

A comprehensive framework  
for understanding the evolutionary  
history of forest birds  
of the Northern Hemisphere

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# A comprehensive framework for understanding the evolutionary history of forest birds of the Northern Hemisphere

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## ABSTRACT

Technological and methodological advances during the past couple of decades in biogeography, paleoecology, phylogenetics and bioinformatics provide a refreshing insight on the evolutionary history of birds. Molecular data of both extinct and extant taxa led to 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 the main forest blocks of the Northern Hemisphere. This paper provides an up-to-date insight in this history from a panel of tools deciphering the imprint of the repeated north-south and east-west changes in the geographic configuration of land masses and in climates since the Mesozoic. Differentiation of most extant bird lineages and species have been shown to start in a much deeper past than formerly thought but recent analyses from molecular phylogenies also support the late Pleistocene model of speciation which has long been hotly debated. The combination of dispersive abilities of birds and geographical connections between tropical and temperate regions make north-south flyways important drivers of differentiation for many lineages. The region of origin and the history of differentiation and colonisation of clades including both resident and long-distance migrants is discussed in the framework of two alternative theories, the “southern home theory” and the “northern home theory”. Then, region-specific characters of the bird faunas and differences between the main forest blocks of the Northern Hemisphere are discussed from hypotheses on dispersal processes in relation to the geographical configuration of land masses and from differential dispersal-colonization rates from tropical regions and subsequent diversification in temperate regions. The causes of the observed decline in diversification rates during the Pleistocene and their differences between the main landmasses in response to Neogene climatic peoration are examined from phylogenetic reconstructions of various clades.

## KEYWORDS

Forest birds,  
phylogenetic systematics,  
historical biogeography,  
tempo and mode of  
speciation,  
migration,  
glacial cycles,  
diversification rates.

## RÉSUMÉ

*Un cadre détaillé pour comprendre l'histoire évolutive des oiseaux forestiers de l'hémisphère nord.*

Les avancées méthodologiques spectaculaires réalisées au cours des deux dernières décennies dans des domaines aussi variés que la biogéographie, la paléoécologie, la phylogénétique et la bio-informatique permettent de retracer sur de nouvelles bases l'histoire évolutive des oiseaux. En particulier, les méthodes modernes d'acquisition de données moléculaire de taxons éteints et actuels ont révolutionné la construction de l'histoire phylogénétique des lignées. Ces avancées éclairent d'un jour nouveau le tempo et le mode ainsi que le contexte spatial et temporel des processus de différenciation qui façonnèrent la composition et la structure des communautés d'oiseaux forestiers des principaux blocs forestiers de l'hémisphère nord (nord-est de l'Amérique du Nord, Europe, Asie

de l'Est). Cet article propose un éclairage nouveau et d'actualité sur cette histoire à partir d'une série d'outils s'efforçant de décoder l'impact de la géographie des masses continentales et des glissements répétés en latitude ou en longitude des ceintures de végétation et de leurs faunes associées depuis le Mésozoïque. Seront plus particulièrement évoqués les points suivants :

- les processus de différenciation de la plupart des lignées, clades et espèces s'avèrent avoir débuté dans un passé beaucoup plus profond que ce qu'on a longtemps pensé. Toutefois, plusieurs phylogénies moléculaires récentes soulignent, voire réhabilitent l'importance du modèle de spéciation pléistocène qui fut longtemps chaudement débattu ;
- la combinaison des capacités dispersives des oiseaux et des connections géographiques entre blocs forestiers tropicaux et tempérés a joué un rôle majeur dans la différenciation de très nombreuses lignées ;
- les foyers d'origine et les histoires de différenciation/colonisation de clades comprenant des espèces sédentaires et des espèces migratrices sont discutés dans le cadre de deux hypothèses alternatives situant l'origine des clades soit en région tropicale ('southern home theory'), soit en région tempérée ('northern home theory') ;
- les caractères et différences des avifaunes forestières propres à chaque grand bloc forestier de l'hémisphère nord sont discutés dans le cadre d'hypothèses sur les processus de dispersion en relation avec la configuration géographique des masses continentales ainsi qu'aux taux différentiels de dispersion-colonisation à partir des régions tropicales avant puis après la colonisation des forêts tempérées par les clades et les espèces ;
- les causes de la décélération observée des taux de diversification des avifaunes forestières au cours du Pléistocène ainsi que leurs différences entre masses continentales en réponse aux péjorations climatiques du Néogène sont analysées à partir de la reconstruction phylogénétique de certains clades.

**MOTS CLÉS**  
Oiseaux forestiers,  
systématique  
phylogénétique,  
biogéographie historique,  
tempo et mode de  
spéciation,  
cycles glaciaires,  
taux de diversification.

## INTRODUCTION

Because more than two thirds of the forested blocks of the Northern Hemisphere are (or have been) forested, woodland birds represent the most important part of their terrestrial bird fauna. At the scale of Eurasia, as many as 39 families, 126 genera, more than 1500 species and billions individual birds are more or less specialized to forest habitats (Keast 1990). From an evolutionary viewpoint, they are a legacy of the common history of birds and plants with close interactions between them since the Eocene (Regal 1977; Herrera & Pellmyr 2002). Major functional interactions include plant pollination (e.g. Grant 1994; Cronk & Ojeda 2008) and especially seed-dispersal (e.g. Herrera 2002; Jordano 2012) with such emblematic examples as the jay-oak and nutcracker-pine associations. The temperate and boreal forested regions of the Northern Hemisphere consist of four main blocks which are either deciduous or mixed deciduous and coniferous, namely the western North American block (which will not be discussed longer because the size, structure and distribution of forested areas are fairly different from those of the other forested blocks), the eastern North American block (part of the North American continent north of the US-Mexican border and east of the 95th western longitude), 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 west of 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 (Appendix 1).

Technological and methodological advances during the past couple of decades provide a refreshing insight on the long-debated evolutionary history of birds associated with the major vegetation belts of the Northern Hemisphere. The use of molecular data of both extinct and extant taxa led to a revolution in reconstructing the phylogenetic history of lineages. Influential methods were PCR-mediated DNA sequencing (Avice 2004; Kraus & Wink 2015) and ancient DNA (aDNA) combined with a burst of paleontological findings (e.g. Wood & De Pietri 2015). The advent of large-scale phylogenomic datasets allows the field of phylogenetics to sequence hundreds to thousands of loci. Enrichment of ultraconserved elements is one of a series of next-generation sequencing (NGS) that can produce large DNA datasets (Faircloth *et al.* 2012). All these advances have been combined with the development of powerful statistical and bioinformatics tools for constructing phylogenies and resolving issues on formerly equivocal relationships within clades. All these advances much contributed to our knowledge on faunal evolution and macroecological issues on broad-scale patterns of abundance, diversity, distribution and diversification (i.e., speciation *minus* extinction). The aim of this paper is to provide a new and refreshing insight in the history and evolution of bird faunas in the forest biomes of the Northern Hemisphere, by using this panel of tools for deciphering the imprint of the repeated north-south and east-west changes in the geographic configuration of land masses and in climates since the Mesozoic.

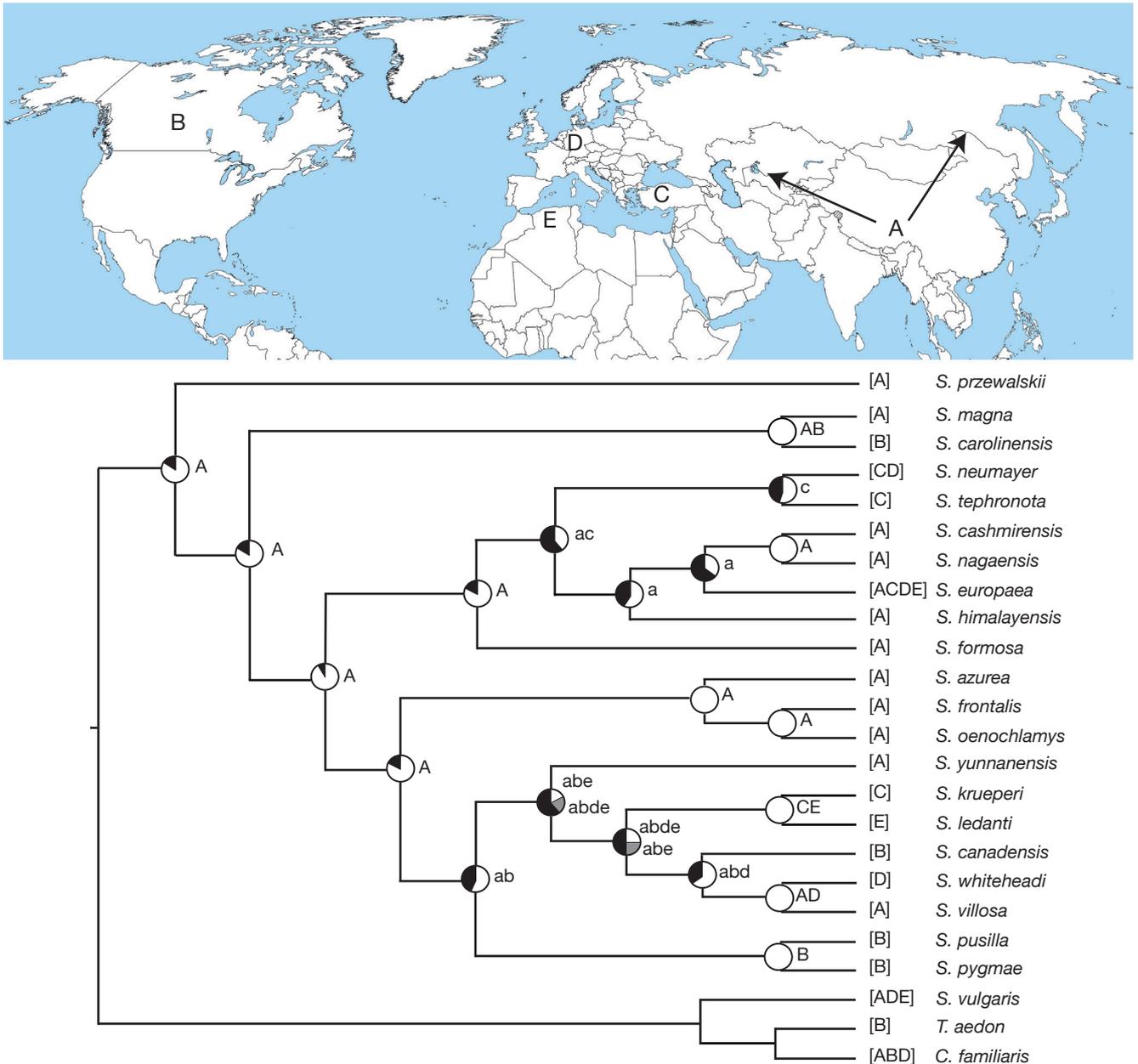


FIG. 1. — Phylogenetic tree of the Sittidae family (with *Sturnus vulgaris* Linnaeus, 1758, *Troglodytes aedon* Vieillot, 1809 and *Certhia familiaris* Linnaeus, 1758 as outgroups), based on the cytb, COI and RAG-1 sequence data, and extant distributional areas. Pie charts indicate relative probabilities of the most likely ancestral ranges for each node with the proportion of white indicating the probability of the best reconstruction, and grey the second best. Ancestral ranges are indicated in capitals for a probability > 70% and in lower case for a probability < 70%. Abbreviations: **A**, Asia; **B**, North America; **C**, Middle East; **D**, Western Europe; **E**, North Africa (after Pasquet *et al.* 2014).

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) 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, Europe and eastern Asia (China and Manchuria) (a forest block also occurs in western North-America but it is much smaller in size and will not be discussed further in

this paper) are mirrored by three huge tropical-equatorial blocks of humid forest in South America, tropical Africa and tropical South-East Asia-Australasia. Given the spatio-temporal context in which birds evolved in a world where climates and geography much changed throughout the history of birds, understanding the history, composition and dynamics of the bird faunas of the northern hemisphere needs to reconsider the role of the major flyways that connect them both in longitude (Nearctic-Palaearctic connections) and in latitude (temperate-tropical connections, i.e., Northern America/Central and South America, Western Europe/Africa, and Eastern Asia/South-eastern Asia).

WHEN AND WHERE DID MODERN FOREST BIRDS ORIGINATE? A wealth of studies using molecular systematics, starting with DNAxDNA hybridization (Sibley & Ahlquist 1990) and especially mitochondrial-DNA (mtDNA, cytochrome b) and DNA gene-sequencing provides a new insight in the spatiotemporal context in which extant bird species evolved. Wetmore's (1959) contention that most modern species date from the Pliocene has been challenged by Selander (1971), among others, who argued, mostly on paleontological grounds, that Pleistocene glacial cycles have been conducive to a burst of speciation in most groups of birds. In fact, recent studies have shown that most of the youngest terrestrial bird species on Earth coalesced in a deep past (Bermingham *et al.* 1992; Zink & Slowinski 1995; Avise 2004) with the majority of modern species of songbirds having a Pliocene origin, which does not mean, however, that substantial Pleistocene speciation did not occur as shown below (Johnson & Cicero 2004; Weir & Schluter 2004; Lovette 2005 but see Zink *et al.* 2004).

Five examples among many others will illustrate various scenarios of differentiation among clades of forest birds that originated in different parts of the Northern Hemisphere:

– a first example is that of the nuthatches of the genus *Sitta* (24–28 species) whose history has recently been reconstructed combining a biogeographic analysis and phylogenetic systematics using two mitochondrial genes and one nuclear gene (Pasquet *et al.* 2014; Fig. 1). A well resolved phylogeny of the genus reveals several clades with a first split, *c.* 20 million years ago (Ma) giving rise to the Przewalskii's nuthatch *Sitta przewalskii* (Berezowski & Bianchi, 1891) which is sister to all other species. Then, the clade *S. carolinensis* Latham, 1790–*S. magna* Ramsay, 1876 split *c.* 17 Ma and is sister to the two other clades which encompass all the other extant species. The genus originated in South-eastern Asia from where several clades dispersed in North America (four species) and in the western Palaearctic (Europe, six species), 17 Ma and 5 Ma, respectively. Interestingly the three endemic “mesogean” nuthatches which occur in coniferous forests in the Mediterranean basin, i.e., the Corsican nuthatch *Sitta whittheheadi* Sharpe, 1884 in Corsica, the Algerian nuthatch *S. ledanti* Vielliard, 1976 in Algeria, and the Kruper's nuthatch *S. kruperi* Pelzeln, 1863 in Turkey do not belong to a monophyletic group but to two separate lineages that diverged at the beginning of the Pliocene, *c.* 5 Ma, with the Corsican nuthatch being a sister species of the North American *S. villosa* Verreaux, 1865 that diverged *c.* 1 Ma;

– as a second example, a near-species-level phylogeny (from protein-coding genes CYTB and/or ND2 of mtDNA, and four nuclear genes) of the speciose (*c.* 832 species) New World clade Emberizoidea, a large and widespread group of songbirds which encompasses the Icteridae, Cardinalidae, Passerellidae, Thraupidae, Parulidae and their close relatives allowed reconstructing the tempo of diversification of this large group (Barker *et al.* 2015). An estimated age of *c.* 20 Ma had been estimated for this group which presumably differentiated in North America after an early lineage of this group, the Passerida, dispersed across Beringia from the Sahul (the continental Australasian mass) where it originated (Barker *et al.* 2004)

as postulated a long time ago by Mayr (1946, 1964). This is a robust result with all replicates yielding  $\geq 0.95$  probability for North America as the area of origin of the group. Then the history of this group was dominated by differentiation within North America with four of the major clades being ancestrally North American (Fig. 2). 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. Then this group of songbirds has accumulated *c.* 791 species in the New World in a series of diversification processes that occurred between *c.* 13 and 7.5 Ma (Fig. 2). The family Emberizidae (41 species) subsequently back dispersed in the Old World *c.* 11.8 Ma. (Barker *et al.* 2015). Within the Emberizoidea, a comprehensive analysis of the phylogenetic relationships of the New World warblers of the family Parulidae has been provided by Lovette *et al.* (2010) from mtDNA (cytochrome b) and nuclear DNA nucleotide characters. This huge family which includes 112–115 species distributed among 24–26 genera is particularly interesting because the breeding distributions of species span from the Arctic to temperate South America with centres of diversity in tropical as well as in temperate forested blocks of eastern North America (Lovette *et al.* 2010). Moreover, the family includes both resident and tropical migratory species, which provides clues for analysing the tempo and mode of diversification processes and for testing hypotheses on the evolution of migratory behaviour (see below). There is a strong molecular phylogenetic support for a monophyletic “core Parulidae” group having differentiated in North America *c.* 5–7 Ma and including all the typical wood-warbler genera (Klein *et al.* 2004; Barker *et al.* 2015; Fig. 2).

Among the Parulines, the 27 species of the genus *Dendroica* is the North America's most spectacular avian radiation (Lovette & Bermingham 1999) with a burst of speciation occurring in the Late Miocene–Early Pliocene later followed by many differentiation events in the late Pleistocene (see below). The *Dendroica* species have been hypothesized to be ecological counterparts of species of the Palaearctic genus *Phylloscopus* (49 species). 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 ecological convergence in similar habitats (Price *et al.* 2000). Most species are migratory and overwinter in the tropics (*Dendroica* in the New World and *Phylloscopus* in the Old World). Molecular phylogenies (mtDNA cytochrome b) showed that the *Phylloscopus* group started to differentiate more than 12 Ma, which is much earlier than the *Dendroica* genus which originated in the Pliocene as mentioned above. Price *et al.* (2000) have shown from ecomorphological and behavioural comparisons of *Dendroica* and *Phylloscopus* communities in New Hampshire (North America) and in Kashmir (Asia) localities, respectively, that the history of the species' radiations so much differs between the two groups that their communities are unlikely to be really convergent even when placed in similar environments. Species in the two regions much differ in foraging behaviour and in relationships between morphology and ecological variables.

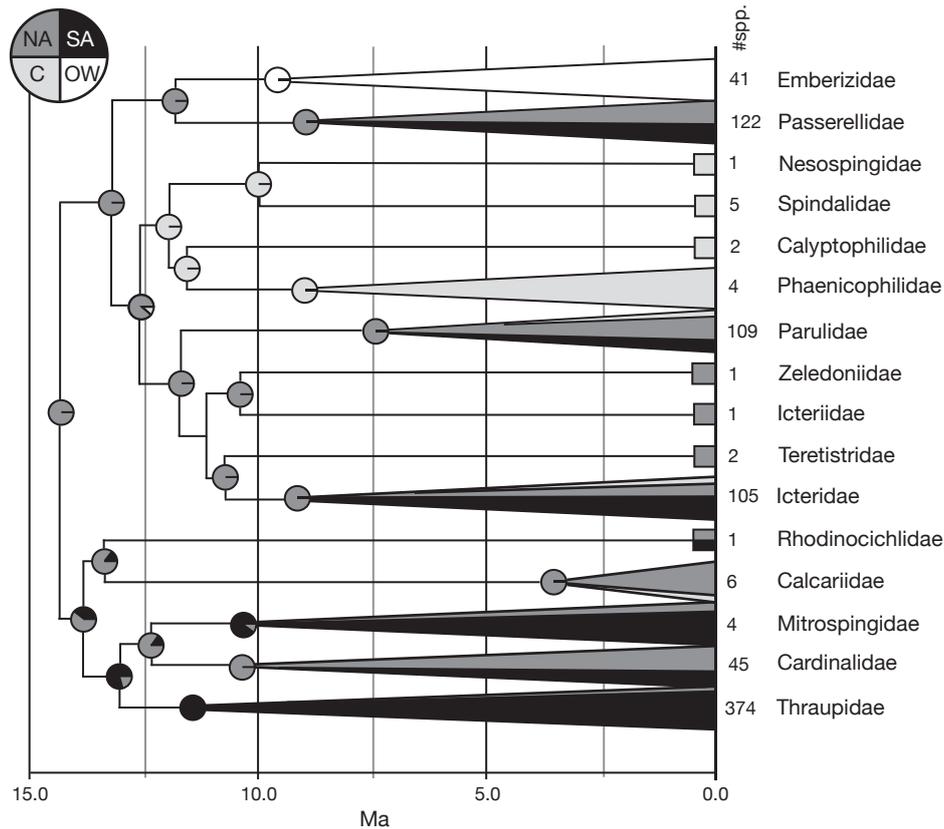


FIG. 2. — Biogeographical reconstruction for the Emberizoidea from a species-level time-scaled phylogeny of the group. Pie graphs at each node indicate the relative likelihood of each state. Width of fill in terminal triangles indicates the percentage of species in each group currently found in each region. Abbreviations: **NA**, North America; **SA**, South America; **C**, Caribbean; **OW**, Old World; **Squares**, lineages with only one species sampled (Barker *et al.* 2015).

*Dendroica* 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 *Dendroica* warblers group of North America is a classic example of fine-scale niche partitioning (MacArthur 1958). Lack (1971: 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 *Dendroica* warblers results from a burst of speciation driven by sexual selection and which results in a “species flock” of ecologically similar coexisting species. 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 well represented in both North and South America includes both temperate resident species and long-distance migrants. This broad distribution and diversity allows to investigate the relative impacts of migration and ecological shifts on avian diversification across North and South America (Bryson *et al.* 2016);

– a third example is the *Sylvia* complex (25 species) which includes many species specialized in mediterranean-type vegetation such as matorrals (a generic name for all kinds of mediterranean-type shrubby or scrubby habitats). The genus

also includes species breeding in tropical Africa. DNAXDNA experiments (Blondel *et al.* 1996) and mitochondrial DNA-sequencing (Böhning-Gaese *et al.* 2003) revealed that the basal split of *Sylvia* (the *atricapilla-borin-abbyssinica* lineages versus all others) occurred *c.* 13–16 Ma. The common whitethroat *S. communis* Latham, 1787 is sister to the Mediterranean species group whose breeding range is restricted to Mediterranean matorrals (Fig. 3). The radiation of the two main clades, the *curruca-bortensis* group and the Mediterranean species group, including *S. communis* Latham, 1787, is estimated as having occurred *c.* 5.5–8.5 Ma. Although the region of origin of the common ancestor of the genus remains unknown, it evolved around the Mediterranean basin during the Pliocene with the three major clades of Mediterranean *Sylvia* warblers having presumably evolved in the three large Mediterranean peninsulas. During the Messinian crisis (5.9 to 5.3 Ma), when the Mediterranean Sea almost completely dried out, the Mediterranean basin was very arid and *Sylvia* habitats must have been restricted to isolated pockets of matorrals. Many episodes of sea level change, climatic upheavals and associated vegetation changes provided opportunities for repeated isolation of populations in isolated refuges (Blondel *et al.* 1996; Shirihi *et al.* 2001). Some of these taxa later came into contact as their habitats spread with matorral vegetation being today more extensive in the Mediterranean region than at any time in the past, as a result of human deforestation;

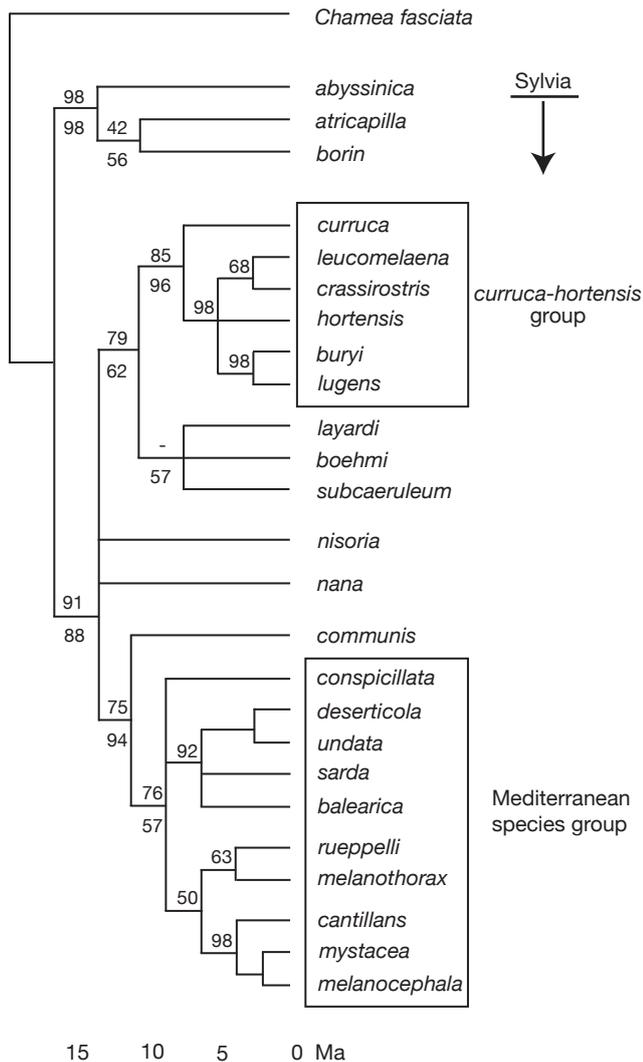


FIG. 3. — Phylogeny of the *Sylvia* complex with Wren Tit *Chamaea fasciata* Gambel, 1845 as an outgroup taxon constructed from mitochondrial cytochrome b gene. Bootstrap values of transition differences (above branches) and bootstrap values of transversion differences (below branches). Branches receiving less than 50% bootstrap support are shown as unresolved polytomies (Böhning-Gaese *et al.* 2003). See text.

– a fourth example which will be discussed further below reports on the divergence time of the twelve species of American thrushes of the genus *Catharus* which includes seven sedentary species breeding in Central and tropical South America and five migratory species breeding in North America. Phylogenetic analyses from cytochrome-b and ND2 genes revealed that this monophyletic group consisting of two clades originated in either Central America or Central America-South America in the early Pliocene to mid-Pleistocene, *c.* 5 Ma, (Outlaw *et al.* 2003);

– a fifth example is that of the grouse group (Tetraoninae) which originated in the Nearctic region 6.3 Ma. (Drovetski 2003). A complete molecular phylogeny of this monophyletic clade (21 species) widely distributed in the Northern Hemisphere has been combined with paleontological data used to calibrate a molecular clock.

Estimates of divergence rates suggested that the radiation of the group coincided with global cooling and climatic oscillations of the Pliocene-Pleistocene. The grouse phylogeny originated in the Pliocene, 6.3 Ma, with diversification beginning *c.* 3.2 Ma. Historical biogeographical reconstructions show that the Western Nearctic played a major role in the radiation of the group and that Eurasia has been colonized independently three times, presumably through the Beringian land bridge, and the Nearctic from Eurasia only once.

#### PLEISTOCENE CLIMATIC INSTABILITY AND BIRD DIFFERENTIATION

Ice ages of the Pleistocene dramatically reshaped biodiversity patterns at a continental scale. Diversification rates have been shown to decrease across the Pleistocene (Ricklefs 2006; McPeck 2008) but this does not mean that Pleistocene climatic upheavals did not produce evolutionary signatures (Klicka & Zink 1997; Avise & Walker 1998; Hewitt 2000, 2004; Zink *et al.* 2004; Lovette 2005). If species retain their climatic niche as climatic conditions change, which is supported by large-scale tests of niche conservatism (Guisan *et al.* 2014; Qian & Ricklefs 2016), birds followed 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 refuges, forming “suture zones” as shown by molecular studies in various groups of plants and animals (Petit *et al.* 1997; Taberlet *et al.* 1998).

A new insight has recently been given on the controversial role of recent ice ages in bird speciation. Dates of origin of passerine bird lineages have been estimated by Weir & Schluter (2004) from mitochondrial sequence divergence and a molecular clock for members of a series of superspecies complexes in boreal, sub-boreal and neotropical forest vegetation belts. Comparing the coalescence times of pairs of species along this latitudinal gradient these authors convincingly showed that speciation was commonly initiated during recent glacial periods with all coalescence events in boreal superspecies dating to the late Pleistocene. In North America, patterns of differentiation and endemism of boreal superspecies are consistent with the fragmentation of the boreal forest 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) which linked geographical patterns of distribution of sister species of wood-warblers to successive glacial advances having produced western species from an eastern ancestor. Weir & Schluter (2004) showed that vicariance events caused by glacial advances have had the largest impact on the most northerly breeding species of extensive boreal forest that was more repeatedly subdivided in isolated refuges than forests 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 46% of tropical superspecies suggesting that avifaunas

directly fragmented by ice sheets experienced rapid rates of diversification, 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. Many of them 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 the same line, genetic transitions occurring transverse to the range of species in mountain ranges as a result of genetic isolation during glaciations have recently been demonstrated by Wallis *et al.* (2016) from molecular studies in several groups of plant, insect and bird species of the Palaearctic mountain chains (e.g. plants and invertebrates in the Pyrenees, mammals and birds in Himalaya). With several others studies, for example that of Töpfer *et al.* (2010) on bullfinches *Pyrrhula* spp., these studies highlight the significance of climatic upheavals and glaciers of the Pleistocene as barriers promoting genetic isolation and bird speciation events.

To conclude from these examples on the tempo of origination of forest birds, three points emerge:

- differentiation of most extant 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) but recent ice ages also played an important role in diversification processes. However broad comparisons based on phylogenies of entire avian genera reveal that Pleistocene-era nodes account for but a small proportion of the total species diversity, something like the tail of the distribution of speciation times (e.g. Lovette & Bermingham 1999; Outlaw *et al.* 2003; Johnson & Cicero 2004);
- major lineages originated in various regions of both the Northern and the Southern Hemispheres as shown by the examples mentioned above so that the histories of differentiation are group-specific;
- 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 & Zink 1997, 1999; Avise & Walker 1998). Recent genomic studies actually show that speciation is a dynamic and complex process in which the incipient species continue to exchange gene 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.

#### TROPICAL-TEMPERATE FLYWAYS AND BIRD DIVERSIFICATION

Between- and within- continents processes of diversification at the biogeographic scale of the Northern Hemisphere have been described since a long time (e.g. Newton 2003) so that they will not be discussed further (see Appendix 2). More interesting is to focus on a new and exciting insight recently provided from phylogenetic studies on the relationships between tropical and temperate regions (north-south flyways) in terms of bird diversification (Blondel 2018). Much of this new information stems from the study of clades that include both resident and long-distance migratory species.

In the framework of the “faunal types” concept (Stegmann 1938) which prevailed before the advent of vicariance biogeography, a long standing tenet is that birds of 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 of speciation (Webster & Purvis 2002). Phylogenetic biogeography, the evolutionary history of long-distance tropical migrants and the origin of the migratory behaviour provide an insight into the biogeographic origin of birds.

A large number of the species of migratory bird 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 & Jones 2002).

Two theories have been proposed for explaining where and when all these long-distance tropical migrants evolved (Salewski & Bruderer 2007). The first theory, the “southern-home-theory” posits that they originated in the tropics where they exploit stable resources and subsequently evolved a migratory habit allowing them to extend their breeding range at higher latitudes for capitalizing on seasonally abundant resources in regions they leave for wintering in their area of origin. 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). This theory has been proposed for both the Palaearctic-Afrotropical and the Nearctic-Neotropical systems (Rappole 1995; Rappole & Jones 2002). The second theory, the “northern-home-theory” hypothesizes that birds having originated in the Northern Hemisphere where they breed are pushed southward annually for avoiding deteriorating seasonal conditions in winter (Bell 2005; Salewski & Bruderer 2007). Testing these theories requires a phylogenetic framework (Zink 2002; Outlaw *et al.* 2003) because: 1) the occurrence of conspecific or congeneric species breeding in both the Northern and the Southern hemispheres says nothing on the ancestral area of origin of taxa; and 2) within a given lineage, migration may be ancestral with extant residency being a derived condition through loss of migratory behaviour.

Clades that include both migrant and resident species are good candidates for testing these hypotheses 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 having reconstructed the ancestral state of migration in an explicit phylogenetic framework show that the migratory behaviour derived from sedentary ancestors (e.g. Outlaw *et al.* 2003; Outlaw & Voelker 2006). These studies concluded that the migratory behaviour among extant birds has evolved relatively recently compared with the total age of the lineages from which migratory species derived. For example, addressing from a molecular phylogeny the evolution of long-distance migration and the historical biogeography of the five migrant and seven resident species of *Catharus* thrushes, Outlaw *et al.* (2003) demonstrated: 1) the nonmonophyly of the migratory species with migratory behaviour having evolved three times; and 2) that the topology of the cladogram indicates that resident behaviour is ancestral with migratory species being sister species of resident species whose ranges are restricted in tropical Central America. A conclusion drawn from this study and several others is that many lineages of long distance migrants breeding in temperate regions of the Northern Hemisphere evolved from historically tropical sedentary ancestors (Rappole 1995). This conclusion supports the “southern-home-theory” and is echoed e.g. by Berthold (2001) and Zink (2002).

Another picture which supports the alternative “northern-home-theory” emerges from studies of the Emberizoidea which, as discussed above, originated in North America (Fig. 2). 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 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 “southern-home-theory” which states that migration evolved through a shift of the breeding range out of ancestral tropical or subtropical regions, rather than an extension of an ancestral temperate non-breeding range to tropical regions. 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. As more comprehensive species-level phylogenies are published with detailed taxon- and area-cladograms, ancestral state reconstructions of migratory behaviour will increase 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 result 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 bird faunas and communities of the main forest blocks of the Northern Hemisphere much differ in spite of their long common evolutionary history. The size of the three main forest blocks is *c.* 1.2, 1.2 and  $1.8 \times 10^6$  km<sup>2</sup> for Europe, eastern Asia and eastern North America, respectively (Latham & Ricklefs 1993a, b). According to the classical species-area relationships, the bird diversity of these three regions of roughly similar size should be of a similar order of magnitude, which is not the case because extant bird faunas include *c.* 732 species in North America, *c.* 533 species in Europe and *c.* 1000 species in eastern Asia. Besides species richness other differences between these bird faunas include:

- a lower taxonomic diversity in Europe compared to the two other regions (Mönkkönen & Viro 1997);
- a larger proportion of the continental-wide bird fauna being associated with forests in eastern North America and eastern Asia (about two thirds of the terrestrial avifauna) than in Europe (about half);
- 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) as compared to 21% only in the primeval oak-hornbeam-lime forest of Białowieża, Poland (Wesołowski *et al.* 2002). The overall numbers of species in the Palearctic-Asian and North America-Neotropics migration systems are quite similar with *c.* 340 species each, while the Palearctic-tropical African system is much smaller with no more than 185 species (Rappole & Jones 2002). Only 48 species of tropical migrants breed in Palearctic forests compared to 112 species in Nearctic forests and 107 in eastern Asian forests (Rappole 1995). Similar patterns of species impoverishment have been found 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 & Ricklefs 1993a). Similar variation in bird and tree species richness does not mean a common variation of tree-bird associations but suggests that the speciation-extinction-dispersal processes have basically but independently been driven by the same factors in the two groups. Explaining these large-scale diversity patterns requires testing hypotheses addressed at time and spatial scales that match the scale of the processes involved.

### *Why fewer species in European forests than in eastern Northern American and eastern Asian ones?*

Two main hypotheses may explain why the three regions of the Northern Hemisphere so much differ 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. In these two regions, as ecological conditions deteriorated during glacial times, temperate biotas were permanently connected with tropical biotas where they could find refuge 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 than 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 allowing a continuous interchange between tropical and temperate bird faunas in response to climatic fluctuations (Webb & Bartlein 1992). The successive waves of Pleistocene glaciations resulted in a 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 (CLIMAP 1976). This explains why extant bird faunas of eastern Asia include representatives of tropical Indo-Malayan families such as Zosteropidae, Pycnonotidae, Timalidae or Campephagidae, and those of eastern North America include representatives of Neotropical families such as Trogonidae, or Cracidae.

In contrast, massive east-west oriented barriers (mountain ranges, seas and large desert belts) always separated the temperate European avifauna from the tropics, preventing it from finding refuge in tropical regions further south. Although the Sahara and desert regions of southwest Asia had more vegetation during glacial times than today, this so-called eremian belt was never forested enough to provide a dispersal link for forest birds between the Afrotropics and Eurasia. Hence Pleistocene glaciations probably hit harder the European bird fauna than that of the two other forest blocks. However, this hypothesis is not supported by phylogenetic analyses which show that less than 10% of the passerine bird species went extinct in the Pleistocene (Zink & Slowinski 1995), a figure supported by the fossil record which shows very low extinction rates during the glacial-interglacial cycles (Willis & MacDonald 2011). In addition, warming effects of the Gulf Stream current 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 northern, 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 for explaining bird richness anomalies posits that differences in diversity patterns among the bird faunas of the three temperate regions of the Northern Hemisphere reflect the dynamics of colonization-differentiation along the tropical-temperate flyways. If, as explained 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 in the north American flyways allowed clades of tropical origin to disperse further north where they subsequently locally differentiate. This “Out of the Tropics” hypothesis proposed by Jablonski *et al.* (2006) for explaining latitudinal gradients of diversity in marine mollusc posits that evolutionary clades that have mostly originated in tropical environments expand their distribution to temperate regions where they subsequently diversify. Intense radiation occurring in temperate regions after ancestral taxa colonised them from the tropics (secondary radiation) is obviously the case for the *Dendroica* wood warblers discussed above (Lovette & Bermingham 1999). The “out of the Tropics” paradigm explains why south-north continental interchange 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 (Appendix 3). One argument supporting the importance of the tropics vs temperate regions for bird diversification is that tropical environments dominated the early Tertiary everywhere on Earth, providing deeper roots for tropical diversity compared to temperate and boreal regions (Wiens & Donoghue 2004).

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 differ between them. For example, many species of the Palearctic leaf warblers of the genus *Phylloscopus* exhibit clear patterns of the Rapoport’s rule whereby species that live farther north have larger ranges (Price *et al.* 1997) with the consequence that niche packing is looser, i.e., fewer species can accumulate in any given habitat. In contrast, in eastern North America, close tree-bird associations and fine habitat selection in Parulids result in a much higher niche-packing, hence higher local species diversity (Price *et al.* 2000) than in Europe.

#### *Neogene diversification rates across scales of space and time*

Besides differential contribution of tropical biotas in colonizing temperate forests, increased environmental instability caused by the Neogene peioration of climatic conditions differently influenced rates of diversification (speciation rates minus extinction rates) between the main landmasses. In the near absence of fossil data, especially from small passerines, testing this hypothesis requires phylogenetic reconstructions (Nee *et al.* 1994; Ricklefs 2006; Jetz *et al.* 2012) because evolutionary trees of different lineages based on mtDNA provide an estimate of combined speciation and extinction rates over time. Tests of Pleistocene diversification of 11 passerine bird lineages suggest a consistent decline in net diversification rates across the Pleistocene (Zink & Slowinski 1995; McPeck 2008, but see Jetz *et al.* 2012). The question is whether the cause of this decline is reduced speciation or increased extinction rates. Again, two non-mutually exclusive hypotheses have been offered for answering this question:

TABLE 1. — Average pairwise percentage dissimilarity (**PD**) of bird communities between two different forest types less than 100 km apart within a region, and average expected number of species (**ES**) in samples of 80 pairs of communities in eastern North America and Europe. PD varies from 0 (all species in common with equal abundances) to 100 (no species in common). **N**, number of comparisons in each region. Differences in **PD** are not significant at the between-region scale but highly significant at the between-continent scale. **ES** values do not differ statistically neither at the between-region scale nor at the between-continent scale (after Mönkkönen 1994).

	<b>N</b>	<b>PD (%)</b>	<b>N</b>	<b>ES</b>
Eastern North America				
Boreal	6	66.2	12	20.8
Sub-boreal	13	69.1	26	19.8
Europe				
Boreal	9	35.5	15	17.6
Sub-boreal	10	43.2	29	20.0

– in Europe, the fact that biotas have been prevented to disperse in tropical refuges during pleniglacial times by barriers to dispersal combined with the geographic displacement and reduction in size of many habitats could have caused more extinction events than in the other forest blocks of the Northern Hemisphere, but this hypothesis is not supported neither by phylogenetic analyses nor by fossil data as explained above; – a slowing down of speciation rates rather than accelerated extinction rates may have resulted from ecological limitations such as competition for limited resources, adaptive radiation or niche filling within clades through evolutionary time (Nee *et al.* 1992, but see Moen & Morlon 2014). Demonstrating a slowdown of diversification rates in temperate regions requires testing the null hypothesis that diversification rates do not differ between temperate and tropical regions. Tests of this hypothesis have been made by comparing the diversity of clades of passerine lineages in large tropical and temperate regions in order to determine the effects of the environment (tropical vs temperate) and the size of the region on rates of diversification. A conclusion strongly supported by data including 14 clades of passerines restricted to South America and 23 clades restricted to North America is that net rates of diversification are higher in tropical regions and decrease with the age of clades, which supports the hypothesis that the filling of ecological space constrains further differentiation (Ricklefs 2006; Fuchs *et al.* 2017 but see Shakya *et al.* 2017). In short, the longstanding tenet of increased avian speciation rates in the Pleistocene does not resist current phylogenetically-based investigations on diversification rates and might have been based on an exaggerated focus on extant species. Future studies from phylogenetic approaches using genomic data (Oyler-McCance *et al.* 2016) should shed light on the tempo and mode of speciation/extinction events of European species during the Neogene.

*Forest bird communities in eastern North America and Europe* Continent-specific histories of differentiation and colonization of bird lineages should translate at the scale of the composition, structure and dynamics of forest bird communities. This discussion will be limited to North American vs European communities because of a lack of

data in Asian communities. As stated above the contribution of tropical migrants is much higher in North American forests (Mönkkönen & Helle 1989; Rappole 1995; Holmes & Sherry 2001) than in European forests where most species are resident or short-distance migrants (Wesołowski & Tomiałojć 1997; Wesołowski 2007). Prominent families of Neotropical origin in North America are Parulidae, Vireonidae, Tyrannidae and Icteridae with 109, 63, 430 and 105 species, respectively. In contrast, Afro-tropical influence in the European bird fauna is negligible (Appendix 3). The main differences between North American and European forest bird communities result from the paramount importance of long-distance migrants which dominate communities in late-seral stages in North America whereas the small number of long-distance migrants in European forests mainly occur in early-seral stages.

Scaling down the structure of bird communities, a striking feature which results from the explosive radiation of several clades, notably that of the Parulidae in North America, discriminates European from North American bird assemblages (Mönkkönen 1994):

- at a continental scale (delta diversity), species richness of forest passerines and allies is higher in the Nearctic (95 species) than in the Palaearctic (78 species);
- at a regional scale of 200 × 200 km<sup>2</sup> squares, a so-called gamma diversity, there are on average ten species more in the eastern Nearctic than in the western Palaearctic region (mean numbers are 53.8 vs 43.6, respectively,  $P < 0.0001$ ), and regional species pools are also structurally and taxonomically more variable in the former region;
- the between-habitat component of diversity (percentage dissimilarity, PD in Table 1, a proxy for beta diversity) 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 two forest types in the western Palaearctic is always less than 50%. This means that habitat selection patterns by birds are finer in North American forests with closer niche packing than in their European counterparts, a typical feature for 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 in relation to forest succession;
- at the local scale of bird communities (alpha diversity), with 18 to 21 species, expected numbers of species in samples of 80 pairs of communities average values did not significantly differ between the two continents. These differences between the two continents presumably result from Nearctic forest associated bird species having experienced higher radiation rates combined with permanent contact between tropical and temperate regions as previously explained in this paper. More opportunities for bird specialization in the floristically richer North American forests should be a worth testing hypothesis. It would also be most interesting to make similar comparisons of diversity and habitat selection patterns between eastern Asian forest birds and those of the two other forest blocks.

## CONCLUSION AND FUTURE PROSPECTS

Bird communities of the three main forest blocks of the Northern Hemisphere have many similarities but also differences which can be investigated from molecular tools which shed light on the tempo and mode of differentiation of clades and on the past relationships of bird faunas at the within- and the between-continent scales. Richer and taxonomically more diverse bird communities in North America than in Europe presumably result from Nearctic forest associated bird species having experienced higher radiation rates as a result of permanent contact during the whole Neogene between tropical and temperate realms rather than from lower extinction rates during glacial times. As more comprehensive species-level phylogenies are published with detailed taxon- and area-cladograms, ancestral state reconstructions will increase our understanding of rates of bird diversification in the various parts of the Northern Hemisphere as well as our understanding of general patterns of change in migratory behaviour across the avian tree of life. One interesting point would be to investigate whether the floristically richer North American forests provided more opportunities for bird specialization, hence more species within the ecological space compared to European forests. 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 two other forest blocks, which would allow to generalize the patterns and processes of forest bird history at the scale of the whole Northern Hemisphere. Such future studies will benefit from the new generation of phylogenetic approaches using genomic data (Joseph & Buchanan 2015; Kraus & Wink 2015; Oyler-McCance *et al.* 2016; Toews *et al.* 2016). However, since most recent species phylogenies are robust, the overall adding of genomic data will probably not change the general patterns but they will provide more fine scale patterns in the phylogenies or gene flow among subspecies groups. Finally, a point which would deserve thorough studies is the extent to which habitat diversity and species diversity have coevolved so that 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 postulated by Rosenzweig (1995).

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## APPENDICES

## APPENDIX 1. — The extant zonation of forest belts of the Northern Hemisphere.

From north to south three main forest belts stretch across the continents of the Northern Hemisphere:

- 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 7000 km from end to end (Imbeau *et al.* 2001). Large parts of the areas today occupied by taiga were under ice during glacial times so that the bird fauna of this biome is relatively poor including a small number of species belonging to the “Siberian” faunal type (*sensu* Stegmann 1938), most of them being widespread over huge areas, and often straddling Eurasia and North America. About 30% of the land birds breeding in boreal forests winter in the tropics, 45% are short-distance migrants, and only 5-15% are permanent residents (Niemi *et al.* 1998);
- 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 species are short-distance migrants and 15-20% are tropical migrants. In both the boreal and nemoral zones of Europe, bird assemblages are taxonomically less speciose and diverse

than those of their North American counterparts, a point which is discussed at length page 36.

- The warm-temperate zone of Europe (mean winter temperature above 4°C and summer mean 21-27°C) is characterized by mediterranean-type forests which have no equivalent in the other forest blocks of the Northern Hemisphere, except in the south-west part of North America in California (which is not discussed in this paper). The bird fauna mostly consists of boreal and temperate species but the high diversity of endemic tree species is not mirrored by a similar diversity of Mediterranean-specific bird species. A striking feature of the Mediterranean forest bird fauna is the very low level of endemism in forest dwelling species. Hence a paradox: the more the forest is mature and dominated by endemic Mediterranean tree species such as holm oak *Quercus ilex* L. or cork oak *Q. suber* L., the less the associated bird assemblages include species of Mediterranean character (Blondel 1998). One hypothesis for explaining this paradox is that the repeated back and forth shifts of vegetation belts and their associated faunas across the western Palaearctic during the Neogene and especially the Pleistocene resulted in repeated mixings of biotas so that they have never been isolated from mid-European forests, preventing allopatric speciation events to occur (see Blondel *et al.* 2010: 45-47; Blondel 2018). This explains the homogeneity and low rate of regional endemism of the forest avifauna over Europe today, including the Mediterranean zone and North Africa (Blondel 1990; Blondel & Vigne 1993; Hewitt 2000).

## APPENDIX 2. — Between- and within-continent east-west relationships of the forest bird faunas.

For most of the Mesozoic, the major land masses of the Northern Hemisphere were connected so that past relationships between North America and the Palaearctic left their imprint before they split during the Jurassic, 100 Ma, separating the formerly continuous Holarctic biotas into two blocks that evolved under conditions of increasing continental isolation. Similarly, a long-standing and wide connection of the same habitat types in the boreal forest biome between Europe and eastern Asia explains many similarities between the two realms. This long history explains that bird faunas of the two continents have many similarities and a wide Holarctic distribution in the boreal zone (coniferous and mixed forests) with 45% and 67% of the resident genera of North America and Europe, respectively, occurring in the two continents (Helle & Mönkkönen 1990).

At the within-continent scale, besides regional differentiation events associated with Pleistocene glaciations, a wide range of Palaearctic taxa exhibit east and west vicariant pairs of species or semi-species whose differentiation is clearly not associated with glacial cycles because of time or space inconsistencies. Examples among maybe one hundred or so include the western capercaillie *Tetrao urogallus* Linnaeus, 1758 and the eastern black-billed capercaillie *T. urogalloides* Middendorf, 1853, the turtle dove *Streptopelia turtur* (Linnaeus, 1758) and the eastern turtle dove *S. orientalis* (Latham, 1790), or the tree pipit *Anthus trivialis* (Linnaeus, 1758) and the Pechora pipit *A. gustavi* Swinhoe, 1863. Deciphering the tempo and mode of differentiation of these taxa from phylogenetic analyses would shed an interesting light on the past relationships between the western and the eastern parts of the Palaearctic.

## APPENDIX 3. — Examples of European forest bird species of tropical origin.

In contrast to the strong Neotropical-North American relationships of forest birds, very few species of European forests originated in the African tropics and most of the few examples of species of Afrotropical origin are not forest specialists. Examples include several species of the Order Coraciiformes with one species of Coraciidae (*Coracias garrulus* Linnaeus, 1758), one species of Alcedinidae (*Alcedo atthis* (Linnaeus, 1758)) and one species of Meropidae (*Merops apiaster* Linnaeus, 1758) (Burt 2004). One species of the Oriole family (29 species), the golden oriole *Oriolus oriolus* (Linnaeus, 1758) is an interesting example of a bird belonging to a family that has colonized Asia from the Australo-Papuan region and then colonized Africa *c.* 11 Ma.

(Jønsson *et al.* 2010). This colonization pattern is a straight forward dispersal from Australia to Asia and then to Africa which is the general patterns proposed for oscine passerines birds (Barker *et al.* 2002). Exceptions to the general rule that most forest lineages of the Afro-tropics are confined to forest habitats in Africa are the species of the *Muscicapa* lineage and allies which originated *c.* 7.4 Ma. in Africa and rapidly expanded in Eurasia (Voelker *et al.* 2016). Except the *Muscicapa* flycatchers none of these species are forest specialists. Among the few other species of tropical origin, *Cisticola juncidis* (Rafinesque, 1810) belongs to a large family (51 species) of birds specialized in open habitats such as savannas and marshland.