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Origin, diversification, and biogeography of forest birds across temperate forest regions in the Northern Hemisphere

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Abstract

Technological and methodological advances in biogeography, phylogenetics, and bioinformatics during the past couple of decades provide greatly enhanced insights into the evolutionary history of birds in space and time. Molecular data, especially next-generation DNA sequencing, have produced a revolution in reconstructing the phylogenetic history of lineages. These advances shed a new light on the mode, tempo, and spatial context of differentiation processes that shaped the composition and structure of extant forest bird communities of temperate forests of the Northern Hemisphere. This paper offers a framework for understanding this history based on analytical tools that allow us to decipher the imprint of changes in the geographic configuration of land masses and in climates since the Mesozoic, with a focus on the temperate-tropical flyways that connect the massive forest blocks of the Northern to those of the Southern Hemispheres. Differentiation of most extant bird lineages and species has been shown to have begun in a deeper past than formerly thought, although recent analyses from molecular phylogenies also support the much-debated Late Pleistocene model of speciation. Geographical connections between tropical and temperate realms make north-south flyways important drivers of differentiation for many lineages. The histories of differentiation and colonisation of clades, including both resident and long-distance migrants, are discussed in relation to two alternative theories, the 'southern home theory' and the 'northern home theory'. The region-specific characters of the bird faunas and differences between the main temperate forest blocks of the Northern Hemisphere are discussed in light of the hypotheses concerning dispersal processes related with geographical configuration of land masses. Differential dispersal-colonisation rates from tropical regions and subsequent diversification in temperate regions (and vice versa) are also considered. The causes of the observed decline in diversification rates during the Pleistocene are examined from phylogenetic reconstructions of various clades.

Highlights

- The origination and differentiation of most forest birds of the Northern Hemisphere started in a deeper past than formerly thought, ranging from nearly 50 million to 5 million years ago.
- Pleistocene-era nodes are far from negligible, as recently demonstrated, and account for a large part of the extant bird species diversity.
- Major lineages originated in various regions of both the Northern and the Southern Hemispheres.
- Tropical-temperate relationships among forest bird faunas are much more pronounced in North-America and eastern Asia than in Europe as a result of strong differences in the geographical configuration of land masses and barriers to dispersal.
- Niche-packing within bird communities is much higher in North American forests than in European forests, which results in finer habitat selection and hence higher local species diversity in the former.
- Scaling down diversity patterns show that the evolutionary histories experienced by Nearctic forest birds result from their close contact with tropical regions.

Keywords: diversification rates, forest birds, glacial cycles, historical biogeography, migration, Northern Hemisphere, phylogenetic systematics, speciation, temperate-tropical flyways

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Introduction

Because more than two thirds of the Northern Hemisphere were forested before large-scale deforestation by humans took place, forest-dependent birds represent a very diverse element of this hemisphere's terrestrial bird fauna. Only at the scale of temperate Eurasia, as many as 39 families and 126 genera, at least 1500 species, and more than ten billion individual birds are more or less dependent on forest habitats (Keast 1990). Temperate and boreal forested regions of the Northern Hemisphere consist of four main blocks, which are either deciduous or mixed deciduous and coniferous. They are the western North American block (which is distinct from the other areas in its size, structure, and distribution of forested areas), the eastern North American block (part of the North American continent north of the US-Mexican border and east of the 95°W), and two blocks in Eurasia, which are separated by large areas of steppe, deserts, and massive mountain ranges, except in the far North where the belt of boreal forests is uninterrupted. These two Eurasian blocks are the western Palearctic block (hereafter named Europe, i.e., part of the Eurasian land mass lying between the Atlantic Ocean and the Ural mountain range), and the eastern Palearctic block (China + Manchuria). Within each forest block, there is a north-south zonation of vegetation belts or biomes (Box 1). Understanding how and when forest lineages of birds evolved and established in these main forest blocks of the Northern Hemisphere has long presented a challenge to biogeographers.

Recent technological and methodological advances in molecular systematics now provide a useful context into which refreshing insight on the long-debated evolutionary history of birds associated with the major vegetation belts of the Northern Hemisphere can be obtained. In particular, the use of molecular data, next generation sequencing (NGS), and the advent of automated and high-throughput DNA sequencing led to new approaches for reconstructing the phylogenetic history of lineages (Avise 2004, Kraus and Wink 2015). Combined with a burst of paleontological findings (e.g., Wood and De Pietri 2015) that facilitate time calibration of molecular results, and with the development of powerful statistical and bioinformatics tools, these advances have contributed to resolve formerly equivocal evolutionary relationships within clades. Here, from selected examples of such approaches, I provide an overview of recent advances in our understanding of the origin, diversification, and biogeography of forest birds across temperate forest regions in the Northern Hemisphere. These approaches have particularly revitalized debates over the effects of the Pleistocene alternation of glacial and interglacial phases on diversification processes (speciation minus extinction) and have greatly contributed to improve our

Box 1 Present-day zonation of forest belts in the Northern Hemisphere. From north to south several forest belts stretch across the continents of the Northern Hemisphere:

1. The boreal zone or taiga is one of the most extensive biogeographic formations on Earth, covering 26% of the world's total forested area between 55°N and 70°N, and extending nearly 7,000 km from end to end (Imbeau et al. 2001). Large parts of the areas today occupied by taiga were under ice during glacial times of the Pleistocene so that the bird fauna of this biome is relatively poor, most species being widespread over huge areas, and often straddling Eurasia and North America.
2. The richest forest belt of the Northern Hemisphere is the broadleaved deciduous forests and mixed forests, the so-called temperate-nemoral forest belt defined by Vera (2000) as lying below 700 m altitude and between 45°N - 58°N and 5°W - 25°E. In Europe, broadleaved deciduous forests extend about ten degrees of latitude further north (*c.* 60°N) than in eastern Asia and eastern North America because of the warming effects of the Gulf Stream. However, they do not extend as far south as in eastern Asia and North America because of a drier summer in southern Europe, which entails a rapid transition to Mediterranean-type woodland. About half the bird species of the broadleaved forest belt are short-distance migrants and 15-20% are tropical migrants, i.e., birds which breed in the temperate forests of the Northern Hemisphere and overwinter in the tropics. Bird assemblages of European forests have fewer species, are taxonomically less diverse, and include less tropical migrants than those of their North American and East Asian counterparts.
3. The warm-temperate zone of Europe (mean winter temperature above 4°C and summer mean 21-27°C) is characterized by Mediterranean-type forests and matorrals which have no equivalent in the other forest blocks of the Northern Hemisphere, except in the south-western part of North America in California (which will not be discussed in this paper). The bird fauna mostly consists of boreal and temperate species, but a striking feature of the Mediterranean forest bird fauna is the very low level of endemism in forest dwelling species (Blondel and Vigne 1993, Blondel et al. 2010, p. 45-47).
4. A small part of forested areas of North America and eastern Asia are tropical. But since the aim of this paper is mostly to address historical and biogeographical issues explaining and comparing extant forest bird faunas of temperate forests, they will not be discussed longer.

knowledge on faunal evolution and macroecological issues on broad-scale patterns of abundance, diversity, and distribution of forest biotas. Because the context in which birds evolved during the Neogene varied much in space and time, I will discuss recent results in light of the repeated climatic variation and north-south and east-west changes in the geographic configuration of land masses since the beginning of the Tertiary, c. 65 Million years ago (Ma).

The tempo of origination and historical biogeography of modern forest birds

World maps of climate classification (e.g., Kottek et al. 2006) and of forest biomes (Walter 1979, Olson et al. 2001, Donoghue and Smith 2004) show that the three blocks of roughly similar size of warm-temperate and temperate-nemoral forests in mid-latitudes of the Northern Hemisphere discussed in this paper, namely in eastern North America, in Europe, and in eastern Asia (China + Manchuria) are mirrored by three vast tropical-equatorial blocks of humid forest in South America, tropical Africa, and tropical south-eastern Asia (Fig. 1). Because many bird species breeding in the forest biomes of the Northern Hemisphere either overwinter or have close relatives breeding in their tropical counterparts, understanding the history and composition of the bird faunas of these forest biomes requires considering the role played during their evolution by the major flyways that connect them, i.e., the temperate – tropical connections between North America/Central and South America, Western Europe/Africa, and eastern Asia/south-eastern Asia.

When and where did modern forest birds originate?

Although Pleistocene climatic upheavals produced much diversification and speciation events in birds (Johnson and Cicero 2004, Weir and Schluter 2004, Lovette 2005), as discussed later, a wealth of recent studies have shown that avian diversification is rooted in a wide range of epochs from the deep past to more recent times. Results from two major phylogenomic analyses of major extant bird groups (Hackett et al. 2008, Prum et al. 2015) showed that extant birds are composed of five major clades whose divergence times are congruent with the paleontological record. In a DNA analysis of 137 passerine species representing all passerine families, Oliveros et al (2019) found that passerine diversification agrees with the fossil and geological records, thus confirming that passerines originated on the Australian landmass *c.* 47 Ma. They also showed how subsequent dispersal and diversification of the group was affected by several climatic and geological events. Since most bird lineages originated in a deep past, the history of avian radiation

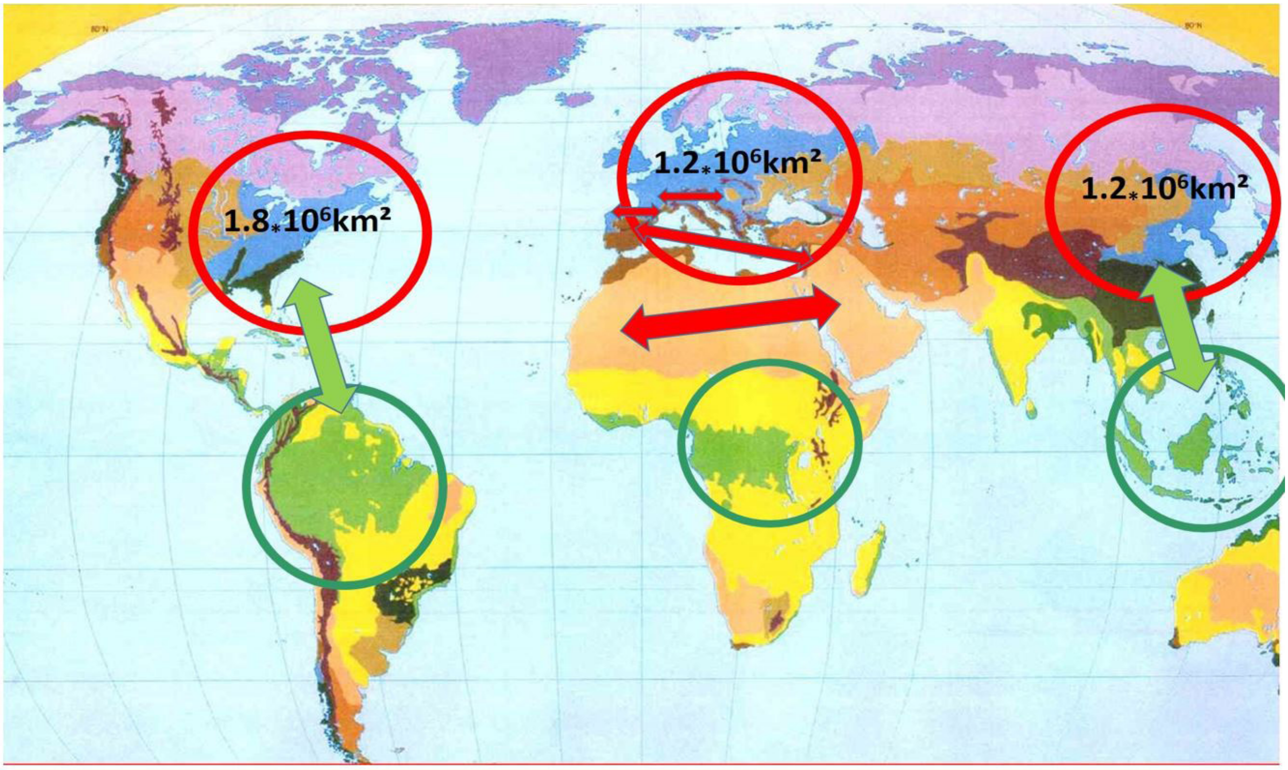

Figure 1. Location and size of the main forest blocks (biomes with different colours, blue for temperate, green for evergreen tropical) in eastern North America, Europe, and eastern Asia (China and Manchuria). The northern forest blocks are the counterparts of the three blocks of tropical forests. Green arrows show that flyways are not interrupted between North and South America and between East Asia and the Indo-Malayan region. The red arrows illustrate the barriers to dispersal between Europe and the Afro-tropical region (map of biomes redrawn from Walter 1979).

and diversification must be interpreted in the context of global climate changes through the Cenozoic, plate tectonics, and mass extinction events. Many studies demonstrate that a large part of terrestrial bird species on Earth coalesced in a deep past (Bermingham et al. 1992, Zink and Slowinski 1995, Avise 2004), with many modern lineages of songbirds having a Miocene-Pliocene origin (e.g., Price et al. 2014 for Himalayan songbirds).

Before analysing the history of the bird faunas of the major forest regions of the Northern Hemisphere in relation to their tropical counterparts, it is worth summarizing the various spatio-temporal scenarios of differentiation of avian clades that are characteristic of present-day forest bird faunas. To this aim, I will use a series of examples of forest dwelling birds, sometimes including clades with species living in both forests and more open habitats. Clades have been chosen for illustrating various possible scenarios of diversification and historical biogeography for both resident and long-distance migrants with a focus on past inter-continental exchanges.

- As a first example of typical forest birds, with 33 genera and 217 species (Dickinson and Remsen 2013), woodpeckers and allies are emblematic birds in all the forest blocks discussed in this paper. The particular suite of evolutionary novelties, both anatomic and behavioural, that allowed woodpeckers to have unique nesting habits and foraging mode of extracting insects (or sap) from woody substrates, has undoubtedly played a role in the diversification and success of this nearly global clade of birds. Inhabiting a wide range of forest habitats, the true woodpeckers (Picidae, Picinae, 24 general, 144 species) have a cosmopolitan distribution with centres of high species richness in the Neotropics and in south-eastern Asia, excluding the Australasian region and Madagascar which have never been colonized. Some regions have unusually great species richness, such as Brazil (51 species) and Myanmar (40 species). A comprehensive well-resolved phylogeny of the group (Shakya et al. 2017) recognizes three subfamilies with the Jynginae (the wrynecks) being sister to all other woodpeckers (Benz et al. 2006). The subfamily Picinae, the typical woodpeckers, is monophyletic and consists of 176 species in 29 genera and five tribes, four of them being monophyletic (Dickinson and Remsen, 2013; Dufort, 2015). These tribes include Old and New World sister taxa (Dufort, 2015; Fuchs et al. 2007, 2013). For example, the four clades of the Picini tribe include species of South and South-East Asia (clade 1), species of the genus *Picus* which are found in South-East Asia and the Palearctic (clade 2), the large African genus *Campethera* and the smaller Asian *Chrysophlegma* (clade 3), species of the New World belonging to the genera *Colaptes*, *Piculus*, *Celeus* and part of *Dryocopus,* as well as some Old World woodpeckers *Mulleripicus* and *Dryocopus* (clade 4). The Melanerpini tribe (often referred to as 'Dendropicini') is a species-rich group (90 species in four main clades) with the New World Melanerpines and the Old World genera *Dendrocopos* (Winkler and Christie 2002). This pied woodpecker assemblage includes the widespread genera *Picoides* and *Dendrocopos* to which recent molecular studies added four other genera from Africa (*Dendropicos),* South America (*Veniliornis),* and Asia (*Hypopicus*, *Sapheopipo*). All of them are nested within the *Dendrocopos*–*Picoides* clade (Fuchs and Pons 2015). Sister relationship between several Old World and New World taxa are illustrated by the large-bodied *Mulleripicus* woodpeckers of South and South-East Asia which are sister to *Dryocopus* of the Old World and the New World, or by *Veniliornis* and *Leuconotopicos* (Melanerpini tribe) which are two monophyletic clades of Neotropical and Nearctic origin, respectively, that separated from each other at *c.* 6 Ma (Shakya et al. 2017). These trans-continental distributions most likely resulted from a combination of multiple dispersal and range contraction events due to climate changes. The family as a whole presumably started to differentiate in the early Miocene *c.* 25 Ma (Benz et al. 2006) with the first split between *Jynx* from the rest of the Picidae (Shakya et al. 2017). Based on Asia-America splits, most divergence events presumably occurred under the warmer climatic conditions that prevailed in the Miocene-Pliocene (Billups and Schrag 2002) with subtropical and temperate Asian species having dispersed eastward into North America. However, Pleistocene glacial events could have accelerated differentiation processes by splitting populations between the New and the Old World (Shakya et al. 2017). Although Short (1982) hypothesized a New World origin for the Picidae, based on the fact that the Neotropics are particularly rich in woodpecker diversity, recent phylogenetic relationships indicate a complex geographic history with many disjunct sister lineages distributed between the New World and Eurasia. Benz et al. (2006) analysis indicates an Old World origin for the family, and Fuchs et al (2007) suggested a tropical-Eurasian origin for the group with divergences between African and New World clades, as well as subsequent intercontinental exchanges that could have occurred synchronously during the Middle Miocene. The Old World (Asia + Africa + Europe) was recovered as the family's area of origin with at least six transitions having occurred between the New and Old world.
- The second example reports on the biogeographical history of the New World thrushes of the genus *Catharus* (12 species) and *Hylocichla* (one species), an interesting model for exploring questions in avian evolution, intercontinental exchanges along temperate-tropical flyways, and the evolution of seasonal migration. This clade is sister to the much larger *Turdus* thrushes clade, which originated in the eastern Palearctic during the Late Miocene, *c.* 7 Ma with an early dispersal into Africa from where a worldwide radiation occurred (Winker and Pruett 2006, Nylander et al. 2008, Nagy et al.

2019). The centre of diversity of *Catharus* thrushes lies in the Neotropics (Central America and/or Central America-South America), where species differentiated between the early Pliocene *c.* 5 Ma and the mid-Pleistocene (Outlaw et al. 2003). Seven species of *Catharus* are resident in the Neotropics and six long-distance migrants, including *Hylocichla mustelina,* breed in North America and overwinter in Mexico, Central America, and South America (Fig. 2). *Catharus guttatus* and *C. occidentalis* likely split from a common ancestor in Mexico within the last three million years. From a large, multi-locus dataset of nuclear loci, Everson et al. (2019) found split-time depths ranging 123–171 Kyr for the *C. fuscescens-minimus-bicknelli* clade of migratory species. This time estimate is much more recent than the previous *c.* 0.4-1 Ma estimates based on mtDNA (Outlaw et al. 2003, Topp et al. 2013, Voelker et al. 2013). This *C. fuscescens-minimus-bicknelli* clade to which *C. ustulatus* is sister (Everson et al. 2019) presumably originated in North America after a dispersal event from South America. Given that the sister group of this clade includes three Mexican-Central American resident species, this lineage probably originated in Mexico-Central America and expanded its range into North America. In sum, the complex *Catharus* history involves several independent transcontinental faunal interchanges. Ancestral character state reconstruction and historical biogeographic analyses suggest a resident ancestor *Catharus* of tropical origin, with migratory behaviour having independently evolved at least three times and differentiation events having occurred in North America after dispersal from the Neotropics.

- The third example is that of the parids, an emblematic group of forest hole-nesting birds which illustrates the tempo and mode of bird differentiation and dispersal across various types of forests, both temperate and tropical. With 59 species (Dickinson and Christidis 2014), parids are found throughout the Holarctic as well as in the Indo-Malayan and Afrotropical zoogeographical regions. The group occurs in a broad array of habitats ranging from tropical rain forest and savannas to boreal taiga. It is particularly species-rich in the Sino-Himalayan mountain range, which is a hotspot of species diversity. The "typical tits" are divided into two sister groups (Johansson et al. 2013) and the spatio-temporal history of their differentiation has been inferred from time-calibrated phylogenetic and biogeographical analyses (see Johansson et al. 2018). Divergence time estimates indicate a Miocene origin for the earliest parid branches, which differentiated from the Remizidae *c.* 18.8 Ma in the mountainous regions of East Asia. The analysis supports monophyly of the parids, including several sister

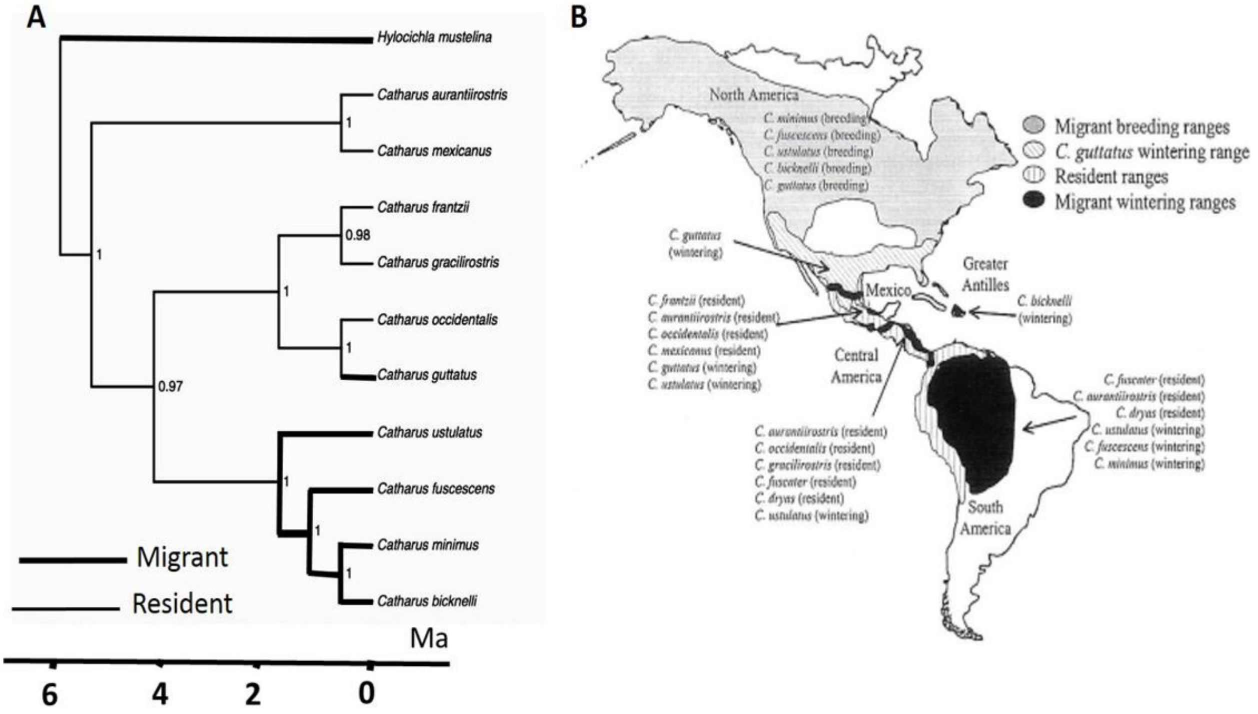

Figure 2. A. Phylogenetic relationships among 11 of the 12 species of the Catharus-Hylocichla clade. Node values denote the Bayesian posterior probabilities of each species quartet (after Everson et al. 2019). B: Map of generalized distributions of the twelve species of Catharus. The five areas of occurrence are North America, Mexico, Central America, South America, and the Greater Antilles. The stage of the life cycle of each species in each area is mentioned after its name (Outlaw et al. 2003).

groups. The first branching event leading to extant species, i.e., between the monotypic *Cephalopyrus flammiceps* of south-eastern Asia and the remaining parids, occurred *c.* 15.1 Ma. Diffusion analysis places the earliest divergence events in the eastern Himalayas and the mountains of western China (Johansson et al. 2018). The main differentiation events within the family started *c.* 8.3 Ma with a split between the "hoarding" and the "non-hoarding" *Parus* s. l. species. First divergences between these two clades occurred at around 6.5 Ma, with several subsequent divergence events within a short time frame (e.g., the separation of the African tits *Melaniparus* spp. from their Indo-Malayan and Palearctic sister clades *c.* 6.3 Ma). Parid species dispersed out of the Sino-Himalayan region between *c.* 8 and 5 Ma. Within this time frame, the ancestor of *Melaniparus* established in the African continent and the first differentiation event of this group took place around the East Africa rift valley *c.* 4.9 Ma. Another major dispersal event involved the North American lineage *Baeolophus,* which split from its Old World sister clades *c.* 6.4 Ma and differentiated on the North American continent *c.* 5.3 Ma. The divergence time of the North American *Poecile* from their Old World relatives is inferred to be younger, *c.* 3.8 Ma. Movements between North America and eastern Asia have been made possible through the Beringian Bridge around 5.4–5.5 Ma. After an early colonization of the Nearctic and repeated exchanges between the continents, back colonization of the Palearctic region occurred in *Poecile* with the re-establishment in Eurasia of *Poecile cinctus* (Gill et al. 2005, Johansson et al. 2013). Then *Cyanistes teneriffae* of the Canary Islands and *C. caeruleus* became separated at 2.7 Ma. Separate estimates based on fossil calibration, as well as those from molecular clock dating, provide almost identical times for differentiation events. Finally, between 5 Ma and present, many divergence events occurred in the Sino-Himalayan region (e.g., *Periparus, Lophophanes* and *Poecile*) as well as in North America (*Baeolophus*). Summing up, the parid group originated between the Miocene and the late Pliocene-early Pleistocene in the Sino-Himalayas and adjacent regions of eastern Asia, which are a hotspot of diversity and centres of differentiation for many groups of plants and animals (Cai et al. 2018). Then, various lineages dispersed into Eurasia, North America, and Africa. Similar patterns of eastern Palearctic origin and dispersal to Eurasia, North America, and Africa have been suggested to explain basal differentiation events within many other passerine bird genera (Voelker 1999) and plant groups (Donoghue & Smith 2004).

- The fourth example is that of the grouse (Tetraoninae) subfamily. This monophyletic group of 21 species is widely distributed throughout the Holarctic and has been considered based on fossil records as having originated in North America prior to the Miocene (Johnsgard 1983, Wang et al. 2013, Mayr 2016). Estimates of divergence rates from a complete molecular phylogeny combined with paleontological data suggested that the radiation of the group coincided with the increasingly high amplitude climatic oscillations part of the global cooling of the Pliocene-Pleistocene (Wang et al. 2013). This analysis suggested that grouse diverged from turkeys (Meleagrinae) *c.* 20 Ma and that the genus *Bonasa* diverged from the common ancestor of all other grouse in the Late Miocene *c.* 12 Ma (Wang et al. 2013). The other three major clades, ptarmigan *Lagopus*, forest grouse *Lyrurus/Tetrao,* and prairie grouse *Centrocercus/Dendragapous/ Tympanuchus* diverged from each other between 3.2 and 1.9 Ma. Dispersal-vicariance analyses (e.g., Ronquist 1997) used by Drovetski (2003) for reconstructing the group's ancestral areas show that the lineage evolved in the north-western Nearctic and occupied the whole Nearctic and some parts of the Palearctic, which was colonized through the Beringian land bridge. The southern ancestor of forest and prairie grouse crossed the Pacific from the south-western Nearctic into the central – eastern Palearctic and differentiated into Nearctic prairie grouse and Palearctic forest grouse. Afterwards, the differentiation of the Palearctic ancestor of *Tetrao/Lyrurus* produced the north-eastern Palearctic *Tetrao* and the south-western Palearctic *Lyrurus,* which became separate disjunct sister species. Summing up, the Western Nearctic played a major role in the radiation of the group and Eurasia has been independently colonized three times through the Beringian land bridge, i.e., first by the ancestor of all grouse in the Late Miocene, then by the ancestor of forest grouse in the Early Pliocene, and finally by the ancestral *Lagopus* in the Early Pleistocene. The Nearctic has been colonized back from Eurasia only once by a common ancestor of forest grouse.
- The fifth example refers to the nuthatches of the genus *Sitta* (24 - 28 species, Päckert et al. 2020a) which are forest-dwelling passerines, except for two rock nuthatches (*S. neumayer* and *S. tephronota*). Nuthatches are widespread throughout the whole Holarctic they colonized from their centre of origin in the mountain ranges of eastern Asia, as inferred by Pasquet et al. (2014). A near-complete investigation of intra- and interspecific differentiation of the genus has been provided by Päckert et al. (2020a) who obtained a time-calibrated multi-locus phylogeny of 27 of the 28 currently recognized species. The differentiation of the family Sittidae from the other Certhioidea has been dated *c.* 20.1 Ma using fossil calibration, and this study confirmed that the genus originated in Southeast Asia, presumably in the region of the Qinghai-Tibet Plateau, a biodiversity hotspot and a biogeographic source for multiple colonization events into adjacent areas including the northern Palearctic (Päckert et al. 2020b). The onset of differentiation of the genus coincides with a Pliocene peak of diversification of the Sino-

Himalayan avifauna that, according to Price et al. (2014), mainly occurred along elevational gradients. Within the genus *Sitta,* the first split gave rise to the *S. przewalskii* – *S. leucopsis* clade which is sister to all other species. Then, the clade *S. carolinensis* - *S. magna* split *c*. 17 Ma and is sister to the two other clades that encompass all the other extant species. The widespread Eurasian nuthatch *S. europaea* is sister to a species-rich monophyletic clade that includes five Sino-Himalayan species. From this highly diverse region of differentiation several clades dispersed to North America (four species) and to the western Palearctic (Europe, six species), 17 Ma and 5 Ma, respectively. Unexpectedly the three endemic "mesogean" nuthatches, which occur in coniferous forests in the Mediterranean basin(i.e., the Corsican nuthatch *S. whiteheadi* in Corsica, the Algerian nuthatch *S. ledanti* in Algeria, and the Krüper's nuthatch *S. krueperi* in Turkey), do not belong to a monophyletic clade but to two separate lineages that diverged at the beginning of the Pliocene, *c*. 5 Ma, with the Corsican nuthatch being sister to the North American *S. villosa* from which it diverged *c.* 1 Ma. Interestingly, latitudinal exchanges between East Asia and both the western Palearctic and North America occurred with distinct phylogroups that have diversified until recently in the Pleistocene. This complex history is typical of a group of species having originated in the Sino-Himalayan region with multiple colonization events and transcontinental exchanges.

- The sixth example is that of the *Sylvia* and allies (genera *Sylvia* and *Curruca*). Although most warblers of this genus do not belong to the bird fauna of mesic temperate forests, including them in this discussion seems relevant because many of them are typical of evergreen Mediterranean matorrals, which are part of the forest biome of the Northern Hemisphere.

According to the most recent and complete phylogeny of Cai et al. (2019), which is based on five mtDNA and seven nuclear markers, the *Sylvia* complex comprises 32 species (including the former *Parophasma galinieri* and *Lioptilus nigricapillus,* which are nested within the *Sylvia* clade). Cai et al (2019) proposed the recognition of two genera corresponding to the two main clades that diverged around the 10 Ma limit, the genus *Sylvia* and the genus *Curruca*. The Sylvia and *Curruca* species are widely distributed from central Eurasia to the tip of South Africa, but 70% of them are restricted within the Mediterranean basin with several island endemics. Although the current distribution of many species suggests a possible role for the Messinian Salinity Crisis (5.96-5.33 Ma) as a driving force in the diversification of this lineage, distribution patterns of several species suggest that Late Miocene-Pliocene Afro-tropical forest upheavals and Paleoclimatic events played primary roles in *Sylvia* divergence and distribution. The extended *Sylvia* phylogeny of Cai et al. (2019) confirms that of Voelker and Light (2011) who indicated an origin of *Sylvia* warblers around the early Miocene *c.* 19.5 Ma. Three well supported clades include all the species (Fig. 3), with a *Sylvia* clade including seven species and two *Curruca* clades encompassing species with broad continental distribution in the Mediterranean area, Asia, Saudi Arabia and Africa, south of the Sahara Desert. Several Mediterranean insular endemics are included in this clade. Asia or Asia+Europe and the Arabian Peninsula are reconstructed as the most likely ancestral areas for this genus. As many as 24 dispersal events have been inferred to explain current distribution patterns of the family. Long-distance migration appears to be the ancestral character state for the entire group, with a sedentary behaviour having evolved at least seven times, especially in island endemics (Fig. 3). Changes in migratory behaviour with species becoming resident independently occurred several times while migratory behaviour subsequently evolved four times from sedentary clades. Mediterranean island endemics result from several vicariance or dispersal events from adjacent ancestral continental areas.

- As a seventh and final example, a near-complete species-level molecular phylogeny of the species-rich (*c*. 832 species) New World clade Emberizoidea exemplifies the tempo and mode of diversification of a widespread group of songbirds, which includes sedentary and long-distance migrants. Emberizoidea encompasses the Icteridae, Cardinalidae, Passerellidae, Thraupidae, Parulidae and their close relatives (Barker et al. 2015). Many of these families include species that are typical of mesic forests of North America (e.g., Parulidae). An age of *c.* 20 million years had been estimated for this group, which presumably differentiated in North America after the early lineage Passerida dispersed across Asia and Beringia from Sahul (the continental Australasian mass) where it originated. The history of this group was dominated by differentiation events within North America, with four of the five major clades accumulating *c*. 791 species in the New World in a series of diversification bouts that occurred between *c*. 13 and 7.5 Ma. One family of the group, the Emberizidae (41 species), back-dispersed from North America to Eurasia across the Beringian land bridge at *c* 11.8 Ma. An analysis of the phylogenetic relationships of the New World warblers of the family Parulidae (112-115 species in 24-26 genera) is particularly interesting because the breeding distributions of species span from the Arctic to temperate South America (Lovette et al. 2010). With both resident and tropical migratory species, this family provides clues for analysing the tempo and mode of diversification processes and for testing hypotheses on the evolution of migratory behaviour in forest-dependent birds, as will be shown later. There is a strong molecular phylogenetic support for a monophyletic "core Parulidae" group having differentiated in North America *c.* 5-7 Ma and which includes all the typical wood-warbler genera (Klein et al. 2004, Barker et al. 2015). Among the Parulines, the 27 species of the genus *Setophaga* represent the

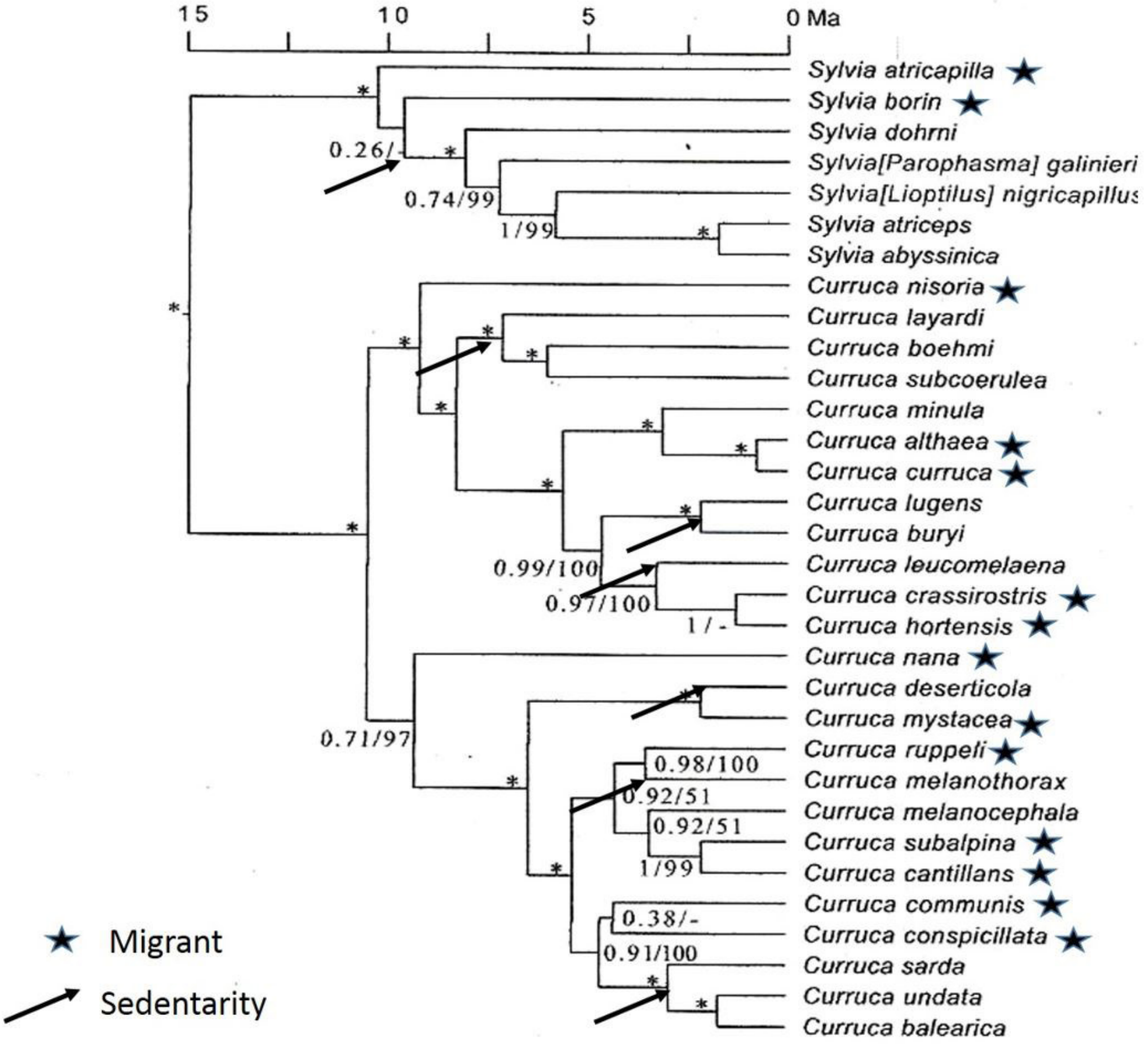

Figure 3. Phylogeny of the Sylviidae (Cai et al. 2019) and migratory state reconstruction (after Voelker and Light 2011). Arrows indicate evolution of sedentary behaviour. Numbers at nodes refer to Bayesian posterior probability/ML bootstrap support. Asterisks indicate 100% bootstrap support.

most spectacular avian radiation in North America (Lovette and Bermingham 1999), with a burst of speciation that occurred in the late Miocene-early Pliocene followed by many differentiation events in the late Pleistocene. Within the Emberizoidea, the large family Passerellidae (26 genera, 129 species), which is sister to Emberizidae and diverged *c.* 11 Ma (Barker et al. 2013), is also a good model for studying the chronology of diversification events. This clade, which is represented in both North and South America, includes both resident species and long-distance migrants. This broad distribution and diversity of movement behaviours allows us to investigate the relative impacts of migration and ecological shifts on avian diversification along the flyways that link North and South American forested biomes (Bryson et al. 2016).

To conclude from these case studies on the tempo of origination of forest birds, four generalizations can be attempted: (i) Differentiation of many present-day forest bird lineages started in a much deeper past than formerly thought, ranging from nearly 50 million to 5 million years ago (e.g., Jetz et al. 2012, Prum et al. 2015); (ii) Recent ice ages played a major role in diversification processes. However, broad comparisons based on phylogenies of entire avian genera reveal that Pleistocene-era nodes account but for a small proportion of the total species diversity, something like the tail of the distribution of speciation events (e.g., Lovette and Bermingham 1999, Johnson and Cicero 2004, Outlaw et al. 2003). In fact, as discussed later in this paper, molecular systematic studies do not indicate a pulse of Pleistocene diversification in birds but suggest instead that diversification rates were lower in the Pleistocene than in earlier epochs of the Neogene (Zink and Slowinski 1995). (iii) Major lineages originated in various regions of both the Northern and the Southern Hemispheres so that the

Box 2. East-west relationships of the forest bird faunas of the Northern Hemisphere

For most of the Mesozoic, the major land masses of the Northern Hemisphere were connected so that past relationships between North America and the Palearctic left their imprint before they started to split during the Eocene 45 Ma, separating the formerly continuous Holarctic biotas into two blocks that evolved under conditions of increasing continental isolation. The existence in the early Tertiary of a widespread 'boreotropical forest' followed by the 'mixed mesophytic forest' (Donoghue and Smith 2004) around the whole Holarctic explains that species from the two continents are phylogenetically connected and share a wide Holarctic distribution in the boreal zone. These similarities decrease from north to south (Helle and Mönkkönnen 1990).

At a within-continent scale, besides regional differentiation events associated with Pleistocene glaciations, a wide range of Palearctic taxa exhibit east - west sister species, whose differentiation is clearly not associated with glacial cycles because of time or space inconsistencies that apparently derived from the same parental form. Examples include the western capercaillie *Tetrao urogallus* and the eastern black-billed capercaillie *T. urogalloides*, the turtle dove *Streptopelia turtur* and the eastern turtle dove *S. orientalis,* or the European greenfinch *Carduelis chloris* and the Oriental greenfinch *C. sinica,* among many others (e.g., Newton 2003). An interesting example is the Eastern and Western Bonelli's warblers, *Phylloscopus orientalis* and *P. Bonelli,* which belong to a clade that includes a third species, the wood warbler *P. sibilatrix,* sister to the *P. Bonelli-P. orientalis* pair. The three species diverged prior to the Pleistocene, *c.* 4.8 Ma (Alström et al. 2018). Deciphering the tempo and mode of differentiation of these taxa from phylogenetic analyses would shed an interesting light on past relationships between the western and the eastern parts of the Palearctic.

histories of differentiation are group specific. (iv) There has been a certain constancy in faunal interchanges between the Old and the New World in most groups, e.g., woodpeckers (several times), thrushes (once), nuthatches (two times), Paridae, and Tetraonidae (several times).

Pleistocene climatic instability and bird differentiation

While ice ages of the Pliocene-Pleistocene dramatically reshaped biodiversity patterns at continental scales, diversification rates have been shown to decrease across the Pleistocene (Zink and Slowinski 1995, Ricklefs 2006, McPeek 2008). This does not mean, however, that Pleistocene speciation events did not occur, as recognised, for example, by Bermingham et al. (1992) who wrote that "Pleistocene speciation appears to be a reasonable scenario of many species of birds". In the same line, re-examining Avise's earlier work on molecular clocks, Avise and Walker (1998,) concluded that it would be premature to "dismiss Pleistocene biogeographic factors as important players in avian evolution, including extended speciation processes", as exemplified by several authors (e.g., Avise and Walker 1998, Hewitt 2000, 2004, Zink et al. 2004, Lovette 2005). If species retained their climatic niche as climatic conditions changed, which is supported by large-scale tests of niche conservatism (Guisan et al. 2014, Qian and Rickelfs 2016), it is likely that organisms like birds tracked the north-south (and east-west) migration of their habitats as climatic conditions repeatedly changed throughout the Pleistocene. Lines isolating different pairs of closely related taxa are often clustered in areas that lie between former refugees, forming "suture zones" as shown by molecular studies in various groups of plants and animals (e.g., Petit et al. 1997, Taberlet et al. 1998, but see Swenson and Howard 2004).

A new insight has recently been given on the controversial role of recent ice ages in bird speciation. While several studies dismissed the Late Pleistocene model of speciation of present-day species (e.g., Zink & Slowinski 1995, Hewitt 1996, Klicka & Zink 1997), others, based on molecular evidence and historical biogeographic reconstructions, have revealed the substantial effect of Pliocene-Pleistocene climatic oscillations on the differentiation of many groups, such as in the subfamily Tetraoninae explained above. Dates of origin for passerine lineages have been estimated by Weir and Schluter (2004) from mitochondrial sequence divergence and a molecular clock for members of a series of superspecies complexes from boreal to Neotropical forest belts. By comparing coalescence times of pairs of species along this large-scale latitudinal gradient, these authors convincingly showed that speciation processes were commonly initiated during recent glacial periods with coalescence events in boreal superspecies dating to the late Pleistocene. In North America, patterns of differentiation and endemism of boreal superspecies are consistent with forest fragmentation by ice sheets during the Mid- and Late Pleistocene, from 0.7 Ma onwards, giving support to the explicit hypothesis proposed a long time ago by Mengel (1964) that linked geographical patterns of distribution of sister species of wood-warblers to successive glacial advances that produced western species from an eastern ancestor. Weir and Schluter (2004) showed that vicariance events caused by glacial advances have had the largest impact on the most northerly breeding species of the extensive belt of boreal forest. These species were more repeatedly and for longer times subdivided in isolated refugees than species further south. Consistent with these findings, the numbers of superspecies that coalesced in the Late Pleistocene decreased from 100% of boreal superspecies to 56% of sub-boreal and to 46% of tropical superspecies (Weir and Schluter 2004), suggesting that bird faunas fragmented by ice sheets experienced rapid rates of differentiation, whereas those distributed farther south were affected to a lesser extent. These findings support the Late Pleistocene speciation model and are consistent with patterns of distribution of many genera of both European and North American birds, which include closely related taxa that are represented by eastern and western forms. Similar processes occur in Asia where the climate cooling that started in the Miocene and peaked during the Pleistocene was associated with phases of aridification of Central Asia, which led to east-west vicariance events in the northern Palearctic, providing characteristic phylogeographic patterns in a number of Eurasian forest-dwelling passerines such as corvids (Haring et al. 2007, Zhang et al. 2012) and tits (Kvist et al. 2003, Tritsch et al. 2017). As a result, many species exhibit clear east-west replacement patterns with range overlap, hybridization or parapatry of sister populations, semi-species or allo-species when they spread again and eventually come into contact. In many cases, intraspecific variation is conducive to incipient speciation. One detailed example of repeated processes of genetic differentiation followed by lineage mixings in relation to the long-term climatic oscillations of the Pleistocene has been provided by Carneiro De Melo Moura et al. (2019) from mitochondrial and nuclear DNA markers in the bee-eater *Merops apiaster*, a species of open habitats. Similar processes presumably also occurred in many forest bird species. Many groups of forest birds, even in the tropics, like the woodpecker group discussed above, presumably had wider distributions in the Miocene when tropical climate extended well into the Northern Hemisphere (Morley 2000). With the Earth cooling in the Pliocene, and especially during the glacial cycles of the Pleistocene, many taxa would have been forced to shift to lower latitudes in tropical regions. Back and forth movements in response to climate change presumably explains many cross-continent relationships among many groups of birds, such as in woodpeckers.

In the same line, genetic transitions occurring transverse to the range of species in mountain ranges, as a result of genetic isolation during Pleistocene glaciations, have recently been demonstrated by Wallis et al. (2016) from molecular studies in several plant and animal groups, including birds of the Palearctic mountain chains (Pyrenees, Alps, Himalayas). Several other studies on the tits *Periparus*, *Parus*, the long-tailed tit *Aegithalos,* and bullfinches *Pyrrhula* spp., have highlighted the significance of climatic upheavals and glaciers as barriers promoting genetic isolation and bird speciation events (Wallis et al. 2016).

Finally, many phylogeographic studies illustrate the role of Pleistocene climatic oscillations and geographical barriers in shaping the current population genetic structure of species in terms of allopatric/parapatric subspecies and species in both the Nearctic and the Palearctic. In contrast to the Nearctic and eastern Asia, which permanently remained connected with tropical regions further south, the western Palearctic realm always remained isolated from the Afrotropics by massive east-west barriers which prevented species from shifting south in tropical regions during glacial periods (see below). As a result, the Mediterranean peninsulas repeatedly acted as refugia during pleniglacial periods, providing opportunities for differentiation events as shown by many examples of range expansion of two or more European lineages from distinct refugia located in the various peninsulas of the southern Palearctic (Taberlet et al. 1998). Therefore, both Pleistocene climatic oscillations and geographical barriers (Pyrenees, Alps, Mediterranean Sea, Sahara Desert) contributed to shape the current genetic structure of many European species. For example, while the North African lineage of the green woodpecker *Picus viridis* split from the Iberian/European clade in the early Pleistocene (1.6–2.2 Ma), giving rise to the North African Levaillant's woodpecker *Picus vaillantii*, divergence between the Iberian and the European lineages occurred during the mid-Pleistocene (Pons et al. 2011). The Iberian Peninsula has been one of the major southern European glacial refugia (Hewitt 2004, Schmitt 2007) where a number of endemic taxa (both at the subspecies and species levels) have diverged from their closest relatives in the central and northern Palearctic (e.g., *Phylloscopus ibericus,* Helbig et al. 1996, *Sylvia inornata*, Brambilla et al. 2008, *Picus viridis*, Pons et al. 2011, 2019, *Troglodytes troglodytes,* Albrecht et al. 2020).

The distribution of mtDNA divergence estimates of various phylogroups shows that speciation processes are usually not "point events in time" resulting from the splitting of an ancestral population into two reproductively isolated species but that the "pace of speciation" is a long-lasting process which probably extended through time from Pliocene origins to Pleistocene completion (Klicka and Zink 1997, 1999, Avise and Walker 1998). Recent genomic studies provide support to this view of speciation as a dynamic and long-lasting process in which the incipient species continue to exchange genetic material long before they reach complete reproductive isolation (Mallet et al. 2016). In fact, when considered together, the seemingly contradictory data on the tempo of speciation between the Late Pleistocene speciation model and many phylogenetic studies provide a robust and complementary picture of avian diversification in the Northern Hemisphere. This makes the Pleistocene speciation model a matter of degree (Lovette 2005) rather than an alternative to models rooting differentiation processes in a deeper past. If a

Pleistocene origin for species is a common scenario, looking at whole genera usually gives more ancient species that are at deeper nodes of the tree.

The diversity of tempos of diversification processes and centres or origin of birds of the Northern Hemisphere raises several important biogeographical questions on the historical relationships of bird faunas at various scales of time and space within and between the forest blocks of both the Northern and the Southern Hemispheres. These questions, addressed below, are particularly interesting in groups that include both resident and long-distance migrants that straddle several continents during their life cycle.

Forest bird diversification within- and between continent and along tropical-temperate flyways

Processes of diversification within-and-between continents at the biogeographic scale of the Northern Hemisphere have long been discussed; therefore, (e.g., Newton 2003) they will not be discussed further (see Box 2).

Given the scope of this study, I will rather focus on the relationships between tropical and temperate regions (north-south flyways) in terms of bird diversification. In this context, estimating rates of speciation and extinction is key for understanding how and why ecological and evolutionary processes explain variation of biological diversity in space and time (Morlon 2014).

Much of what we know today stems from the study of clades that include both resident and long-distance migratory species. Many species of birds perform spectacular migrations by travelling twice a year up to tens of thousands of kilometres between their breeding and wintering grounds. At the scale of North America, north of Mexico, more than half of the species are Nearctic-Neotropical migrants that shift seasonally between their breeding and wintering grounds (338 of 650 species; Rappole 1995). Whenever this phenomenon involves geographic disjunction between the temperate breeding grounds in the Northern Hemisphere and wintering ranges in tropical regions of the Southern Hemisphere, the conditions that triggered the evolution of seasonal migration behaviour remain poorly understood. Besides abiotic and biotic drivers of such migrations, which have been studied (e.g., by Dufour et al. 2020), we need studies that integrate theories about the evolution of bird migration with the biogeographic origin and history of migratory clades (Zink 2002, Salewski and Bruderer 2007, Louchart 2008, Winger et al. 2014, 2019). This is because migration may be a key innovation enabling lineages to radiate in new environments (Winker 2000). Comparing on a global scale bird clades that include both migratory and resident species should shed light on these relationships. We must keep in mind, however, that birds' geographic migration likely evolved, at least in part, as a response to the onset of seasonal environments on a geologic time-scale (see Somveille et al. 2018, Winger et al. 2019) and that loss of migratory behaviour frequently occurs (Dufour et al. 2020). This suggests that initially migratory lineages may have adapted to novel ecological opportunities by returning to a resident state. This reasoning is supported by the findings of Kondo et al. (2008) who demonstrated that the sedentary behaviour of subtropical species may represent secondary drop-offs of temperate long-distance migrants (see also Bruderer and Salewski 2008, Winger et al. 2012). Secondary loss or gain of a migratory behaviour often independently occurs within lineages as a response to varying ecological conditions, as exemplified above by several species of *Catharus* (Fig. 2) and of *Sylvia* (Fig. 3).

In the framework of the "faunal types" concept (Stegmann 1938) which prevailed long ago before the advent of vicariance biogeography, a long-standing tenet was that birds from the Northern hemisphere evolved within the temperate regions with only a small fraction of them originating in the tropics. Historical biogeography (e.g., Voelker 1999) has discounted the notion that centres of diversity reflect the centre of origin of lineages so that current ranges of species cannot be considered as proxies for their ranges at the time when they differentiated (Webster and Purvis 2002). Phylogenetic biogeography, the evolutionary history of long-distance tropical migrants, and the origin of migratory behaviour provide important insights for understanding the biogeographic origin of lineages, although the region where a migratory behaviour evolved is not necessarily the same as their biogeographic region of origin (Bruderer and Salewski 2008, Salewski and Bruderer 2007).

Two theories have been proposed for explaining where and when long-distance tropical migrants evolved (Salewski and Bruderer 2007). The first theory, the "southern-home-theory" (SHT) posits that they originated in the tropics where they exploited stable resources and subsequently evolved a migratory habit that allowed them to extend their breeding range at higher latitudes for capitalizing on seasonally abundant resources in regions they left for wintering in their area of origin (Gauthreaux 1982, Levey and Stiles 1992, Rappole 1995).The rationale is that population pressures in the area of origin force exploration and exploitation of seasonally abundant resources away from the ancestral home, followed by a return to the tropics upon seasonal decline of these resources (Zink 2002). The presence in the tropics of close sedentary relatives of these migratory species supports sedentary behaviour as ancestral in those lineages (Rappole 1995, Berthold 2001), as it is obviously the case in the *Catharus* group discussed above. This theory has been proposed for both the Palearctic-Afrotropical and the Nearctic-Neotropical systems (Rappole 1995, Rappole and Jones 2002). Some short-distance movements of tropical species could be precursors of true long-distance seasonal migration. The second theory, the "northern-home-theory" (NHT) hypothesizes that birds that originated from resident temperate species in the Northern Hemisphere where they breed are pushed southward annually to avoid deteriorating seasonal conditions in winter (Gauthreaux 1982, Bell 2000, 2005, Salewski and Bruderer 2007). Since support for either of these two hypotheses presumably depends on the evolutionary history of the clades examined (see Winger et al. 2014 for Emberizoidea), testing them requires a robust and comprehensive phylogenetic framework (Zink 2002, Outlaw et al. 2003) because (i) the occurrence of conspecific or congeneric species breeding in both the Northern and the Southern hemisphere does not say anything on their ancestral area of origin, and (ii) within a given lineage, migration may be ancestral with extant residency being a derived trait through loss of migratory behaviour or *vice versa*. Large-scale phylogenetic studies investigating the evolutionary origins of long-distance migration are scarce (Winger et al. 2014), but Dufour et al. (2020) recently provided a thorough investigation of the biogeographic and climatic context of the evolutionary emergence of long-distance bird migration worldwide (see also Gomez et al. 2016). Using two recent phylogenies of nearly all extant bird species (9,819 species), Dufour et al (2020) reconstructed the temporal and biogeographic scenario under which seasonal geographic migration evolved in major migratory bird orders (NHT *vs* SHT) by retracing the biogeographic origin of the lineages that have developed a migratory behaviour. Surprisingly, the ancestor of the huge order Passeriformes was estimated as a strict migrant, with the first drop-off to a sedentary behaviour being estimated to occur around 39.7 Ma. Subsequently, residency became the dominant strategy within Passeriformes from mid-Oligocene onwards.

A large number of migratory species which currently breed in the Nearctic and in eastern Asia have conspecifics or congeners in tropical regions of Central/South America and south-eastern Asia. In contrast, very few of the tropical long-distance migrant species which breed in Europe have conspecific populations breeding in the Afrotropics (Rappole and Jones 2002). Clades that include both long-distance migrant and resident species are good candidates for testing the NHT *vs* SHT, assuming that the phylogenetic signal of migration within lineages indicates whether the extant migratory behaviour has evolved *in situ* or has arisen once or several times from sedentary ancestors (Winger et al. 2012). Many studies that have reconstructed the ancestral state of migration in an explicit phylogenetic framework show that the migratory behaviour derives from sedentary ancestors (e.g., Outlaw et al. 2003, Outlaw and Voelker 2006, Winker and Pruett 2006). Usually, but not necessarily, migratory behaviour has evolved relatively recently compared with the total age of the lineages from which migratory species derived, presumably because gain of drop-off of migratory behaviour is a response to Pliocene-Pleistocene climate changes. For example, the *Catharus* genus is particularly interesting for its contribution to the study of seasonal migration, divergence, and speciation in birds (Outlaw et al. 2003, Winker and Pruett 2006, Delmore et al. 2016, Everson et al. 2019). By analysing from a phylogenetic framework the evolution of long-distance migration and the historical biogeography of the five migrant and seven resident species of the *Catharus-Hylocichla* thrushes discussed above, Outlaw et al. (2003) demonstrated the non-monophyly of the migratory species and estimated that migratory behaviour has independently evolved at least three times in that group (Winker and Pruett 2006). Everson et al. (2019) have further shown that the migratory and resident lineages in *Catharus* are intermixed in phylogenies. Of the ten *Catharus* species, only two are strictly resident (*C. gracilirostris* and *C. fuscater*) and three (*C. aurantiirostris, C. mexicanus* and *C. occidentalis*) exhibit limited - distance movements. The phylogeny indicates that residency is ancestral at all nodes of the cladogram but for one (Fig. 2) with migratory species being sister species of resident species whose ranges are restricted in tropical Central America. Interestingly, the breeding and wintering ranges of *C. minimus* occur to the north and south of the breeding and wintering ranges of *C. bicknelli*, a distributional condition among diverging migratory lineages known as leapfrog migration (Everson et al. 2019). The evolution of the genus *Catharus* likely illustrates the case of many lineages of long-distance migrants breeding in temperate regions which have differentiated from historically tropical sedentary ancestors (Rappole 1995), with migratory behaviour being a derived character state. This conclusion which supports the “southern-home-theory” is echoed by Berthold (2001) and Zink (2002).

Another picture supporting the alternative “northern-home-theory” emerges from studies of the Emberizoidea which, as discussed above, originated in North America. Within the Emberizoidea, the New World Parulidae are interesting for testing the evolution of migratory behaviour because this huge monophyletic group, encompassing 112-115 species distributed in 24-26 genera (Lovette et al. 2010), spans a wide spectrum of migratory behaviours from mostly sedentary tropical genera to some champions of long-distance migration. Using a variety of models, Winger et al. (2012) demonstrated that, contrary to the *Catharus* thrushes discussed above, the migratory character of this group is ancestral, and that the migratory behaviour has been lost and regained many times during the radiation of the group, which started *c* 7.5 Ma. An important point made by Winger et al. (2012), however, is that their results neither support nor contradict the prediction of the NHT, which states that migration evolved through an extension of an ancestral temperate non-breeding range to tropical regions to avoid deteriorated winter conditions. They only imply that the ancestral Parulid was probably a Nearctic–Neotropical migrant, and that extant sedentary taxa represent a derived condition within the family. Obtaining more species-level phylogenies with adequate taxon and geographic sampling to enable better character state reconstructions of migratory behaviour is key to improve our understanding of general patterns of change in migratory behaviour across the avian tree of life.

To conclude, as for the tempo of species origination, the evolution of migratory behaviour is group-specific and may arise at various stages of the phylogeny of the group and in different regions, either temperate or tropical.

Region-specific attributes of the forest avifaunas of the Northern Hemisphere

A common heritage differently reshaped by geography and history

The three main blocks of temperate forests of the Northern Hemisphere are of a similar order of magnitude in size (*c.* 1.2, 1.2, and 1.8 x 10^6 km^2 for Europe, eastern Asia, and eastern North America, respectively; Latham and Ricklefs 1993a, b) and lie at similar latitudes (Fig. 1) so that plant and animal species associated with them experienced the same early evolutionary history before continents split as a result of plate tectonics (Donoghue and Smith 2004). Therefore, according to the classical species-area relationships, the bird diversity of these three forest blocks should be of a similar order of magnitude. However, this is not the case since the present-day bird faunas of these regions greatly differ in numbers, including *c.* 732 species in eastern North America, *c.* 550 species in Europe, and *c.* 1000 species in eastern Asia. Similar continent-wide differences also occur in tree species richness, with three times as many tree species in mesic forests of eastern Asia (729 species) as in eastern North America (253 species) and six times more than in European forests (124 species; Latham and Ricklefs 1993a). Similar variation in bird and tree species richness suggests that speciation-extinction-dispersal processes have basically, but independently, been driven by the same factors in the two groups. The questions to be addressed refer to the causes underlying these differential diversities across the three blocks of temperate forest, that is, historical versus contemporary local/regional processes. Besides species richness, other differences between these bird faunas include: (i) a lower phylogenetic diversity in Europe compared to the two other regions (Mönkkönen and Viro 1997), (ii) a larger proportion of the terrestrial bird fauna is associated with forests in eastern North American and eastern Asia (about two thirds of the terrestrial avifauna) than in Europe (about half), and (iii) a much higher proportion of long-distance tropical migrants in eastern North America and eastern Asia than in Europe. The percentage of tropical migrants amounts to 68% in North American forests (Terborgh 1989) compared to 21% only in remnants of the near pristine nemoral forests of Europe, such as in the primeval oak-hornbeam-lime forest of Białowieża, Poland (Wesołowski et al. 2002). The overall numbers of tropical migrants in the North America-Neotropics and East Palearctic- tropical-Asian flyways systems are quite similar with *c*. 340 species each, while the west Palearctic-tropical African system includes 185 species only (Rappole and Jones 2002). Only 48 species of tropical migrants breed in European forests compared to 112 species in Nearctic forests and 107 in eastern Asian forests (Rappole 1995). Explaining these large-scale diversity patterns and inter-biomes discrepancies requires testing hypotheses at temporal and spatial scales that match the scale at which the processes involved operate.

Why are there fewer species in European forests than in eastern North American and eastern Asian?

Two main hypotheses may explain why the three forested regions of the Northern Hemisphere differ so much in species richness. The first hypothesis posits that extinction rates associated with climatic Pleistocene alternations depended on the differences of geographical configuration of land masses and barriers to dispersal in the two continents (Huntley 1993), and the second hypothesis proposes that the extant bird faunas result from differential dispersal-colonization rates from tropical regions and subsequent diversification in temperate regions.

Arguments supporting the first hypothesis refer to the absence of massive east-west barriers to dispersal between temperate and tropical areas in both North America where barriers are north-south oriented (Rocky Mountains), and eastern Asia where there are no mountainous barriers at all (Fig. 1). In these two regions, as ecological conditions repeatedly deteriorated during glacial times, temperate biotas were permanently connected with tropical biotas that could have acted as refuges during glacial periods. In addition, climate cooling during Quaternary ice ages was much less severe in eastern Asia where continental ice sheets never reached the mid-latitudes as they did in Europe. The rationale of this hypothesis is that in both North America and eastern Asia, birds remained connected to the tropics over the whole Tertiary-Quaternary, permitting a continuous interchange between tropical and temperate bird faunas as climatic conditions changed (Webb and Bartlein 1992). The twenty or so waves of Pleistocene glaciations resulted in a repeated back-and-forth north-south movement of forest belts and their associate faunas, which always remained in close contact with tropical forests to the south through the temperate-tropical flyways (CLIMAP 1976). This is the most likely explanation for the presence in the extant bird faunas of temperate forests of eastern Asia of representatives of tropical Indo-Malayan families such as Zosteropidae, Pycnonotidae, Timaliidae or Campephagidae, and for the presence in both North and South America of representatives of many families such as Trochilidae, Parulidae or Tyrannidae.

In contrast, massive east-west oriented barriers (mountain ranges, seas, and large desert belts) always isolated the temperate European avifauna from the tropics (Fig. 1). Although the Sahara and desert regions of southwestern Asia had more vegetation during glacial times than today, they were never forested enough to provide a dispersal link for forest birds between the Afrotropics and Eurasia. Hence, Pleistocene glaciations probably hit harder the European biotas, including the bird fauna, than those of the other forest blocks. However, at least for birds, this hypothesis is not supported by phylogenetic analyses which show that only a small proportion of passerine bird species went extinct in the Pleistocene (see e.g., Zink and Slowinski 1995, Louca and Pennell 2020), which is also supported by the fossil record showing very low extinction rates during the glacial-interglacial cycles (Willis and MacDonald 2011). In addition, warming effects of the Gulf Stream result in a 10° north shift in vegetation belts in Europe, making distance between the breeding grounds to the tropics much longer than in the two other regions. Tropical winter quarters are also more northerly distributed, hence closer to breeding grounds for Nearctic migrants (e.g., Mexico, Central America, the Caribbean area, and even the southern parts of North America) than for Palearctic migrants.

The second hypothesis explaining bird richness anomalies between the three temperate regions of the Northern Hemisphere posits that differences in diversity patterns among their forest bird faunas reflect the dynamics of colonization-differentiation along the tropical-temperate flyways. If, as discussed in the first section, many extant bird species of temperate forests or their ancestors originated in the tropics, the permanent connections between tropical and temperate regions in eastern Asia and their close proximity to the North American flyways allowed clades of tropical origin to disperse and differentiate further north in mesic forests of the Northern Hemisphere *after* they colonized them, especially because, as shown by Rolland et al. (2014), migration triggers speciation whenever migratory lineages settled down and become resident. The ancestral migratory behaviour of Passeriformes (Dufour et al. 2020) suggests that the vast majority of resident species of this order observed today (*c.* 85%) could result from repeated losses of migratory behaviour after dispersive processes in the evolutionary history of the clade, as exemplified by many Parulid species and several *Sylvia* species as explained above. This migratory behaviour certainly favoured the spread of Passeriformes and their diversification across the globe (Dufour et al. 2020; see also Bruderer and Salewski 2008, Ericson et al. 2002). One example is the large suborder *Tyranni* (*c.* 1000 species) which diversified in South America after it colonized this continent (Claramunt and Cracraft 2015), whereas the other suborder (*Passeri*, *c.* 5,000 species) probably diversified in Australia and New Guinea before dispersing elsewhere in the world. Migratory behaviour was a successful life history strategy for coping with seasonal climates, which may have triggered high speciation rates (Winger et al. 2012, Rolland et al. 2014) and allowed the Passeriformes to take advantage of the global cooling and fragmentation of biomes and to diversify into many new habitats and ecological niches.

According to the ‘Out of the Tropics’ hypothesis (OTH) proposed by Jablonski et al. (2006) to explain latitudinal diversity gradients in marine molluscs, dispersal is a primary driver for producing these gradients. Clades that have originated in tropical environments expand their distribution to temperate regions where they subsequently diversify. Intense radiation occurring in temperate regions *after* ancestral taxa colonized them from the tropics (secondary radiation) is probably the case for many bird clades (Lovette and Bermingham 1999). This OTH paradigm is consistent with a south-north continental interchange that has been more marked within the New World (Mönkkönen et al. 1992) with large groups such as Tyrannidae and Parulidae being widespread in both South America and North America than in Europe, where the northward spread of Afrotropical species has been prevented by barriers to dispersal that existed long before the establishment of modern bird faunas. One argument supporting the importance of tropical *vs* temperate regions for bird diversification is that tropical environments dominated the early Tertiary everywhere on Earth, providing deeper roots for diversity in tropical regions compared to temperate and boreal regions (Wiens and Donoghue 2004). This is in line with the view that most bird diversity is tropical with many temperate clades having evolved from tropical ancestors. However, such a view has been recently challenged by Harvey et al. (2020) who provided a new perspective on the mechanisms of bird accumulation in the tropics. Following a phylogenetic approach with the largest tropical bird radiation, the suboscine passerines in the Neotropics, these authors have shown that mechanisms best explaining high tropical diversity do not necessarily rely on high regional speciation rates in stable tropical environments. Rather, they result from the gradual accumulation over time of species with higher speciation rates occurring in lineages from regions located at environmental extremes, where species diversity is low and species would originate faster. In an attempt to distinguish between the OTH and the Tropical Conservatism Hypothesis (TCH), which makes different predictions about dispersal across latitudes and the phylogenetic clustering of assemblages in temperate regions, Duchêne and Cardillo (2015) used the geographic and phylogenetic data of more than 9,000 bird species to reconstruct the ancestral latitudinal zone for each node in each of 100 bird phylogenetic estimates. By estimating the frequency of ancestor-descendant dispersal within and across latitudinal zones and quantifying phylogenetic clustering separately for bird assemblages within the Old World and the New World, these authors demonstrated that latitudinal distributions are relatively conserved since 60–96% of nodes had the same inferred latitude as their immediate ancestral node. They also found that dispersal events out of the tropics were much less frequent (4–5%) than dispersal events in the tropics (15–21%), which strongly supports the TCH and is opposite to what would be expected under the OTH. Both the deeper origins of tropical clades and the comparatively recent, but infrequent, dispersal events into temperate regions explain the strong disparity in tropical and temperate species richness in birds. These results make the OTH at most tentative, especially since one may question the reliability of obtaining speciation and extinction rates estimates from time-calibrated phylogenies of extant species. In a recent study, Louca and Pennell (2020) argued that determining past diversification rates from generalized birth-death models still remains difficult because "there exists an infinite number of alternative diversification scenarios that are equally likely to have generated any given extant timetree" (also see Morlon et al. 2020). In a similar line, Marin and Hedges (2016) found that variation in diversity patterns along latitudinal gradients is better explained by time (age of lineages) than by diversification rates, which do not significantly differ between tropical and temperate areas. Under this scenario higher diversities in the tropics would result from climatic stability, with younger and less species-rich assemblages occupying higher latitudes. One additional finding making the OTH unlikely has been provided by Tilston-Smith et al. (2017) who showed that diversification begins at the intraspecific level. From genetic data of 210 New World bird species distributed across a broad latitudinal gradient, these authors demonstrated that lower latitude species had on average greater phylogeographic diversity than higher latitude species and that intraspecific diversity showed evidence of greater persistence in the tropics. This makes latitudinal gradient in species richness originating at least partly from population-level processes within species. These processes are consistent with hypotheses implicating time and environmental stability in the formation of diversity gradients. Therefore, the debate on what has driven differences in diversity between tropical and extratropical regions has shifted from a set of hypotheses considering mostly unidirectional south-north movements to evidence-based conclusions that faunal interchange between higher and lower latitudes was a bidirectional process, i.e., into- and out of the tropics. In the case of oscines in the Neotropics, phylogenetic data suggest that they colonized South America from the north, which is consistent with the idea that entry into a new region triggers diversification, and that diversification is higher and/or continues for longer in areas with greater carrying capacity and environmental stability (Kennedy et al. 2014), as exemplified by the *Tyranni*. Similar processes of rapid radiation followed by bidirectional exchanges also occurred within and out the Qinghai-Tibet Plateau in many animal groups, including passerine birds (Päckert et al. 2020b), as well as plants (e.g., Ebersbach et al. 2017 for the *Saxifraga* genus). This region is a hotspot of species diversity where many groups diversified and colonized both the Old and the New World though continental interchanges.

One additional hypothesis for explaining the differences between North American and European bird communities is that patterns of habitat diversity and habitat selection by birds much differ between them as a result of contrasted biogeographic histories. As an example, the Palearctic leaf warblers of the genus *Phylloscopus* (77-78 species) have been hypothesized to be ecological counterparts and functional equivalents of the North American Parulids of the genus *Setophaga* (Alström et al. 2018). Indeed, these two groups are dominant components of their respective communities in broad-leaved forests, and they have been hypothesized to be functionally equivalent as a result of morphological and ecological convergence in similar habitats (Price et al. 2000). Most species in these two groups are migratory and overwinter in the tropics (*Setophaga* in the New World and *Phylloscopus* in the Old World). However, close tree-bird associations and fine habitat selection in Parulids result in a much higher niche-packing, hence higher local species diversity than *Phylloscopus* species in Eurasia (Price et al. 2000). Palearctic leaf warblers of the genus *Phylloscopus* follow Rapoport's rule whereby species that live farther north occupy larger geographical ranges than those that breed further south (Price et al. 1997) with the consequence that niche packing is looser, i.e., fewer species can accumulate in any given habitat. A complete species-level phylogeny showed that the *Phylloscopus* group started to differentiate more than 11.7 Ma with divergence times between sister species ranging from 0.5 Ma to 6.1 Ma (Alström et al 2018), which is much earlier than the *Setophaga* genus that originated in the Pliocene, as mentioned above. Price et al. (2000) have shown from ecomorphological and behavioural comparisons of *Setophaga* and *Phyllocopus* communities in New Hampshire (North America) and in Kashmir (Asia) localities, respectively, that the history of the species' radiations differs so much between the two groups that their communities are unlikely to be really convergent even when placed in similar environments. Species in the two regions differ greatly in foraging behaviour and in relationships between morphology and ecological variables. *Setophaga* species are ecologically more similar than are *Phylloscopus* species, which results in a much closer species' packing in the former, with no equivalent in the Old World. Indeed, the *Setophaga* group of warblers in North America is a classic example of fine-scale niche partitioning (e.g., MacArthur 1958), and Lack (1971, p. 132) pointed out that these warblers "present a more complex case of ecological interdigitation than any found in European passerine species", which is mirrored by narrow habitat-bird associations. According to Price et al. (2000), the striking similarity of *Setophaga* warblers results from a burst of speciation driven by sexual selection, which in turn results in a "species flock" of ecologically similar coexisting species. Examining the evolution of visual pigments in the New World *Setophaga* and the Old World *Phylloscopus*, Bloch et al (2015) showed that the former, which are especially colourful and sexually dimorphic, indeed experienced an episode of accelerated evolution.

Neogene diversification rates across scales of space and time

Besides differential contribution of tropical biotas in colonizing the three blocks of temperate forests of the Northern Hemisphere, increased environmental instability caused by the late Neogene/Quaternary climatic transition and alternation of glacial episodes is assumed to have differently influenced rates of diversification across the main landmasses, hence the composition and structure of bird communities. Demonstrating these differences requires testing the null hypothesis that diversification rates do not differ between temperate and tropical regions. In the near absence of fossil data, especially from small passerines, testing these predictions relies upon using "reconstructed phylogenies" of extant species and comparing alternative models of diversification (Nee et al. 1994, Ricklefs 2006, Jetz et al. 2012, Morlon 2014). Early tests of Pleistocene diversification of 11 passerine bird lineages in North America showed a consistent decline in net diversification rates across the Pleistocene (Zink and Slowinski 1995), a conclusion also reached by McPeek (2008) who suggested that lineage accumulation resulted from a strong decrease in speciation rate with increasing species richness. The question is whether the cause of this decline is reduced speciation or increased extinction rates. Again, two non-mutually exclusive hypotheses may answer this question: (i) The geographic displacement and reduction in size of many habitats as a result of global cooling could have caused many extinction events, especially in Europe where biotas were prevented from shifting further south in tropical refugees. However, this hypothesis is not supported neither by phylogenetic analyses nor by fossil data as explained above; (ii) A slowing down of speciation rates rather than accelerated extinction rates may have resulted from ecological limitations such as competition for limited resources or niche filling within clades through evolutionary time (Nee et al. 1992, Price et al. 2014, but see Moen and Morlon 2014). As shown by Zink and Slowinski (1995), the cumulative distribution of reconstructed speciation events in mtDNA phylogenies of North American lineages reveals longer intervals between successive speciation events in the course of the Pleistocene, suggesting a decrease in speciation rates through this epoch. Based on a phylogeny of 358 songbird species distributed along the eastern elevational gradient in the Himalayas, the findings of Price et al. (2014) also suggest that speciation rates are set by niche filling, i.e., ecological competition for resources. From data including 14 clades of passerines restricted to South America and 23 clades restricted to North America, Ricklefs (2006) also concluded that net rates of diversification are higher in tropical regions and decrease with the age of clades, a conclusion which supports the hypothesis that the filling of ecological space constrains further differentiation. A similar conclusion has also been reached by Price et al. (2014) in Himalayan songbirds (but see Weir and Schluter 2007). Because many conclusions on diversification rates are still tentative and controversial, more comparative studies are needed to elucidate the tempo and mode of speciation and extinction rates and their variation across time and space.

The imprint of history and tropical-temperate relationships in the construction of bird communities in eastern North American and European forests

To which extent continent-specific histories of differentiation-colonization of bird lineages translate at the scale of the composition, structure, and dynamics of forest bird assemblages? This discussion will be limited to North American *vs* European communities because of a lack of comparable data in Asian communities. As stated and explained above, the contribution of tropical migrants to local bird communities is much higher in North American forests (Mönkkönen and Helle 1989, Rappole 1995, Holmes and Sherry 2001) than in European forests where most species are resident or short-distance migrants (e.g., Wesołowski and Tomiałojć 1997, Wesołowski 2007). Prominent families which are widespread in the Neotropics and have representatives breeding in North America are Parulidae, Vireonidae, Tyrannidae and Icteridae, whereas the European forest avifauna hardly harbours any species of Afrotropical origin. In addition, long-distance migrants dominate breeding bird communities in late-seral stages of forest successions in North America, whereas the small number of long-distance migrants in European forests mainly occur in early-seral stages.

When the structure and composition of bird communities is scaled down from continent-wide faunas to local communities, several features arise when comparing North American and European bird assemblages (Mönkkönen 1994): (i) At a continental scale (the so-called *delta* diversity), species richness of forest passerines and allies is higher in the Nearctic (*c.* 95 species) than in the Palearctic (*c.* 78 species); (ii) At a regional scale of 200 x 200 km^2 squares (*gamma* diversity), there are on average ten species more in the eastern Nearctic than in the western Palearctic region (mean numbers are 53.8 *vs* 43.6), and regional species pools are also structurally and phylogenetically more variable in the former region; (iii) The between-habitat component of diversity (percentage dissimilarity, a proxy for *beta* diversity, see Blondel 2018) is greater in North American than in European forest bird assemblages since on average two-thirds of species pairs change with forest type in the Nearctic, while the turnover between pairs of forest types in the western Palearctic is always less than 50%. This indicates that habitat selection patterns of birds are finer in North American forests, with closer niche packing than in their European counterparts, a typical feature exemplified by wood-warblers (Lovette et al. 2010). Mönkkönen et al. (1992) also showed that North American long-distance migrants tend to prefer a relatively narrow range of habitats within forest succession; (iv) At a local scale of bird communities (*alpha* diversity), with 18 to 21 species, expected numbers of species in samples of 80 pairs of communities did not significantly differ between the two continents, which means that patterns of resource partitioning could be similar in the two continents. These differences result from the different histories experienced by Nearctic forest birds which benefitted from higher radiation rates and permanent contact with tropical regions, as explained earlier in this paper. More opportunities for bird specialization in the floristically richer North American forests should be a hypothesis worth testing. It would be very interesting also to make similar comparisons of diversity and habitat selection patterns between eastern Asian forest birds and those of the two other forest blocks of the Northern Hemisphere.

Conclusion and future prospects

Bird communities of the three main temperate forest regions of the Northern Hemisphere show many similarities, but they also exhibit substantial differences which seem to have arisen mainly from tropical-temperate relationships of bird faunas and differences in the tempo and mode of component clade diversification. High diversification rates in Nearctic forest bird species due to a permanent contact between tropical and temperate realms during Neogene-Quaternary, rather than low extinction rate during Pleistocene glacial times, led to richer and more taxonomically diverse forest bird communities in North America than in Europe. As more species-level phylogenies are published with comprehensive taxonomic and geographic sampling, applying the new generation of phylogenetic comparative methods has the potential to increase our understanding of how variation in diversification rates in the various parts of the Northern Hemisphere can explain differences in bird communities, as well as general patterns of change in migratory behaviour across the avian tree of life (Morlon 2014). It would also be interesting to investigate whether the floristically richer North American forests are associated with more diverse functional structures of bird communities than their European counterparts since this could provide more opportunities for bird specialization and allow more species to coexist within the ecological space. Completing this general framework would require similar comparisons of diversification rates, diversity, and habitat selection patterns between eastern Asian forest birds and those of the other two forest regions, which would allow one to generalize the patterns and processes of forest bird history at the scale of the whole Northern Hemisphere.

Besides additional specimen material, which is critical for keeping the ‘library of life’ as complete as possible as a basis for innovative studies (Winker 2004), future studies will benefit from (i) the fast production of phylogenetic hypotheses using genomic data (Joseph and Buchanan 2015, Kraus and Wink 2015, Oyler-McCance et al. 2016, Toews et al. 2016), (ii) a myriad of new approaches and methods for analysing trait-dependent diversification, and (iii) performing ancestral state reconstructions, even if these can be challenging (e.g., Ree and Sanmartin 2018, Sukumaran and Knowles 2018, Pannetier et al. 2021). Because extant time-calibrated phylogenies cannot always allow to determine historical diversification rates, paleontological data often remain crucial for answering macroevolutionary questions (Louca and Pennell 2020). At finer scales of biological resolution, patterns of differentiation and population structure of species should be provided and compared for each forest region and between regions whenever possible using new and promising phylogeographic approaches (see e.g., Xue & Hickerson 2020).

Finally, these forest communities are a legacy of the common history of birds and plants, with close interactions between them since the Eocene (Regal 1977, Herrera and Pellmyr 2002). Major functional interactions include plant pollination (e.g., Grant 1994, Cronk and Ojeda 2008) and seed-dispersal (e.g., Herrera 2002, Jordano 2012), with emblematic examples such as many species of hummingbirds and sunbirds pollinating herbs, shrubs and small trees, and the jay-oak and nutcracker-pine associations for seed dispersal. Therefore, the extent to which habitat and species diversity have coevolved, as hypothesized by Rosenzweig (1995), deserves further attention. A high diversity of pollinating and seed dispersing animal species promotes specialization and differentiation among trees, which in turn offers a higher habitat diversity for animals. As a final word, despite many conceptual and technological advances provided by molecular techniques and a number of macroevolutionary approaches and models, many of the results of this paper remain tentative and challenging so that conclusions must be drawn cautiously.

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