: Aramus guarauna) Eurypygiidae (family with a single species: Eurypyga helias)
	Chile	Phytotomidae (plantcutters, part of Cotingidae) Chionididae (sheathbills, Chionidae) Thinocoridae (seedsnipes)
	Neotropical region except Antilles	Dendrocolaptidae (woodcreepers, part of Furnariidae) Tinamidae (tinamous, as a single family part of Tinamiformes)
	Brazil and Chile	Pterotochidae (tapaculos, part of Rhinocryptidae) Cariamidae (seriemas) Palamedeidae (screamers, Anhimidae)

Antilles	Todidae (todies)
Brazil	Steatornithidae (family with a single species: <i>Steatornis caripensis</i>) Opisthocomidae (as a single family with a single species: <i>Opisthocomus hoazin</i> , part of Opisthocomiformes) Psophiidae (trumpeters)
Oriental	
Oriental region (mainland and islands)	Phyllornithidae (green bulbuls in Wallace's time)
Indochina and Indo-Malaya	Liotrichidae (hill-tits, corresponding family cannot be found) Eurylaemidae (broadbills, Eurylaimidae)
Australian	
Austro-Malaya and Australia	Paradisaeidae (bird-of-paradise, Paradisaeidae) Casuariidae (cassowaries and emu)
Australian region (mainland and islands)	Meliphagidae (honeyeaters) Platycercidae (rosellas, part of Psittaculidae)
Polynesia	Drepanididae (Hawaiian honeycreepers) Didunculidae (<i>Didunculus strigirostris</i> , part of Columbidae) Rhynchotidae (family with a single species: <i>Rhynchotos jubatus</i>)
Australian region except New Zealand	Trichoglossidae (lories, part of Psittaculidae) Megapodiidae (megapodes)
Austro-Malaya and New Zealand	Nestoridae (nestorid parrots)
New Zealand	Stringopidae (family with a single species: <i>Strigops habroptila</i>) Apterygidae (kiwis)
Nearctic	
California	Chamaeidae (considered to be <i>Chamaea fasciata</i> , part of Paradoxornithidae)

For studying the biogeographical origin of the above groups of birds I mainly followed the traditional biogeographic division applying some practical modifications described in the methods.

1.2. Phylogenetic histories in Neognathae birds

Modern birds originated in the Late Cretaceous in the continents of Western Gondwana, and their diversification has been accelerated after the Cretaceous-Paleogene boundary (Brusatte et al. 2015, Claramunt and Cracraft 2015). The Neornithes are divided into two major groups which clades separated more than 100 Mya. The Palaeognathae contains the tinamous and ratites, whilst the groups of Galloanseres and Neoaves are included in the Neognathae. In the next subsections I focus on the evolution of the latter group in overviewing their radiation, especially in Accipitriformes and the Turdidae and their closest relatives.

1.2.1. Major radiations of Neognathae

The Neognathae have been split into two major clades around 100-70 Mya forming a basal branch including Galliformes and Anseriformes, and a highly diverse one containing the rest of all extant birds of this group. The common ancestor of landfowls and waterfowls appeared around the Cretaceous-Paleogene boundary in a terrestrial region corresponding to South America, and the two clades evolved separately thereafter (Brusatte et al. 2015, Burleigh et al. 2015, Claramunt and Cracraft 2015, Prum et al. 2015).

These researches also suggest that nearly all orders of the Neognathae diverged approximately 50 Mya, and by that time they spread into Africa, Madagascar, India, and North America (Brusatte et al. 2015, Claramunt and Cracraft 2015). The biogeographic patterns of early radiation of these groups are unclear in some points due to methodological limitations.

Nevertheless, the diversification of avian lineages increased fast after that, leading to a highly diverse group of vertebrates amounting to ten thousand species (Jetz et al. 2012, Ksepka and Phillips 2015). This acceleration is more likely based on the geobiospheric changes described above which is also reflected in the geographical distribution of diversification rates and species richness (Voskamp et al. 2017). The

most species-rich areas include the tropical regions where passerine lineages with high diversification rates are presented (but see also temperate East Asia and North America), whilst lineages with higher diversification rate among non-passerines are almost exclusively typical in the Northern Hemisphere (Jetz et al. 2012).

The detailed evolutionary history and origin of Neognathae itself would demand a longer monograph, thus I briefly summarise only some major considerations. The historical biogeography of landfowls is obscure but the different results can be combined to form an acceptable explanation. It is widely recognised that Africa and the Indomalayan regions were significant hotspots in the early radiations of Galliformes (Wang et al. 2017). However, the most basal clades were found to be originated in Australasia and South America, in the order of branching, and the common ancestor of the rest of the landfowls was suggested to disperse from South America to Africa. This is only supported by the West Gondwanian origin of Neognathae (Claramunt and Cracraft 2015) with the acceptance of the possible dispersal routes of Megapodidae to Australasia via Antarctica (Wang et al. 2017).

Although many more important groups and their histories could be described besides the basal branches, let only consider the top of the tree, indicating the core landbirds (Telluraves). Out of the two major clades, one contains the Accipitriformes, while the other includes the Turdidae, which separated around 70-60 Mya (Brusatte et al. 2015, Claramunt and Cracraft 2015). The accipitrid birds of prey form the oldest group among its relatives and are sisters to the owls (Strigiformes) and the rest of the Afroaves (see for detailed phylogenetic and biogeographic history of some relevant groups e.g. owls, Wink et al. 2009, woodpeckers, Fuchs et al. 2017, kingfishers, Andersen et al. 2017). Therefore the name of ‘diurnal raptors’ may be misleading in a phylogenetic perspective: although accipitrid and falconid raptors share similar ecology and behaviour, they are not closely related groups (Mahmood et al. 2014, Cenizo et al. 2016). The sister taxa of Falconiformes are represented by the parrots (Psittaciformes) and the seriemas (Cariamiformes) and these three are basal to the lineages of perching birds (Passeriformes, Brusatte et al. 2015, Claramunt and Cracraft 2015).

Thorough description on the evolutionary history and diversification of passerine birds are available in recent studies. For the contribution of islands to the diversity in this group, see Jønsson and Holt (2015), whereas for the origin and diversification of songbirds in the New World look up Selvatti et al. (2015), and for the role of tectonic collisions in the radiation of oscines the paper of Moyle et al. (2016) is recommended.

1.2.2. Phylogeny of Accipitriformes

Although both natural and sexual selection influence the species richness of accipitrids, the former one plays a more prominent role in their diversification (Krüger 2008). Consequently, 240-270 extant or extinct species are known recently.

Many phylogenetic studies were published to clarify the relationships within a specific group of raptors but only some of those included multiple gene sequences or involved a comprehensive set of taxa and almost none of them dated the radiations of the birds of prey (see discussion in Griffiths et al. 2007, do Amaral et al. 2009 and their references).

The common ancestor of buteonine hawks (Buteoninae) originated between 27-13 Mya (do Amaral et al. 2009) which interval covers the estimated age of the first appearance of the ancestor of aquiline eagles (Aquilini, Helbig et al. 2005). Nevertheless, some of the buteonine hawks seem to form a younger clade than aquiline eagles according to several studies (Griffiths et al. 2007). Moreover, none of these subfamilies are monophyletic, except for the secretarybird (*Sagittarius serpentarius*, Sagittariidae), the osprey (*Pandion haliaetus*, Pandionidae), and the large clade containing the rest of the accipitrids.

Based on these uncertainties, it would be hard to form statements on the phylogenetic relationships among the subfamilies of raptors, since several taxonomic and classification changes have been proposed (Griffiths et al. 2007, do Amaral et al. 2009). Therefore the phylogenetic revision of the Accipitriformes is badly needed.

1.2.3. Phylogeny of Turdidae

Many studies of thrushes aimed to investigate the phylogeny and biogeography of the group, either focusing on one genus (i.e., *Catharus*, Outlaw et al. 2003, Winker and Pruett 2006, Voelker et al. 2013, *Turdus*, Voelker et al. 2007, 2009), or through wider taxonomic range (Klicka et al. 2005, Nylander et al. 2008).

The early radiation of *Turdus* was dated to around 7 Mya (Nylander et al. 2008, Voelker et al. 2009), however the results of Jetz et al. (2012) showed that the first appearance of the common ancestor of this group occurred approximately 15 Mya. These contrasting time intervals suggest to revise the biogeographic history of *Turdus* thrushes.

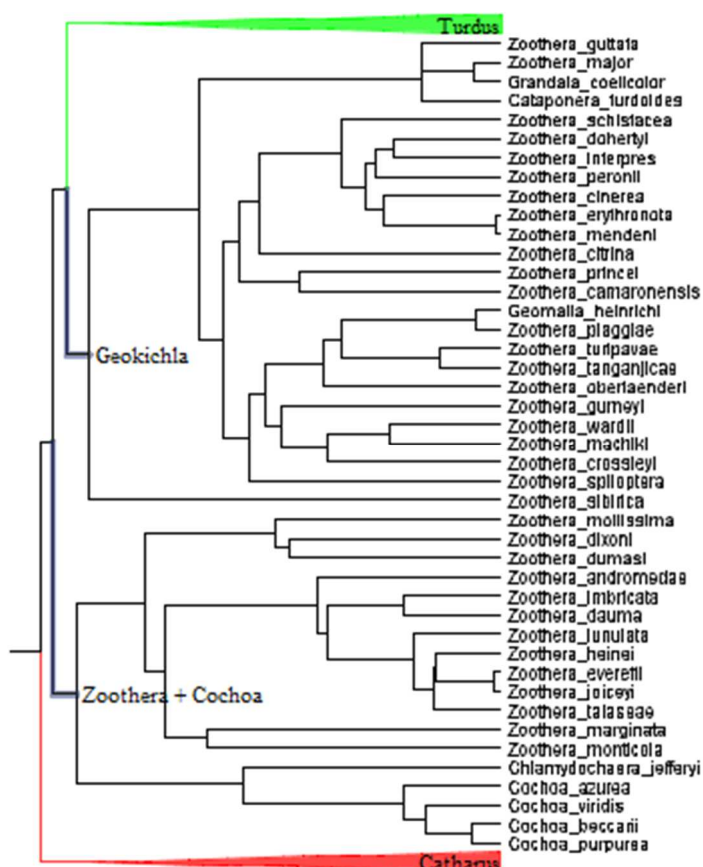


Figure 1. Suggestion for revision of Geokichla and Zoothera. Phylogeny of species is based on Jetz et al. (2012). See Results for novel findings.

Although this group originates from Southeast Asia, the importance of Indomalayan islands was also suggested (e.g. Nylander et al. 2008, Voelker et al. 2009). The biogeographic history of Turdidae becomes more unclear in the case of Central and South American species, despite the hypothesised trans-Atlantic movements. The most basal group of thrushes, the *Catharus* (Voelker and Klicka 2008, but see also Klicka et al. 2005) has also been originated in Central and/or South America (Outlaw et al. 2003).

The two branches of *Zoothera* is considered as polyphyletic taxa (Klicka et al. 2005, Jetz et al. 2012). Nevertheless, all *Geokichla* have been classified as *Zoothera*, together with *Zoothera naevia* and *Z. pinicola*. However, they were previously considered as monotypic genera, *Ixoreus naevius* and *Ridgwayia pinicola*, respectively (Olsson and Alström 2013). Currently, *Zoothera* includes all former *Geokichla* species (e.g. Voelker and Outlaw 2008), that should be split into two generic groups (Figure 1): (1) the monophyletic *Geokichla* and (2) the core *Zoothera* related to the subgenus *Cochoa* (Jetz et al. 2012). The core *Zoothera* is suggested to be monophyletic including the four, *Catharus* related species, *Z. naevia*, *Z. pinicola*, *Z. margaretae*, and *Z. leucolaema* after their taxonomic revision.

1.3. Phylogeny, migration and biogeography

After reviewing the geo-biospheric changes and the major radiations of modern birds, especially focusing on the Accipitriformes and the Turdidae, I summarise the main hypotheses on the origin of migration in birds including the differences of geographically distinct migratory systems and the brief overview of migratory behaviour and related traits.

The space limitation of this work does not allow to present longer description of the relationships among migration and other traits. For more detail in these topics the monographs of Newton (2008), Cox (2010), and Milner-Gulland et al. (2011), or also Dingle (2014) are recommended that are also referred below.

1.3.1. The origins of migration in birds

Behavioural traits, such as migration are unable to be fossilised and hence current ideas are only inferred from phylogenetic or biogeographic studies. The theories of the evolution of migration in birds are categorised into three groups (Rappole and Jones 2002, Bruderer and Salewski 2008, Louchart 2008).

The ‘tropical origin’ hypothesis assumes that migratory birds derive from populations or species occupying regions where environmental conditions were annually constant. Starting from those source patches, northern areas were gradually colonised to exploit the seasonally available food resources for reproduction. However, the decreased chance to survival, e.g. during winter food limitation forced these populations or species to return to south. According to a stepping-stone model competition for food led tropical resident species to colonise the subtropics developing partial migratory behaviour (Cox 1985). These birds continued to spread to higher latitudes where they were able to breed successfully but returned to the tropics in winters. An example for the ‘tropical origin’ hypothesis was provided for *Catharus* thrushes (Outlaw et al. 2003 and the references therein for more examples). The North American, migratory thrushes are sister to tropical species, and the ancestral range for them found to be in the Neotropic. This pattern can also be true for intraspecific comparison of populations e.g. in North American chipping sparrows (*Spizaella passerina*, Milá et al. 2006), in which case the northern, long-distance migrant populations descend from non-migratory Mexican populations.

The ‘northern origin’ hypothesis proposes that climatic or other ecological changes on the breeding ranges of northern species could have led to the evolution of migration due to the leaving of the highly seasonal habitats of temperate and arctic species during winter (Bell 2005, Bruderer and Salewski 2008). However, this hypothesis has received relatively low support to date.

Both the tropical and the northern origin hypotheses predicts that the migration evolved from resident populations or species simultaneously with the range expansion of these birds. Compared to them, the ‘shifting home’ hypothesis suggests the

narrowing of formerly wider tropical belt as the source of the evolution of migration (Louchart 2008). According to this hypothesis which considering paleoclimatic changes, migration evolved as a consequence of winter range shift rather than assuming the existence of an ancestral northern or southern breeding range.

Nevertheless, the shifting home is parallel to the idea of the origin of migration without the expansion of the breeding ranges, as suggested by intra-tropical migrants (e.g. Boyle et al. 2011). Variation and predictability of food sources or the ability to explore and to use these sources appear to prompt some avian taxa for migration (Bell 2011).

1.3.2. Migratory systems in birds

The two major, geographically distinguishable migratory systems are represented by the Palearctic-Afrotropical and the Nearctic-Neotropical systems (Newton 2008). The most striking difference between the two is the result of zonality. The vegetation zones follow an East-West direction in the Old World, whilst it follows a North-South axis in the New World, particularly regarding the orientation of significant ecological barriers.

Hundreds of species are migrating from the whole Palearctic region to sub-Saharan Africa crossing broad plateaus and mountains (>2000 m) or extremely arid (<50-100 mm of annual precipitation) areas during the journey (Newton 2008). However, the land bridge between North and South America, and the Caribbean islands provide more continuous routes for migration than in the Old World, where the Mediterranean Sea and the Sahara present hazardous areas for the passage of migrants. To a certain extent, the Mexican Plateau may form such a barrier, as indicated by several bird species wintering on its Northern border.

Furthermore, the distinction of Western Palearctic-Afrotropical and East Palearctic-Australasian migratory systems is supported by several reasons. The Europe-African migratory routes resemble the New World routes in the sense that birds face gradual changes of landscapes along these routes, contrary to the more homogenous landscapes

along the East Asian migratory flyways. Birds breeding on northern latitudes in East Asia tend to be canalised along nearly barrier-free, continuous routes during migration.

The importance of this significant difference is supported by the number of migratory species. While more than 200 species winter south of the Sahara in Africa, and this number is even larger in south of Central America, only 161 species migrate to Malaysia (Newton 2008). Moreover, the number of species overwintering south of the Equatorial forest belt is 42 in South America and 28 in Africa, however, only 14 in Australasia (Dingle 2014).

These evidences clearly justify the categorisation of species by migratory systems and their separate inclusion in the analyses as it is treated in this dissertation on accipitrid raptors.

1.3.3. Migration and other life history traits

Migratory behaviour influences and is affected by many ecological, behavioural and life history related factors, including the distribution and diversification of birds (Newton 2008). Here I mainly focus on those which seem to be significant in relation to the studied groups of birds.

Body mass is a fundamental factor in determining nearly all aspects of birds' life, which could be related to overcome the limitation of food and/or harsh weather. In relation to migration, body measurements affect, e.g. the timing and length of the journey, the speed of flight and the manoeuvrability, and hence the mortality of birds (e.g. Newton 2008, Cox 2010).

Before leaving the breeding/wintering range and at the stopover sites birds must refuel their fat reserves to have enough energy source for migration. Therefore the diet and hunting/feeding strategies also influence both body mass and migration (Newton 2008, Cox 2010). These strategies may require divergently adapted morphological structures (e.g. Dingle 2014), thus differences in body measurements (e.g. body mass, wing/tail ratio) and feeding 'equipment' (e.g. bill length) in relation to migration are

connected to resource partitioning and consequently to niche segregation (Brown 1976).

Feeding on seasonally available food sources is well-known in birds (del Hoyo et al. 2016), and evolutionary changes in foraging behaviour in sedentary/migratory lineages is documented for several groups (e.g. Rainio et al. 2012, Telleria et al. 2013, Moyle et al. 2015). Nevertheless, niche partitioning includes seeking for suitable habitats where food is available in appropriate quality and quantity, thus habitat type in temperate-tropical migratory systems could govern the availability of suitable routes and destination areas. For example, most of the North American and East Asian long-distance migrants winter in forests, however it is less frequent in migrants from the rest of the Palearctic (Rappole and Jones 2002, Newton 2008).

Life-history trade-offs, including the so far mentioned factors, are associated with migratory behaviour (e.g. Dingle 2014). Furthermore, because migration has a reproductive cost due to the higher risk of mortality, it is expected to be offset by further mechanisms: for example, larger clutch sizes were found in many migratory species (e.g., Bruderer and Salewski 2009 Jahn and Cueto 2012, Barve and Mason 2015, but see also Böhning-Gaese et al. 2000).

The complexity of the impact and interaction of involved factors in relation to migration is not entirely clear. Although an increasing number of papers are published in this subject, comprehensive and/or well-designed analyses are still lacking for several groups of birds. Thus my aims were (1) to estimate the evolutionary origin of migration, (2) which could not have been done without a historical biogeographic framework, and (3) to investigate relationships between life history-related traits and migration in a phylogenetic context, (4) including correlated evolutionary patterns in Accipitriformes and *Turdus* thrushes.

1.4. Objectives and hypotheses

Studying spatiotemporal patterns in the evolution of behavioural traits in birds requires biogeographical analyses and ancestral state estimations of traits considering common phylogenetic histories of species. However, investigating recent correlations among ecological and life history factors could also uncover significant consequences of historical events.

In this work, I focus on the evolution of migration in birds. Migration is one of the most complex phenomena related to many components of ecology (e.g. climate, biogeography) and behaviour (e.g. reproduction and survival). Accordingly, my aims were to (1) find climatic drivers of the biogeographic origin of the studied groups, (2) investigate the evolutionary origin of migration, and (3) several aspects of traits related to migration in these birds.

I chose two well-studied, widely known groups which play important roles in past and recent human culture. Both raptors and thrushes are widespread taxa, although some of the species in each group have very limited distributions that is fundamental for identifying their biogeographical origins. Furthermore, the suggested southern origin for both groups (Ericson 2012, Nylander et al. 2008) allows to compare differences regarding tropical hotspots. Out of a larger set, significant diversity in migratory behaviour and mobility, feeding ecology, reproductive biology, and body measurements, can be observed among the members of both groups (Ferguson-Lees and Christie 2001, del Hoyo et al. 2016), providing an opportunity to investigate relationships of several traits.

Nevertheless, considering all similarities and differences between Accipitriformes order and the Turdidae family, the question arises: whether is it possible to draw general conclusions which apply for these two groups or even in wider taxonomic ranges? Hence, I designed a comparative phylogenetic framework to investigate the following hypotheses:

1. Larger birds are more likely to become residents or vice versa, resident species might become larger.
2. Food is a major limiting factor during both winter and on the move.
 - a. Species with a more generalist diet are more likely to survive at temperate latitudes and be able to stay in winters.
 - b. In contrast, species feeding on alternative food sources are able to cope more easily with food limitations, hence food generalism or the ability of switching between food sources are more frequent among migratory species.
3. Differences in geographically distinct flyways are detectable (e.g. barriers, continuity).
 - a. The availability of suitable habitat types could have influenced the presence of corridors for tropical-temperate dispersal during the evolution of tropical-temperate migration systems.
 - b. Novel niches, as a consequence of the shift in grassy and forested habitats (changes in zonality) could have driven the radiation of birds into areas to be colonised.
4. Because migration may be costly due to the higher mortality during the migratory journey, a definable shift to higher numbers in reproductive attempts, as measured by clutch size, is expectable.

2. Materials and methods

I used an integrative approach to study the evolution of migration and the historical biogeography in two groups of birds, applying modern phylogenetic comparative methods.

Gene sequences for building phylogenetic trees were obtained from GenBank (<http://ncbi.nlm.nih.gov/>). Bioclimatic variables in raster format were downloaded from the WorldClim database (<http://www.worldclim.org/>). Distribution patterns were collected following the map library of BirdLife International (2015). Data on body measurements, clutch size, feeding ecology, migratory behaviour, and habitat selection were mainly collected from Ferguson-Lees and Christie (2001), Dunning (2008) and from Jetz et al. (2008) for raptors, and from del Hoyo et al. (2016) for thrushes.

Analyses were carried out in the R statistical environment attempting to use the latest version available (R Development Core Team 2017). In all other cases, the appropriate software is referred.

2.1. Estimation of phylogenetic relationships

Gene sequences for *12S* and *16S ribosomal RNA*, *ATP synthase subunit 6* and *subunit 8*, *β -fibronigen intron 7*, *cytochrome c oxidase subunit 1*, *cytochrome b*, *NADH-ubiquinone oxidoreductase subunit 2* and *subunit 6* and *recombinase activating gene 1* were searched in the database of GenBank (Table 2). The raw genetic information was processed using ‘ape’ (Paradis et al. 2004) and ‘seqinr’ (Charif and Lobry 2007) packages in R. MAFFT program was used for sequence alignment (Katoh et al. 2005), and the alignments were run through Gblocks (Castresana 2000) for cleaning purposes.

The RAxML (Stamatakis 2006) approach was applied on the created supermatrix to identify the best starting tree for the Bayesian MCMC analyses implemented in BEAST v1.8.3 (Drummond and Rambaut 2007). The best fitted substitution model for each of

the ten genes, based on result of the model test in the ‘phangorn’ package of R (Schliep 2011) was set for each partition uniquely.

Table 2. Availability of gene sequences used for the reconstruction of the phylogeny of Accipitriformes and Turdidae.

Gene	Number of species	Length of base pairs	Substitution model
Accipitriformes			
12S ribosomal RNA	74	900	TIM2+I+G
16S ribosomal RNA	53	1527	GTR+I+G
ATP synthase subunit 6	56	684	TrN+I+G
ATP synthase subunit 8	56	168	TrN+I+G
β-fibronigen intron 7	69	922	TVM+G
Cytochrome c oxidase subunit 1	86	1551	TIM2+I+G
Cytochrome b	164	1146	TIM3+I+G
NADH-ubiquinone oxidoreductase subunit 2	151	1047	GTR+I+G
NADH-ubiquinone oxidoreductase subunit 6	66	525	GTR+I+G
Recombinase activating gene 1	87	2872	GTR+I+G
Turdidae			
12S ribosomal RNA	61	385	GTR+I+G
16S ribosomal RNA	10	430	HKY+I
ATP synthase subunit 6	7	684	GTR+I
ATP synthase subunit 8	7	168	GTR+I
β-fibronigen intron 7	2	850	GTR
Cytochrome c oxidase subunit 1	36	649	GTR+I+G
Cytochrome b	71	1032	GTR+I+G
NADH-ubiquinone oxidoreductase subunit 2	66	1034	GTR+I+G
NADH-ubiquinone oxidoreductase subunit 6	6	519	GTR+G
Recombinase activating gene 1	5	1435	HKY+I

Uncorrelated relaxed molecular clocks approach was used for molecular dating (Drummond et al. 2006). Fossil calibration points were added to set divergent times to a maximum of 4 Mya for *Buteo galapagoensis*, 5.1 Mya for *B. solitarius*, and a minimum of 37 Mya for *Pandion haliaetus* in accipitrid raptors (do Amaral et al. 2009). Similarly in thrushes, priors were set for a minimum of 2.5 Mya for *Turdus rufiventris*,

T. rufopalliatus, *T. ignobilis*, and *T. plebejus* (Emslie 1998), 2.6 Mya for *T. pilaris*, *T. philomelos*, and *T. torquatus* (PaleoDB collection 124956, 124960, Harrison 1987) 3.5 Mya for *T. viscivorus*, and *T. merula* (Clot et al. 1976), and 5.3 Mya for *T. iliacus* (Jánossy 1991).

Independent Bayesian estimations were allowed to run for 50,000,000 generations then the results were combined. A maximum clade credibility tree for Accipitriformes was performed after removing 10% of the resulted trees as burn-in, using TreeAnnotator v1.8.3. (Rambaut and Drummond 2016). The Bayesian analyses and the creation of the final consensus tree were similar with small modifications in *Turdus*. Additionally, to investigate the taxonomic relationships among 155 species of the Turdidae family a consensus tree sampled after 5,000,000 generations were used as starting tree for the analyses detailed above. Two more fossil calibration points were used in this case setting the divergent times to a minimum of 2 Mya for *Catharus guttatus* and *Hylocichla mustelina* (Emslie 1998).

2.2. Biogeographic models and analyses

Although the analytical approaches were the same for both raptors and thrushes, the biogeographic regionalisation was modified due to practical reasons. Therefore, breeding distribution of 180 accipitrid species was scored as present/absent depending on the distribution pattern of the species in Nearctic, Palearctic, Neotropical, Afrotropical, Malagasy, Indomalayan, following the maps in Ferguson-Lees and Christie (2001). However, the distribution patterns of 72 *Turdus* species required the split of some realms into subregions, thus Nearctic, Mexican, Neotropical, West and East Palearctic, Afrotropical, Indomalayan, Australasian, and Antarctic (Figure 2).

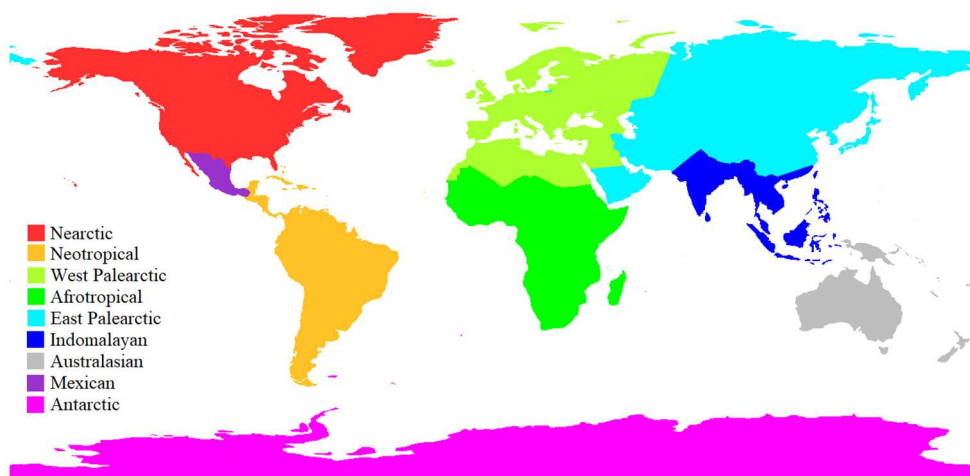


Figure 2. Biogeographic regionalisation used in the analyses. Colours correspond to those used to represent the results of the historical biogeographic estimations.

This classification serves as operative biogeographic units, and although it is based on Wallace’s biogeographic division, it is not identical to it. Because numerous species are exclusively or partially distributed in Mexico, the distinction of the Mexican region from the neighbouring realms is advisable. Moreover, because Australasian species were not present in the dataset due to the clear underrepresentation of the genus *Turdus*, this region was excluded from the analyses. Only *Turdus poliocephalus* is present in some islands of the Australasian and Indomalayan regions, however it is clustered into a mainly East Palearctic clade, thus its dispersal to these islands is more probable than the other direction.

Ancestral range estimations were performed using probabilistic historical biogeography methods in the ‘BioGeoBEARS’ package of R (Matzke 2013). The Dispersal-Vicariance (DIVA, Ronquist 1997), the Dispersal-Extinction-Cladogenesis (DEC, Ree et al. 2005, Ree and Smith 2008), and the BayArea model (Landis et al. 2013), paired each with founder-event speciation, were included and compared (Figure 3). For *Turdus* thrushes, the above approaches were complemented by a recently developed method, known as the biogeographical stochastic mapping (BSM, Matzke 2016), which was repeated 50 times on the model with the lowest Akaike Information Criterion (AIC) value. Although all three of the main biogeographic models can

basically deal with dispersal, extinction and narrow sympatry, in DIVA both narrow and widespread vicariance, in DEC subset sympatry and narrow vicariance, and in BayArea widespread sympatry are also allowed to be estimated.

		Ranges		Character mapping	DIVA	DEC (GeoSSE, LAGRANGE)	BayArea, BBM (RASPB)	Parameter of BioGeoBEARS Supermodel
		Before	After					
Anagenetic	Dispersal				✓	✓	✓	d (& x.b)
	Extinction				✓	✓	✓	e (& u.b)
	Range-switching			✓				a (& x.b)
Cladogenetic	Sympatry (narrow)			✓	✓	✓	✓	y (& ms0ly)
	Sympatry (widespread)						✓	y (& ms0ly)
	Sympatry (subset)					✓		s (& ms0ly)
	Vicariance (narrow)				✓	✓		v (& ms0ly)
	Vicariance (widespread)				✓			v (& ms0ly)
	Founder							j (& x, ms0lj)

Figure 3. Comparison of the three major biogeographic regions using the combinations of assumed processes. (Detailed summary and this figure are available at: <http://phylo.wikidot.com/biogeobears> - created by Nicolas J. Matzke.)

2.3. Comparative phylogenetic methods

Migratory behaviour was categorised as (1) non-migrant, (2) partial migrant, when part of the populations of a species perform seasonal movements and distinguishable breeding-only and year-round distribution areas can be delimited, and (3) complete migrant, when all of the populations of a species considered to be migrant and the presence of breeding-only and wintering-only areas in its distribution pattern are the typical (e.g. do Amaral et al. 2009). In correlated evolutionary analyses only binary categories could be used, thus the above three type of behaviour were re-coded as non-migratory and migratory, merging partial and complete migrants into the latter.

Importantly, because a significant proportion of *Turdus* species (17%) are frequently move on an East-West (along-latitudinal) axis, either being migratory or not, a new variable was scored 1 if the pattern is described in the literature for the species, and in any other cases it was assigned 0.

Average values for body mass of males and females measured in grams were used where both were accessible, otherwise data on the available sex was included to maximise the number of species in the analyses.

Flying skills inseparably depend on morphological parameters, in particular on the ratio of wing to tail as a metric of aerodynamic characteristics of birds which significantly affects the duration, length, or technique of flight during migration (e.g. Newton 2008). Therefore, based on the length of wing and tail in millimetres, eight categories were derived to measure body shape in Accipitriformes, calculating the direction of the deviation from the average length: (1) both wing and tail are shorter than average, (2) shorter wing and longer tail, (3) longer wing and longer tail, and (4) longer wing and shorter tail were assigned into the appropriate category identified for both small- and large-bodied species. The raw data for length of the body, wing, and bill (in relation to different food sources) were used in the case of *Turdus*.

Diet was a major factor in both groups. Main prey types of accipitrid raptors were listed into nine categories: (1) bird, (2) mammal, (3) reptile, (4) fish, (5) amphibian, (6) crustacean, (7) insect, (8) worm (invertebrate prey other than insects), and (9) carrion. Each category was assigned a score based on its share in the diet, whereas dietary breadth and reliance on warm-blooded prey or carcasses (the mean dietary score of mammals, birds, and carrion) were calculated for both breeding and non-breeding season (following e.g. Roulin and Wink 2004). In turn, thrushes are considered to be more omnivorous, however diet breadth was calculated for both seasons, similarly as described above, to measure differences in feeding behaviour (degree of omnivory). Furthermore for this group, change in food types between seasons was derived from the dissimilarity in main food types compared between the breeding and the non-breeding seasons. If this was the same in both seasons the score was 0 (means no changes) else 1.

Hunting behaviours of raptors were classified as hunting (1) in the air, (2) on the ground, or (3) by both ways. Habitat preference was classified as open habitat (grassland, savannah, and water surface) or closed (forest). Some more variables related to breeding phenology and ecology were used for thrushes, including the length of breeding season and the range of altitude.

2.3.1. Ancestral state estimation of traits

Bayesian ancestral state estimation was performed in BEAST (Drummond and Rambaut 2007) to infer the migratory behaviour at ancestral nodes in the phylogeny of birds of prey. Considering uncertainties in phylogenetic hypotheses, the Bayesian estimation is better than former methods. The outcome of this analysis indicates the probability of migratory or non-migratory states at each node, based on the trait values of its ancestor and descendants.

Evolutionary changes and ancestral states in migratory behaviour of thrushes were investigated by allowing the estimation of transition rates between non-migratory and migratory states. The ancestral state for the root (i.e. the ancient behaviour of the common ancestor of all *Turdus*) was estimated along the phylogeny using the maximum likelihood method. These types of analyses were done in the ‘MultiState’ module of BayesTraits 2.0 (Pagel et al. 2004), which software is suitable for estimating ancestral states and how discrete traits evolved on phylogenetic trees applying Bayesian approach with maximum likelihood estimation of parameters.

Furthermore, stochastic character mapping was applied to map migratory behaviour on the phylogeny of *Turdus*, simulated 1000 times in the ‘phytools’ package in R (Revell 2012). This analysis was done on the binary categorisation of migration, as well as on the partition of non-migratory, partial and complete migratory categories.

2.3.2. Analyses of correlated evolution

Correlated evolution between migration and one of the predictors was tested using ‘Discrete’ module of BayesTraits (Pagel et al. 2004, Pagel and Meade 2006). Applying this method, transition rates of correlated evolution can be estimated between a pair of traits on a phylogeny, also including the evaluation of directions that have significant information content for the evolution of migration. Because this approach can only be applied for binary traits, all of the explanatory variables were re-coded.

The distribution (tropical, non-tropical) and diet specialism (generalist, specialist) were included for birds of prey. Diet specialism was derived from diet breadth, hence a species is considered to be specialist if less than five prey types is consumed, otherwise it is generalist.

In the case of thrushes the following variables were included: (1) main food type in, and outside of the breeding seasons, (2) shift in food type between seasons, and (3) the ability to make movements along latitudes. Binary values were assigned to main food type (invertebrates, fruits/seeds), to difference in consumed food type between seasons (the same type, shift from insectivorous to herbivorous or vice versa), and to the ability of moving along latitudes (not typical, typical).

2.3.3. Models and model selection

A multivariate phylogenetic generalized linear mixed model implemented in the ‘MCMCglmm’ package in R (Hadfield and Nakagawa 2010) was used to determine the effects of body size, habitat type, diet breadth, reliance on warm-blooded prey, and the geographical location on migratory behaviour in accipitrid birds of prey. The interaction between habitat and geographical occurrence was also included to model the differences in habitat use among the species of Old versus New World.

Furthermore, in a second set of analyses, the multivariate phylogenetic generalized least squares (PGLS) approach was applied with Brownian motion fitting in the ‘nlme’ package in R (Pinheiro et al. 2015), including habitat, hunting strategy, clutch size,

dietary factors, wing-tail ratio, and body size dimorphism as predictors, to investigate the differences among migratory systems in raptors. A model selection procedure of the ‘MuMIn’ package in R was used to identify the most important variables (Bartón 2015), considering only those models which has small difference to the best model ($\Delta AIC < 4$). To filter out the strong impact of species’ distribution on migratory behaviour found after the first runs of model selection the dataset was split into three classes of migratory system: (1) species of North and South America ($N = 40$), (2) species of West Palearctic-Afrotropical migratory system ($N = 50$), and (3) species of East Palearctic-Indomalayan migratory system ($N = 33$).

Similar methods were used for *Turdus* thrushes with some changes listed below. The relationships between migratory behaviour and each explanatory variable were identified using PGLS approach. Moreover, this design is especially important to find factors that are associated with migration and which could be included in correlated evolutionary analyses described above. Data fit was tested through two model sets: (1) all pairwise models for species with all available variables ($N = 60$), and (2) omitting missing values per variable, where the number of included species varied between 66 and 72. Analyses were repeated on 100 different phylogenetic trees to check the effect of phylogenetic hypotheses.

Best-fitted λ values were generated from likelihood-profiles of λ (Kamilar and Cooper 2013) derived from 500 runs on randomly selected values between 0 and 1, in each PGLS run. Pagel’s λ (Pagel 1997, 1999) is a possible representation of phylogenetic signal (0 means that closer species on the phylogeny are not more similar than distant relatives, whilst 1 indicates dependency), which is a statistical measure of trait relatedness to phylogeny (Kamilar and Cooper 2013). To identify the degree of difference in models where λ was set to 0 and 1, likelihood ratio tests were applied.

Averaged λ , estimated value of parameters, standard error, t and p-values were calculated over the 100 runs, while the importance of explanatory variables was estimated by using model selection as described above. The strength of this design is sought in the identification of truly significant factors after permitting the variation of

the sample size, and calculating the average values of 100 runs that allows to control the effect of phylogenetic history.

2.4. Bioclimatic analyses

The bioclimatic variables have been made with the purpose of creating biologically more meaningful climatic information that indicate annual tendencies, seasonality, and limiting environmental factors (see the full list of variables and their calculation methods at <http://www.worldclim.org/bioclim>). Variables of ten arc-minute resolution were used, and first correlations among variables were calculated to avoid confounding results (Hijmans 2015) where clusters were built based on Pearson's correlation coefficient. Uncorrelated variables (on separated branches with a preference for quarters) were included into computer learning maximum entropy modelling implemented in Maxent 3.3 (Phillips and Dudík 2008).

By this way, temperature seasonality, mean temperature of driest quarter, mean temperature of warmest quarter, precipitation seasonality, and precipitation of driest quarter were selected as predictors for 110 species in Accipitriformes. Similarly, isothermality, temperature seasonality, mean temperature of driest quarter, mean temperature of warmest quarter, annual precipitation, precipitation seasonality, precipitation of driest quarter, and precipitation of warmest quarter were used for 71 *Turdus* species. *Turdus daguae* was excluded from the bioclimatic analyses due to its consideration as subspecies of *Turdus albicollis* and consequently the inaccurate determination of its distribution pattern. Furthermore, the calculation could not be performed for *Nesocichla eremita*, *T. bewsheri*, *T. helleri*, and *T. olivaceofuscus* because of the extremely small distribution of these species where MaxEnt was not able to be trained.

Coordinates were sampled from distribution shape files of migratory species (BirdLife International 2015). Coordinates from the distribution of each species were randomly pinned based on the proportion of breeding range size of species compared to the largest range. One thousand points from the largest range, and proportionally less

from the others were selected. All runs were replicated five times by cross-validation and the projections were extended for the whole distribution of species, including both wintering and year-round areas where those were applicable.

3. Results

In this chapter, I briefly summarise my formerly published finding regarding the phylogeny and the evolution of migration of raptors and thrushes, and I also provide the results of two new analyses that have not been published yet: (1) a comprehensive phylogenetic reconstruction of 155 species from the Turdidae family and (2) some bioclimatic analyses of *Turdus* thrushes complement the previous results.

3.1. Evolutionary origin of migration in birds of prey

The identification of temporal and spatial origin of migration requires the reconstruction of phylogenetic relationships among lineages possibly with dating and the estimation of ancestral biogeographic regions of the group in interest. In the following subsections I collected the results of the ancestral area estimation, migratory trait reconstruction and evolutionary analyses of migration in accipitrid raptors based on our previously published papers (Nagy and Tökölyi 2014, Nagy et al. 2017).

3.1.1. *Phylogeny of accipitrid birds of prey*

The crown Accipitriformes, i.e. the split between the secretarybird (Sagitariidae) and the rest of the raptor species was found to have occurred around 57-37 Mya, during the Eocene. The second oldest descent of the osprey (Pandionidae) out the rest of the group is estimated to have originated 50-37 Mya. The two earliest branches within the core Accipitridae resulted in the appearance of elanid kites (Elaninae) between 45-29 Mya and the group including Gypaetinae and Perninae around 35-23 Mya. All of the major lineages according the aforementioned studies are been identified here with an accelerated diversification rate from the Miocene to recent times (Figure 4).



3.1.2. Historical biogeography and the origin of migration

Based on the best supported biogeographic model (DEC with founder-event speciation) a southern origin was inferred for all raptor subfamilies. According to these analyses, Accipitrinae, Aegypiinae and Gypaetinae have an Afrotropical origin, whereas Elaninae and Perninae derive from the Neotropics. The ancestors of Buteoninae and Harpiinae had a joint Afrotropical/Neotropical distribution, whilst Aquilinae have an Afrotropical/Neotropical and Indomalayan origin, although the probabilities of these latter results are low (<0.3). Circeatinae were assigned to the Indomalayan region with relatively high probability. Lastly, the most likely ancestral distribution of Haliaeetinae was located in Australasia (Table 3, Figure 5).

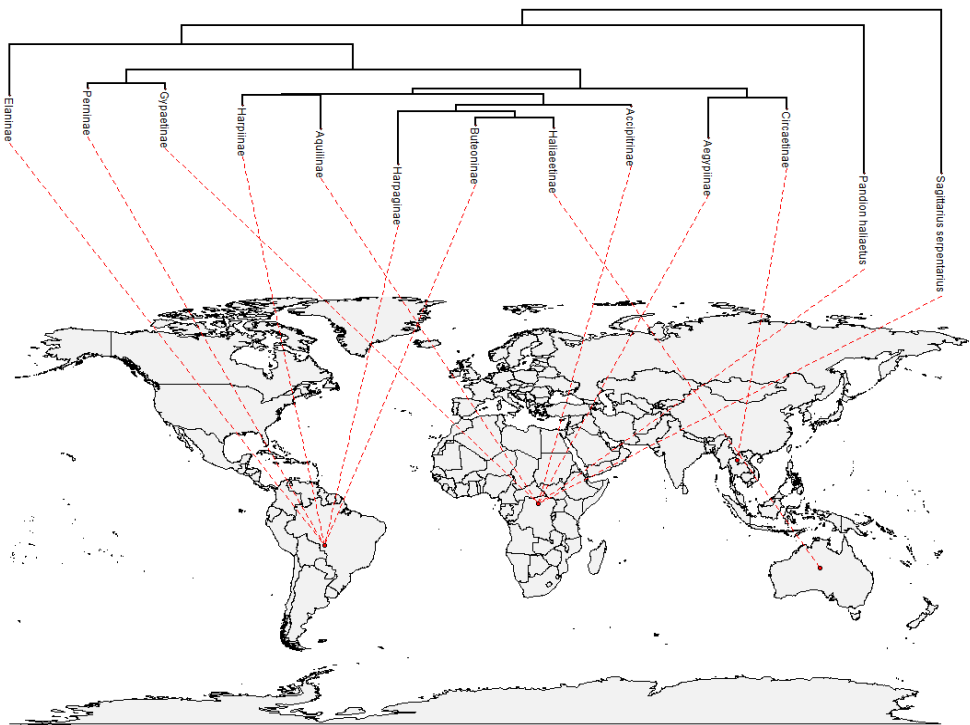


Figure 5. Mapped phylogeny of Accipitriformes, indicating the most probable ancestral area of each subfamily.

The estimation of ancient behavioural showed multiple independent origin of migratory behaviour in Accipitriformes. Taking the *Buteo* hawks, *Accipiter* hawks, or *Haliaeetus* eagles as examples, each group constitute of closely related species that are

mainly migratory, consequently the most likely state for the ancestor of these species is being migratory. However, most of these independent events concern a single species, thus the appearance of migration is limited to the split off from its ancestor. Hence, migration could have evolved in these lineages recently, beginning during the Early Pliocene. Moreover, the oldest among the nodes that are undoubtedly estimated as migratory, the ancestor of the goshawk (*Accipiter gentilis*) and the harriers (*Circus* spp.), is aged to around 16-10 Mya.

Table 3. Geographic origin of subfamilies in Accipitriformes based on the best fitting biogeographic model (DEC+J).

Subfamily	Genera	Age (Mya - interval)	Ancestral distribution	Probability
Accipitrinae	Accipiter, Circus, Kaupifalco, Melierax, Urotriorchis	23.0; 15.1	Afrotropical	0.79
Aegyptiinae	Aegyptius, Gyps, Necrosyrtes, Sarcogyps, Torgos, Trionoceph	12.6; 7.4	Afrotropical	0.78
Aquilinae	Aquila, Hieraaetus, Ictinaetus, Lophaelix, Nisaetus, Oroaetus, Polemaetus, Spizaetus, Spizastur, Stephanoaetus	15.4; 9.8	Neotropical / Afrotropical / Indomalayan	0.26
Buteoninae	Busarellus, Butastur, Buteo, Buteogallus, Geranoaetus, Geranospiza, Harpyhaliaetus, Ictinia, Leucopternis, Parabuteo, Rostrhamus	16.7; 10.3	Neotropical / Afrotropical	0.24
Circaetinae	Circaetus, Dryotriorchis, Pithecophaga, Spilornis, Terathopius	22.5; 13.8	Indomalayan	0.87
Elaninae	Elanus, Gampsonyx	29.4; 14.4	Neotropical	0.15
Gypaetinae	Gypaetus, Gypohierax, Neophron, Polyboroides	29.0; 18.5	Afrotropical	0.99
Haliaeetinae	Haliaeetus, Haliastur, Ichthyophaga, Milvus	15.7; 9.8	Australasian	0.30
Harpiinae	Harpia, Harpyopsis, Macheiramphus, Morphnus	24.4; 13.6	Neotropical / Afrotropical	0.20
Perninae	Aviceda, Chondrohierax, Elanoides, Eutriorchis, Hamirostra, Leptodon, Lophoictinia, Pernis	29.4; 18.7	Neotropical	0.15

Evolutionary analysis revealed that both complete and partial migration evolved from a non-migratory state suggesting that partial migration is not an intermediate state between complete migration and the lack of migration (Figure 6).

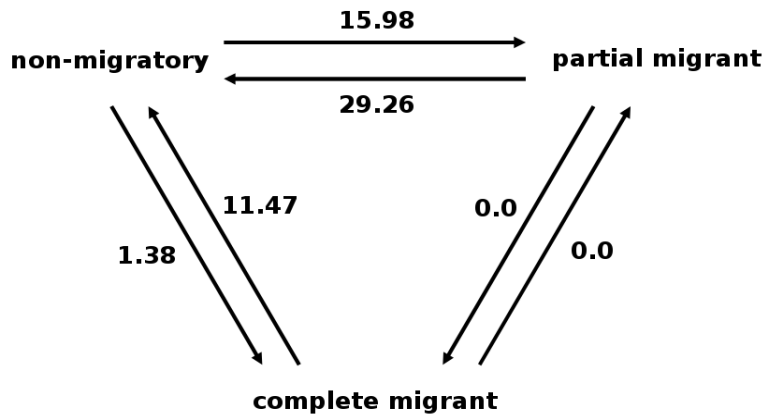


Figure 6. Evolutionary transition rates among levels of migratory behaviour in accipitrid birds of prey.

Finally, tropical origin of migratory species is broadly supported due to the inference of tropical or partly tropical ancestral area for most of the migratory lineages. Few exceptions differ from this pattern, for instance *Aquila heliaca* and *A. nipalensis* evolved within the Palearctic from non-migratory ancestors. Similarly, *Buteo platypterus* and *B. nitidus* seem to have originated in the Nearctic from non-migratory ancestors, although the posterior support for the phylogenetic reconstruction is low.

3.1.3. Bioclimatic effects on migration in different migratory systems

Maximum entropy modelling allowed the prediction of the wintering ranges of migratory raptor species based on the breeding distribution where the presence of the species is confirmed or highly probable. Wintering regions for migratory species are at least as suitable for survival as their breeding ranges, i.e. species seek to find areas with similar level of climatic limitations.

Environmental variables related to temperature are the most important limiting factors for 12 of the 17 long-distance migratory accipitrid raptors, and for a total of 70 species among all. Highest values were gained for temperature seasonality, mean

temperature of driest quarter and precipitation of driest quarter among Palearctic migrants, and for mean temperature of warmest quarter, precipitation seasonality among Nearctic migratory species which indicate differences between these migratory systems. Furthermore, bioclimatic limitation is one of the major factors in the East Palearctic-Indomalayan migratory system (see Table A1 and Figure A1 in the Appendix).

3.1.4. Migration and life history traits in raptors

The first set of multivariate analyses of the ecological factors influencing migration suggests that winter diet specialisation and habitat are associated with migration: (1) species with generalist winter diet, and (2) in connection with open habitats are more likely to be migratory. Additionally, directional tests of migratory behaviour paired with geographic distribution and diet breadth were performed (Figure 7). According to these analyses, migration appeared with a higher rate in lineages with a tropical distribution and transitions to a non-tropical distribution are more likely in migratory than in non-migratory lineages (see e.g. the genera of *Buteo*, *Accipiter*, *Circus*, *Hieraaetus*, *Elanus*, *Circaetus*). Switches in the geographic distribution from a tropical to a non-tropical distribution or vice versa in non-migratory lineages are lacking, whilst they are relatively common among migrants. Furthermore, migration more likely arises in specialist lineages than in generalists, and a generalist diet is more likely to have evolved in migrants than in non-migrants. Hence, it appears that a wider range of diet is an evolutionary response to the selective environments imposed by migratoriness, rather than predisposing species for migration.

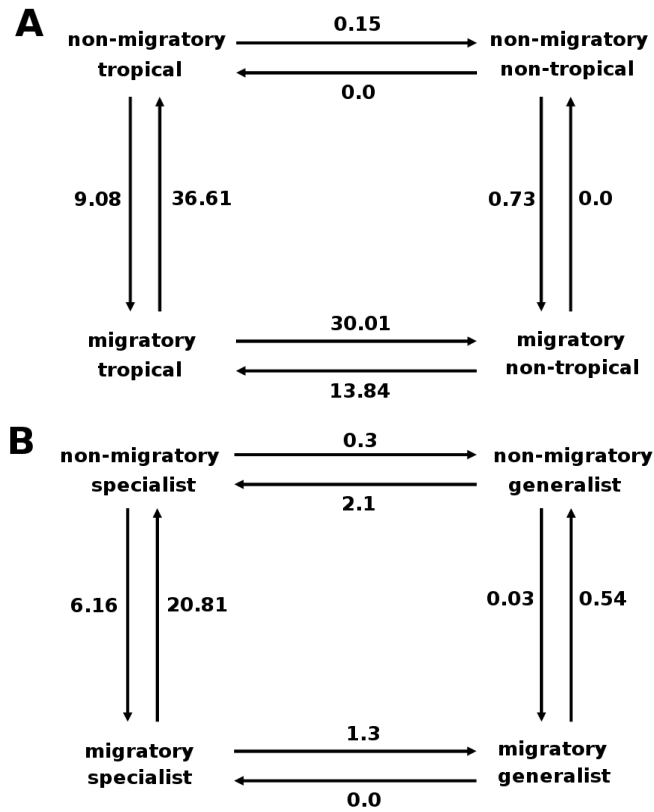


Figure 7. Transition rates from correlated evolutionary tests between migratory behaviour and (A) geographic distribution, (B) diet specificity in raptors.

However, in a second set of analysis, distribution, either categorised species on a continental level or classified them into tropical/non-tropical or both regions, has masked the effect of the other variables. Therefore, separating the species into migratory systems was justified. The highly significant variables in the models selected for North and South America and West Palearctic-Afrotropical regions are clutch size and hunting strategy with high importance. Parameter estimates for clutch size were similar, however hunting strategy was positively correlated with migration for North and South America, whereas it was negative for West Palearctic-Afrotropic. Reliance on warm-blooded prey or carcasses was significant only in the set of Nearctic-Neotropic, but with a low importance. For East Palearctic-Indomalayan regions when bioclimate (as categorical variable) was included in the model selection procedure strongly supported differences were found in clutch size with a high importance level for both factors.

Figure 8. Phylogeny of 155 species in Turdidae, first published here.

3.2. Phylogeny, migration and biogeography of *Turdus* Thrushes

Considering the aforementioned taxonomical uncertainties the use of *Turdus* (s.l.) as a model system including *Nesocichla eremita* and *Psophocichla litsitsirupa* was straightforward. The results are presented following Nagy et al. (2019). Furthermore, I provide bioclimatic estimation for environmental limitation in *Turdus* species and a detailed phylogenetic analysis of Turdidae (first published here, Figure 8) to identify future research directions.

3.2.1. Phylogeny of the Turdidae

The two monophyletic groups following the current naming of species are the *Catharus*, with uniquely high posterior probabilities and the three species of *Sialia*. The majority of *Turdus* with relatively well-supported nodes form the youngest clade within the family including *Nesocichla eremita* and *Psophocichla litsitsirupa*, however five species (*T. rufopalliatu*s, *T. maranonicus*, *T. lawrencii*, *T. subalaris*, *T. hauxwelli*) clustered within *Myadestes*, which group has lower posterior probabilities. Therefore, *Turdus* is polyphyletic and *Myadestes* is paraphyletic. However, reconsidering the taxonomic position of the above five species could prove or refuse the monophyly of *Turdus*. Moreover, one of the earliest divergence of Turdidae contains mainly the genera of *Alethe*, *Myophonus* and *Brachypteryx*, and together with two other species (*Chamaetylas fuelleborni*, *Heinrichia calligyna*) they form a monophyletic clade (Figure A2 in the Appendix).

The two most problematic genera are represented by the *Zoothera* and *Geokichla*. Most of the species formerly classified as *Geokichla* are referred to as *Zoothera* in some sources, but it seems to be debatable. The type species of *Zoothera*, however, is the long-billed thrush (*Zoothera monticola*, Vigors 1832, Proc. Zool. Soc. London). The clade containing this species is more closely related to the group including *Catharus*, hence the true *Zoothera* is considered to be monophyletic (Figure A2 in the Appendix). The species in the other group of *Zoothera* that contains the former *Geokichla* spp.

should be transferred to *Geokichla*, which is also presumably monophyletic as the sister to *Turdus* (Table 4).

Table 4. Species suggested for nomenclature revision. Names indicated in bold are also considered as *Geokichla* in Voelker and Outlaw (2008).

Current name*	Suggested name	Suggested genus	Related to
<i>Zoothera guttata</i>	<i>Geokichla guttata</i>		
<i>Zoothera schistacea</i>	<i>Geokichla schistacea</i>		
<i>Zoothera dohertyi</i>	<i>Geokichla dohertyi</i>		
<i>Zoothera interpres</i>	<i>Geokichla interpres</i>		
<i>Zoothera peronii</i>	<i>Geokichla peronii</i>		
<i>Zoothera cinerea</i>	<i>Geokichla cinerea</i>		
<i>Zoothera erythronota</i>	<i>Geokichla erythronota</i>		
<i>Zoothera mendeni</i>	<i>Geokichla mendeni</i>		
<i>Zoothera citrina</i>	<i>Geokichla citrina</i>		
<i>Zoothera princei</i>	<i>Geokichla princei</i>	<i>Geokichla</i> ¹	<i>Turdus</i>
<i>Zoothera camaronensis</i>	<i>Geokichla camaronensis</i>		
<i>Zoothera piaggiae</i>	<i>Geokichla piaggiae</i>		
<i>Zoothera tanganjicae</i>	<i>Geokichla tanganjicae</i>		
<i>Zoothera oberlaenderi</i>	<i>Geokichla oberlaenderi</i>		
<i>Zoothera gurneyi</i>	<i>Geokichla gurneyi</i>		
<i>Zoothera wardii</i>	<i>Geokichla wardii</i>		
<i>Zoothera crossleyi</i>	<i>Geokichla crossleyi</i>		
<i>Zoothera spiloptera</i>	<i>Geokichla spiloptera</i>		
<i>Zoothera sibirica</i>	<i>Geokichla sibirica</i>		
<i>Zoothera mollissima</i>			
<i>Zoothera dixonii</i>			
<i>Zoothera andromedae</i>			
<i>Zoothera dauma</i>			
<i>Zoothera lunulata</i>			
<i>Zoothera heinei</i>		<i>Zoothera</i> ¹	<i>Catharus</i>
<i>Zoothera everetti</i>			and allies ¹
<i>Zoothera talaseae</i>			
<i>Zoothera marginata</i>			
<i>Zoothera monticola</i>			
<i>Zoothera margaretae</i>			
<i>Zoothera heinrichi</i>			
<i>Chlamydochaera jefferyi</i>	<i>Cochoa jefferyi</i>		<i>Zoothera</i>
<i>Cochoa viridis</i>		<i>Cochoa</i> ¹	+
<i>Cochoa purpurea</i>			<i>Catharus</i>
<i>Zoothera naevia</i>	<i>Ixoreus naevius</i>		Included in:
<i>Zoothera pinicola</i>	<i>Ridgwayia pinicola</i>		<i>Catharus</i> clade ¹
<i>Grandala coelicolor</i>	<i>Sialia coelicolor</i>		

¹ These clades have > 0.99 posterior probabilities on the phylogeny published here.

* These names are used in some sources, e.g. Jetz et al. (2012), GenBank.

Nevertheless, the low posterior probabilities could be the result of the underrepresentation of available genetic sequences of the concerned species (Table A2). For example, most of the *Zoothera* spp. have just a few records or some species have short sequences (e.g. *Turdus iliacus*, *Hylocichla mustelina*). Further molecular genetic determination of these species could improve the accuracy of the similar phylogenetic reconstructions.

3.2.2. Biogeographic history of *Turdus* radiation

According to the best fitting biogeographic model (DEC with founder-event speciation), the possible ancestral regions for all *Turdus* species are located in East Palearctic and/or Afrotropical realms (Figure A5 in the Appendix). The two earliest clades containing *Turdus mupinensis* and *Psophocichla litsitsirupa* as well as *T. viscivorus* and *T. philomelos* suggest very early dispersal from South-east Asia to Europe and Africa, or eventually vice versa (Figure 9).

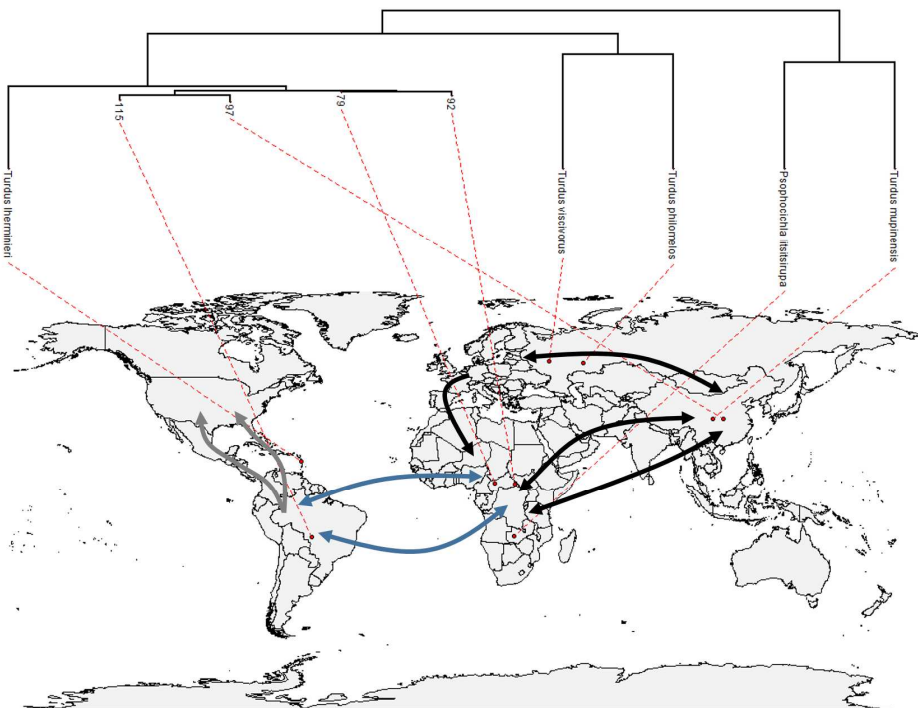


Figure 9. Mapped phylogeny of *Turdus* thrushes, indicating major dispersal routes during their early evolution.

Nevertheless, the common ancestor of 68 species is assumed to be of Afrotropical/Neotropical ancestral origin, which suggest multiple trans-Atlantic movements starting from the Middle Miocene to recent times, as the examples of *T. lherminieri*, *T. plebejus*, and *Nesocichla eremita* show. The colonisation of Mexico and North America occurred in five independent lineages from the direction of South America within the past 6-2 Mya.

The summary of fifty biogeographical stochastic mappings also supports the result of the best fitting model (Figure A6 in the Appendix). The estimated speciation events including the possible processes are dominated by sympatry, anagenetic dispersal events, founder event speciation, and vicariance, in a descending order.

3.2.3. The evolution of migration, life history traits and bioclimate

Out of the studied 72 *Turdus* species, 17 species is migratory. The results indicate that migration emerged as an ancestral behaviour in an early phase of the evolution of this group (Figure 10). Transition rates among states also confirm this finding due to the loss of migration in multiple times. Furthermore, in *Turdus*, complete migration could only have evolved or lost via partial migration.

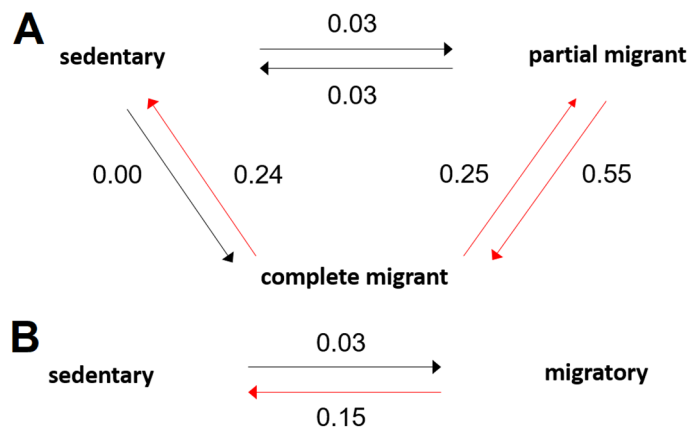


Figure 10. Evolutionary transition rates among levels of migratory behaviour in *Turdus* thrushes: (A) three-level estimation, (B) two-level estimation.

Based on the resulted values for 100 different phylogenies in PGLS analyses, it can be concluded that tree structure has no effect on the models output. The estimated λ values show moderate level of phylogenetic signal in many cases where likelihood ratio test reveals significant differences from pre-set λ values. This implies that migratory behaviour and the related traits probably evolved more dependently than independently among the lineages of *Turdus* thrushes.

Five out of the variables of substantial support were highly significant. Migratory behaviour is more frequent in non-tropical species compared to those that breed in both climatic belts, and less frequent in tropical species than in species with breeding areas located in both tropical and non-tropical regions. Clutch size is higher in migratory species which could imply shifts of main food type between breeding and non-breeding seasons. The important factors relevant to migration indicate that migratory species tend to be more mobile (rarities, i.e. frequently seen outside their distribution ranges), and most of them frequently move along-latitudinal (East-West) axis.

Correlated evolution between migration and the ability of along-latitudinal movements show that appearance and disappearance of East-West movements could have frequently changed on migratory lineages, but the loss of this trait is most frequent in sedentary lineages (Figure 11).

Based on the analysis of migration and main food type during the breeding season, transition rates show that the emergence of sedentariness could be more frequent than the evolution of migratory behaviour in herbivorous lineages. Additionally, a shift in the main food type from fruits/seeds to invertebrates is moderately typical of non-migratory lineages, however, analysis based on the main food type during non-breeding season shows that the transition from fruits/seeds to invertebrates likely has a higher rate in migratory lineages, than vice versa. The rates of changes in migratory behaviour on herbivorous lineages are likely to represent corresponding transitions in the main food type in the breeding season, however with a substantially lower value (Figure 11).

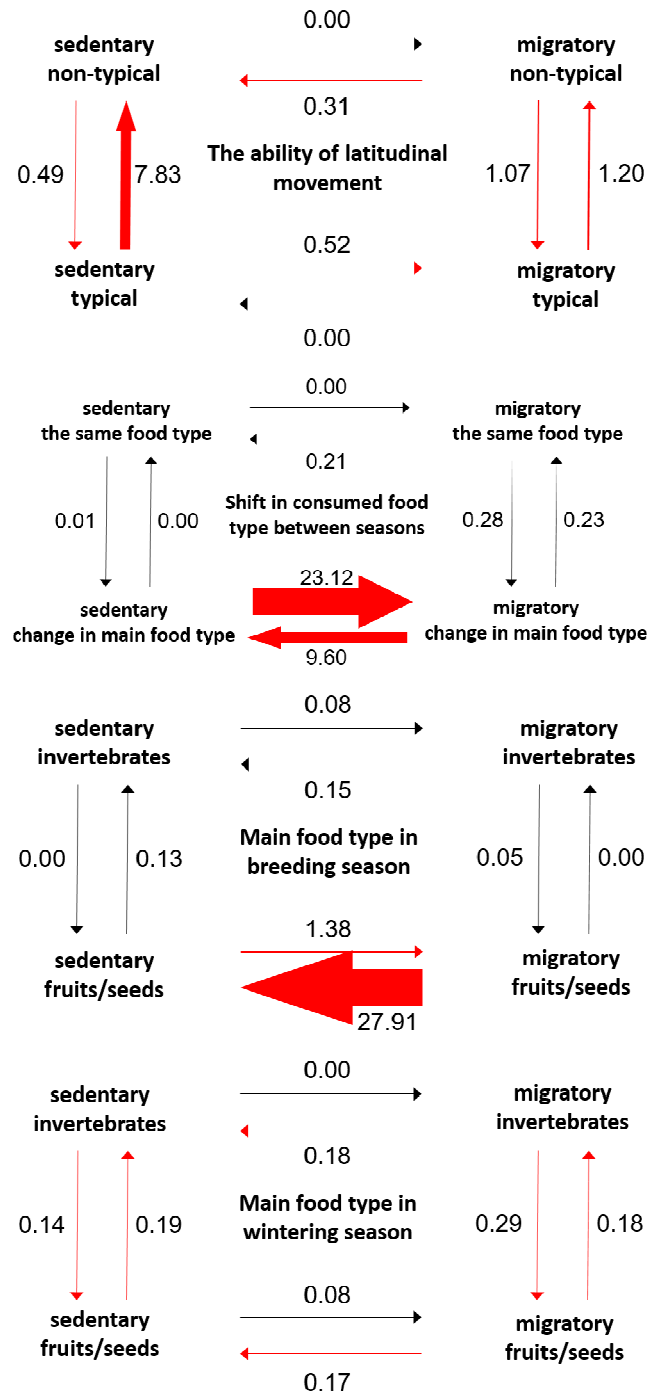


Figure 11. Results of correlated evolutionary analyses between migratory behaviour and predictor variables in *Turdus*.

Analysis of migration and the shift in main food type between seasons demonstrates that change in main food type is highly associated with changes in migratory behaviour. Hence, migration could appear more frequently in lineages with the ability to frequently change food sources. Furthermore, transition rates show a shift in diet from consumption of the same food type in both seasons to the frequent alternation between herbivorous and insectivorous behaviour in migratory lineages where inversion has also similar rate.

Bioclimatic limitation among 67 *Turdus* species is dominated by temperature related factors (N = 39). Temperature seasonality, mean temperature of the warmest quarter, precipitation of the driest quarter and precipitation of the warmest quarter showed the highest importance values, drawing attention to recent climatic changes, which may be even more significant in species having small distribution areas. However, among migratory species the proportion of temperature related variables is 9/17, which indicates that temperature or precipitation could equally determine the suitable areas for both breeding and wintering within this group (Table A3 and Figure A4 in the Appendix).

4. Discussion

In this chapter, I discuss the most comprehensive phylogeny of Accipitriformes to date. My findings provide the first evidence of the probable southern (Paleotropical) origin of this group of raptors completed with the most probable evolutionary origin of migratory behaviour. Although differences among geographically identified migratory systems have been detected previously (e.g. Newton 2008), our papers (Nagy and Tökölyi 2014, Nagy et al. 2017) were the first to find substantial dissimilarities among geographic regions in migratory behaviour in relation to life history traits and climatic conditions.

Furthermore, the broadest phylogenetic inference for the relationships of the genera within the Turdidae family is first published here supporting the need for thorough taxonomic revisions and suggesting further molecular phylogenetic considerations. Moreover, the most comprehensive historical biogeographic estimation and the evolution of migration in *Turdus* is also discussed in this chapter (Nagy et al. 2019).

4.1. Phylogeny, historical biogeography and migratory systems in raptors

All available genetic information was combined to produce a multi-gene phylogeny of Accipitriformes including approximately two-third of extant species. The phylogenetic hypothesis obtained from this analysis supports previous reports (e.g. Wink and Sauer-Gürth 2004, Helbig et al. 2005, Lerner and Mindell 2005, Griffiths et al. 2007, do Amaral et al. 2009), showing that several traditionally established subfamilies (e.g. Aegypiinae, Buteoninae, Aquilinae, Accipitrinae) are in fact polyphyletic or paraphyletic.

For instance, Old World vultures form a polyphyletic clade containing: (1) Gypaetinae which is monophyletic with Perninae and includes the bearded vulture (*Gypaetus barbatus*) and the Egyptian vulture (*Neophron percnopterus*) and (2)

Aegypiinae which comprises all remaining Old World vultures and is the sister clade of Circaetinae. Accipiter hawks are paraphyletic and should include harriers (*Circus* spp.), which are closely related to the clade containing goshawks (see also Pathak 2018 and the references therein). In addition, widespread paraphyly is observed in aquiline eagles and buteonine hawks, similarly to previous studies (Helbig et al. 2005, do Amaral et al. 2009).

Otherwise, several differences were found in the higher level relationships of Accipitridae compared to previous works (e.g. Lerner and Mindell 2005, Griffiths et al. 2007). Aquilinae and Harpiinae are sister clades, however with a moderate support (posterior probability: 0.45). *Harpagus* kites are inferred as the sister group of the clade containing Buteoninae and Haliaeetinae with relatively high support (0.83). Finally, the sister relationship between the clade including Aquilinae and Harpiinae on one side and the superclade of Buteoninae, Haliaeetinae and Accipitrinae on the other is strongly supported (1.0).

Ancestral state reconstruction applied on the above discussed phylogenetic hypothesis suggests that migratory behaviour evolved multiple times among accipitrid birds of prey. Most of these events probably occurred during the Pliocene or Pleistocene, i.e. within 5 Mya. By comparison, do Amaral et al. (2009) reconstructed the origin of migration in one *Buteo* clade at approximately 5 Mya which is supported by these findings. Nevertheless, in true hawks (Accipitrinae), migration appears to be more ancient behaviour and has evolved approximately 14-12 Mya, during the Middle/Late Miocene (Nagy and Tökölyi 2014). More direct estimates based on the age distribution of fossilized individuals found at Olduvai Gorge, in Tanzania, suggest that this location served as wintering site for shorebirds belonging to Scolopacidae and Charadriidae 1.9-1.74 Mya, implying that migration was present at this time (Louchart 2008 and the references therein). Hence, the origin of migration in accipitrid hawks appears to be one of the oldest dates published so far. Similar estimates are important if we want to understand the evolution of migration in a constantly changing spatiotemporal context at a global scale (Louchart 2008).

During the Late Miocene, the Earth's climate had globally cooled (Zachos et al. 2001), which resulted in the expansion of grasslands and contraction of forest habitats, e.g. the shift of habitat zones in Africa, possibly opening new spaces of niche segregation for predatory birds (Brown 1976, Bobe and Behrensmeyer 2004, Bonnefille 2010). The analyses suggest that accipitrid hawks appeared shortly before this period, probably in the Afrotropical realm and colonised the whole world rapidly thereafter. Since most extant species belonging to this lineage are at least partly migratory today, it is likely that their ancestor also performed seasonal migratory movements (Nagy and Tökölyi 2014). Alternatively, migration could have evolved separately in these lineages due to similar selective environments (i.e. as a consequence of convergent evolution rather than shared phylogenetic background).

Migration is a phylogenetically instable trait that can evolve very quickly (see e.g. Zink 2011), independent evolution in multiple lineages in similarly selective environments is a plausible explanation for the occurrence of migratory behaviour in closely related species. However, this is clearly less parsimonious in explaining the evolution of migration in true hawks, because this group contains both temperate-tropical and intra-tropical migrants on different continents, which would imply simultaneous, independent selection for migration in a wide variety of environments on different parts of the world.

The estimation of historical biogeography and ancestral migratory behaviour suggests that in raptors migration appeared mostly in species of southern origin, possibly independently in different geographical migratory systems (do Amaral et al. 2009, Nagy and Tökölyi 2014, Nagy et al. 2017). This is further strengthened by directional analyses which suggest that migration is more likely to evolve in tropical species and that migratory raptors are more likely to switch to a non-tropical breeding range. Therefore, parallel evolution of migratory behaviour and range expansions is highly suggested. Interestingly, the transition rate from a tropical to non-tropical distribution (and vice versa) is very low in non-migratory lineages, but not in migrants, implying that range expansions were greatly intensified by migration in raptors.

The tropical (southern) origin of migratory raptors is in line with the results of previous studies in a variety of taxonomic groups (e.g. Joseph et al. 1999, Outlaw et al. 2003, Milá et al. 2006). The origin of all major lineages within Accipitridae can be traced back to one of the southern biogeographic realms of Gondwanian origin. Hence, both migratory and non-migratory species currently inhabiting the temperate zone descend from the tropics. According to the findings, migration is more likely to emerge in the tropics than in the temperate zone. Migratory raptors are more likely to disperse and switch from a tropical distribution to a non-tropical one. Therefore, the relationship between the colonisation of the temperate zone and the evolution of migration could be the reverse of what is assumed (the lack of forested habitats in North Africa act as a dispersal barrier, effectively filtering range expansions from South, Rappole and Jones 2003), i.e. migratory birds more likely to colonise novel habitats and expand their distributions to North. Since all accipitrid birds of prey have tropical origin, their ancestors should have undergone range expansions to the temperate regions considering that some of the species (but not necessarily all) became migratory.

The results also indicate that winter diet specialisation, under different pressure e.g. in West and East Palearctic, predicts the occurrence of migration in accipitrid birds of prey, with migratory species relying on more variable diet. The ability to feed on different food types could increase rate of survival in the temperate zone where food availability is much lower during the winter (Newton 2008). This could partly explain interspecific differences in migratoriness. Interestingly, the association between migration and reliance on warm-blooded prey or carcass was only weakly significant in species filtered to the New World, suggesting that these food sources alone might not be enough to sustain most species in the temperate zone during winter. For instance, two of the four vulture species that occur in Europe (*Gyps fulvus*, *Neophron percnopterus*) are migratory, despite the fact that their major food source (carcass) is most likely available during the whole year. However, the availability of carcasses might also show seasonal fluctuations (e.g. Kendall et al. 2012).

Furthermore, the results show for raptors that clutch sizes are larger in migratory species than in residents (more examples for wider taxonomic range in Martin 1995,

Jahn and Cueto 2012, Barve and Mason 2015) in each of the three migratory systems (Nagy et al. 2017). Increase in clutch size could be a consequence of the compensation against higher mortality during migration (see e.g. Ketterson and Nolan 1982, Rappole et al. 1989, Bell 1996, Alerstam et al. 2003). For instance, Schmutz and Fyfe (1987) found that numerous migratory ferruginous hawks (*Buteo regalis*) did not survive their first year. The hazards of migration were also emphasized in Klaassen et al. (2014) where they demonstrated that mortality during migration is six times higher than in other times of the year. However, uncovering other direct and indirect factors underlying the correlation between the higher clutch size and migratory behaviour, such as food predictability, environmental seasonality, require further investigations.

Additionally, the success of raising young depends on the level of success by different hunting and feeding strategies. More successful hunters are expected to provide more prey items and/or in better quality to feed the young. For example, McDonald et al. (2004) showed that larger female brown falcons (*Falco berigora*), having higher wing–tail ratios exhibited higher reproductive success. Thus, increased breeding performance may induce enhanced preference for migratory behaviours due to more effective hunting (birds with higher level of flying skills can be predicted as more successful hunters) during the migratory route and on the wintering grounds under different climatic conditions. Nevertheless, these findings support the idea that seasonal climate may be related to the increased cost of breeding under unpredictable environmental conditions (Jetz and Rubenstein 2011, Rice et al. 2013, Thomson et al. 2014, Rubenstein 2015).

Moreover, the importance of different prey classes in predicting hunting strategies for different distribution areas is supported here. Previous studies have detected morphological adaptations to a wide variety of prey (e.g. Rutz et al. 2006, Hertel et al. 2014) among different groups of raptors (Fowler et al. 2009, Sustaita and Hertel 2010). For instance, the results of Otterbeck et al. (2015) imply beneficial effects of prey specialisation, as pairs of Eurasian sparrowhawks (*Accipiter nisus*) were able to raise more young related to higher constancy in prey size, which indirectly enhance higher

success in hunting behaviour. A study on northern goshawks (*Accipiter gentilis*) also showed similar results (Pérez-Camacho et al. 2015).

Hunting behaviour is substantially different for birds of prey between the migratory systems of the New World and West Palearctic/Africa (Ferguson-Lees and Christie 2001). These strategies are associated with resource partitioning and niche segregation among raptors with overlapping ranges (Brown 1976, Gamauf et al. 1998, Piana 2013). Specifically, wintering areas in Africa include mainly open lands such as savannahs, whereas the majority of South America is forested. Therefore, most of West Palearctic-African migratory raptors inhabit open/semi-open landscapes, whereas a larger proportion of the Nearctic-Neotropic migrants are connected to woody landscapes (e.g. *Circus*, *Buteo* spp., respectively, do Amaral et al. 2009, BirdLife International 2015). Such variation may lead to differences in hunting strategies. For example, Terraube et al. (2014) found that foraging on diverse diet was related to higher hunting success in migratory Montagu's harriers (*Circus pygargus*).

The results of maximum entropy modelling suggest that climatic limitations experienced on the wintering grounds make those areas for migratory species equally suitable as their breeding ranges (see also Zurell et al. 2018). This partly explains why species overwinter in Africa, while others regularly migrate to South-East Asia, often from areas outside of assumptions (e.g. *Aquila clanga*, *A. nipalensis*, and other diurnal raptors such as *Falco amurensis*, *F. vespertinus*).

Significant results obtained for East Palearctic-Indomalayan species highly supported that breeding and wintering areas of these species are not separated by geographical and consequently strict ecological barriers (Greenberg et al. 2008, Germei et al. 2009, but see also Polakowski et al. 2014). The continuity of habitats equally enhances the development of short- and long-distance migratory strategies, as predicted by the maximum entropy modelling. In comparison, breeding and wintering areas are prominently separated by barriers both in the New World and in West Palearctic/Africa. The Mexican Plateau, the Gulf of Mexico, and the Caribbean Sea serve as barriers for migratory species in Central America, similarly the Mediterranean Sea and the Sahara are barriers for migrating birds from the Western Palearctic to Africa. In a study of

satellite-tracked raptors, Strandberg et al. (2009) summarized the difficulties of birds crossing the Sahara and found similarly high mortality rate for migratory juveniles as in previous studies (e.g. Schmutz and Fyfe 1987).

Nevertheless, these findings are applicable on wider taxonomical scales, as the importance of hunting and reproductive strategies in modulating distribution ranges is predictable for migratory predatory birds. For example, European populations of the insectivorous Eurasian scops owls (*Otus scops*) migrate to Africa across the Sahara, while a related species, the oriental scops owl (*Otus sunia*) has continuous breeding and wintering areas in South-East Asia (König and Weick 2008, BirdLife International 2015). In Falconiformes, the other diurnal group of raptors, vicariant and migratory species show remarkable geographical segregations. Although this order is phylogenetically not closely related to Accipitriformes (e.g. Jarvis et al. 2014, Mahmood et al. 2014, Prum et al. 2015, Cenizo et al. 2016), they share similar ecological and morphological characteristics. For instance, red-footed falcons (*F. vespertinus*) breed in the West Palearctic and winter in Africa, whereas their sister and vicariant species, the amur falcons (*F. amurensis*) inhabit the East Palearctic and also winter in Africa. This might be a result of parallel evolutionary histories of the two species because both are insectivorous and connected to relatively open habitats. Although habitat, migration, and diversification rate of falcons are highly associated, the splits among falconid taxa are frequently younger than the estimated ancestral migratory behaviour (Fuchs et al. 2015).

In summary, (1) migratory behaviour in raptor lineages could be emerged either as an ancestral behaviour or a recent adaptation, (2) the dominant differences between the three migratory systems of diurnal birds of prey are related to the connectivity of breeding and wintering ranges, (3) bioclimatic conditions can emerge as limiting factors on varying levels in biogeographic regions that are considered to be homogenous, (4) diet specialisation, hunting success and reproductive success measured as clutch size are associated with migration on both evolutionary and recent scales, and finally (5) the importance of life history attributes in predicting distribution is enhanced by distances and discontinuities between breeding and wintering grounds.

4.2. Phylogeny, migration and biogeography in the genus *Turdus*

The results suggest association between the early colonisation of the Southern Hemisphere and the evolution of migration in *Turdus* thrushes. Specifically, the process of ‘along-latitudinal first’ type of migration could have enhanced the early diversification of thrushes due to the colonisation of Africa possibly from two different directions: either (1) from the north, through Europe, supported by the distribution of the earliest splits of *Turdus viscivorus* and *T. philomelos*, or (2) from the south (east), through India, as supported by the distribution of *T. mupinensis* and *Psophocichla litsitsirupa*. High probability of mobility, inducing migration as an ancestral behaviour within this group is further confirmed by evidence of latitudinal dispersal and speciation (Mazerolle et al. 2005, Faaborg et al. 2010, but see also Winger et al. 2012, 2014) which was also predicted for Amazonian birds (Salisbury et al. 2012). The north-south migratory pattern could have emerged subsequently in thrushes as an adaptation to bio-geospheric and climatic changes which also led to variation of climatic niche dynamics and high diversification rate in some other groups (see e.g. Rolland et al. 2014, Cooney et al. 2016, Gómez et al. 2016).

On the one hand, the orogeneic events before the Late Tertiary, especially the uplift of the Tibetan Plateau, may have forced birds to move along an East-West axis in Asia. For instance, Arnaiz-Villena et al. (2014) discussed that the evolution of Carduelini finches may have associated with the changes during the Late Miocene. This period may also influence the evolution of the accentors, Prunellidae (Drovetski et al. 2013), a radiation that might parallel the evolutionary history of *Turdus* in the temperate zone. Additional examples can be observed in warblers, Parulidae and Phylloscopidae (Price 2010, Winger et al. 2012, Bloch et al. 2015) and also in buntings, Emberizidae (Packert et al. 2015). Moreover, a supported Southeast Asian origin of *Turdus* and the whole Turdidae is suggested by examining the distribution of the earliest splits (*Brachypteryx* and *Myophonus* spp.) within the family (Figure A2 in the Appendix, see also Klicka et al. 2005). Further biogeographic analyses are needed to answer this question.

On the other hand, movements along latitudes could have evolved earlier, facilitated by the more contiguous tropical zone from East Asia through northern Africa to South America. That pattern provided a corridor to the radiation of *Turdus* thrushes, followed by the appearance of meridional migration within the group. Consequently, the increased genetic differences due to speciation may have resulted as a response to variation in migratory behaviour (Sol et al. 2005, Pulido 2007, Winger et al. 2012, 2014). Similar correlation between migratory behaviour and speciation rate has been found in other bird groups (e.g. falconid raptors, Fuchs et al. 2015). Based on the results and the chronology of the phylogenetic trees used in the analyses, the colonisation of South America more likely occurred from the direction of Africa rather than from North America, which assumption is in accordance with the South American origin of White-throated Thrush (*T. assimilis*) and its allies (Núñez-Zapata et al. 2016). The youngest clade of a larger set of Neotropical species possibly originated from Afrotropical ancestors, thus it is doubtful to assume northern colonisation routes. Nevertheless, the uplift of the Andes in the Late Tertiary (Gregory-Wodzicki 2000, Hooghiemstra and Van der Hammen 2004, Barke and Lamb 2006) directed dispersal routes from South America to the north, thus orographically channelising thrushes to North America.

However, in case of *T. iliacus*, a species nested in the older Neotropical clade, together with some North American and other Eurasian species, a probable trans-Beringian re-settlement of Eurasian regions is presumable which pattern can be found in e.g. winter wren (*Troglodytes troglodytes*), pine grosbeak (*Pinicola enucleator*) among passerines (Drovetski et al. 2004, 2010), and also in three-toed woodpecker (*Picoides tridactylus*, Zink et al. 1995, 2002). Furthermore, *Catharus* thrushes, forming an outgroup to *Turdus* (Outlaw et al. 2003, Winker and Pruett 2006), could have originated from North America (Voelker et al. 2013) after their split and colonised the northern regions from the direction of Asia as can be inferred from its sister relation to *Zoothera*. In contrast, a Central or South American origin is also supported for the *Catharus* (Outlaw et al. 2003) which are in line with the findings presented and discussed here. The entire clarification of this uncertainty needs further biogeographic analyses at the family level.

These contradictory patterns call for reanalysing the biogeographic history of the Turdidae after a deep taxonomic revision of the family. I found that in some sources, species belonging to the genera of *Geokichla* and *Zoothera* are altogether named as *Zoothera* which is incorrect. My broad scale phylogenetic estimation shows that the true *Zoothera* is sister to the clade containing *Catharus*, and all *Geokichla* spp. are sister to *Turdus* which supports previous results (del Hoyo et al. 2016 following Voelker and Outlaw 2008).

Previous studies in relation to the evolution of migration have also shown that species are able to remain migratory if they occupy boreal regions, including mountainous habitats. For example, in the Carduelini tribe, most species are distributed in either mountainous or boreal areas (Arnaiz-Villena et al. 2001, BirdLife International 2015), while migratory/highly mobile species frequently move on an axis along the latitudes. However, the loss of migration in crossbills (*Loxia* spp.) compared to their sister taxa, including migratory *Carduelis* species (see a comprehensive phylogenetic review in Nagy 2017), may have been driven by their adaptation to feeding on pine seed (Benkman 2003, Parchman et al. 2006, Nguembock et al. 2009, Thompson 2016), which food source is abundantly available during winter. In contrast, other example is the Siberian accentor (*Prunella montanella*), a long-distance migrant and also a regular vagrant in Western Europe and North America, it has many non-migrant relatives (Drovetski et al. 2013, del Hoyo et al. 2016). These strategies, i.e. adaptation to specific food sources or wintering under similar climatic conditions closer to the breeding grounds could be regarded as evidences for a risk avoidance strategy similar to cases where migratory species move on an axis along the latitudes rather than crossing the Himalayas (e.g. *Phylloscopus* genus, Price 2010). The loss of migration thus seems to be more frequent in the evolution of similarly behaving passerine groups, as it is often related to changes in foraging (e.g. Moyle et al. 2015, but see also Fuchs et al. 2015).

However, in *Turdus* thrushes, shifts in consumed food types between breeding and wintering seasons were relatively common in migratory lineages and could have been the result of flexibility to changing environmental conditions during migration and on

breeding/wintering sites. Species with the ability of easily changing food sources, could change migratory behaviour more frequently (see e.g. Parulidae, Gómez et al. 2016 or a synthesis by Cooney et al. 2016). Although sedentary *Turdus* thrushes are mainly tropical or subtropical species, the ‘insectivorous first’ hypothesis has been proposed as a reasonable assumption to explain why evolutionary directions show that changes in the main food type occurred frequently in migratory lineages and led to the sedentariness of herbivorous taxa (Rainio et al. 2012, Telleria et al. 2013, but see Moyle et al. 2015). However, please note that clear causal relationships are hardly defined and only possible changes between evolutionary states can be highlighted, thus further investigations will be required to resolve this uncertainty.

Correlated evolutionary analyses showed shifts from insectivorous to frugivorous behaviour during the non-breeding season. These shifts might have been associated with the appearance of migratory behaviour during the evolution, which flexibility is supported by many examples (e.g. *Sturnus vulgaris*, *Carpodacus erythrinus*, *Emberiza koslowi*, *Prunella himalayana*) of feeding behaviour in present bird species (Elkins 2010, del Hoyo et al. 2016). A clear trend in a recent shift in food types emerges not only in resident species but also in migratory birds, as they are increasingly dependent on plant materials, including fruits (Telleria et al. 2013). Further work on bill shape and size that should be highly correlated with different types of consumed food may support these findings.

In addition, being a herbivorous resident bird or an insectivorous migrant has important conservation consequences (Rainio et al. 2012). It has long been known that migration and reproductive success have important trade-offs (Alerstam et al. 2003, Newton 2008), for example, in a case study of wood thrushes (*Hyloichia mustelina*), resident birds had higher survival rates than vagrants (Rappole et al. 1989), as migrants are more frequently exposed to mortality factors than residents (e.g. Ketterson and Nolan 1982, Bell 1996). Migratory strategies have already been suggested as one of the possible explanations of the variation in adult survival among *Turdus* and *Catharus* species (Boyce and Martin 2017). These may result in the increased clutch sizes seen in migratory species as documented here for *Turdus* (see for other examples: Martin

1995, Jahn and Cueto 2012, Barve and Mason 2015) as a mechanism to offset losses during migration.

Maximum entropy modelling showed that temperature related factors are the most limiting components of current climate in *Turdus* thrushes, equally among migratory and non-migratory species. For these small-bodied birds these results have remarkable significance in predictable future distribution and migratory behaviour of species as a consequence of ongoing climatic changes (Møller et al. 2010).

To sum up the main results: (1) the presented findings provide estimations for the biogeographical origin of the genus *Turdus* by locating their most likely ancestral area into East Asia, (2) besides the support of the ‘along-latitudinal first’ hypothesis for migration as probable explanation for distribution pattern in early colonisation of the Western Palearctic and Africa, (3) followed by emerged trans-Atlantic events, and finally (4) correlated evolution between migration and food types, distinguishing seasonal shifts in the latter, predicts important plasticity in responding to changing climate of geological history.

4.3. Synthesis

I found consistent patterns which are equally applicable for both Accipitriformes and Turdidae, along with dissimilarities rooted in the different histories of the two groups. However, inferring more general statements for wider taxonomic range requires further research.

First, the southern origin of core landbirds is supported by the historical biogeographic analyses of the studied groups, which is in line with the findings of previous studies (e.g. Ericson 2012, Brusatte et al. 2015). However, the importance of Africa and Southeast Asia in the early diversification of the Accipitriformes and of the Turdidae, respectively, is in contrast with the South American origin of landbirds (Claramunt and Cracraft 2015). In that work, biogeographic analyses of 230 species were conducted. More than one-third of the species were partially or exclusively distributed in South America, also including basal clades from this region. Further,

considering that among the endemic species of each realm, the majority were of South American origin, it could have biased the estimated origin of landbirds towards the Neotropics. Despite the fact that in my taxon sets a large number of Neotropical species were included, I found that South America could be an early destination rather than the source of origin. Thus, the hotspot nature of Southeast Asia and Africa is confirmed for these groups (see also Ericson et al. 2003, Ericson 2012). Nevertheless, further analyses involving more species from different bird families are recommended.

Second, the emergence of grassland vegetation and hence the shift in forested habitats provided novel niches available during the Late Miocene which accelerated the diversification of both Accipitriformes and Turdidae, similarly to a general pattern in all birds (e.g. Jetz et al. 2012). For instance, the majority of long-distance migrants in the Nearctic winter in forests, whereas almost none of the Palearctic migrants follow this strategy (Rappole and Jones 2002). The lack of forested habitats in North Africa could have been a dispersal barrier. Therefore, climatic changes including the intensified aridisation, completed with the orogenetic events during the Miocene could have caused the appearance of barely liveable areas which facilitated the evolution of migration in birds.

Third, recent bioclimatic conditions showed several limiting factors, mostly related to temperature that have equal impact on birds' behaviour on both of their breeding and wintering areas. The differences in the geographically identifiable migratory systems (e.g. Newton 2008) are related to the connectivity of the distribution of species. Hence, the East Palearctic migratory system significantly differs from the West Palearctic or from the Nearctic-Neotropic systems, especially in Accipitriformes. Additionally, many *Turdus* species are endemic, with patch-like distributions to south of China, and species breeding in northern East Asia have expanded range to the western regions (Figure A3 in the Appendix). The result of maximum entropy modelling may show significant signs for predicted population changes in passerine birds (Møller et al. 2010, Zurell et al. 2018). For instance, weakly suitable areas were found for several species (e.g. *Turdus iliacus*, *T. torquatus*, *T. subalaris*, *T. naumanni*), which may indicate decline in population sizes or complete disappearance of species from those areas.

These findings can be used in development of biodiversity conservation programmes, especially for species distributed on very small areas.

Fourth, migration appeared multiple times, independently in raptors from non-migratory ancestors, whilst thrushes originated from migratory ancestors which is a substantial difference in the origin of migration between the two groups. Furthermore, migratory behaviour seems to be more facultative among accipitrid raptors which is also indicated by the frequency of vagrants (Ferguson-Lees and Christie 2001). However, in *Turdus* thrushes, migration might be a heritage rooting in the ‘along-latitudinal’ mobility of ancestors.

Fifth, one of the most important components related to migration is represented by feeding ecology patterns of birds (e.g. Boyle et al. 2011, Rainio et al. 2012, Terraube et al. 2014). Although raptors and thrushes depend on significantly different food sources, the evolution of migration highly correlated with evolutionary aspects of feeding behaviour in both groups. Migration could have evolved in species with higher plasticity in diet or on the other way around. Either being a generalist (larger diet breadth in some raptor species, but do not forget that most thrushes are omnivorous), or being able to easily adapt to different food sources (change in main food type in thrushes) are highly associated with migratory lineages. Consequently, migratory species could have easily survived during migration.

Sixth, alongside survival, reproductive success is the other major factor in the evolution of organisms. I measured reproductive attempts in birds by clutch size and compared it with migratory strategy. The generalisation of my findings support that migratory birds suffer from higher mortality during migration (e.g. Alerstam et al. 2003, Jahn and Cueto 2012, Barve and Mason 2015, Boyce and Martin 2017), which correlates with increased numbers in clutch sizes that may be an evidence for the trade-off between migration and reproduction/survival. Increased clutch size for migrants has been detected here in all three migratory systems of accipitrid birds of prey and also in *Turdus* thrushes, indicating that this phenomenon could appear multiple times, phylogenetically independently. Also investigating these finding in other bird families would be beneficial.

5. Summary

Migration forms a significant part in the life cycle of temperate bird species. The regular movements appear to have originated in parallel with the postglacial northern expansion of tropical species, however, our knowledge is still poor regarding the early states and climatic backgrounds in the evolutionary history of migration. Nevertheless, this phenomenon is also influenced by several environmental and ecological factors, such as surviving inappropriate climatic conditions. Hence, understanding the origins and evolution of migratory behaviour requires integration of the biogeographic history and ecology of birds in a phylogenetic context.

My aim was to find general conclusions in a wider taxonomic range, specifically: (1) to find climatic drivers of the biogeographic origin of the studied groups, (2) investigate the evolutionary origin of migration, and (3) several aspects of traits related to migration in these birds. I chose two well-studied, widely known, but phylogenetically distinct model groups of landbirds (Telluraves), similar in some aspects (e.g. diverse feeding ecology, reproductive biology, species with very limited distribution), but different enough for comparisons and contrasts.

Therefore, I designed three studies applying comparative phylogenetic framework in each. First, molecular phylogenetic reconstruction and ancestral area estimation were performed to investigate historical biogeography in 179 accipitrid birds of prey (Accipitriformes). Ancestral state estimation, completed with correlated evolutionary analyses were applied to infer the origins and evolutionary changes in migratory behaviour in this group. Second, phylogenetic generalized least squares (PGLS) method was used to examine the relationships among distribution patterns, diet, hunting strategies, body measurements, clutch size, and migratory behaviour. Furthermore, maximum entropy modeling was applied to investigate the bioclimatic suitability of geographical ranges for migratory raptors.

According to the results, migration evolved multiple times in birds of prey. One of the earliest events occurred in true hawks (Accipitrinae) during the Middle Miocene. In most cases, a tropical origin was inferred for the non-migratory ancestors of migratory lineages. Correlated evolutionary analyses indicate that migration evolved in the tropics, suggesting that temperate species might be descendants of tropical ones. Diet generalism is associated with migration among raptors. Moreover, clutch size and hunting strategies proved to be the most important variables in the three migratory systems. However, the geographic dissimilarities may mask important relationships between life history traits and migratory behaviours. Indeed, the European-African and the North-South American migratory systems are fundamentally different from the East Asian system, owing to the presence versus absence of ecological barriers.

The second group of birds in the third study was the Turdidae (Passeriformes). Standard set of methods were used to build the phylogenetic tree of Turdidae, which is first published here. The above described approaches for raptors were also applied in *Turdus* thrushes to identify relationships between distribution patterns, diet, body measurements, clutch size, and migratory behaviour. The main biogeographic models (DIVA, DEC, BayArea) were compared to infer historical biogeographic within the group.

The results show that the most probable ancestor regions for all 72 *Turdus* species were located in the East Palearctic and/or Afrotropical realms. Several trans-Atlantic movements occurred between 11-4 Mya, including the earliest events found to date. Migration emerged as an ancestral behaviour of the genus. Clutch size and main food types are associated with migratory behaviour. Correlated evolution between migration and along-latitudinal mobility, main food type, and the shift in main food type between seasons show high importance. Along-latitudinal movements may have evolved earlier, simultaneously with the radiations of *Turdus* thrushes, followed by the appearance of north-south migration, in connection with the orographic and climatic changes. The increased clutch sizes observed in migratory species could be important mechanism to compensate losses to mortality during migration. The results of bioclimatic analyses

imply possible conservation applications and predict the need of attention to important patterns in changes of distribution and population trends in small passerines.

Finally, the generalisation of my findings can be summarised as follows. (1) The southern origin of core landbirds is supported by the historical biogeographic analyses of the studied groups. (2) The hotspot nature of Southeast Asia and Africa is confirmed, thus South America could be an early destination rather than the source of origin. (3) The emergence of grassland vegetation and hence the shift in forested habitats provided novel niches available during the Late Miocene which accelerated the diversification of both Accipitriformes and Turdidae, similarly to a general pattern in all birds. (4) Recent bioclimatic conditions showed several limiting factors, mostly related to temperature that have equal impacts on birds' behaviour on both of their breeding and wintering areas. (5) The differences in the geographically identifiable migratory systems are related to the connectivity of the distribution of species. (6) The result of maximum entropy modeling may show significant signs for predicted population changes in passerine birds. (7) Migration evolved multiple times, independently in raptors from non-migratory ancestors, whilst thrushes originated from migratory ancestors, which is a substantial difference in the origin of migration between the two groups. (8) Migratory behaviour seems to be more facultative among accipitrid raptors, however, in *Turdus* thrushes, migration might be a heritage rooting in the 'along-latitudinal' mobility of ancestors. (9) Migration could have evolved in species with higher plasticity in diet or on the other way around. Either being a generalist (larger diet breadth in some raptor species or the omnivory of thrushes), or being able to easily adapt to different food sources (change in main food type in thrushes) are highly associated with migratory lineages. (10) Migratory birds suffer from higher mortality during migration, which can be observed as increased numbers in clutch sizes that may be an evidence for the trade-off between migration and reproduction/survival. This phenomenon could have appeared multiple times, phylogenetically independently.

Publications in peer-reviewed journals related to the thesis:

Nagy, Jenő and Tökölyi, Jácint (2014). Phylogeny, historical biogeography and the evolution of migration in accipitrid birds of prey (Aves: Accipitriformes). *Ornis Hungarica*, 22, 15–35.

Nagy, Jenő, Végvári, Zsolt, and Varga, Zoltán (2017). Life history traits, bio-climate and migratory systems of accipitrid birds of prey (Aves: Accipitriformes). *Biological Journal of the Linnean Society*, 121, 63–71.

Nagy, Jenő, Végvári, Zsolt, and Varga, Zoltán (2019). Phylogeny, migration and life history: filling the gaps in the origin and biogeography of the Turdus thrushes. *Journal of Ornithology*, 160, 529–543.

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Összefoglalás

Az emberiség történetében számos példát találhatunk arra, miként töltenek be a madarak különböző szerepeket a kultúrában és hitvilágban. Köszönhető ez titokzatos viselkedésüknek (vonulás), pompás tollazatuknak (paradicsommadarak) és elképesztő leleményességüknek (ággal vadászó új-kaledón varjak). Gondolhatunk az egyiptomiak sólyomfejű isteneire vagy a görögök „főnixére”, a rómaiak augúri tisztségére, vagy akár hozzánk közelebbi példákra is, úgy, mint a mongolok „aranszárnyú sasmadara” vagy a magyarok „turulmadara”.

Eme nagymértékű érdeklődés vezetett odáig, hogy napjaikban már tudományosan megalapozott ismeretek tömkelege áll rendelkezésünkre a madarak életmenetéről, ökológiájáról és viselkedéséről. Azonban a tudás bővülése szükségszerűen újabb kérdések megválaszolását vonja maga után.

Jelen dokumentum az elmúlt, közel egy évtized kutatómunkájának összefoglalása és értékelése. Az angol nyelven írt doktori értekezés a nemzetközi tudományos közönség elérését célozza meg, ugyanakkor legalább ennyire fontosnak tartom a hazai nyilvánossághoz való eljutást is. Ennek érdekében a következő néhány oldalon igyekszem minél bővebb összefoglalását adni a ragadozó madarak és az énekesek (azon belül is a rigók) kapcsán végzett vizsgálataimnak és legfőbb eredményeimnek.

Háttér

A Föld kérgét alkotó kőzetlemezek mozgásuk során jelentős felszínformáló tevékenységet végeznek. Az ütközések, felgyűrődések és alábukó lemezek alakították ki és alakítják az egyes földrészek domborzati viszonyait. A nagyszabású változások következményeként bolygónk klímája és bioszférája folyamatosan átformálódik. A Harmadidőszaki kontinensvándorlások és hegységképződések hozták létre a ma ismert arculatot. A Tibeti-fennsík és a Himalája felgyűrődése az Eocénban kezdődött, míg Afrika összekapcsolódása Ázsiával az Oligocén időszakra tehető. A Miocén

időszakban mind Afrika területén, mind pedig az Andok kiemelkedésével, Dél-Amerikában jelentős változások mentek végbe. Ez az időszak különösen jelentős az újmadárszabásúak (*Neognathae*) evolúciója szempontjából is.

A Föld klímája ciklikus változást mutat, melyet nemcsak a tektonikus események, hanem a Milanković–Bacsák-ciklus és biotikus tényezők egyaránt befolyásolnak. A Paleocén-Eocén hőmérsékleti maximumot követően a klíma lehűlésnek indult, ahogy az Antarktisz jégtakarója egyre inkább kiteljesedett az Oligocén időszak alatt. A Miocén és a Pleisztocén melegebb időszakai ellenére ez a jégképződés folytatódott, és az Északi-sark, valamint a szárazföldi jégtakarók megjelenése következtében a világtengerek szintje lecsökkent. Napjaink egyre szélsőségesebb viszonyai ellenére egy viszonylag hűvös időszak uralja Földünk klímáját.

A Középső-Miocén alatt elkezdődött változások új élőhelyek megjelenését eredményezték. A lehűlés és fokozatos szárazodás következtében Afrika füves és erdős élőhelyei alapvetően átalakultak. Az erdővel borított területek délebbre tolódtak és északon megjelentek az első szavanna formációk. Ez a változás a többi földrészhez viszonyítva egyedülállónak tekinthető. Mindazonáltal terjeszkedési és differenciálódási lehetőséget biztosított a madarak és más állatcsoportok számára.

Az eddigi kutatások azt mutatják, hogy közel az összes *Neognathae* leszármazási vonal kialakult már 50 millió évvel ezelőtt, és a fajképződési folyamatok jelentősen felgyorsultak ezt követően. Vizsgálódásaim során a szárazföldi madarak (*Telluraves*) két csoportjával foglalkoztam kiemelkedően. Egyrészt a vágómadár-alakúakat (*Accipitriformes*), másrészt pedig a rigók családját (*Turdidae*) választottam modellrendszerként. Mindkét csoport jelentős viselkedésbeli, ökológiai és alaktani sokféleséget mutat, mely alkalmassá teszi őket az összehasonlításra. Ugyanakkor eléggé különböznek ahhoz, hogy szélesebb körben érvényes megállapításokat is vizsgáljunk.

A ragadozó madarak evolúcióját célzó vizsgálatok csupán az utóbbi néhány évben szolgáltak átfogó eredményekkel, melyhez az én és társszerzőim munkája is jelentősen hozzájárult. Korábbi ismereteink alapján csupán az ölyvek (*Buteoninae*) eredetéről voltak pontos ismereteink. A halászsast (*Pandion haliaetus*), valamint a

kígyászkeselyűt (*Sagittarius serpentarius*) magában foglaló családokat leszámítva további monofiletikus alcsaládokat nem sikerült elkülöníteni. Ezért egy átfogó filogenetikai elemzés szükségesnek bizonyult.

Hasonlóan tisztázatlan eseteket foglal magában a rigófélék családja is, ahol nemcsak filogenetikai, de nevezéktani bizonytalanságokat úgyszintén találhatunk. Korábbi források alapján a fajok többsége a *Turdus* és *Zoothera* nemekbe tartozik. Ez utóbbi azonban magában foglalja a máshol *Gokichla* nembe sorolt fajokat is. A felsorolt bizonytalanságok megkövetelték a rigók rokonsági kapcsolatainak, genetikai adatok alapján történő újratérképezését.

A vizsgált csoportok őseinek elterjedését illetően, korábbi tanulmányok alapján trópusi eredet valószínűsíthető. Azonban, néhány esetben csupán feltételezéseket közöltek a téma kutatói. Ezek a hézagok korszerű biogeográfiai elemzések segítségével kitölthetővé válnak. Ezért a főbb fajkelekezési modellek összehasonlítása újabb megvilágításba helyezheti a két csoport eredetéről alkotott elképzeléseinket.

A rokonsági kapcsolatok és a történeti biogeográfia ismeretében célszerűnek adódott a madarak körében rendkívül jellemző viselkedés, a rendszeres vonulás eredetének és formálódásának vizsgálata. Több elképzelés is született a vonulás első megjelenését illetően. A trópusi eredet hipotézis szerint a vonulás az egyenlítő közelében élő populációk fokozatos terjeszkedésének következménye. A madarak találtak olyan területeket magasabb szélességi körökön is, melyek az év bizonyos szakaszaiban alkalmasak voltak a költésre. Az elterjedési terület kiterjesztésével egyetemben jelenhetett meg a vonulási viselkedés, az új költő, és az eredeti terület között. Ezzel szemben az északi eredet hipotézis alapján a magasabb szélességi körökön bekövetkező környezeti változások következményeként jelent meg a vonulás. Ez az elképzelés eddig viszonylag kevés csoport esetében igazolódott. A legújabb feltételezés szerint az elterjedési terület szűkülése eredményezte a költő és telelő területek szétválását. A földtörténet során a szélesebb trópusi öv zsugorodása vont maga után a területek elkülönülését és így a rendszeres vonulás megjelenését.

Ugyanakkor nem csak időben, hanem térben is különbséget lehet tenni a vonulási mintázatokban. Alapvetően három jelentős vonulási rendszert különíthetünk el: Észak-

és Dél-Amerika, Afrika és Európa, valamint Északkelet-Ázsia és az Indonézszigetvilág vonulási rendszereit. A legszembetűnőbb különbség közöttük, hogy míg az első kettő esetében jelentős földrajzi akadályai vannak a vonulásnak (Mexikói-fennsík, Karibi-térség, Földközi-tenger, Szahara), addig utóbbi gyakorlatilag folytonos rendszert alkot. Felmerülhet a kérdés, hogy milyen további eltérések, esetleg hasonlóságok mutathatóak ki az egyes régiókban?

Az előbb áttekintett szempontokra alapozva, első lépésben 179 ragadozó, valamint 155 rigó faj törzsfáját hoztam létre a genetikai adatbázisban elérhető szekvenciák alapján. Az elkészült fák a biogeográfiai és összehasonlító filogenetikai vizsgálatok fontos részét képezték. Modern módszerek felhasználásával a vonulás kialakulását és a vele összefüggő tényezőket vizsgáltam a következő állítások próbájaként:

1. Nagytestű fajoknál gyakrabban kialakul a vonulás, hacsak nem a vonulás következménye a testméret növekedése.
2. A táplálék erős korlátozó tényező, mind a téli időszakban, mind pedig a vonulás során.
 - a. Minél változatosabb táplálékot fogyaszt egy faj, annál nagyobb eséllyel képes túlélni a mérsékelt égövben, sőt a téli időszakban is képes költőterülete közelében maradni.
 - b. Ezzel ellentétben, azok a fajok, melyek képesek különböző táplálékforrásokat hasznosítani, könnyebben átvészeltetik a fő táplálékforrásban mutatkozó hiányokat. Ennélfogva ez a jelenség gyakoribb a vonuló fajok körében, másrészt a vonuló fajok könnyebben váltanak táplálékforrást.
3. Fontos eltérések azonosíthatóak a földrajzilag elkülöníthető vonulási rendszerekben.
 - a. A trópusi-mérsékelt övi vonulási rendszerek kialakulásában fontos szerepet töltenek be az eltérő élőhelyek, melyek alkalmas folyosókat jelölhetnek ki a létrejövő vonulási útvonalak számára.

- b. Az újonnan elérhetővé váló élőhelyek (niche-k), úgy, mint a füves és erdei élőhelyek arányának megváltozása a Miocénben, elősegíthették a madarak szétterjedését.
4. Mivel a vonulás költséges a nagymértékű elhullási arány miatt, ezért a vonuló fajok esetében megnövekedett fészekalj-méret várható a szaporodási siker növelése érdekében.

Eredmények

A vizsgált 179 ragadozó madárfaj közös őse több, mint 60 millió évvel ezelőtt jelenhetett meg. Ezt követően vált el a kígyászkeselyű, majd a halászsas a többi fajtól (57-37 millió éve). Két további korai elválás következteben (50-20 millió éve) az Elaninae alcsalád, valamint a Gypaetinae/Perninae rokonsági kör különült el a többi alcsaládtól. Az összes faj közös őse valószínűsíthetően afrikai eredetű, de bármely alcsaládot vesszük figyelembe, minden esetben valamely trópusi terület adódik ősi elterjedési területnek.

A vonulás több különböző leszármazási vonalon, függetlenül jelenhetett meg a ragadozók körében. A teljes vonulás (a faj/populációk összessége vonuló), illetve a részleges vonulás (bizonyos populációk, vagy egyes földrajzi egységek tekintetében figyelhető meg vonulás) egyaránt a nem vonuló állapotból származtatható, átmenet nélkül. Következésképpen, a viselkedésbeli változás párhuzamosan mehetett végbe a fajok mérsékelt égöv irányába történő terjeszkedésével. A bioklimatikus elemzések kimutatták, hogy mind a vonuló, mind pedig a nem vonuló fajok esetében valamely hőmérséklettel összefüggő változó az, amely meghatározza az elterjedési terület megfelelőségét. A bioklimatikus változók alapján jól elkülöníthetők az említett vonulási rendszerek. A különböző életmenet-jellegek és ökológiai tényezők közül a táplálkozás változatossága, az élőhely és a fészekalj-méret mutatott jelentős összefüggést. A vonulási viselkedés megjelenése vontatta maga után a szélesebb táplálékforráshoz való alkalmazkodást, mely nyilván az élőhelyek változatosságában is megnyilvánul. Afrikában a nyílt élőhelyekhez, míg máshol főként az erdő borította területekhez kellett alkalmazkodniuk a vonuló fajoknak. Fontos eredmény, hogy

mindhárom vonulási rendszerben kimutathatóan több tojást raknak a vonuló fajok a nem vonulókhöz képest.

A rigófélék (*Turdidae*) filogenetikai rokonságával kapcsolatban itt teszem közzé először azt a törzsfát, mely az utóbbi évtizedek legátfogóbb fajkészletén alapszik. Az eredmények értelmében a *Turdus* nemzetség polifiletikus (a fajok eltérő őstől származnak – legalábbis a jelenlegi nevezéktan alapján), amennyiben azt az 5 fajt is figyelembe vesszük, melyek más ágakkal mutatnak rokonságot. A galléros rigót (*Zoothera monticola*) magában foglaló elágazás monofiletikus egységnek (a közös őst és annak leszármazottait is tartalmazza) tekinthető. Mivel ez a faj a nemzetség típusfaja, ezért ez a vonal kell, hogy alkossa a valódi *Zoothera* nemzetséget, melynek legközelebbi testvércsoportja az amerikai fülemülrigókat (*Catharus*) is magában foglaló ág. A másik, szintén monofiletikus csoport, a *Turdus* testvércsoportja. Az ide tartozó fajokat egységesen, a *Geokichla* nembe szükséges sorolni, mert egyértelműen elkülönülnek az előbb említett *Zoothera* vonaltól. A 72 *Turdus* faj eredete egyértelműen trópusi. Valószínűleg Délkelet-Ázsia és/vagy Afrika lehetett a közös ős elterjedési területe. A csoport szétterjedése során, viszonylag hamar elérte Dél-Amerikát (15-10 millió éve), melyet többszöri transz-atlantikus áttelepülés követett. Alapvető különbség, a ragadozókkal szemben, hogy a vonulási viselkedés lehetett az ősi állapot, melyet a szétterjedés során mutatkozó és a mai, vonuló fajok többségénél megfigyelhető költési elterjedés kelet-nyugati lefutása is alátámaszt. A vonulás megjelenése szoros összefüggést mutat a rigók kelet-nyugati mozgékonyásával. Ebben a csoportban is kimutatható a táplálkozás-biológia és fészekalj-méret vonuló fajoknál mutatott eltérése. A vonulási viselkedés a táplálékforrásban történő váltás képességével nagyban összefügg. Ez magyarázata lehet annak a megfigyelésnek is, hogy számos énekes madár költési és telelési időszakban eltérő táplálékot fogyaszt. Hasonlóan a ragadozókhöz, a vonuló rigófajok esetében is, megnövekedett fészekalj-méret jellemző a nem vonuló fajokhoz viszonyítva. Végezetül, eddig még bioklimatikus elemzéseket nem közöltek rigókra, mely eredmények alapján fontos természetvédelmi kérdésekben nyílnak újabb lehetőségek. Az elterjedési területek megfelelősége azt mutatja, hogy egyes peremterületek kevésbé alkalmasak a fajok

számára, ami előrevetítheti a közeljövőben bekövetkező, lehetséges elterjedési és populációs változásokat.

Szintézis

Eredményeim alapján fontos következtetéseket lehet levonni szélesebb taxonómiai körben. Annak ellenére, hogy a ragadozó madarak és az rigók két, eltérő csoport, mégis sikerült mindkét modellrendszerben hasonló mintázatot találni.

Először is, megerősítést nyert a szárazföldi madarak trópusi eredete. Azonban a korábbi elképzelésekkel ellentétben, Délkelet-Ázsia és Afrika bizonyult fontos fajképződési göcsterületnek. Az itt bemutatott két csoport alapján Dél-Amerika egy nagyon korai célterületnek, mintsem a szétterjedés forrásának tekinthető. További, sokfajos elemzések segíthetnek a kérdés tisztázásában.

Másodszor, az újonnan megjelenő füves élőhelyek, valamint az erdős területek arányának változása a Késő-Miocén lehülés és szárazodás következtében, alapvetően beindíthatta a madárcsoportok szétterjedését, felgyorsítva ezzel a fajképződést. Mindazonáltal viselkedésbeli változásokat is előidézhetett, melyek a vonulás kialakulását segítették.

Harmadszor, a jelenkori viszonyok bioklimatikus modellezése lehetővé tette a fajok számára megfelelő területek azonosítását. Habár a legtöbb faj érzékeny valamely hőmérsékleti változóval szemben, a földrajzilag elkülöníthető vonulási rendszerekben is különbségek mutatkoznak. Ez részint a nagyobb ökológiai akadályok meglétének vagy hiányának is köszönhető. Minden esetre, a modellek alkalmazhatónak bizonyulnak olyan fontos előrejelzések elkészítésére, melyek természetvédelmi szempontból jelentősek lehetnek, előre vetítve a fajok elterjedésében és populációs mintázataiban történő lehetséges változásokat.

Negyedszer, a vonulás kialakulása más-más csoportokban eltérő lehet. A ragadozók esetében nem vonuló ősből leszármazott vonalakon, többször, egymástól függetlenül jelent meg ez a viselkedési forma. Ebben a csoportban inkább fakultatív jellege van a viselkedésnek, melyet a nagyszámú, kóborló egyedek megfigyelése is alátámaszt.

Ezzel ellentétben, a rigók esetében sokkal mélyebben gyökerezik a vonulás, és egyfajta örökségnek tekinthető, összefüggésben a rendszeres kelet-nyugati mozgásokkal.

Ötödször, az egyik legfontosabb, vonulással összefüggő tényező a fajok táplálkozása. Az eredményekből kitűnik, hogy a vonulás kialakulhat akkor is, ha egy faj több, különböző táplálékforrást képes hasznosítani, de akkor is, ha képes a táplálékforrások közötti, rugalmas váltásra.

Végezetül, a vonulás során elszenvedett veszteségek és a madarak szaporodási sikere között csereviszony áll fenn. Több esetben kimutatható megnövekedett fészekalj-méret vonuló fajoknál. Ez a mintázat megerősíti az előbb említett összefüggés jelentőségét. További madárcsoportokon végzett vizsgálatok segíthetnek annak feltárásában, hogy ez a csereviszony többször, származástól (filogenetikailag) függetlenül jelenik meg a madárvilágban.

Az értekezés alapját képező közlemények:

Nagy Jenő és Tökölyi Jácint (2014). Phylogeny, historical biogeography and the evolution of migration in accipitrid birds of prey (Aves: Accipitriformes). *Ornis Hungarica*, 22, 15–35.

Nagy Jenő, Végvári Zsolt és Varga Zoltán (2017). Life history traits, bio-climate and migratory systems of accipitrid birds of prey (Aves: Accipitriformes). *Biological Journal of the Linnean Society*, 121, 63–71.

Nagy Jenő, Végvári Zsolt és Varga Zoltán (2019). Phylogeny, migration and life history: filling the gaps in the origin and biogeography of the Turdus thrushes. *Journal of Ornithology*, 160, 529–543.

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References

- Alerstam, T., Hedenström, A., and Åkesson, S. (2003). Long-distance migration: evolution and determinants. *Oikos*, 103, 247–260.
- do Amaral, F. R., Sheldon, F. H., Gamauf, A., Haring, E., Riesing, M., Silveira, L. F., and Wajntal, A. (2009). Patterns and processes of diversification in a widespread and ecologically diverse avian group, the buteonine hawks (Aves, Accipitridae). *Molecular Phylogenetics and Evolution*, 53, 703–715.
- Andersen, M. J., McCullough, J. M., Mauck III, W. M., Smith, B. T., and Moyle, R. G. (2017). A phylogeny of kingfishers reveals an Indomalayan origin and elevated rates of diversification on oceanic islands. *Journal of Biogeography*, 45, 269–281.
- Arnaiz-Villena, A., Guillén, J., Ruiz-del-Valle, V., Lowy, E., Zamora, J., Varela, P., Stefani, D., and Allende, L. M. (2001). Phylogeography of crossbills, bullfinches, grosbeaks, and rosefinches. *CMLS Cellular and Molecular Life Sciences*, 58, 1–8.
- Arnaiz-Villena, A., Ruiz-del-Valle, V., Gomez-Prieto, P., Rey, D., Enriquez-de-Salamanca, M., Marco, J., Muniz, E., Martin-Villa, M., and Areces, C. (2014). Carduelini new systematics: Crimson-winged Finch (*Rhodopechys sanguineus*) is included in “Arid-Zone” Carduelini finches by mitochondrial DNA phylogeny. *The Open Ornithology Journal*, 7, 55–62.
- Bairlein, F. (2008). The mysteries of bird migration - Still much to be learnt. *British Birds*, 101, 68–81.
- Barke, R., and Lamb, S. (2006). Late Cenozoic uplift of the Eastern Cordillera, Bolivian Andes. *Earth and Planetary Science Letters*, 249, 350–367.
- Bartoń, K. (2015). MuMIn: multi-model inference. R package version 1.13.4. URL: <http://CRAN.R-project.org/package=MuMIn/>.
- Barve, S., and Mason, N. A. (2015). Interspecific competition affects evolutionary links between cavity nesting, migration and clutch size in Old World flycatchers (Muscicapidae). *Ibis*, 157, 299–311.
- Bell, C. P. (1996). The relationship between geographic variation in clutch size and migration pattern in the Yellow Wagtail. *Bird Study*, 43, 333–341.
- Bell, C. P. (2005). The origin and development of bird migration: comments on Rappole and Jones, and an alternative evolutionary model. *Ardea*, 93, 115–123.
- Bell, C. P. (2011). Resource buffering and the evolution of bird migration. *Evolutionary Ecology*, 25, 91–106.
- Benkman, C. W. (2003). Divergent selection drives the adaptive radiation of crossbills. *Evolution*, 57, 1176–1181.
- BirdLife International (2015). IUCN Red List for birds. URL: <http://www.birdlife.org/>.
- Bloch, N. I., Morrow, J. M., Chang, B. S. W., and Price, T. D. (2015). SWS2 visual pigment evolution as a test of historically contingent patterns of plumage color evolution in warblers. *Evolution*, 69, 341–356.
- Bobe, R., and Behrensmeyer, A. K. (2004). The expansion of grassland ecosystems in Africa in relation to mammalian evolution and the origin of the genus *Homo*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 207, 399–420.
- Bonnefille, R. (2010). Cenozoic vegetation, climate changes and hominid evolution in tropical Africa. *Global and Planetary Change*, 72, 390–411.
- Boyce, A. J., and Martin, T. E. (2017). Contrasting latitudinal patterns of life-history divergence in two genera of new world thrushes (Turdinae). *Journal of Avian Biology*, 48, 581–590.

- Boyle, W. A., Conway, C. J., and Bronstein, J. L. (2011).** Why do some, but not all, tropical birds migrate? A comparative study of diet breadth and fruit preference. *Evolutionary Ecology*, 25, 219–236.
- Böhning-Gaese, K., Halbe, B., Lemoine, N., and Oberrath, R. (2000).** Factors influencing the clutch size, number of broods and annual fecundity of North American and European land birds. *Evolutionary Ecology Research*, 2, 823–839.
- Brown, L. (1976).** Birds of prey: their biology and ecology. *A & W Publishers, New York*.
- Bruderer, B., and Salewski, V. (2008).** Evolution of bird migration in a biogeographical context. *Journal of Biogeography*, 35, 1951–1959.
- Bruderer, B., and Salewski, V. (2009).** Lower annual fecundity in long-distance migrants than in less migratory birds of temperate Europe. *Journal of Ornithology*, 150, 281–286.
- Brusatte, S. L., O'Connor, J. K., and Jarvis, E. D. (2015).** The origin and diversification of birds. *Current Biology*, 25, 888–898.
- Buhl, M. L. (1947).** The goddesses of the Egyptian tree cult. *Journal of Near Eastern Studies*, 6, 80–97.
- Burleigh, J. G., Kimball, R. T., and Braun, E. L. (2015).** Building the avian tree of life using a large-scale, sparse supermatrix. *Molecular Phylogenetics and Evolution*, 84, 53–63.
- Castresana, J. (2000).** Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Molecular Biology and Evolution*, 17, 540–552.
- Cawood, P. A., Kröner, A., Collins, W. J., Kusky, T. M., Mooney, W. D., and Windley, B. F. (2009).** Accretionary orogens through Earth history. *The Geological Society, London, Special Publications*, 318, 1–36.
- Cenizo, M., Noriega, J. I., and Reguero, M. A. (2016).** A stem falconid bird from the Lower Eocene of Antarctica and the early southern radiation of the falcons. *Journal of Ornithology*, 157, 885–894.
- Charif, D., and Lobry, J. R. (2007).** SeqinR 1.0-2: a contributed package to the R project for statistical computing devoted to biological sequences retrieval and analysis. *Structural Approaches to Sequence Evolution*, 207–232.
- Chorowicz, J. (2005).** The east African rift system. *Journal of African Earth Sciences*, 43, 379–410.
- Claramunt, S., and Cracraft, J. (2015).** A new time tree reveals Earth history's imprint on the evolution of modern birds. *Science Advances*, 1, e1501005.
- Clot, A., Chaline, J., Heintz, E., Jammot, D., Mourer-Chauviré, C., and Rage, J. C. (1976).** Montoussé 5 (Hautes-Pyrénées), un nouveau remplissage de fissure à faune de vertébrés du Pléistocène inférieur. *Geobios*, 9, 511–514.
- Condie, K. C. (1997).** Plate tectonics and crustal evolution. Butterworth-Heinemann, Oxford.
- Cooney, C. R., Seddon, N., and Tobias, J. A. (2016).** Widespread correlations between climatic niche evolution and species diversification in birds. *Journal of Animal Ecology*, 85, 869–878.
- Coward, M. P., and Ries, A. C. (2003).** Tectonic development of North African basins. *Geological Society, London, Special Publications*, 207, 61–83.
- Cox, G. W. (1985).** The evolution of avian migration systems between temperate and tropical regions of the New World. *The American Naturalist*, 126, 451–474.
- Cox, G. W. (2010).** Bird migration and global change. *Island Press, Washington*.
- DeCelles, P. G., Kapp, P., Gehrels, G. E., and Ding, L. (2014).** Paleocene-Eocene foreland basin evolution in the Himalaya of southern Tibet and Nepal: Implications for the age of initial India-Asia collision. *Tectonics*, 33, 824–849.
- deMenocal, P. B. (2004).** African climate change and faunal evolution during the Pliocene^Pleistocene. *Earth and Planetary Science Letters*, 220, 3–24.

- Dingle, H. (2014).** Migration: the biology of life on the move. *Oxford University Press, New York*.
- Drovetski, S. V., Zink, R. M., Rohwer, S., Fadeev, I. V., Nesterov, E. V., Karagodin, I., Koblik, E. A., and Red'kin, Y. A. (2004).** Complex biogeographic history of a Holarctic passerine. *Proceedings of the Royal Society of London B*, 271, 545–551.
- Drovetski, S. V., Zink, R. M., Ericson, P. G. P., and Fadeev, I. V. (2010).** A multilocus study of pine grosbeak phylogeography supports the pattern of greater intercontinental divergence in Holarctic boreal forest birds than in birds inhabiting other high-latitude habitats. *Journal of biogeography*, 37, 696–706.
- Drovetski, S. V., Semenov, G., Drovetskaya, S. S., Fadeev, I. V., Red'kin, Y. A., and Voelker, G. (2013).** Geographic mode of speciation in a mountain specialist Avian family endemic to the Palearctic. *Ecology and Evolution*, 3, 1518–1528.
- Drummond, A. J., Ho, S. Y., Phillips, M. J., and Rambaut, A. (2006).** Relaxed phylogenetics and dating with confidence. *PLoS Biology*, 4, e88.
- Drummond, A. J., and Rambaut, A. (2007).** BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, 7, 214.
- Du Bois, C. G. (1904).** Mythology of the Mission Indians. *The Journal of American Folklore*, 17, 185–188.
- Dunning, J. B. (2008).** CRC handbook of avian body masses. *CRC Press, Boca Raton*.
- Dupont-Nivet, G., Hoorn, C., and Konert, M. (2008).** Tibetan uplift prior to the Eocene-Oligocene climate transition: Evidence from pollen analysis of the Xining Basin. *Geology*, 36, 987–990.
- Elias, S. A., Short, S. K., Nelson, C. H., and Birks, H. H. (1996).** Life and times of the Bering land bridge. *Nature*, 382, 60–63.
- Elkins, N. (2010).** Weather and bird behaviour. *T & A D Poyser, London*.
- Emslie, S. D. (1998).** Avian community, climate, and sea-level changes in the Plio-Pleistocene of the Florida Peninsula. *Ornithological Monographs*, 1–113.
- Ericson, P. G. P., Irestedt, M., and Johansson, U. S. (2003).** Evolution, biogeography, and patterns of diversification in passerine birds. *Journal of Avian Biology*, 34, 3–15.
- Ericson, P. G. P. (2012).** Evolution of terrestrial birds in three continents: biogeography and parallel radiations. *Journal of Biogeography*, 39, 813–824.
- Faaborg, J., Holmes, R. T., Anders, A. D., Bildstein, K. L., Dugger, K. M., Gauthreaux, S. A., Heglund, P., Hobson, K. A., Jahn, A. E., Johnson, D. H., Latta, S. C., Levey, D. J., Marra, P. P., Merkord, C. L., Nol, E., Rothstein, S. I., Sherry, T. W., Sillett, T. S., Thompson, F. R., and Warnock, N. (2010).** Recent advances in understanding migration systems of New World land birds. *Ecological Monographs*, 80, 3–48.
- Ferguson-Lees, J., and Christie, D. A. (2001).** Raptors of the world. *Houghton Mifflin Company, Boston*.
- Flower, B. P., and Kennett, J. P. (1994).** The middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 108, 537–555.
- Fowler, D. W., Freedman, E. A., and Scannella, J. B. (2009).** Predatory functional morphology in raptors: interdigital variation in talon size is related to prey restraint and immobilisation technique. *PLoS One*, 4, e7999.
- Fuchs, J., Johnson, J. A., and Mindell, D. P. (2015).** Rapid diversification of falcons (Aves: Falconidae) due to expansion of open habitats in the Late Miocene. *Molecular Phylogenetics and Evolution*, 82, 166–182.

- Fuchs, J., Pons, J.-M., and Bowie, R. C. K. (2017).** Biogeography and diversification dynamics of the African woodpeckers. *Molecular Phylogenetics and Evolution*, 108, 88–100.
- Gamauf, A., Preleuthner, M., and Winkler, H. (1998).** Philippine birds of prey: interrelations among habitat, morphology, and behavior. *The Auk*, 115, 713–726.
- Germi, F., Young, G. S., Salim, A., Pangimangen, W., and Schellekens, M. (2009).** Over-ocean raptor migration in a monsoon regime: spring and autumn 2007 on Sangihe, North Sulawesi, Indonesia. *Forktail*, 25, 104–116.
- Gómez, C., Tenorio, E. A., Montoya, P., and Cadena, C. D. (2016).** Niche-tracking migrants and niche-switching residents: evolution of climatic niches in New World warblers (Parulidae). *Proceedings of the Royal Society of London B*, 283, 20152458.
- Green, S. J. (2009).** Malevolent gods and Promethean birds: Contesting augury in Augustus's Rome. In *Transactions of the American Philological Association* 139, pp. 147–167. *The Johns Hopkins University Press*.
- Greenberg, R., Kozlenko, A., Etterson, M., and Dietsch, T. (2008).** Patterns of density, diversity, and the distribution of migratory strategies in the Russian boreal forest avifauna. *Journal of Biogeography*, 35, 2049–2060.
- Gregory-Wodzicki, K. M. (2000).** Uplift history of the Central and Northern Andes: a review. *Geological Society of America Bulletin*, 112, 1091–1105.
- Griffiths, C. S., Barrowclough, G. F., Groth, J. G., and Mertz, L. A. (2007).** Phylogeny, diversity, and classification of the Accipitridae based on DNA sequences of the RAG-1 exon. *Journal of Avian Biology*, 38, 587–602.
- Hadfield, J. D., and Nakagawa, S. (2010).** General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology*, 23, 494–508.
- Haq, B. U., Hardenbol, J., and Vail, P. R. (1987).** Chronology of fluctuating sea levels since the Triassic. *Science*, 235, 1156–1167.
- Harrison, C. J. O. (1987).** Pleistocene and prehistoric birds of south-west Britain. *Proceedings of the University of Bristol Spelaeological Society*, 18, 81–104.
- Harrison, T. M., Copeland, P., Kidd, W. S. F., and Yin, A. (1992).** Raising Tibet. *Science*, 255, 1663–1670.
- Heather, P. J. (1939).** Some animal beliefs from Aristotle. *Folklore*, 50, 243–258.
- Hedges, S. B. (1996).** Historical biogeography of West Indian vertebrates. *Annual Review of Ecology and Systematics*, 27, 163–196.
- Helbig, A. J., Kocum, A., Seibold, I., and Braun, M. J. (2005).** A multi-gene phylogeny of aquiline eagles (Aves: Accipitriformes) reveals extensive paraphyly at the genus level. *Molecular Phylogenetics and Evolution*, 35, 147–164.
- Hernández Fernández, M., and Vrba, E. S. (2006).** Plio-Pleistocene climatic change in the Turkana Basin (East Africa): Evidence from large mammal faunas. *Journal of Human Evolution*, 50, 595–626.
- Hertel, F., Maldonado, J. E., and Sustaita, D. (2014).** Wing and hindlimb myology of vultures and raptors (Accipitriformes) in relation to locomotion and foraging. *Acta Zoologica*, 96, 283–295.
- Hijmans, R. J. (2015).** raster: geographic data analysis and modeling. R package version 2.4–15. URL: <http://CRAN.Rproject.org/package=raster/>.
- Holt, B. G., Lessard, J.-P., Borregaard, M. K., Fritz, S. A., Araújo, M. B., Dimitrov, D., Fabre, P.-H., Graham, C. H., Grave, G. R., Jönsson, K. A., Nogués-Bravo, D., Wang, Z., Whittaker, R. J., Fjeldsa, J., and Rahbek, C. (2012).** An update of Wallace's zoogeographic regions of the world. *Science*, 1228282.

- Hooghiemstra, H., and Van der Hammen, T. (2004).** Quaternary Ice-Age dynamics in the Colombian Andes: developing an understanding of our legacy. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359, 173–181.
- Hopkins, D. M. (1959).** Cenozoic history of the Bering land bridge. *Science*, 129, 1519–1528.
- del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A., and de Juana, E. (2016).** Handbook of the Birds of the World Alive. *Lynx Edicions, Barcelona*. URL: <http://www.hbw.com/>.
- Iturralde-Vinent, M. A., and MacPhee, R. D. E. (1999).** Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bulletin of the American Museum of Natural History*, 238, 1–95.
- Jahn, A. E., and Cueto, V. R. (2012).** The potential for comparative research across New World bird migration systems. *Journal of Ornithology*, 153, 199–205.
- Jarvis, E. D., Mirarab, S., Aberer, A. J., Li, B., Houde, P., Li, C., Ho, S. Y. W., Faircloth, B. C., Nabholz, B. Howard, J. T., Suh, A., Weber, C. C., da Fonseca, R. R., Li, J., Zhang, F., Li, H., Zhou, L., Narula, N., Liu, L., Ganapathy, G., Boussau, B., Bayzid, Md. S., Zavidovych, V., Subramanian, S., Gabaldón T., Capella-Gutiérrez, S., Huerta-Cepas, J., Rekepalli, B., Munch, K., Schierup, M., Lindow, B., Warren, W. C., Ray, D., Green, R. E., Bruford, M. W., Zhan, X., Dixon, A., Li, S., Li, N., Huang, Y., Derryberry, E. P., Bertelsen, M. F., Sheldon, F., H., Brumfield, R., T., Mello, C., V., Lovell, P. V., Wirthlin, M., Schneider, M. P. C., Prosdocimi, F., Samaniego, J. A., Velazquez, A. M. V., Alfaro-Núñez, A., Campos, P. F., Peterson, B., Sicheritz-Ponten, T., Pas, A., Bailey, T., Scofield, P., Bunce, M., Lambert, D. M., Zhou, Q., Perelman, P., Driskell, A. C., Shapiro, B., Xiong, Z., Zeng, Y., Liu, S., Li, Z., Liu, B., Wu, K., Xiao, J., Yinqi, X., Zheng, Q., Zhang, Y., Yang, H., Wang, J., Smeds, L., Rheindt, F. E., Braun, M., Fjeldsa, J., Orlando, L., Barker, F. K., Jönsson, K. A., Johnson, W., Koepfli, K. P., O'Brien, S., Haussler, D., Ryder, O., A., Rahbek, C., Willerslev, E., Graves, G. R., Glenn, T. C., McCormack, J., Burt, D., Ellegren, H., Alström, P., Edwards, S. V., Stamatakis, A., Mindell, D. P., Cracraft, J., Braun, E. L., Warnow, T., Jun, W., Gilbert, M. T. P., and Zhang, G. (2014).** Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science*, 346, 1320–1331.
- Jánossy, D. (1991).** Late Miocene bird remains from Polgárdi (W-Hungary). *Aquila*, 98, 13–35.
- Jetz, W., Sekercioglu, C. H., and Böhning-Gaese, K. (2008).** The worldwide variation in avian clutch size across species and space. *PLoS Biology*, 6, 2650–2657.
- Jetz, W., and Rubenstein, D. R. (2011).** Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biology*, 21, 72–78.
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., and Mooers, A. O. (2012).** The global diversity of birds in space and time. *Nature*, 491, 444–448.
- Jönsson, K. A., and Holt, B. G. (2015).** Islands contribute disproportionately high amounts of evolutionary diversity in passerine birds. *Nature Communications*, 6, 8538.
- Joseph, L., Lessa, E. P., and Christidis, L. (1999).** Phylogeny and biogeography in the evolution of migration: shorebirds of the Charadrius complex. *Journal of Biogeography*, 26, 329–342.
- Kamilar, J. M., and Cooper, N. (2013).** Phylogenetic signal in primate behaviour, ecology and life history. *Philosophical Transactions of the Royal Society B*, 368, 20120341.
- Katoh, K., Kuma, K. I., Toh, H., and Miyata, T. (2005).** MAFFT version 5: improvement in accuracy of multiple sequence alignment. *Nucleic Acids Research*, 33, 511–518.
- Kendall, C., Virani, M. Z., Kirui, P., Thomsett, S., and Githiru, M. (2012).** Mechanisms of coexistence in vultures: understanding the patterns of vulture abundance at carcasses in Masai Mara National Reserve, Kenya. *The Condor*, 114, 523–531.

- Ketterson, E. D., and Nolan Jr, V. (1982).** The role of migration and winter mortality in the life history of a temperate-zone migrant, the Dark-eyed Junco, as determined from demographic analyses of winter populations. *The Auk*, 99, 243–259.
- Klaassen, R. H. G., Hake, M., Strandberg, R., Koks, B. J., Trierweiler, C., Exo, K. M., Bairlein, F., and Alerstam, T. (2014).** When and where does mortality occur in migratory birds? Direct evidence from long-term satellite tracking of raptors. *The Journal of Animal Ecology*, 83, 176–184.
- Klicka, J., Voelker, G., and Spellman, G. M. (2005).** A molecular phylogenetic analysis of the “true thrushes” (Aves: Turdinae). *Molecular Phylogenetics and Evolution*, 34, 486–500.
- König, C., and Weick, F. (2008).** Owls of the world. *Christopher Helm Publishers, London*.
- Kreft, H., and Jetz, W. (2013).** Comment on “An update of Wallace’s zoogeographic regions of the world”. *Science*, 341, 343.
- Krüger, O. (2008).** Engines of speciation: a comparative study in birds of prey. *Journal of Evolutionary Biology*, 21, 861–872.
- Ksepka, D. T., and Phillips, M. J. (2015).** Avian diversification patterns across the K-Pg boundary: Influence of calibrations, datasets, and model misspecification. *Annals of the Missouri Botanical Garden*, 100, 300–328.
- Kutzbach, J. E., Prell, W. L., and Ruddiman, Wm. F. (1993).** Sensitivity of Eurasian climate to surface uplift of the Tibetan Plateau. *The Journal of Geology*, 101, 177–190.
- Landis, M. J., Matzke, N. J., Moore, B. R., and Huelsenbeck, J. P. (2013).** Bayesian analysis of biogeography when the number of areas is large. *Systematic biology*, 62, 789–804.
- Lerner, H. R. L., and Mindell, D. P. (2005).** Phylogeny of eagles, Old World vultures, and other Accipitridae based on nuclear and mitochondrial DNA. *Molecular Phylogenetics and Evolution*, 37, 327–346.
- Louchart, A. (2008).** Emergence of long distance bird migrations: a new model integrating global climate changes. *Naturwissenschaften*, 95, 1109–1119.
- Mahmood, M. T., McLenachan, P. A., Gibb, G. C., and Penny, D. (2014).** Phylogenetic position of avian nocturnal and diurnal raptors. *Genome Biology and Evolution*, 6, 326–332.
- March, H. C. (1898).** The mythology of wise birds. *The Journal of the Anthropological Institute of Great Britain and Ireland*, 27, 209–232.
- Marincovich Jr, L., and Gladenkov, A. Y. (1999).** Evidence for an early opening of the Bering Strait. *Nature*, 397, 149–151.
- Martin, T. E. (1995).** Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs*, 65, 101–127.
- Matzke, N. J. (2013).** Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *University of California, Berkeley*.
- Matzke, N. J. (2016).** Stochastic mapping under biogeographical models. PhyloWiki BioGeoBEARS website. URL: http://phylo.wikidot.com/biogeobears#stochastic_mapping/.
- Mazerolle, D. F., Hobson, K. A., and Wassenaar, L. I. (2005).** Stable isotope and band-encounter analyses delineate migratory patterns and catchment areas of white-throated sparrows at a migration monitoring station. *Oecologia*, 144, 541–549.
- McDonald, P. G., Olsen, P. D., and Cockburn, A. (2004).** Selection on body size in a raptor with pronounced reversed sexual size dimorphism: are bigger females better? *Behavioral Ecology*, 16, 48–56.
- Mercer, J. M., and Roth, V. L. (2003).** The effects of Cenozoic global change on squirrel phylogeny. *Science*, 299, 1568–1572.

- Milá, B., Smith, T. B., and Wayne, R. K. (2006).** Postglacial population expansion drives the evolution of long-distance migration in a songbird. *Evolution*, 60, 2403–2409.
- Milner-Gulland, E. J., Fryxell, J. M., and Sinclair, A. R. E. (2011).** Animal migration: a synthesis. *Oxford University Press, New York*.
- Molnar, P., England, P., and Martinod, J. (1993).** Mantle dynamics, uplift of the Tibetan Plateau, and the Indian monsoon. *Reviews of Geophysics*, 31, 357–396.
- Molnar, P., Boos, W. R., and Battisti, D. S. (2010).** Orographic controls on climate and paleoclimate of Asia: thermal and mechanical roles for the Tibetan Plateau. *Annual Review of Earth and Planetary Sciences*, 38, 77–102.
- Møller, A. P., Fiedler, W., and Berthold, P. (2010).** Effects of climate change on birds. *Oxford University Press, New York*.
- Moyle, R. G., Hosner, P. A., Jones, A. W., and Outlaw, D. C. (2015).** Phylogeny and biogeography of *Ficedula* flycatchers (Aves: Muscicapidae): novel results from fresh source material. *Molecular Phylogenetics and Evolution*, 82, 87–94.
- Moyle, R. G., Oliveros, C. H., Andersen, M. J., Hosner, P. A., Benz, B. W., Manthey, J. D., Travers, S. L., Brown, R. M., and Faircloth, B. C. (2016).** Tectonic collision and uplift of Wallacea triggered the global songbird radiation. *Nature Communications*, 7, 12709.
- Müller, R. D., Sdrolas, M., Gaina, C., Steinberger, B., and Heine, C. (2008).** Long-term sea-level fluctuations driven by ocean basin dynamics. *Science*, 319, 1357–1362.
- Nagy, J., and Tökölyi, J. (2014).** Phylogeny, historical biogeography and the evolution of migration in accipitrid birds of prey (Aves: Accipitriformes). *Ornis Hungarica*, 22, 15–35.
- Nagy, J. (2017).** Phylogeny and evolution of the European Goldfinch (*Carduelis carduelis*) and its allies—a review of the “bird of the year”. *Ornis Hungarica*, 25, 1–10.
- Nagy, J., Végvári, Zs., and Varga, Z. (2017).** Life history traits, bio-climate and migratory systems of accipitrid birds of prey (Aves: Accipitriformes). *Biological Journal of the Linnean Society*, 121, 63–71.
- Nagy, J., Végvári, Zs., and Varga, Z. (2019).** Phylogeny, migration and life history: filling the gaps in the origin and biogeography of the *Turdus* thrushes. *Journal of Ornithology*, 160, 529–543.
- Najman, Y., Appel, E., Boudagher-Fadel, M., Bown, P., Carter, A., Garzanti, E., Godin, L., Han, J., Liebke, U., Oliver, G., Parrish, R., and Vezzoli, G. (2010).** Timing of India-Asia collision: Geological, biostratigraphic, and palaeomagnetic constraints. *Journal of Geophysical Research: Solid Earth*, 115, B12416.
- Newton, I. (2008).** The migration ecology of birds. *Academic Press, London*.
- Nguembock, B., Fjeldsa, J., Couloux, A., and Pasquet, E. (2009).** Molecular phylogeny of *Carduelinae* (Aves, Passeriformes, Fringillidae) proves polyphyletic origin of the genera *Serinus* and *Carduelis* and suggests redefined generic limits. *Molecular Phylogenetics and Evolution*, 51, 169–181.
- Noodén, L. (1992).** Animal symbolism in Celtic mythology. *University of Michigan*.
- Núñez-Zapata, J., Peterson, A. T., and Navarro-Sigüenza, A. G. (2016).** Pleistocene diversification and speciation of White-throated Thrush (*Turdus assimilis*; Aves: Turdidae). *Journal of Ornithology*, 157, 1073–1085.
- Nylander, J. A. A., Olsson, U., Alström, P., and Sanmartin, I. (2008).** Accounting for phylogenetic uncertainty in biogeography: A Bayesian approach to dispersal-vicariance analysis of the thrushes (Aves: *Turdus*). *Systematic Biology*, 57, 257–268.
- Olsson, U., and Alström, P. (2013).** Molecular evidence suggests that the enigmatic Sulawesi endemic *Geomalia heinrichi* belongs in the genus *Zoothera* (Turdidae, Aves). *Chinese Birds*, 4, 155–160.

- Otterbeck, A., Lindén, A., and Roualet, É. (2015).** Advantage of specialism: reproductive output is related to prey choice in a small raptor. *Oecologia*, 179, 129–137.
- Outlaw, D. C., Voelker, G., Mila, B., and Gorman, D. J. (2003).** Evolution of long-distance migration in and historical biogeography of *Catharus* thrushes: a molecular phylogenetic approach. *The Auk*, 120, 299–310.
- Packert, M., Sun, Y., Strutzenberger, P., Valchuk, O., Tietze, D. T., and Martens, J. (2015).** Phylogenetic relationships of endemic bunting species (Aves, Passeriformes, Emberizidae, *Emberiza koslowi*) from the eastern Qinghai-Tibet Plateau. *Vertebrate Zoology*, 65, 135–150.
- Pagel, M. (1997).** Inferring evolutionary processes from phylogenies. *Zoologica Scripta*, 26, 331–348.
- Pagel, M. (1999).** Inferring the historical patterns of biological evolution. *Nature*, 401, 877.
- Pagel, M., Meade, A., and Barker, D. (2004).** Bayesian estimation of ancestral character states on phylogenies. *Systematic biology*, 53, 673–684.
- Pagel, M., and Meade, A. (2006).** Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *The American Naturalist*, 167, 808–825.
- Paradis, E., Claude, J., and Strimmer, K. (2004).** APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, 20, 289–290.
- Parchman, T. L., Benkman, C. W., and Britch, S. C. (2006).** Patterns of genetic variation in the adaptive radiation of New World crossbills (Aves: Loxia). *Molecular Ecology*, 15, 1873–1887.
- Pathak, V. (2018).** Phylogeny of the Accipiters. *Long Island University, New York*.
- Pérez-Camacho, L., García-Salgado, G., Rebollo, S., Martínez-Hestekamp, S., and Fernández-Pereira, J. M. (2015).** Higher reproductive success of small males and greater recruitment of large females may explain strong reversed sexual dimorphism (RSD) in the northern goshawk. *Oecologia*, 177, 379–387.
- Phillips, S. J., and Dudík, M. (2008).** Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, 31, 161–175.
- Piana, R. P. (2013).** Ecology and conservation of a diurnal raptor community within a protected area in northwestern Peru. *Manchester Metropolitan University, Manchester*.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., and R Development Core Team. (2015).** nlme: linear and nonlinear mixed effects models. R package version 3.1–121. URL: <http://CRAN.R-project.org/package=nlme/>.
- Piqué, A., Tricart, P., Guiraud, R., Laville, E., Bouaziz, S., Amrhar, M., and Ouali, R. A. (2002).** The Mesozoic–Cenozoic Atlas belt (North Africa): an overview. *Geodinamica Acta*, 15, 185–208.
- Polakowski, M., Jankowiak, L., Kasprzykowski, Z., Bela, G., Kosmicki, A., Janczyszyn, A., Niemczyk, A., and Kilon, D. (2014).** Autumn migratory movements of raptors along the southern Baltic coast. *Ornis Fennica*, 91, 39–47.
- Price, T. D. (2010).** The roles of time and ecology in the continental radiation of the Old World leaf warblers (*Phylloscopus* and *Seicercus*). *Philosophical Transactions of the Royal Society of London B*, 365, 1749–1762.
- Pulido, F. (2007).** The genetics and evolution of avian migration. *AIBS Bulletin*, 57, 165–174.
- Prum, R. O., Berv, J. S., Dornburg, A., Field, D. J., Townsend, J. P., Lemmon, E. M., and Lemmon, A. R. (2015).** A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature*, 526, 569–573.

- Rainio, M. J., Kanerva, M., Wahlberg, N., Nikinmaa, M., and Eeva, T. (2012).** Variation of basal EROD activities in ten passerine bird species—relationships with diet and migration status. *PLoS One*, 7, e33926.
- Rambaut, A., and Drummond, A. J. (2016).** TreeAnnotator v1.8.3. *University of Edinburgh, Edinburgh, UK*. URL: <http://beast.bio.ed.ac.uk/treeannotator/>.
- Rappole, J. H., Ramos, M. A., and Winker, K. (1989).** Wintering Wood Thrush movements and mortality in southern Veracruz. *The Auk*, 106, 402–410.
- Rappole, J. H., and Jones, P. (2002).** Evolution of old and new world migration systems. *Ardea*, 90, 525–537.
- Ravelo, A. C., Andreasen, D. H., Lyle, M., Lyle, A. O., and Wara, M. W. (2004).** Regional climate shifts caused by gradual global cooling in the Pliocene epoch. *Nature*, 429, 263–267.
- R Development Core Team (2017).** R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*. URL: <http://www.R-project.org/>.
- Rea, D. K., Snoeckx, H., and Joseph, L. H. (1998).** Late Cenozoic eolian deposition in the North Pacific: Asian drying, Tibetan uplift, and cooling of the northern hemisphere. *Paleoceanography*, 13, 215–224.
- Ree, R. H., Moore, B. R., Webb, C. O., and Donoghue, M. J. (2005).** A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution*, 59, 2299–2311.
- Ree, R. H., and Smith, S. A. (2008).** Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic biology*, 57, 4–14.
- Revell, L. J. (2012).** phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3, 217–223.
- Rice, A. M., Vallin, N., Kulma, K., Arntsen, H., Husby, A., Tobler, M., and Qvarnström, A. (2013).** Optimizing the trade-off between offspring number and quality in unpredictable environments: Testing the role of differential androgen transfer to collared flycatcher eggs. *Hormones and Behavior*, 63, 813–822.
- Ricklefs, R., and Bermingham, E. (2008).** The West Indies as a laboratory of biogeography and evolution. *Philosophical Transactions of the Royal Society of London B*, 363, 2393–2413.
- Rolland, J., Jiguet, F., Jonsson, K. A., Condamine, F. L., and Morlon, H. (2014).** Settling down of seasonal migrants promotes bird diversification. *Proceedings of the Royal Society B*, 281, 20140473.
- Ronquist, F. (1997).** Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, 46, 195–203.
- Roulin, A., and Wink, M. (2004).** Predator-prey relationships and the evolution of colour polymorphism: a comparative analysis in diurnal raptors. *Biological Journal of the Linnean Society*, 81, 565–578.
- Rubenstein, D. R. (2015).** Superb starlings: cooperation and conflict in an unpredictable environment. In Koenig, W. D., and Dickinson, J. L., (eds.): *Cooperative breeding in vertebrates: studies of ecology, evolution, and behaviour*. *Cambridge University Press*, 181–196.
- Ruddiman, W. F., and Kutzbach, J. E. (1989).** Forcing of late Cenozoic northern hemisphere climate by plateau uplift in southern Asia and the American West. *Journal of Geophysical Research: Atmospheres*, 94, 18409–18427.
- Rutz, C., Whittingham, M. J., and Newton, I. (2006).** Age-dependent diet choice in an avian top predator. *Proceedings of the Royal Society of London B*, 273, 579–586.

- Sacek, V. (2014).** Drainage reversal of the Amazon River due to the coupling of surface and lithospheric processes. *Earth and Planetary Science Letters*, 401, 301–312.
- Salisbury, C. L., Seddon, N., Cooney, C. R., and Tobias, J. A. (2012).** The latitudinal gradient in dispersal constraints: ecological specialisation drives diversification in tropical birds. *Ecology Letters*, 15, 847–855.
- Sanders, W. J., and Miller, E. R. (2002).** New proboscideans from the early Miocene of Wadi Moghara, Egypt. *Journal of Vertebrate Paleontology*, 22, 388–404.
- Schliep, K. P. (2011).** phangorn: phylogenetic analysis in R. *Bioinformatics*, 27, 592–593.
- Schmutz, J. K., and Fyfe, R. W. (1987).** Migration and mortality of Alberta ferruginous hawks. *The Condor*, 89, 169–174.
- Scotese, C. R., and McKerrow, W. S. (1990).** Revised world maps and introduction. *Geological Society, London, Memoirs*, 12, 1–21.
- Scotese, C. R. (2004).** A continental drift flipbook. *The Journal of Geology*, 112, 729–741.
- Selvatti, A. P., Gonzaga, L. P., and de Moraes Russo, C. A. (2015).** A Paleogene origin for crown passerines and the diversification of the Oscines in the New World. *Molecular Phylogenetics and Evolution*, 88, 1–15.
- Sepulchre, P., Ramstein, G., Fluteau, F., Schuster, M., Tiercelin, J. J., and Brunet, M. (2006).** Tectonic uplift and Eastern Africa aridification. *Science*, 313, 1419–1423.
- Sol, D., Stirling, D. G., and Lefebvre, L. (2005).** Behavioural drive or behavioural inhibition in evolution: subspecific diversification in holarctic passerines. *Evolution*, 59, 2669–2677.
- Somveille, M., Rodrigues, A. S. L., and Manica, A. (2015).** Why do birds migrate? A macroecological perspective. *Global Ecology and Biogeography*, 24, 664–674.
- Stamatakis, A. (2006).** RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22, 2688–2690.
- Strandberg, R., Klaassen, R. H. G., Hake, M., and Alerstam, T. (2009).** How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors. *Biology Letters*, rsbl20090785.
- Sustaita, D., and Hertel, F. (2010).** In vivo bite and grip forces, morphology and prey-killing behavior of North American accipiters (Accipitridae) and falcons (Falconidae). *The Journal of Experimental Biology*, 213, 2617–2628.
- Tellería, J. L., Blázquez, M., De La Hera, I., and Pérez-Tris, J. (2013).** Migratory and resident Blackcaps *Sylvia atricapilla* wintering in southern Spain show no resource partitioning. *Ibis*, 155, 750–761.
- Terraube, J., Guixé, D., and Arroyo, B. (2014).** Diet composition and foraging success in generalist predators: Are specialist individuals better foragers? *Basic and Applied Ecology*, 15, 616–624.
- Thompson, J. N. (2016).** Coevolution, local adaptation and ecological speciation. *Molecular Ecology*, 25, 5608–5610.
- Thomson, R. L., Griesser, M., Laaksonen, T., and Korpimäki, E. (2014).** Brood size manipulations in a spatially and temporally varying environment: male Tengmalm’s owls pass increased reproductive costs to offspring. *Oecologia*, 176, 423–430.
- Udvardy, M. D. F. (1975).** A classification of the biogeographical provinces of the world. *International Union of Conservation of Nature and Natural Resources, Morges, IUCN Occasional Paper*, 18, 1–48.
- Voelker, G., and Klicka, J. (2008).** Systematics of *Zoothera* thrushes, and a synthesis of true thrush molecular systematic relationships. *Molecular Phylogenetics and Evolution*, 49, 377–381.
- Voelker, G., and Outlaw, R. K. (2008).** Establishing a perimeter position: speciation around the Indian Ocean Basin. *Journal of Evolutionary Biology*, 21, 1779–1788.

- Voelker, G., Rohwer, S., Bowie, R. C. K., and Outlaw, D. C. (2007).** Molecular systematics of a speciose, cosmopolitan songbird genus: Defining the limits of, and relationships among, the *Turdus* thrushes. *Molecular Phylogenetics and Evolution*, 42, 422–434.
- Voelker, G., Rohwer, S., Outlaw, D. C., and Bowie, R. C. K. (2009).** Repeated trans-Atlantic dispersal catalysed a global songbird radiation. *Global Ecology and Biogeography*, 18, 41–49.
- Voelker, G., Bowie, R. C. K., and Klicka, J. (2013).** Gene trees, species trees and Earth history combine to shed light on the evolution of migration in a model avian system. *Molecular Ecology*, 22, 3333–3344.
- Voskamp, A., Baker, D. J., Stephens, P. A., Valdes, P. J., and Willis, S. G. (2017).** Global patterns in the divergence between phylogenetic diversity and species richness in terrestrial birds. *Journal of biogeography*, 44, 709–721.
- Waida, M. (1978).** Birds in the mythology of sacred kingship. *East and West*, 28, 283–289.
- Wallace, A. R. (1876).** The geographical distribution of animals: with a study of the relations of living and extinct faunas as elucidating the past changes of the Earth's surface: in two volumes. *Harper & Brothers Publishers, New York*.
- Wang, N., Kimball, R. T., Braun, E. L., Liang, B., and Zhang, Z. (2017).** Ancestral range reconstruction of Galliformes: the effects of topology and taxon sampling. *Journal of Biogeography*, 44, 122–135.
- Winger, B. M., Lovette, I. J., and Winker, D. W. (2012).** Ancestry and evolution of seasonal migration in the Parulidae. *Proceedings of the Royal Society B*, 279, 610–618.
- Winger, B. M., Barker, F. K., and Ree, R. H. (2014).** Temperate origins of long-distance seasonal migration in New World songbirds. *Proceedings of the National Academy of Sciences*, 111, 12115–12120.
- Wink, M., and Sauer-Gürth, H. (2004).** Phylogenetic relationships in diurnal raptors based on nucleotide sequences of mitochondrial and nuclear marker genes. *Raptors Worldwide*, 483–498.
- Wink, M., El-Sayed, A.-A., Sauer-Gürth, H., and Gonzalez, J. (2009).** Molecular phylogeny of owls (Strigiformes) inferred from DNA sequences of the mitochondrial cytochrome b and the nuclear RAG-1 gene. *Ardea*, 97, 581–591.
- Winker, K., and Pruett, C. L. (2006).** Seasonal migration, speciation, and morphological convergence in the genus *Catharus* (Turdidae). *The Auk*, 123, 1052–1068.
- Zachos, J., Pagani, M., Sloan, S., Thomas, E., and Billups, K. (2001).** Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, 292, 686–693.
- Zhang, R., Jiang, D., Ramstein, G., Zhang, Z., Lippert, P. C., and Yu, E. (2018).** Changes in Tibetan Plateau latitude as an important factor for understanding East Asian climate since the Eocene: A modeling study. *Earth and Planetary Science Letters*, 484, 295–308.
- Zheng, H., Powell, C. M., An, Z., Zhou, J., and Dong, G. (2000).** Pliocene uplift of the northern Tibetan Plateau. *Geology*, 28, 715–718.
- Zhisheng, A., Kutzbach, J. E., Prell, W. L., and Porter, S. C. (2001).** Evolution of Asian monsoons and phased uplift of the Himalaya–Tibetan plateau since Late Miocene times. *Nature*, 411, 62–66.
- Zink, R. M., Rohwer, S., Andreev, A. V., and Dittmann, D. L. (1995).** Trans-Beringia comparisons of mitochondrial DNA differentiation in birds. *The Condor*, 97, 639–649.
- Zink, R. M., Rohwer, S., Drovetski, S., Blackwell-Rago, R. C., and Farrell, S. L. (2002).** Holarctic phylogeography and species limits of three-toed woodpeckers. *The Condor*, 104, 167–170.
- Zink, R. M. (2011).** The evolution of avian migration. *Biological Journal of the Linnean Society*, 104, 237–250.

Zurell, D., Gallien, L., Graham, C. H., and Zimmermann, N. E. (2018). Do long-distance migratory birds track their niche through seasons? *Journal of Biogeography*, jbi13351.

Appendix

Table A1. Variable importance (%) based on model averages of maximum entropy modelling of Accipitriformes. Highest values are indicated in bold.

Species	AUC	Temperature			Precipitation	
		Seasonality	Mean of driest quarter	Mean of warmest quarter	Seasonality	Mean of driest quarter
<i>Accipiter bicolor</i>	0.5775	2.8821	20.1638	20.9257	14.4276	41.6008
<i>Accipiter gularis</i>	0.6084	8.8615	33.6877	13.6120	22.8412	20.9977
<i>Accipiter rufiventris</i>	0.7063	12.0605	8.7965	77.0273	2.0561	0.0597
<i>Accipiter soloensis</i>	0.6665	17.6452	25.3855	14.3132	18.2337	24.4224
<i>Accipiter superciliosus</i>	0.6117	36.7241	10.9351	12.5675	23.9845	15.7888
<i>Accipiter tachiro</i>	0.6751	30.4718	8.7588	22.0374	10.2314	28.5006
<i>Accipiter virgatus</i>	0.6371	15.4676	23.6768	18.6124	32.0842	10.1590
<i>Aquila adalberti</i>	0.5793	20.0000	20.0000	0.0000	20.0000	0.0000
<i>Aquila clanga</i>	0.6088	25.7949	9.7968	18.9838	37.8676	7.5569
<i>Aquila nipalensis</i>	0.6485	29.6088	26.4372	24.0238	13.7935	6.1366
<i>Aquila pomarina</i>	0.6152	60.4439	22.6187	1.3688	14.5157	1.0529
<i>Aquila spilogaster</i>	0.6376	28.0270	14.4686	21.3440	32.1121	4.0484
<i>Aquila verreauxii</i>	0.6382	23.7901	5.3092	19.0278	33.9892	17.8836
<i>Aviceda subcristata</i>	0.6719	22.0618	36.8531	13.8189	7.9079	19.3584
<i>Busarellus nigricollis</i>	0.5712	31.9156	8.0318	27.9035	14.0035	18.1457
<i>Butastur indicus</i>	0.6237	6.8384	36.6606	27.9970	10.0013	18.5027
<i>Butastur rufipennis</i>	0.6076	18.2757	9.1735	9.1819	12.6368	50.7321
<i>Buteo albicaudatus</i>	0.5876	38.2173	11.9837	13.8247	28.5702	7.4041
<i>Buteo augur</i>	0.5996	56.3220	8.5484	4.0589	14.7441	16.3267
<i>Buteo auguralis</i>	0.6566	19.0870	17.5819	29.0799	18.4333	15.8178
<i>Buteo brachypterus</i>	0.6955	0.0000	92.1458	6.2502	0.0000	1.6040
<i>Buteo galapagoensis</i>	0.7080	0.0000	99.6691	0.0000	0.3309	0.0000
<i>Buteo hemilasius</i>	0.6075	22.4618	26.5569	13.8746	17.6161	19.4906
<i>Buteo lagopus</i>	0.6105	30.5498	34.9786	8.2842	5.7809	20.4066
<i>Buteo leucorrhous</i>	0.6131	14.6050	20.9765	11.5287	20.5552	32.3345
<i>Buteo magnirostris</i>	0.5615	27.3516	22.5798	21.6361	11.5487	16.8838
<i>Buteo nitidus</i>	0.5874	17.7024	31.8704	12.5396	23.0103	14.8774
<i>Buteo oreophilus</i>	0.6067	32.1914	0.0000	4.8620	20.5270	22.4197
<i>Buteo platypterus</i>	0.6034	13.8594	9.2688	35.6660	19.2602	21.9456
<i>Buteo polyosoma</i>	0.6487	41.7965	18.6154	11.1895	20.4361	7.9626
<i>Buteo ridgwayi</i>	0.5820	0.0000	0.0000	7.4693	52.5307	0.0000

Buteo rufofuscus	0.7176	38.5291	24.5875	14.3132	3.2338	19.3364
Buteo solitarius	0.5913	17.7975	0.0000	0.0000	20.0000	2.2025
Buteo swainsoni	0.5865	13.5509	12.9989	12.2489	44.9985	16.2030
Buteo ventralis	0.6455	40.9127	5.2521	2.1622	29.7519	21.9211
Buteogallus aequinoctialis	0.5726	63.9353	32.6783	0.0000	0.8126	2.5737
Buteogallus meridionalis	0.5726	6.2558	20.0990	11.9749	28.2502	33.4201
Buteogallus urubitinga	0.5803	15.9414	7.8778	21.4820	27.5068	27.1920
Chondrohierax uncinatus	0.5897	33.7893	17.9841	18.7248	20.3114	9.1903
Circaetus cinerascens	0.6327	16.7817	30.1851	24.4052	17.3438	11.2842
Circaetus cinereus	0.6353	15.0790	36.6986	25.9145	16.2506	6.0573
Circaetus fasciolatus	0.6286	24.2080	0.1667	0.7350	19.2738	55.6164
Circaetus gallicus	0.6167	28.5044	20.7921	6.9520	10.8168	32.9348
Circaetus pectoralis	0.6230	25.8889	38.6965	4.7078	4.3677	26.3392
Circus macrourus	0.6025	27.5128	13.9147	11.0623	13.9852	33.5250
Circus pygargus	0.6337	26.1671	37.9561	9.1452	7.0901	19.6416
Circus ranivorus	0.6634	29.9850	22.1361	12.0309	9.2375	26.6105
Elanoides forficatus	0.6101	25.4745	7.9612	30.4219	10.7288	25.4136
Elanus leucurus	0.5763	13.8236	13.1735	11.5880	16.3899	45.0251
Eutriorchis astur	0.7364	99.4340	0.0000	0.0000	0.0000	0.5660
Gampsonyx swainsonii	0.5763	24.2134	31.2097	8.0576	21.0146	15.5048
Geranoaetus melanoleucus	0.5905	29.0866	25.4574	13.4945	5.7049	26.2566
Geranospiza caerulescens	0.5755	30.2031	20.6452	14.1284	24.3966	10.6267
Gypaetus barbatus	0.6408	17.3276	20.1334	10.1857	16.1987	36.1546
Gypohierax angolensis	0.6747	22.3998	10.6530	4.3783	48.9391	13.6297
Gyps africanus	0.6416	18.5189	36.9203	17.8346	21.7634	4.9628
Gyps bengalensis	0.6088	7.6420	21.4871	11.3494	12.0077	47.5138
Gyps coprotheres	0.6790	23.4709	2.8933	4.3986	47.5324	21.7048
Gyps himalayensis	0.6385	26.6750	35.0803	10.8022	7.0853	20.3572
Gyps indicus	0.6580	4.8145	16.7370	0.3575	17.9602	60.1307
Gyps rueppelli	0.6519	33.9388	7.0409	43.3959	6.3444	9.2799
Gyps tenuirostris	0.6719	36.3831	22.1041	29.7341	6.5988	5.1799
Haliaeetus leucogaster	0.6220	14.5741	12.1093	23.4767	11.1031	38.7369
Haliaeetus vocifer	0.6120	23.2881	17.0076	20.0685	19.9606	19.6753
Haliaeetus vociferoides	0.6258	0.0000	4.9703	1.5644	0.0000	93.4653
Haliastur indus	0.6021	30.6512	11.2684	26.8069	8.1029	23.1705
Haliastur sphenurus	0.5971	15.0644	28.1733	5.1867	22.4651	29.1104

Harpagus bidentatus	0.6011	25.7893	12.1258	3.1275	33.7557	25.2016
Harpagus diodon	0.6803	24.1316	28.1446	24.7198	9.3386	13.6654
Harpia harpyja	0.5837	36.7218	15.3027	14.3611	13.9727	19.6416
Harpyhaliaetus coronatus	0.6273	23.2163	17.6731	13.9302	30.9216	14.2587
Harpyhaliaetus solitarius	0.6760	7.3604	29.3392	54.6728	5.0049	3.6226
Hieraaetus ayresii	0.6572	24.5886	28.8528	5.1580	23.3039	18.0967
Hieraaetus fasciatus	0.6751	8.3289	12.3862	23.9886	43.4684	11.8279
Hieraaetus kienerii	0.6121	17.7559	24.9280	19.9182	18.7101	18.6878
Hieraaetus pennatus	0.6519	17.5735	44.1645	14.1110	14.5278	9.6232
Ichthyophaga ichthyaetus	0.6432	24.3393	16.6997	9.5299	12.7913	36.6398
Ictinaetus malayensis	0.6660	22.6218	19.0851	21.2527	20.9916	16.0488
Ictinia mississippiensis	0.6082	15.4787	25.1076	1.5610	29.2383	28.6144
Kaupifalco monogrammicus	0.6211	35.3591	10.6754	25.3751	11.7064	16.8840
Leptodon cayanensis	0.5722	21.8244	17.8307	20.4419	32.4169	7.4861
Leucopternis albicollis	0.5909	39.7131	5.7504	23.9656	14.3376	16.2334
Lophaetus occipitalis	0.6305	31.1870	16.4565	13.4180	19.5013	19.4373
Melierax canorus	0.6579	25.2795	7.1308	6.7302	17.6343	43.2253
Melierax poliopterus	0.6465	42.4794	18.4659	2.8607	11.3891	24.8049
Micronisus gabar	0.6285	16.4029	47.6350	15.1479	12.0497	8.7644
Morphnus guianensis	0.5780	36.2583	10.2694	15.6186	11.6459	26.2078
Necrosyrtes monachus	0.6121	29.3329	5.9549	12.9672	28.6406	23.1044
Nisaetus alboniger	0.6432	2.1777	39.1643	21.6554	5.2955	31.7072
Nisaetus nanus	0.6433	14.6254	2.2100	5.4250	55.7615	21.9780
Nisaetus nipalensis	0.6629	37.7057	9.3436	23.2839	7.0032	22.6636
Oroaetus isidori	0.7322	35.2481	36.4059	0.6540	15.1483	12.5438
Pandion haliaetus	0.5822	21.0256	41.7847	12.8679	11.3616	12.9602
Parabuteo unicinctus	0.5889	10.5526	28.5396	8.2531	23.2534	29.4013
Pernis apivorus	0.6007	38.2969	17.8378	14.6928	9.3246	19.8479
Pithecophaga jefferyi	0.6203	20.0000	8.9018	0.0000	0.0000	51.0982
Polemaetus bellicosus	0.6085	5.0596	36.8848	32.9008	15.6723	9.4825
Polyboroides typus	0.6265	61.1766	3.8870	11.5796	19.7787	3.5782

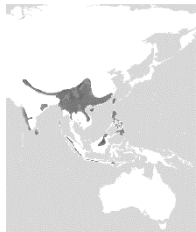
Sagittarius serpentarius	0.6434	16.5037	19.1092	27.9871	27.3708	9.0293
Sarcogyps calvus	0.6313	22.8221	7.8934	24.2783	15.1353	29.8709
Spizaetus africanus	0.6635	36.0250	0.7200	4.0309	36.3997	22.8243
Spizaetus cirrhatus	0.6255	25.9924	17.7362	23.8628	21.1260	11.2827
Spizaetus lanceolatus	0.5889	0.0000	20.0000	0.0000	40.0000	0.0000
Spizaetus ornatus	0.5999	10.0716	39.0099	12.1350	3.6638	35.1196
Spizaetus tyrannus	0.5995	35.6045	25.0454	10.6216	12.8925	15.8360
Spizastur melanoleucus	0.5914	21.4397	27.2993	28.0042	10.8741	12.3828
Stephanoaetus coronatus	0.6786	14.7338	6.2570	10.2712	8.6270	60.1110
Terathopius ECAUDATUS	0.6138	27.4434	16.8967	18.0402	19.6686	17.9511
Torgos tracheliotos	0.6292	31.1885	22.4269	25.3035	16.7497	4.3314
Trigonoceps occipitalis	0.6748	12.6347	12.8205	9.2255	34.7579	30.5613

Figure A1. Suitable areas for raptor species within their distribution ranges. The colour gradient indicates the degree of suitability (from 0 – white, to 1 – black).

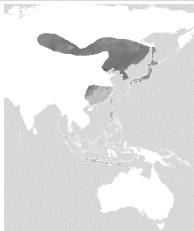
Accipiter bicolor



Accipiter virgatus



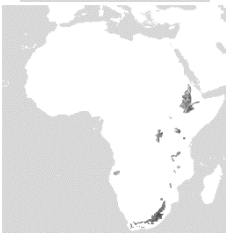
Accipiter gularis



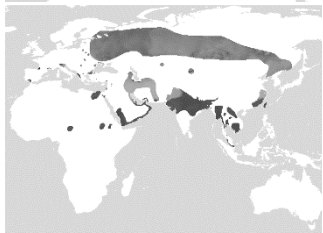
Aquila adalberti



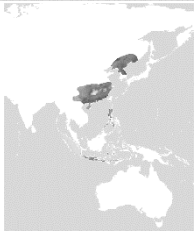
Accipiter rufiventris



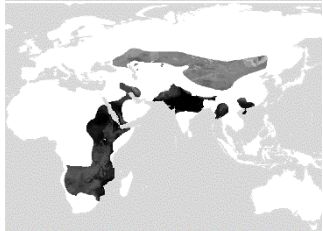
Aquila clanga



Accipiter soloensis



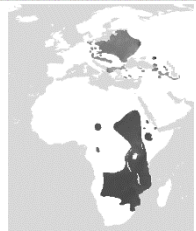
Aquila nipalensis



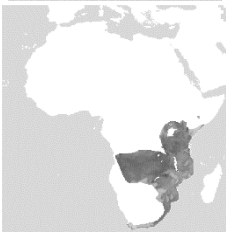
Accipiter superciliosus



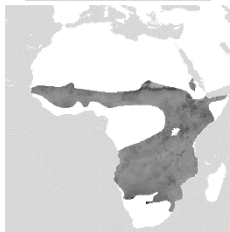
Aquila pomarina



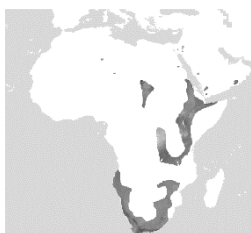
Accipiter tachiro



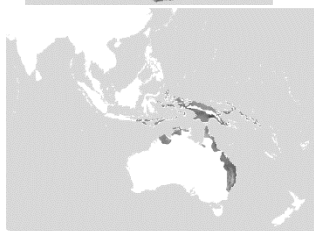
Aquila spilogaster



Aquila verreauxii



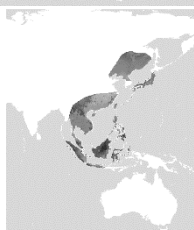
Aviceda subcristata



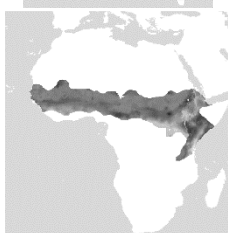
Busarellus nigricollis



Butastur indicus



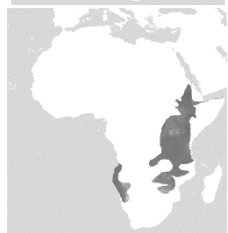
Butastur rufipennis



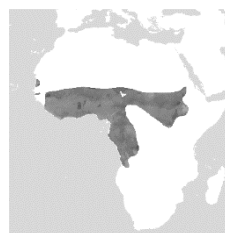
Buteo albicaudatus



Buteo augur



Buteo auguralis



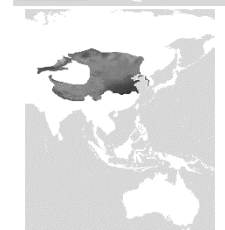
Buteo brachypterus



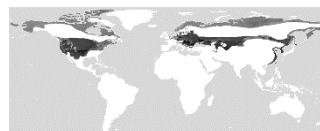
Buteo galapagoensis



Buteo hemilasius



Buteo lagopus



Buteo leucorrhous



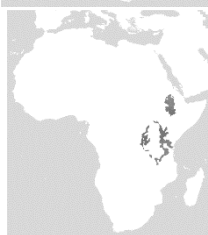
Buteo magnirostris



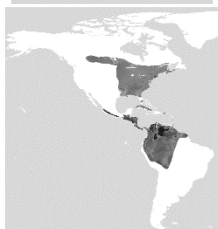
Buteo nitidus



Buteo oreophilus



Buteo platypterus



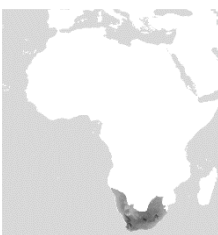
Buteo polyosoma



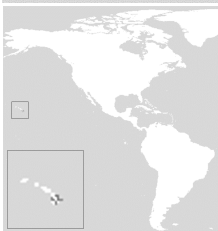
Buteo ridgwayi



Buteo rufofuscus



Buteo solitarius



Buteo swainsoni



Buteo ventralis



*Buteogallus
aequinoctialis*



*Buteogallus
meridionalis*



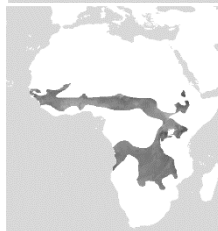
*Buteogallus
urubitinga*



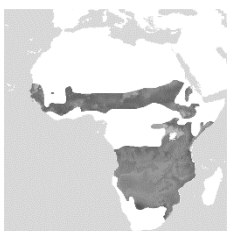
*Chondrohierax
uncinatus*



*Circetus
cinerascens*



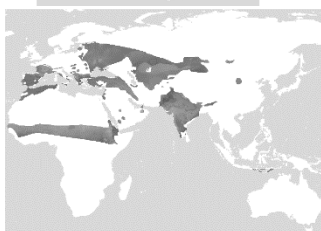
Circaetus cinereus



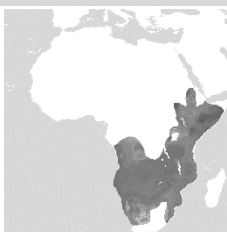
Circaetus fasciolatus



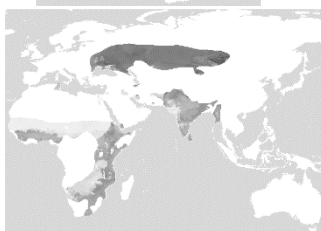
Circaetus gallicus



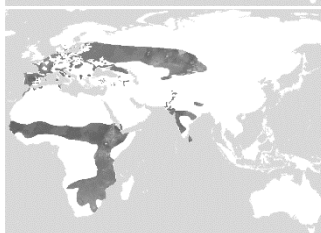
Circaetus pectoralis



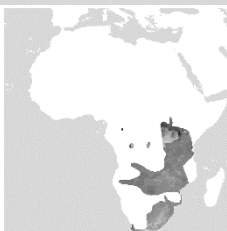
Circus macrourus



Circus pygargus



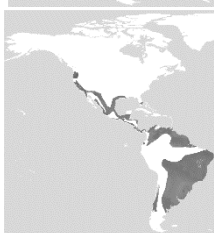
Circus ranivorus



Elanoides forficatus



Elanus leucurus



Eutriorchis astur



Gampsonyx swainsonii



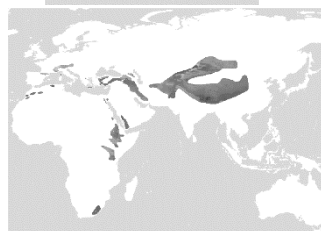
Geranoaetus melanoleucus



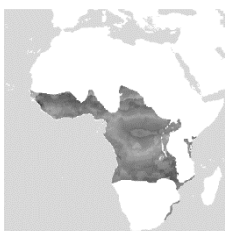
Geranospiza caerulescens



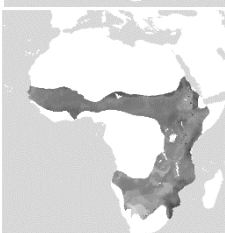
Gypaetus barbatus



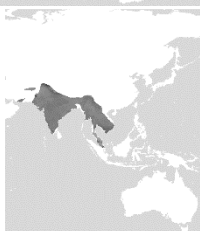
*Gypohierax
angolensis*



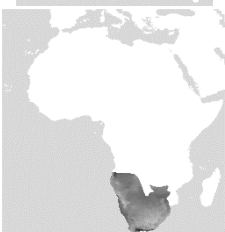
Gyps africanus



Gyps bengalensis



Gyps coprotheres



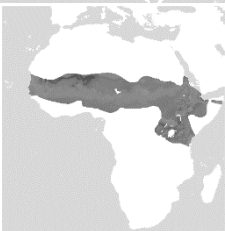
Gyps himalayensis



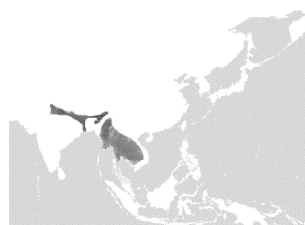
Gyps indicus



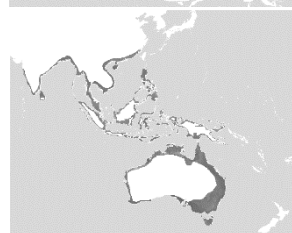
Gyps rueppelli



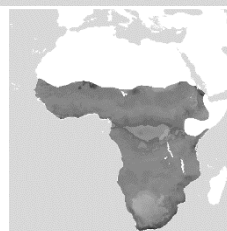
Gyps tenuirostris



*Haliaeetus
leucogaster*



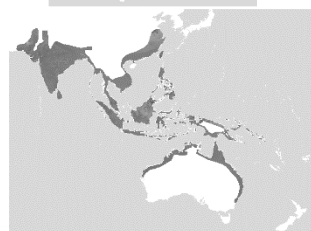
Haliaeetus vocifer



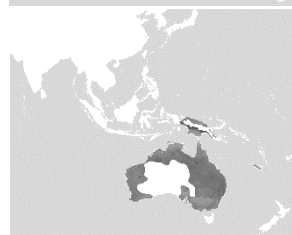
*Haliaeetus
vociferoides*



Haliastur indus



*Haliastur
sphenurus*



*Harpagus
bidentatus*



Harpagus diodon



Harpia harpyja



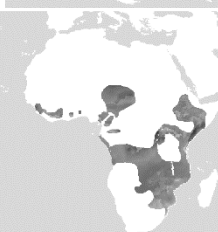
Harpyhaliaetus coronatus



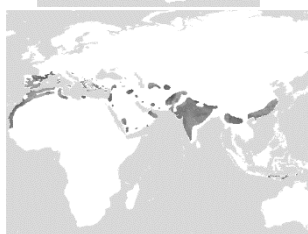
Harpyhaliaetus solitarius



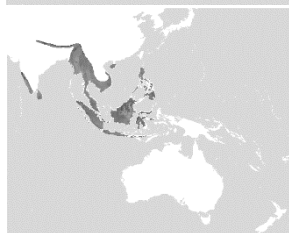
Hieraaetus ayresii



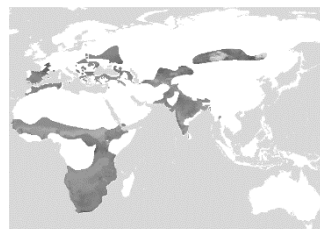
Hieraaetus fasciatus



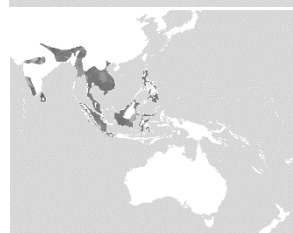
Hieraaetus kienerii



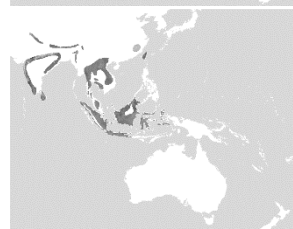
Hieraaetus pennatus



Ichthyophaga ichthyaetus



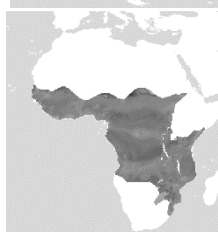
Ictinaetus malayensis



Ictinia mississippiensis



Kaupifalco monogrammicus



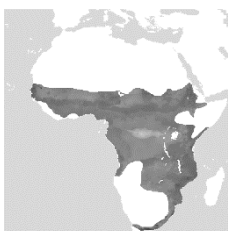
Leptodon cayanensis



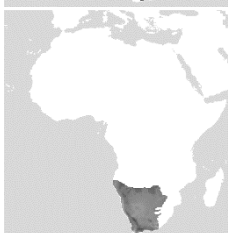
Leucopternis albigollis



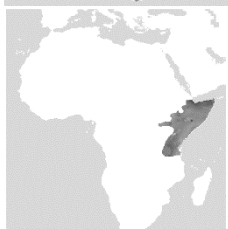
Lophaetus
occipitalis



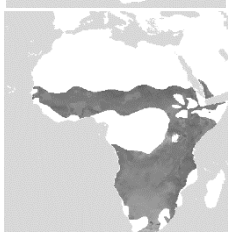
Melierax
canorus



Melierax
poliopterus



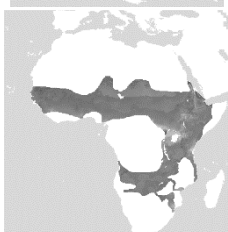
Micronisus
gabari



Morphnus
guianensis



Necrosyrtes
monachus



Nisaetus
alboniger



Nisaetus
nanus



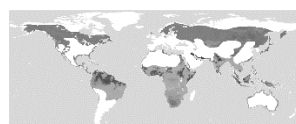
Nisaetus
nipalensis



Oroaetus
isidori



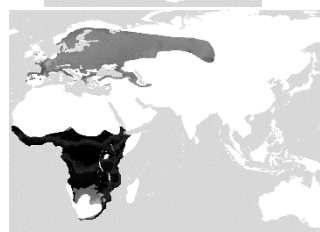
Pandion
haliaetus



Parabuteo
unicinctus



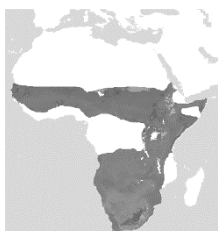
Pernis
apivorus



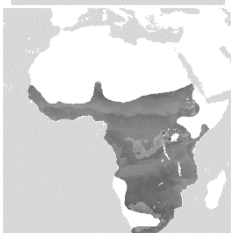
Pithecophaga
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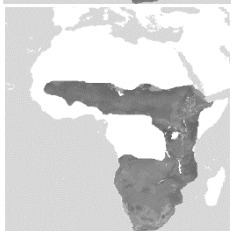
*Polemaetus
bellicosus*



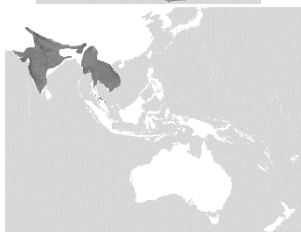
*Polyboroides
typus*



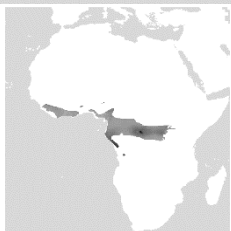
*Sagittarius
serpentarius*



Sarcogyps calvus



*Spizaetus
africanus*



*Spizaetus
cirrhatus*



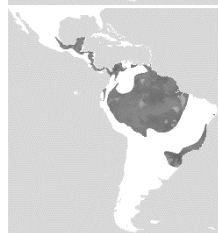
*Spizaetus
lanceolatus*



Spizaetus ornatus



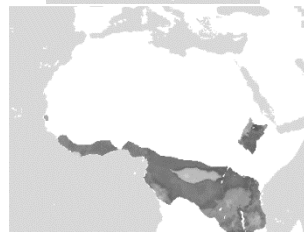
*Spizaetus
tyrannus*



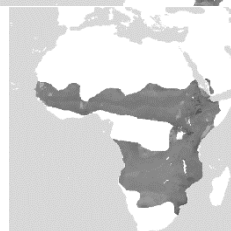
*Spizastur
melanoleucus*



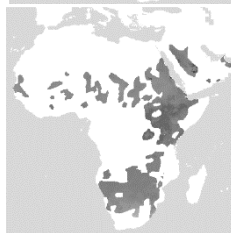
*Stephanoaetus
coronatus*



*Terathopius
ECAUDATUS*



*Torgos
tracheliotos*



*Trigonoceps
occipitalis*

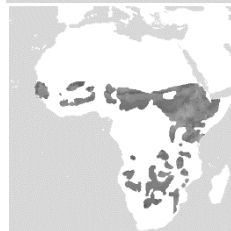


Table A2. Data on species of Turdidae in detail. N is the number of records, Bp is the average length of base pairs.

Species	N	Bp.	Species	N	Bp.	Species	N	Bp.
Alethe choloensis	4	846.50	Psophocichla litsitsirupa	9	775.78	Turdus olivaceus	23	659.70
Alethe diademata	58	796.33	Sialia currucoides	9	659.33	Turdus olivater	9	723.78
Alethe poliocephala	37	843.95	Sialia mexicana	39	546.64	Turdus pallidus	34	591.41
Alethe poliophrys	5	903.80	Sialia sialis	21	550.38	Turdus pelios	12	261.55
Brachypteryx hyperythra	2	1075	Stizorhina fraseri	2	664.57	Turdus philomelos	8	691.50
Brachypteryx leucophrys	16	741.75	Turdus albicollis	7	664.57	Turdus pilaris	26	691.50
Brachypteryx montana	57	727.03	Turdus albocinctus	45	768.11	Turdus plebejus	19	641.68
Brachypteryx stellata	5	727.03	Turdus amaurochalinus	9	722.78		10	715.20
	6	851.17		30	643.43	Turdus plumbeus	11	868.41
Catharus aurantiirostris	16	713.81	Turdus assimilis	45	1045.62	Turdus poliocephalus	64	884.44
Catharus bicknelli	11	743.93	Turdus aurantius	10	811.10	Turdus reevei	7	744.14
Catharus dryas	3	743.93	Turdus bewsheri	11	731.27	Turdus rubrocanus	11	782.91
Catharus frantzii	28	693.43	Turdus boubou	8	651.25	Turdus ruficollis	16	701.81
Catharus fuscater	12	892.15	Turdus cardis	17	666.18	Turdus rufitorques	5	689.20
Catharus fuscescens	22	647.41	Turdus celanops	8	693.25	Turdus rufiventris	23	1432.30
Catharus gracilirostris	57	726.82	Turdus chiguanco	14	773.50	Turdus rufopalliat	93	1071.02
Catharus guttatus	20	687.70	Turdus chrysolaus	33	636.27	Turdus serranus	7	744.29
Catharus mexicanus	16	903.94	Turdus daguae	12	1095.92	Turdus subalaris	8	578.75
Catharus minimus	13	733.23	Turdus dissimilis	8	559.13	Turdus swalesi	7	742.43
Catharus occidentalis	20	848.27	Turdus falcklandii	11	761.88	Turdus tephronotus	3	817
Catharus ustulatus	19	807.36	Turdus feae	7	695.50	Turdus torquatus	75	440.24
Chaetops aurantius	5	807.36	Turdus flavipes	4	695.50	Turdus unicolor	5	724.40
Chaetops frenatus	2	557	Turdus fulviventris	10	714	Turdus viscivorus	25	747.52
Chamaetylas fuelleborni	13	870.62	Turdus fumigatus	7	743.29	Zoothera andromedae	5	712.80
	4	994.75		18	746.78			

Chlamydochaera jefferyi	7	761.71	Turdus fuscater	10	696.50	Zoothera camaronensis	9	754.22
Cichlherminia lherminieri	114	628.82	Turdus grayi	43	865.93	Zoothera cinerea	3	877.67
Cichlopsis leucogenys	5	879.20	Turdus haplochrous	7	695	Zoothera crossleyi	6	795
Cochoa purpurea	5	518.40	Turdus hauxwelli	27	706.11	Zoothera dauma	86	692.44
Cochoa viridis	10	783.40	Turdus helleri	21	535.62	Zoothera dixonii	20	757.25
Entomodestes coracinus	2	732.50	Turdus hortulorum	11	2179	Zoothera dohertyi	2	886.50
Entomodestes leucotis	21	729	Turdus ignobilis	294	587.19	Zoothera erythronota	2	1017
Geokichla citrina	30	748.80	Turdus iliacus	63	381.49	Zoothera everetti	2	599.50
Geokichla interpres	2	1019.50	Turdus infuscatus	4	698	Zoothera gurneyi	7	914.86
Grandala coelicolor	7	746.29	Turdus jamaicensis	7	742.14	Zoothera guttata	2	952.50
Heinrichia calligyna	9	699	Turdus kessleri	6	673.50	Zoothera heinei	5	895.20
Hylocichla mustelina	53	447.85	Turdus lawrencii	15	656.53	Zoothera heinrichi	2	866
Ixoreus naevius	25	644.04	Turdus leucomelas	32	618.94	Zoothera lunulata	6	899.50
Myadestes coloratus	12	863.92	Turdus leucops	14	942	Zoothera margaretae	3	811.67
Myadestes elisabeth	4	909.25	Turdus libonyana	14	699.64	Zoothera marginata	5	895.20
Myadestes genibarbis	35	863.77	Turdus ludoviciae	3	791.33	Zoothera mendeni	4	690.50
Myadestes melanops	12	816.92	Turdus maculirostris	9	809.67	Zoothera mollissima	53	826.85
Myadestes obscurus	6	802.50	Turdus maranonicus	14	629.64	Zoothera monticola	7	911.57
Myadestes occidentalis	40	912.03	Turdus menachensis	3	340.67	Zoothera oberlaenderi	3	745.67
Myadestes ralloides	39	793.05	Turdus merula	625	700.09	Zoothera peronii	2	995
Myadestes townsendi	29	812.66	Turdus migratorius	125	713.04	Zoothera piaggiae	2	1007.50
Myadestes unicolor	26	804.77	Turdus mupinensis	7	647.57	Zoothera pinicola	11	583.36
Myophonus borneensis	3	951	Turdus naumanni	32	1116.78	Zoothera princei	10	768.90
Myophonus caeruleus	12	777.17	Turdus nigrescens	7	742.43	Zoothera schistacea	6	810.33
Myophonus glaucinus	4	742	Turdus nigriceps	16	656.94	Zoothera sibirica	11	780.09
Myophonus melanurus	4	671.50	Turdus nudigenis	33	728.27	Zoothera spiloptera	2	968.50

Neocossyphus poensis	13	854.08	Turdus obscurus	18	751.94	Zoothera talaseae	5	894.60
Neocossyphus rufus	14	743.29	Turdus obsoletus	10	714.90	Zoothera tanganjicae	2	970
Nesocichla eremita	7	826.43	Turdus olivaceofuscus	19	805.84	Zoothera wardii	4	797.75

Figure A2. Phylogeny of Turdidae. Numbers indicate posterior probability values.

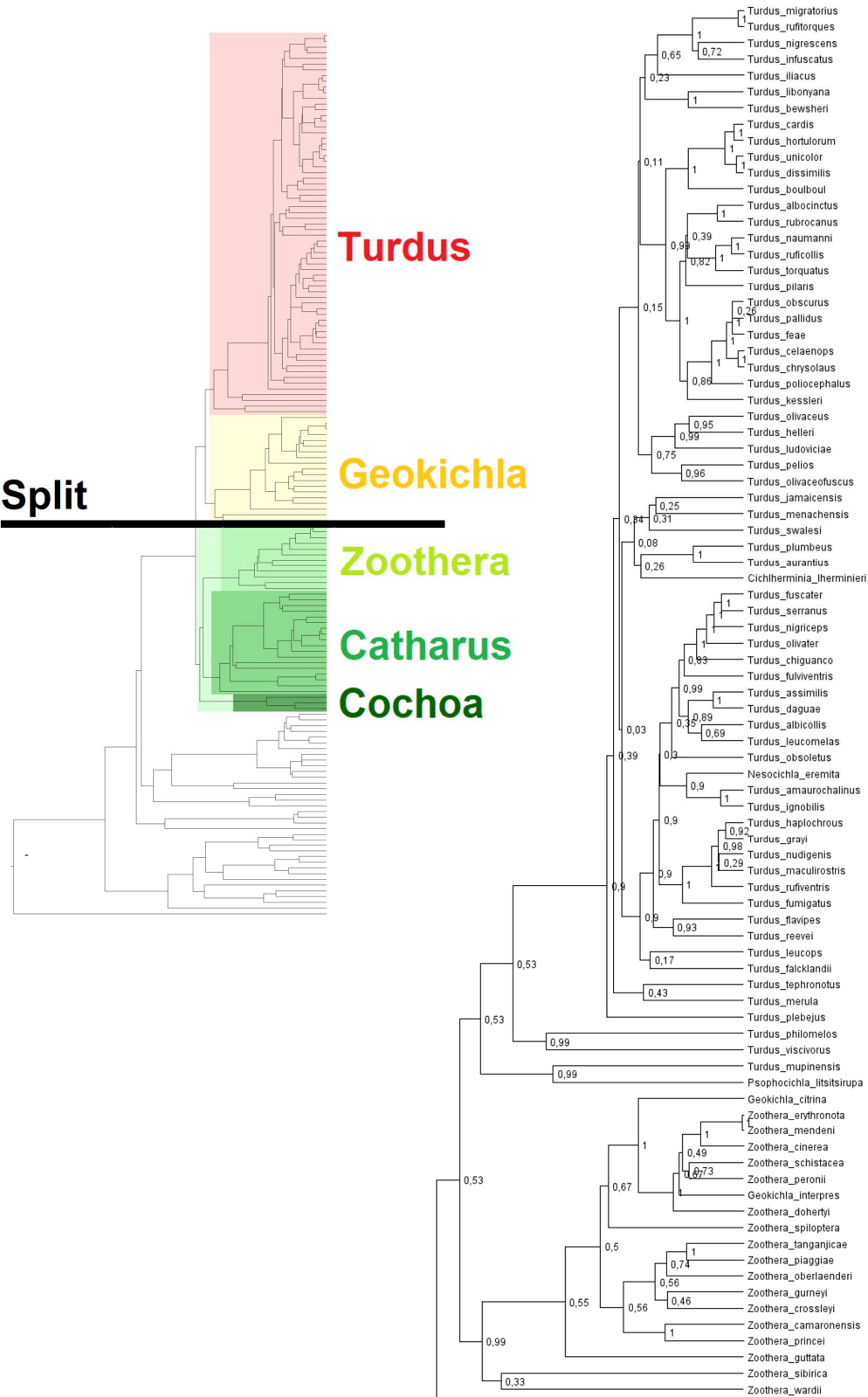


Figure A2. Continue.

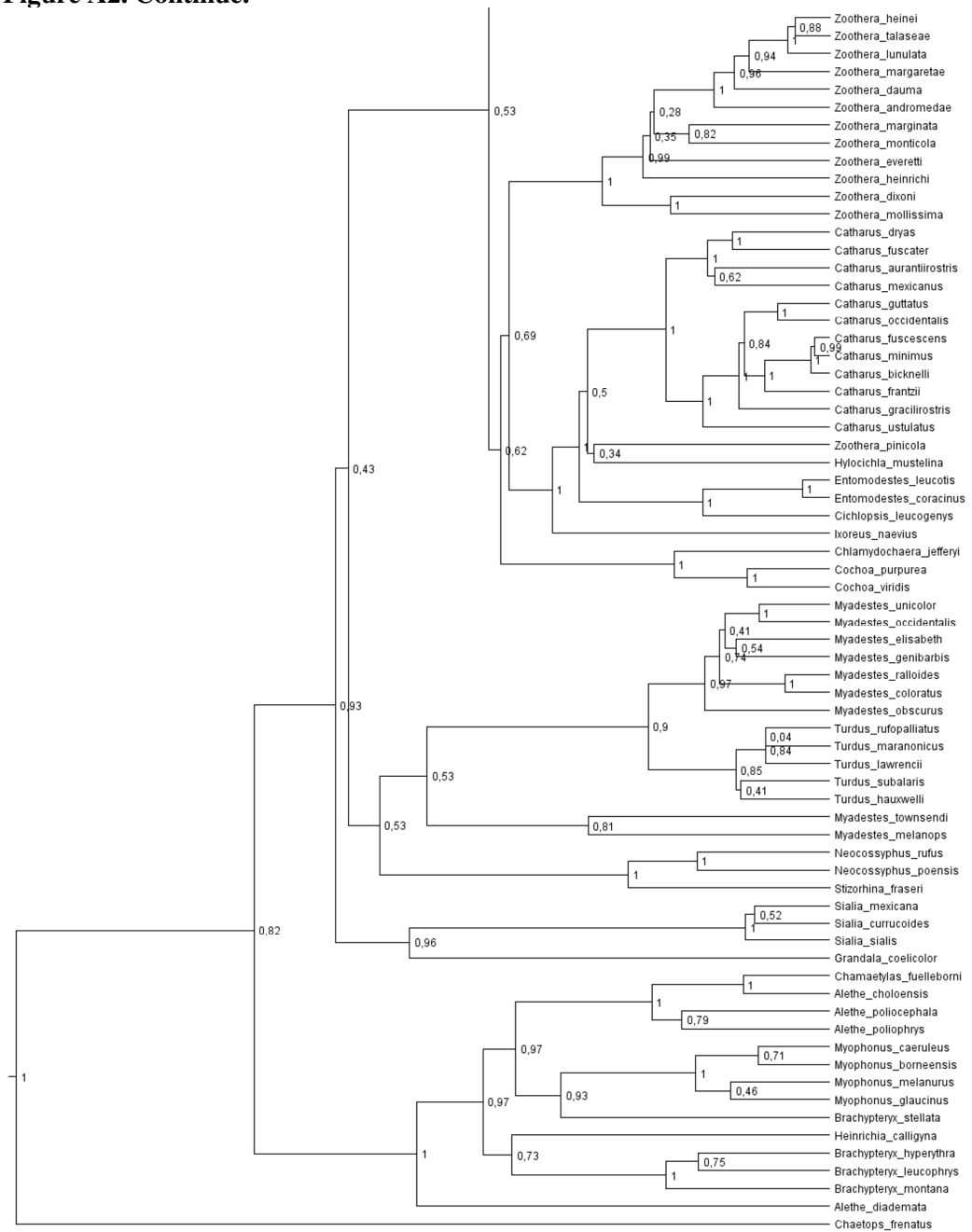


Figure A3. The density map of 72 *Turdus* species. Most of the migratory species breed in an extended area along an East-West axis. This pattern of breeding and wintering areas might be a fingerprint, as a consequences of the ‘along-latitudinal first’ type of migration in this group.

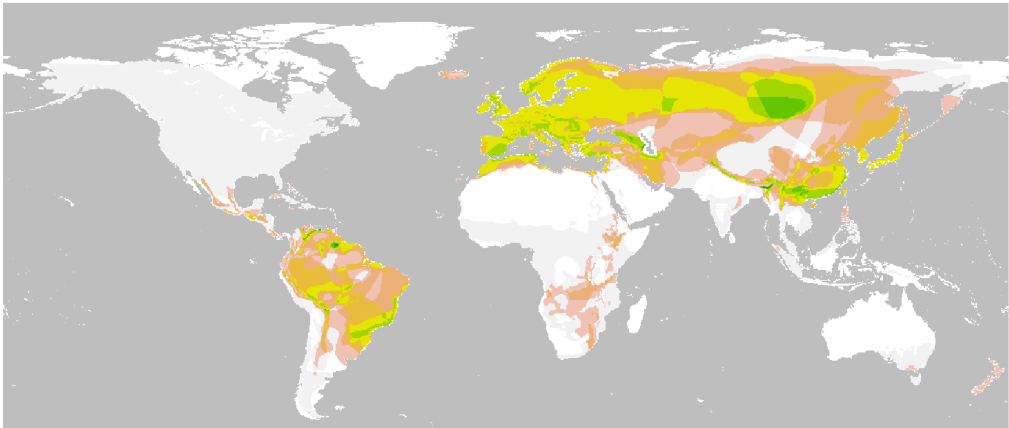


Table A3. Variable importance (%) based on model averages of maximum entropy modelling of *Turdus* species. Highest values are indicated in bold.

Species	AUC	Temperature				Precipitation			
		Isothermality	Seasonality	Mean of driest quarter	Mean of warmest quarter	Annual	Seasonality	Mean of driest quarter	Mean of warmest quarter
<i>Psophocichla litsitsirupa</i>	0.7421	9.106	12.3046	19.611	9.3201	22.541	18.2467	1.4764	7.3942
<i>Turdus albicollis</i>	0.6566	16.0821	7.3944	10.7276	17.0413	11.7841	14.9304	14.7637	7.2764
<i>Turdus albocinctus</i>	0.7621	0	0.0006	0	47.7582	20.8287	24.4569	3.707	3.2487
<i>Turdus amaurochalinus</i>	0.7101	36.274	12.3993	15.4375	10.5174	4.4997	3.0958	13.2435	4.5329
<i>Turdus assimilis</i>	0.7148	5.2852	11.9602	0.2679	3.5476	6.2543	4.8475	67.2116	0.6258
<i>Turdus aurantius</i>	0.5937	1.0274	28.0512	0	0	20	0	0	10.9215
<i>Turdus boulboul</i>	0.6856	11.45	3.1545	42.3402	3.4561	2.7133	3.0395	27.7219	6.1244
<i>Turdus cardis</i>	0.7431	1.0909	25.002	10.685	5.2567	5.3051	0.4416	47.2972	4.9216
<i>Turdus celaenops</i>	0.6666	0	0	0	50	0	0	0	0
<i>Turdus chiguanco</i>	0.6703	1.5648	18.6668	11.2483	5.4367	20.0255	2.6411	16.6975	23.7193
<i>Turdus chrysolaus</i>	0.6132	20.753	17.9901	0.9717	1.5735	0	17.6734	20	21.0381
<i>Turdus dissimilis</i>	0.7849	13.7561	11.377	4.9428	5.3815	15.7852	4.7474	40.0802	3.9298
<i>Turdus falcklandii</i>	0.6878	11.2813	33.0343	8.9165	4.7412	3.0998	11.6397	4.8515	22.4358
<i>Turdus feae</i>	0.7126	40.5188	0	0	1.3047	1.7193	0	18.6214	37.8357
<i>Turdus flavipes</i>	0.6886	0	1.0179	8.9923	26.7945	0	48.3043	1.586	13.3049
<i>Turdus fulviventris</i>	0.62	20	0.1235	0	20	0	19.8473	0	20.0292
<i>Turdus fumigatus</i>	0.7104	4.7749	5.4767	10.413	12.9422	12.7755	25.7701	13.1469	14.7007
<i>Turdus fuscater</i>	0.6781	6.1273	16.8343	0	21.5784	1.7872	19.4606	0.0153	34.1969
<i>Turdus grayi</i>	0.7852	2.9878	3.7297	3.5833	9.1057	28.2152	22.2608	11.9712	18.1462
<i>Turdus haplochrous</i>	0.6988	0	0	17.5618	77.3301	0	0	5.1082	0
<i>Turdus hauxwelli</i>	0.6876	11.5662	12.226	4.0422	22.1939	20.7257	7.8259	17.4806	3.9395
<i>Turdus hortulorum</i>	0.6709	16.001	13.6748	17.4625	22.3852	11.4422	10.6994	4.2342	4.1007
<i>Turdus ignobilis</i>	0.765	7.1184	5.973	19.4409	16.1059	5.5181	12.288	10.0301	23.5257
<i>Turdus iliacus</i>	0.5992	18.4372	10.9324	12.6912	15.1624	8.6451	21.9235	2.1988	10.0094
<i>Turdus infuscatus</i>	0.6113	18.5263	0.7141	38.7142	0.5888	0	0	0	1.4566
<i>Turdus jamaicensis</i>	0.5722	0	20	20	0	0	0	0	0
<i>Turdus kessleri</i>	0.6813	0.5458	5.6383	54.5198	11.7398	2.2681	10.0415	13.628	1.6186
<i>Turdus lawrencii</i>	0.7337	15.1744	22.6383	9.064	11.2016	18.3894	9.9419	5.5155	8.0748
<i>Turdus leucomelas</i>	0.6722	8.7543	13.2216	10.9832	9.8599	23.4284	19.6829	5.6523	8.4174
<i>Turdus leucops</i>	0.7801	15.5763	25.3312	0	30.7546	27.7673	0	0.0723	0.4983
<i>Turdus lherminieri</i>	0.8	0.5035	4.6301	32.5644	0.7689	12.9029	48.6301	0	0
<i>Turdus libonyanus</i>	0.7041	8.1455	12.0461	4.9986	8.3609	11.297	18.841	28.7536	7.5572
<i>Turdus ludoviciae</i>	0.6363	0	0	20	0	0	20	20	20
<i>Turdus maculirostris</i>	0.6852	0	0	0	100	0	0	0	0

Turdus maranonicus	0.5948	0	0	0	0	60	0	0	0
Turdus menachensis	0.6907	7.6376	22.9636	17.991	20	0	1.5874	0	29.8204
Turdus merula	0.6568	13.7297	14.1141	16.7122	14.9563	6.3641	10.2921	7.6954	16.1361
Turdus migratorius	0.6215	5.826	16.159	16.1252	12.2783	10.5272	8.8983	15.1639	15.0221
Turdus mupinensis	0.7157	35.3879	2.4061	6.2155	8.2163	0.7773	11.2259	22.0042	13.7668
Turdus naumanni	0.6512	23.8019	8.5258	23.5718	22.0934	8.4692	8.5727	1.848	3.1173
Turdus nigrescens	0.65	0	25	0	25	0	25	0	0
Turdus nigriceps	0.6804	0	0	0	20.609	62.2562	0.5049	14.5785	2.0514
Turdus nudigenis	0.6829	22.3742	13.4854	34.1368	2.7003	4.9309	15.4548	4.6476	2.27
Turdus obscurus	0.6672	37.8345	4.2552	2.2846	16.7638	7.1454	14.1826	4.4096	13.1243
Turdus obsoletus	0.5645	32.4987	57.3417	0	0	0	7.5013	0	2.6583
Turdus olivaceus	0.7063	10.6869	21.1136	8.1789	1.3292	18.7134	11.3719	10.5878	18.0183
Turdus olivater	0.6492	60.1506	8.4892	1.1303	20	10.23	0	0	0
Turdus pallidus	0.7325	22.1312	4.7173	2.9172	38.6817	2.4299	3.6336	11.9238	13.5654
Turdus pelios	0.6644	10.1854	3.4713	8.584	41.804	15.6296	9.6533	5.6148	5.0576
Turdus philomelos	0.598	12.575	17.8547	4.1444	16.5848	5.9901	8.4412	8.5214	25.8884
Turdus pilaris	0.6027	16.7342	5.1403	4.7224	12.5105	2.7689	20.3327	34.6927	3.0983
Turdus plebejus	0.7347	0	11.3499	0	1.5605	42.7247	44.3649	0	0
Turdus plumbeus	0.7487	0	0	0.028	0.0232	2.7041	5.374	0	91.8707
Turdus poliocephalus	0.6234	0	0.0012	2.6251	0	0	0	97.3737	0
Turdus reevei	0.6127	2.7509	0	7.033	82.7079	0	0	1.8179	5.6904
Turdus rubrocanus	0.7134	33.3678	3.1759	3.4508	19.4012	25.8161	1.7977	9.8987	3.0918
Turdus ruficollis	0.6587	7.723	12.3704	16.961	12.5474	18.0306	9.0005	8.365	15.002
Turdus rufitorques	0.5838	0	19.9128	20	0	0.0872	0	0	20
Turdus rufiventris	0.7209	12.3371	11.6209	6.2668	25.8174	11.3652	14.7115	6.837	11.0442
Turdus rufopalliatus	0.6436	1.9842	0	0	63.1861	4.9987	6.9492	6.8266	16.0553
Turdus serranus	0.6307	0.7506	89.5609	0.2365	0.8102	3.4899	4.9653	0.1867	0
Turdus subalaris	0.7759	13.4567	13.8538	12.5051	2.3627	0.8008	7.346	28.3141	21.3609
Turdus swalesi	0.7689	0	12.0484	0	25	0	25	37.9516	0
Turdus tephronotus	0.6793	7.6752	28.455	0	2.1018	16.5845	21.658	14.7321	8.7934
Turdus torquatus	0.6724	8.5953	18.1021	7.9698	5.1465	3.3301	46.9532	3.1102	6.7928
Turdus unicolor	0.6747	70.7362	0	0	18.9276	6.9415	0	3.3947	0
Turdus viscivorus	0.6184	11.4926	10.0933	13.4896	19.0564	18.1065	8.3392	4.8326	14.5899

Figure A4. Suitable areas for *Turdus* thrushes within their distribution ranges. The colour gradient indicates the degree of suitability (from 0 – white, to 1 – black).



Turdus
falcklandii



Turdus
feae



Turdus
flavipes



Turdus
fulviventris



Turdus
fumigatus



Turdus
fuscater



Turdus
grayi



Turdus
haplochrous



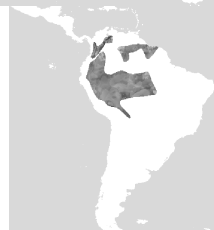
Turdus
hauxwelli



Turdus
hortulorum



Turdus
ignobilis



Turdus
iliacus



Turdus
infuscatus



Turdus
jamaicensis



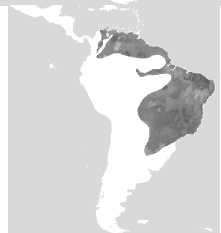
Turdus kessleri



Turdus lawrencii



Turdus leucomelas



Turdus leucops



Turdus herminieri



Turdus libonyanus



Turdus ludoviciae



Turdus maculirostris



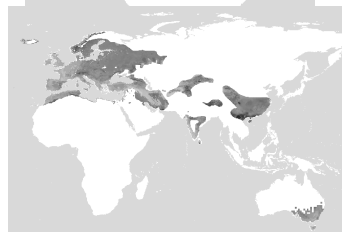
Turdus maranonicus



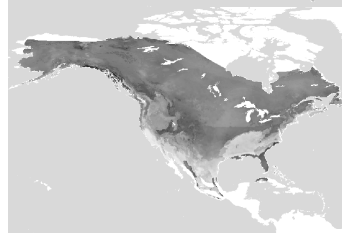
Turdus menachensis



Turdus merula



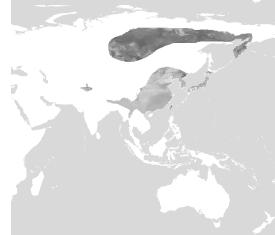
Turdus migratorius



Turdus mupinensis



Turdus naumanni



Turdus nigrescens



Turdus nigriceps



Turdus nudigenis



Turdus obscurus



Turdus obsoletus

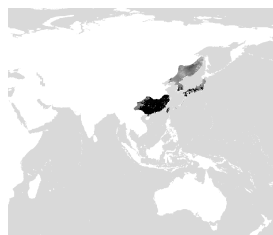


Turdus olivaceus



Turdus olivater

Turdus pallidus



Turdus pelios



Turdus philomelos



Turdus pilaris



Turdus plebejus



Turdus plumbeus



Turdus poliocephalus



Turdus reevei



Turdus rubrocanus



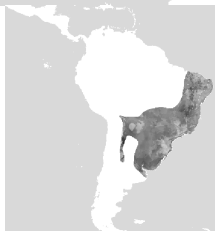
Turdus ruficollis



Turdus rufitorques



Turdus rufiventris



Turdus rufopalliatus



Turdus serranus



Turdus subalaris



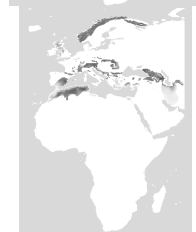
Turdus swalesi



Turdus tephronotus



Turdus torquatus



Turdus unicolor



Turdus viscivorus

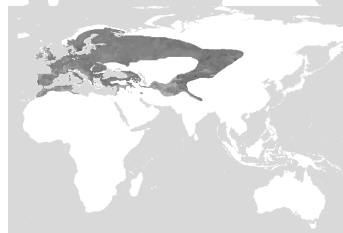


Figure A5. Results of the six biogeographic models for *Turdus* thrushes, ordered by descending AIC values: (A) DEC+j, (B) DIVA+j, (C) BayArea+j, (D) DEC, (E) DIVA, (F) BayArea. Pies indicate the most probable ancestral states.

(A) DEC+j

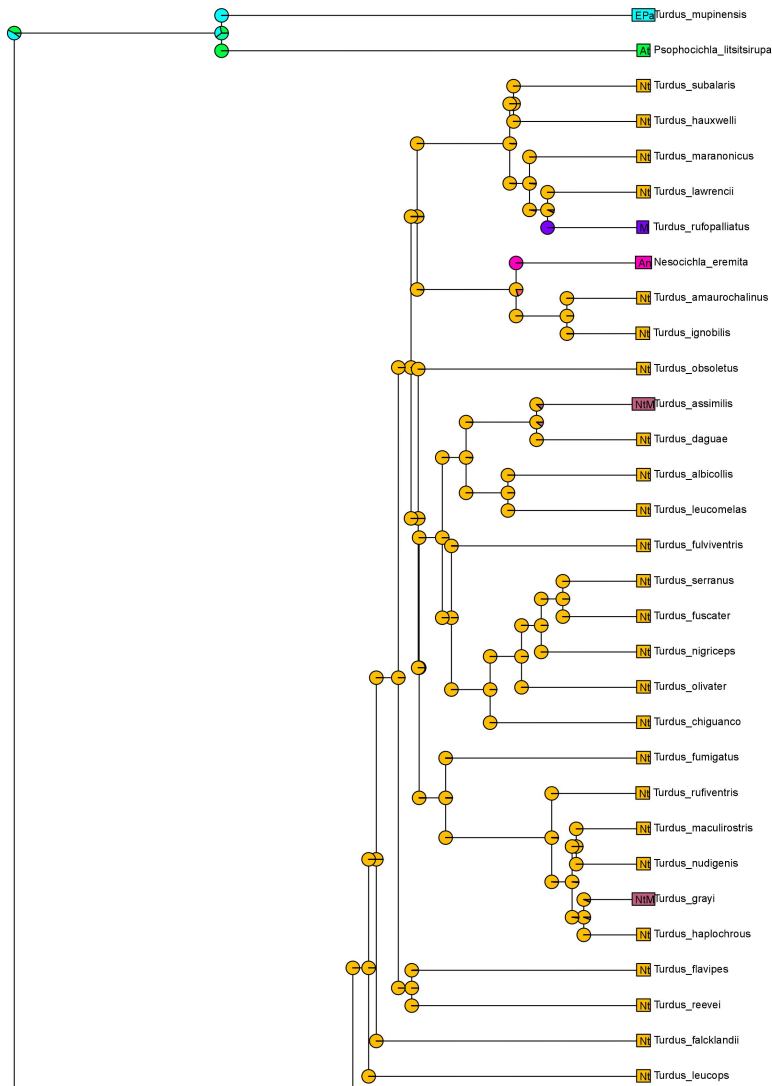


Figure A5. (A) DEC+j, continue.

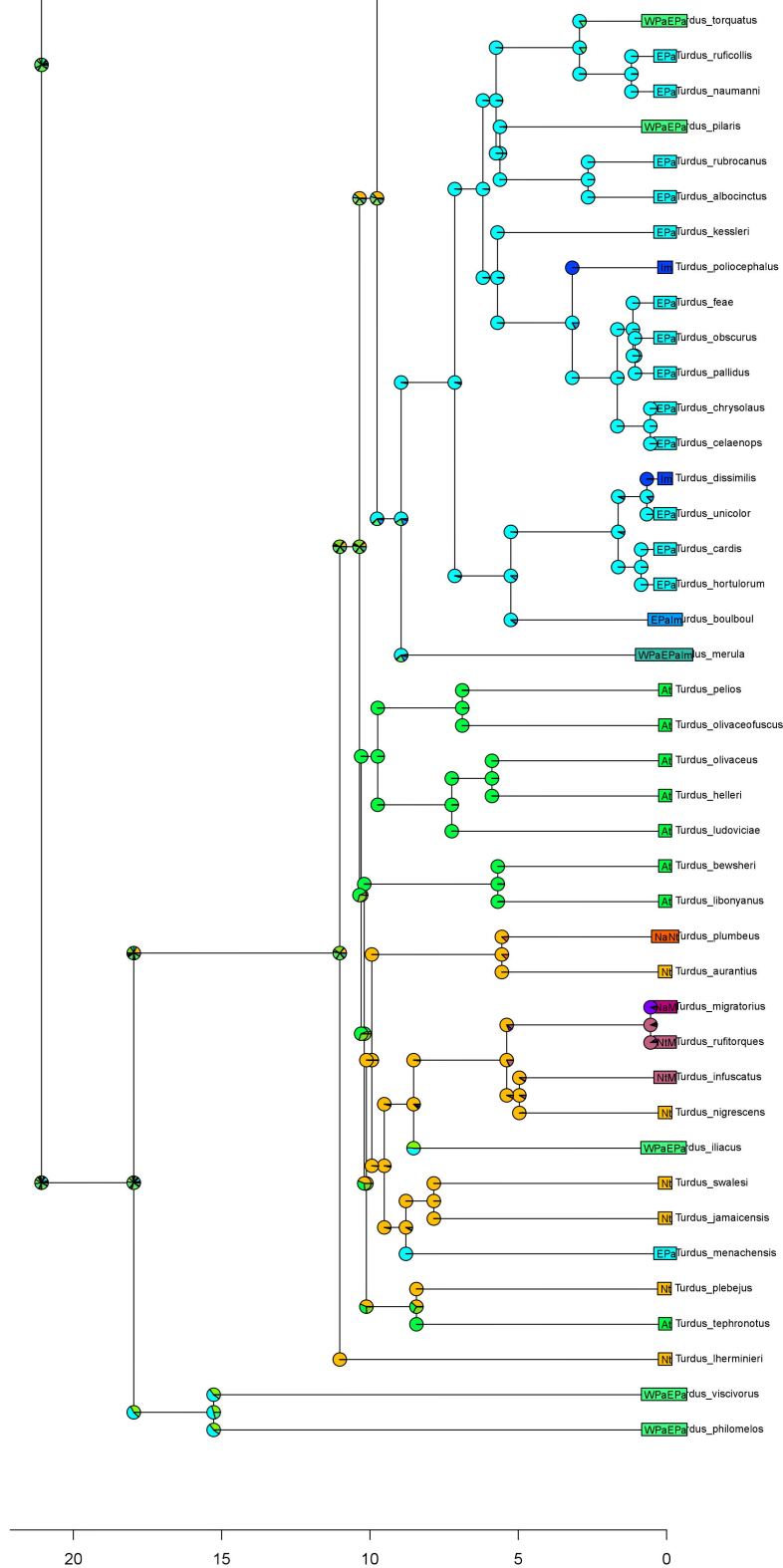


Figure A5. (B) DIVA+j.

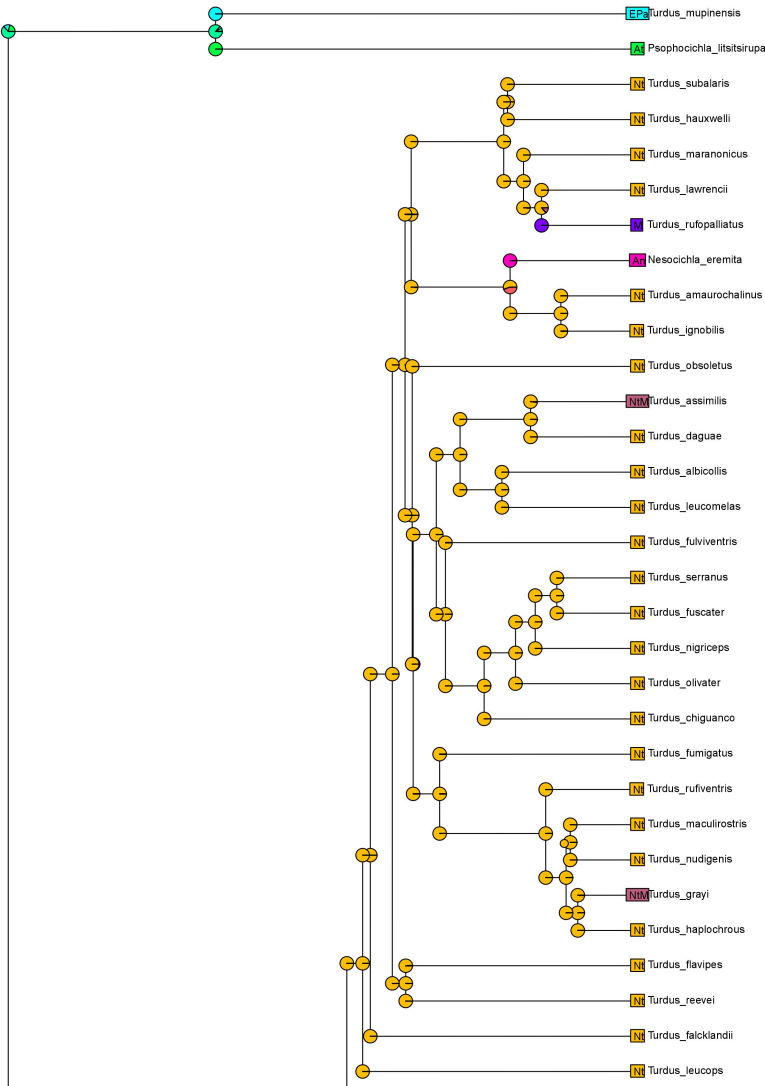


Figure A5. (B) DIVA+j, continue.

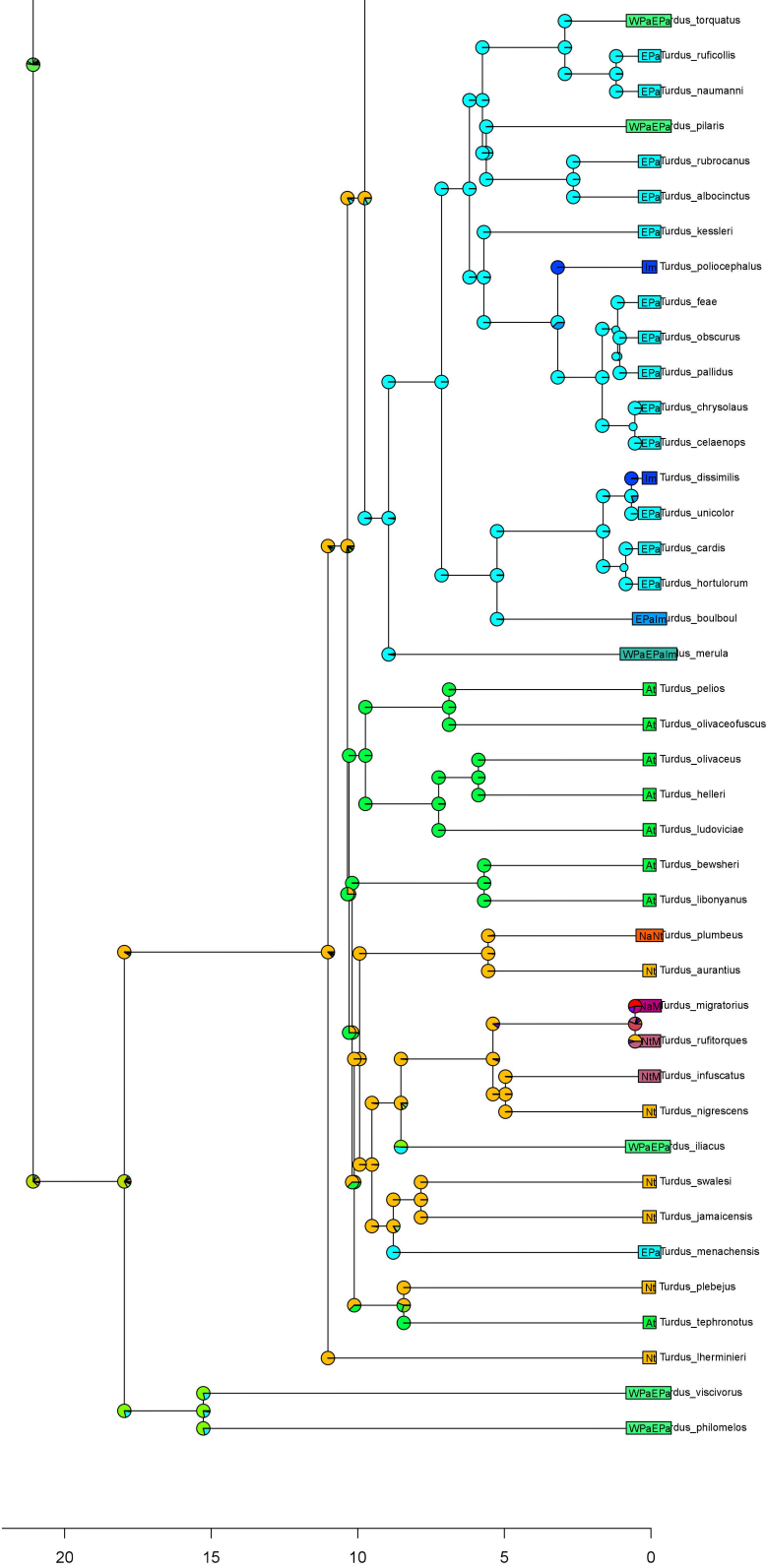


Figure A5. (C) BayArea+j.

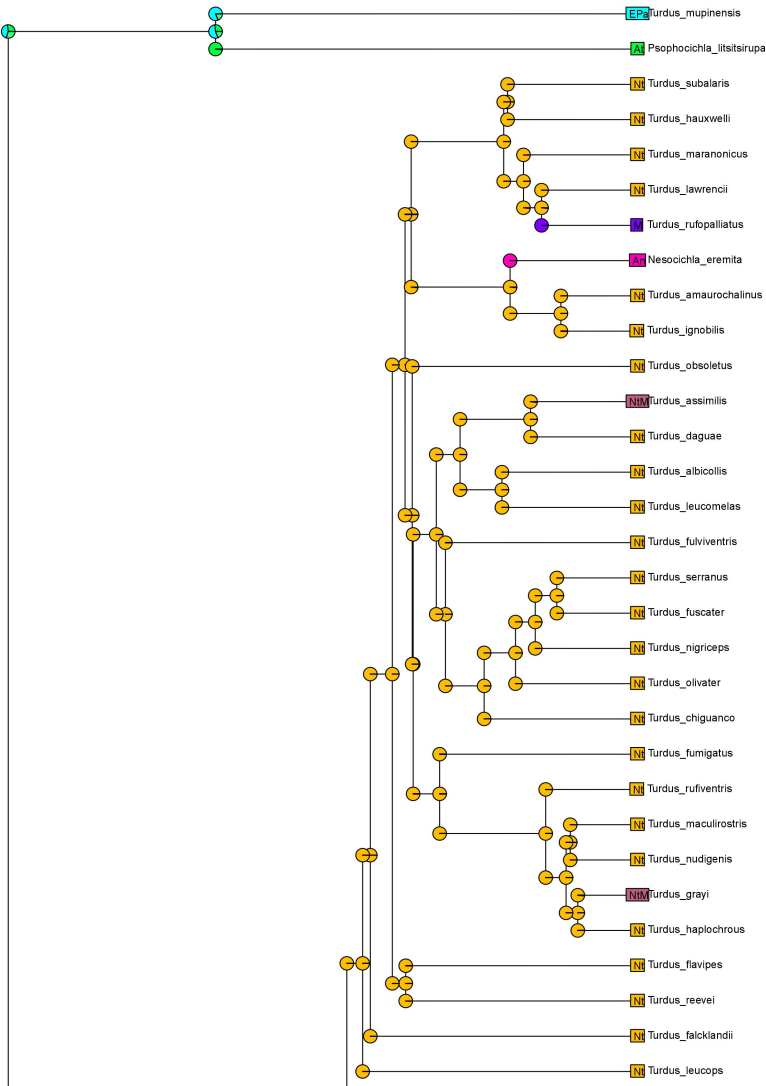


Figure A5. (C) BayArea+j, continue.

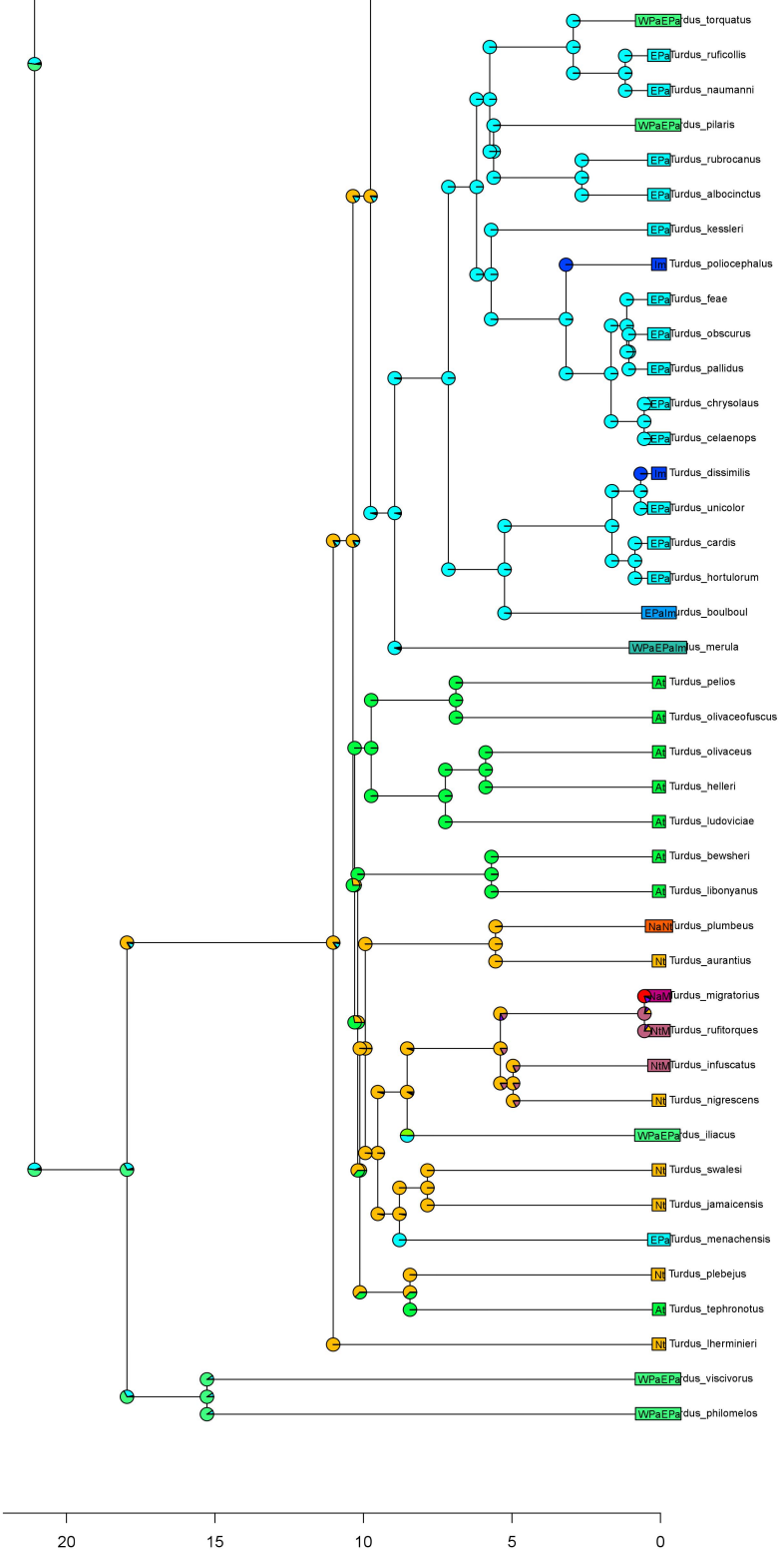


Figure A5. (D) DEC.

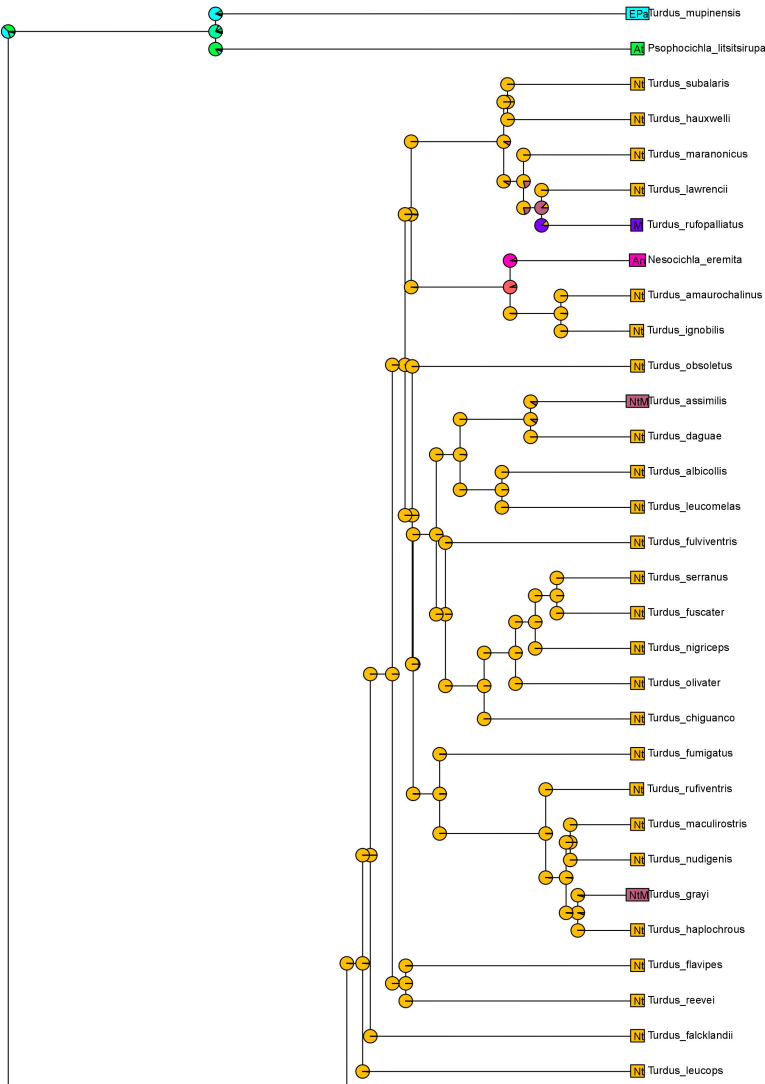


Figure A5. (D) DEC, continue.

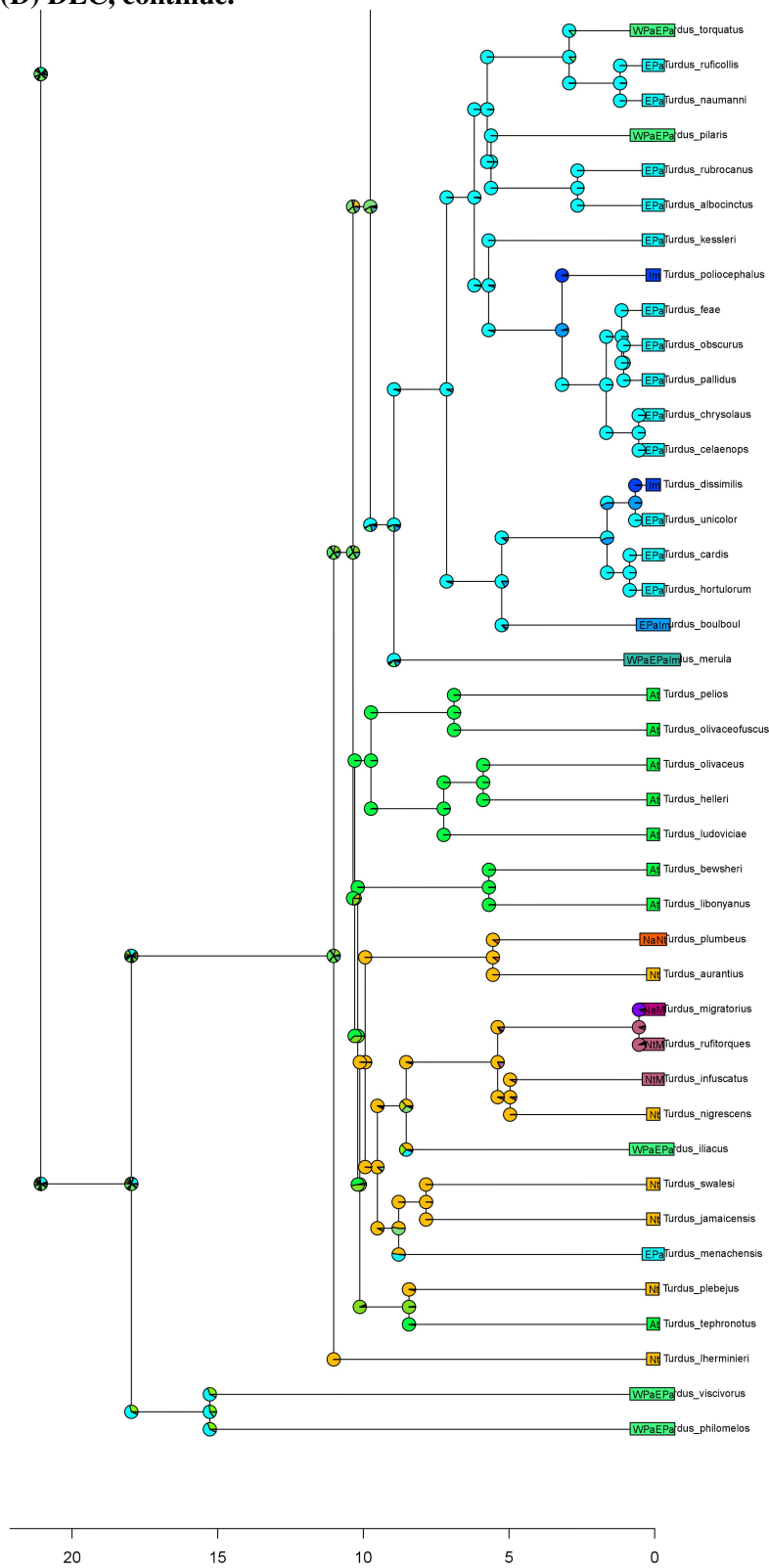


Figure A5. (E) DIVA.

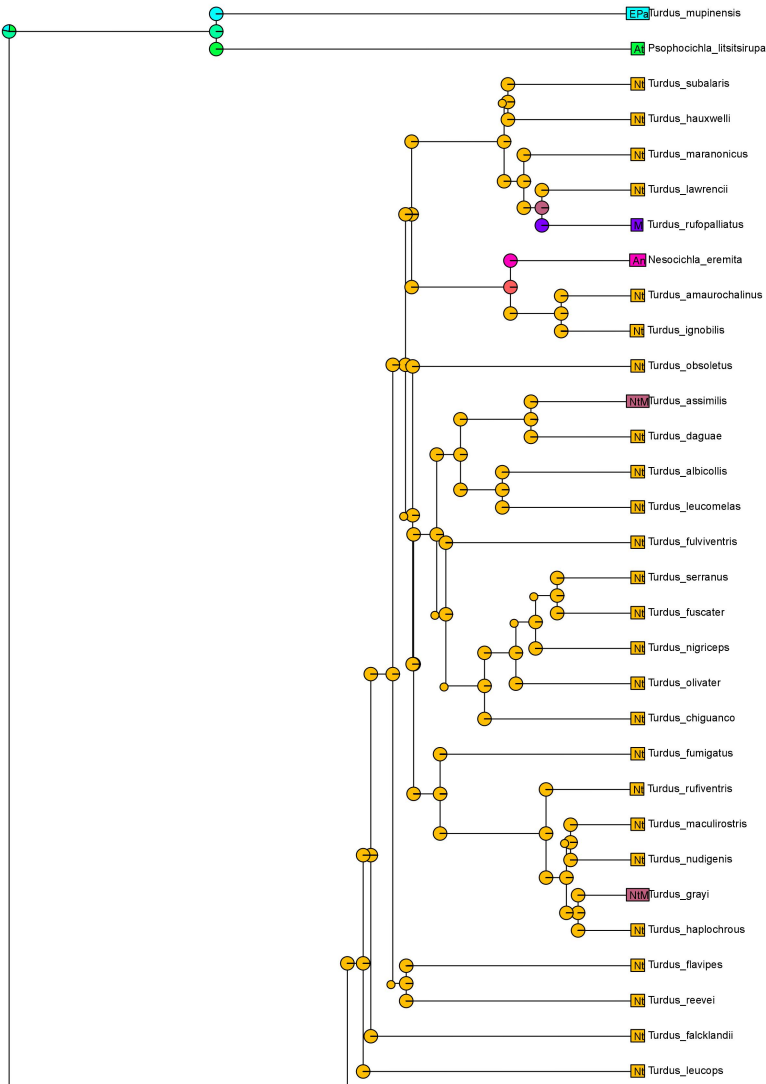


Figure A5. (E) DIVA, continue.

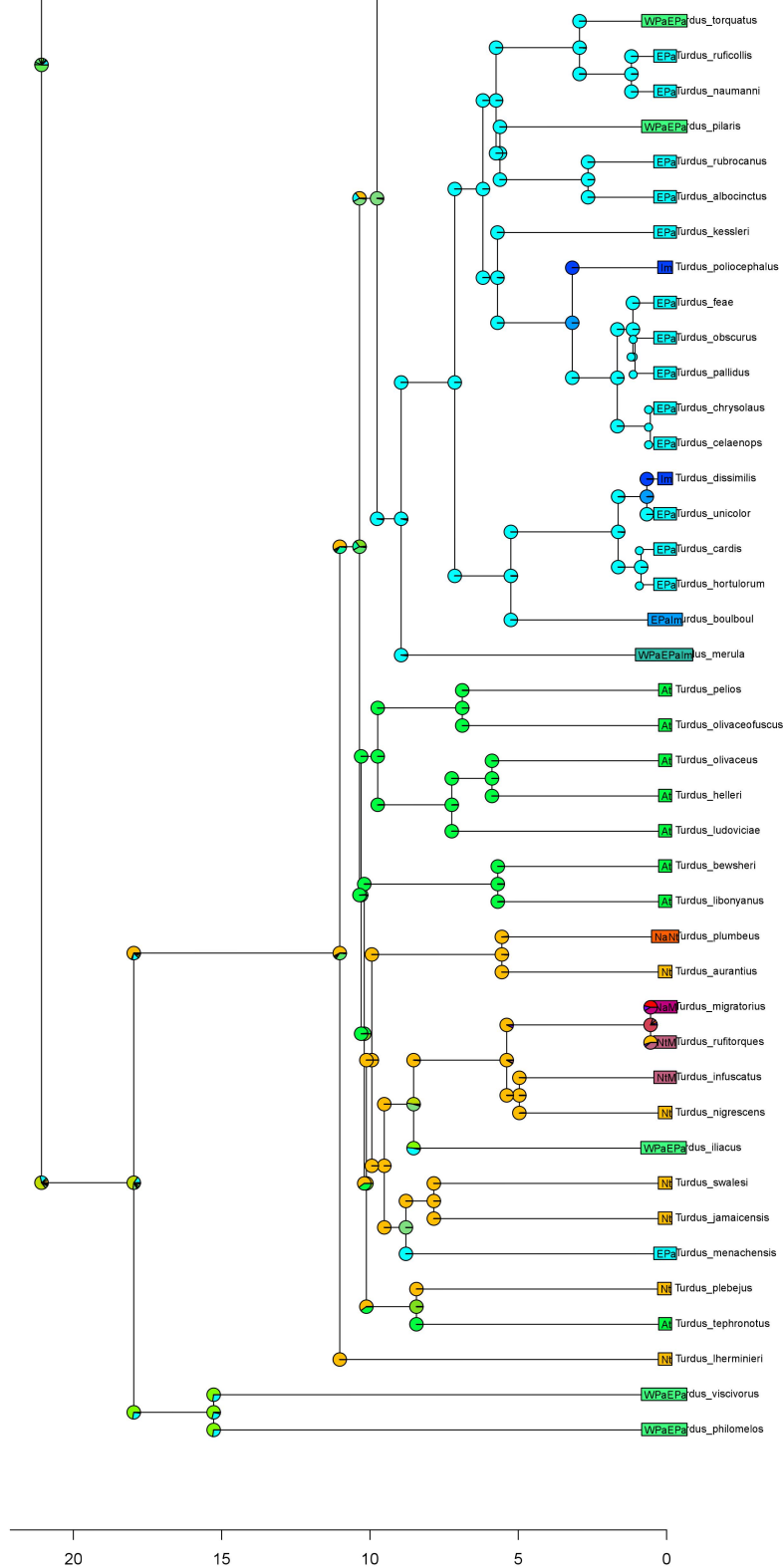


Figure A5. (F) BayArea.

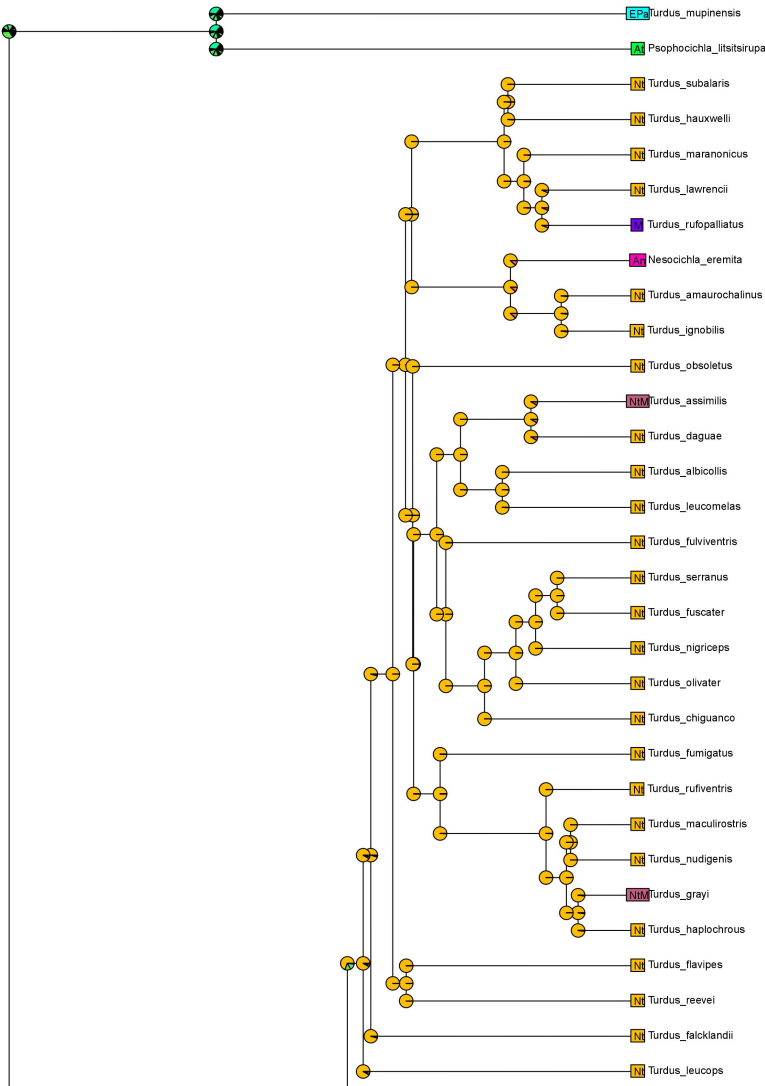


Figure A5. (F) BayArea, continue.

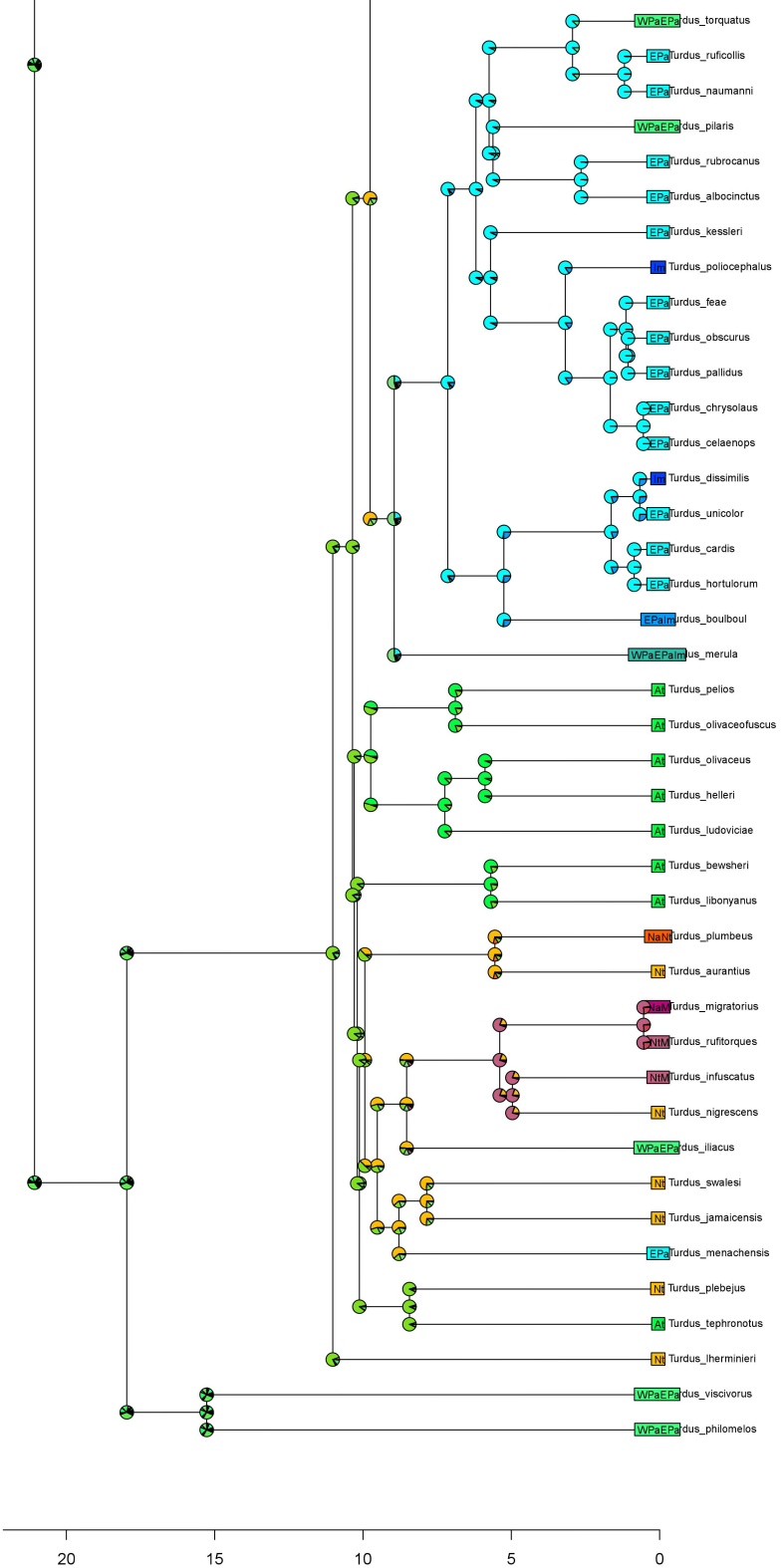


Figure A6. Results of biogeographic stochastic mapping for 72 *Turdus* species. Colours are corresponding to the biogeographic regionalisation on Figure 2.

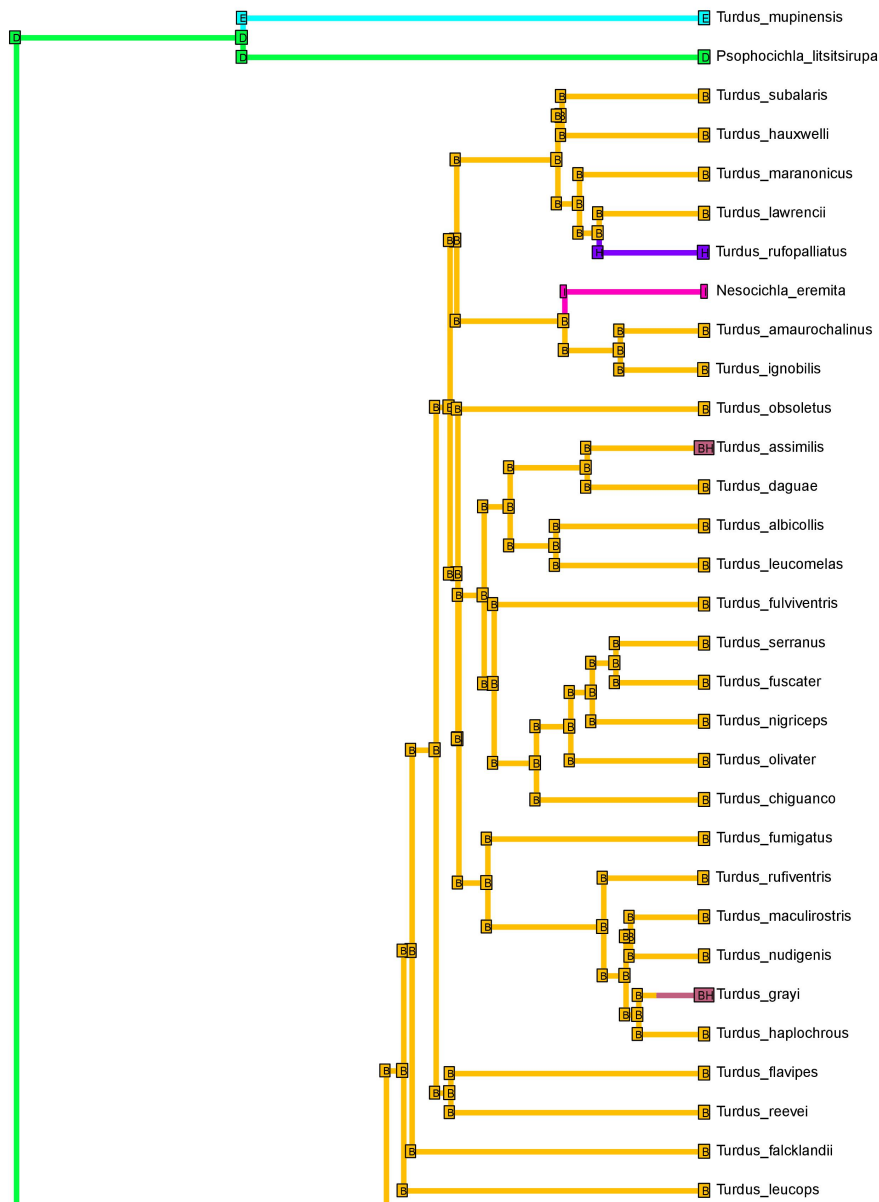


Figure A6. Continue.

