Journal of Biogeography (*J. Biogeogr.*) (2011)

ORIGINAL ARTICLE

Horizontal and elevational phylogeographic patterns of Himalayan and Southeast Asian forest passerines (Aves: Passeriformes)

Martin Päckert[1]*, Jochen Martens[2], Yue-Hua Sun[3], Lucia Liu Severinghaus[4], Alexander A. Nazarenko[5], Ji Ting[3], Till Töpfer[6] and Dieter Thomas Tietze[1]

[1]*Senckenberg Naturhistorische Sammlungen, Museum für Tierkunde, Königsbrücker Landstraße 159, 01109 Dresden, Germany,* [2]*Institut für Zoologie, Johannes Gutenberg-Universität, 55099 Mainz, Germany,* [3]*Key Laboratory of Animal Ecology and Conservation, Institute of Zoology, Chinese Academy of Science, 100101 Beijing, P.R. China,* [4]*Biodiversity Research Center, Academia Sinica, Taipei, 115, Taiwan,* [5]*Institute of Biology and Soil Sciences, Far-East Branch, Russian Academy of Sciences, 690022, Vladivostok, Russia,* [6]*Biodiversity and Climate Research Center (BiK-F), Senckenberganlage 25, 60325 Frankfurt am Main, Germany*

*Correspondence: Martin Päckert, Senckenberg Naturhistorische Sammlungen, Museum für Tierkunde, Königsbrücker Landstraße 159, 01109 Dresden, Germany.
E-mail: martin.paeckert@senckenberg.de

ABSTRACT

Aim Zoogeographic patterns in the Himalayas and their neighbouring Southeast Asian mountain ranges include elevational parapatry and ecological segregation, particularly among passerine bird species. We estimate timings of lineage splits among close relatives from the north Palaearctic, the Sino-Himalayan mountain forests and from adjacent Southeast Asia. We also compare phylogeographic affinities and timing of radiation among members of avian communities from different elevational belts.

Location East Asia.

Methods We reconstructed molecular phylogenies based on a mitochondrial marker (cytochrome *b*) and multilocus data sets for seven passerine groups: Aegithalidae, Certhiidae (*Certhia*), Fringillidae (*Pyrrhula*), Paridae (*Periparus*), Phylloscopidae, Regulidae and Timaliidae (*Garrulax sensu lato*). Molecular dating was carried out using a Bayesian approach applying a relaxed clock in BEAST. Time estimates were inferred from three independent calibrations based on either a fixed mean substitution rate or fixed node ages. The biogeographic history of each group was reconstructed using a parsimony-based approach.

Results Passerine radiation in Southeast Asia can be divided into roughly three major phases of separation events. We infer that an initial Miocene radiation within the Southeast Asian region included invasions of (sub)tropical faunal elements from the Indo-Burmese region to the Himalayan foothills and further successive invasions to Central Asia and Taiwan towards the early Pliocene. During two further Pliocene/Pleistocene phases, the subalpine mountain belt of the Sino-Himalayas was initially invaded by boreal species with clear phylogenetic affinities to the north Palaearctic taiga belt. Most terminal splits between boreal Himalayan/Chinese sister taxa were dated to the Pleistocene.

Main conclusions Extant patterns of elevational parapatry and faunal transition in the Sino-Himalayas originated from successive invasions from different climatic regions. The initiation of Southeast Asian passerine diversification and colonization of the Himalayan foothills in the mid-Miocene coincides with the postulated onset of Asian monsoon climate and the resulting floral and faunal turnovers. Patterns of elevational parapatry were established by southward invasions of boreal avifaunal elements to the subalpine Sino-Himalayan forest belt that were strongly connected to climate cooling towards the end of the Pliocene. Current patterns of allopatry and parapatry in boreal species (groups) were shaped through Pleistocene forest fragmentation in East Asia.

Keywords

Ancestral area reconstruction, bird evolution, faunal transition, molecular clock, parapatry, Passeriformes, phylogeography, rate smoothing, Sino-Himalayas.

http://wileyonlinelibrary.com/journal/jbi
doi:10.1111/j.1365-2699.2011.02606.x

INTRODUCTION

One important hotspot of avian biodiversity in the Northern Hemisphere comprises several large Eurasian mountain ranges: the Himalayan mountains, the neighbouring sub-Himalayan Indo-Burmese region, and the south-western Chinese mountain systems of the provinces Gansu, Qinghai, Sichuan, Shaanxi, Yunnan and forested regions of south-eastern Tibet (Roselaar *et al.*, 2007). Fifteen Himalayan bird species are entirely endemic, and four Endemic Bird Areas (EBA) defined by BirdLife International (Stattersfield *et al.*, 1998) largely or partly overlap with the Himalayas. Given the growing focus on molecular methods and bioacoustics in avian systematics, some passerine genera were recently re-evaluated (Alström, 2006; Rheindt, 2006; Martens *et al.*, 2011). As a result of such taxonomic progress, a large number of subspecies were promoted to species level, and these constitute the largest part of a recent increase in currently accepted species numbers (review in Sangster, 2009). Nevertheless, several Asian bird species were in fact described as new to science, with a focus on cryptic taxa in species-rich genera such as leaf-warblers, Phylloscopidae (two recent examples are *Phylloscopus occisinensis* Martens *et al.*, 2008 and *Phylloscopus calciatilis* Alström *et al.*, 2010).

The zoogeographic composition of the Himalayan avifauna has been analysed mainly on a horizontal plane (Martens & Eck, 1995; Johansson *et al.*, 2007; Renner & Rappole, 2011). However, efforts have been made to categorize the elevational zonation of avian communities in the Himalayas with affinities to different zoogeographic regions. Zuxiang (1982) distinguished four different elevational zones from the southern slopes of the Himalayas that comprised an exclusively Oriental avifauna below 2600 m a.s.l. and a Palaearctic avifauna above 3200 m, with a transition zone in between. Martens (1984) compared regional distribution patterns of Himalayan birds, mammals and arthropods, and drew similar conclusions: species of the moist subalpine forests (*Rhododendron*–coniferous zone up to the tree line; 2800–4200 m a.s.l.) appear to reach further north into south-western China and have closest relatives in the northern parts of the Palaearctic, whereas tropical Oriental species reached the Himalayas from the south along the river valleys and today rarely occur above 2000 m (Martens, 1984; Fig. 1).

The large number of molecular studies from the past 10 years on Himalayan and Southeast Asian birds focused mainly on systematic and taxonomic problems, and used a phylogenetic rather than a phylogeographic approach. Price & Gross (2005) postulated *in situ* speciation within the Himalayas, but Johansson *et al.* (2007) refuted that hypothesis, based on their comprehensive reconstruction of the biogeographic history of Old World warblers (genera *Phylloscopus* and *Seicercus*). They suggested that Himalayan warblers originated from dispersal or range expansion of an ancestral species into the Himalayas from the east. Most warbler species pairs included in the latter study were estimated to have diverged earlier than the Pleistocene, except for a few splits separating Himalayan endemics from their parapatric Chinese sister species (Johansson *et al.*, 2007). In a recent comparative study, genetic lineage splits between Himalayan and Chinese sister taxa from five passerine genera were dated to a time interval of 0.3–4 Ma, with most confidence intervals overlapping the Pliocene–Pleistocene boundary (Päckert *et al.*, 2009).

In this paper, we compare phylogeographic reconstructions based on mitochondrial and concatenated multi-gene sequence data for several passerine genera from seven families. We provide time estimates for the phylogeographic splits between Himalayan species and their close relatives from adjacent biogeographic regions, inferred from molecular dating using a Bayesian approach. Apart from the horizontal scenarios, we distinguish between avian communities from three elevational ecozones in the Himalayas and the neighbouring Chinese mountains in order to reconstruct separate timelines for subalpine communities of the higher elevations and for the (sub)tropical communities of the foothills. Complex patterns of elevational parapatry in the Himalayas and adjacent Chinese and Southeast Asian mountain systems are particularly apparent in treecreepers, leaf-warblers and tits, but the timing and circumstances of their origin are yet to be fully understood (Martens & Eck, 1995; Martens *et al.*, 2011). In a comparative approach across seven passerine families, we evaluate whether a common phylogenetic pattern can be inferred for congruent Eurasian zoogeographic patterns, and whether lineage separa-

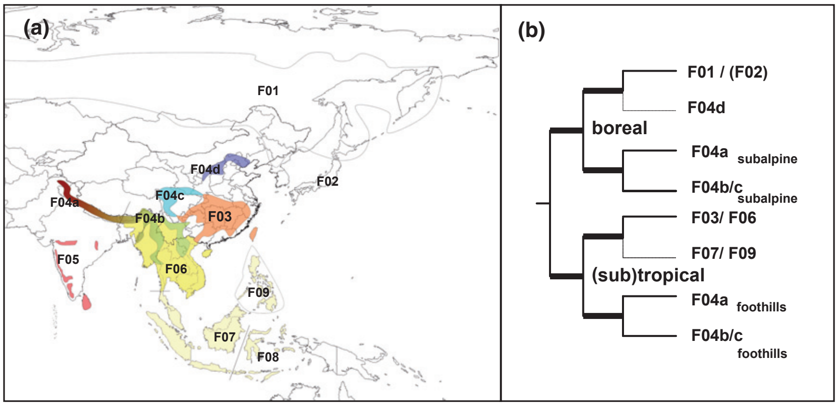

Figure 1 (a) Key forest regions for Southeast Asian birds, bioregions F01–F09 modified after Collar *et al.* (2001). (b) Frequent phylogeographic pattern among closest relatives of congeneric Eurasian passerines according to molecular data (this study; cf. Päckert *et al.*, 2009).

tion among horizontally adjacent bioregions or ecoregions at different elevations can be dated back to the same evolutionary time periods.

MATERIALS AND METHODS

Sequence data

We compiled mitochondrial cytochrome *b* (cyt *b*) sequence data from several previous phylogenetic studies and compared these focusing on phylogeographic patterns and age estimates for lineage splits among Sino-Himalayan populations (subspecies). The following north Palaearctic and Southeast Asian passerine families/genera were studied (list of materials, sequence accession numbers and references are given in Appendix S1 in the Supporting Information): crests and kinglets of the genus *Regulus* (Regulidae); tits and chickadees of the family Paridae, with a focus on coal tit and allies of genus *Periparus*; treecreepers of the genus *Certhia* (Certhiidae); long-tailed tits and bushtits of the family Aegithalidae; bullfinches of the genus *Pyrrhula* (Fringillidae); laughing-thrushes of several different groups (Timaliidae; see below); and Palaearctic and tropical species of Old World leaf-warblers of the genera *Phylloscopus* and *Seicercus* (Phylloscopidae).

Molecular dating was performed based on cyt *b* data alone, and based on concatenated sequence data sets comprising both mitochondrial and nuclear genes for all genera: 16S rDNA (16S), 12S rDNA (12S), control region (CR), NADH dehydrogenase, subunit 2 (ND2), fibrinogen intron 7 (fib7), myoglobin intron 2 (myo2), glyceraldehyde-3-phosphate dehydrogenase intron 11 (GAPDH11), transforming growth factor beta intron 2 (TGFB2) and ornithine decarboxylase introns 6–7 (ODC6) (the combinations of markers differ slightly among genera). For tits, chickadees, treecreepers, kinglets and some Old World warblers, these additional genetic markers had to be newly amplified and sequenced from the material of the original studies (see Appendix S1). Primer pairs, polymerase chain reaction (PCR) settings and sequencing conditions for 16S rDNA, GAPDH and fibrinogen intron 7 followed Päckert *et al.* (2010), and for amplification of myoglobin and 12S rDNA we followed the protocols in Johansson *et al.* (2007).

Apart from those genera that included Palaearctic species, we analysed a further cyt *b* data set of the predominantly (sub)tropical Southeast Asian laughing-thrushes of genus *Garrulax* (*sensu* Dickinson, 2003; Appendix S1), with a focus on the subfamily Leiothrichinae. This group was shown to be a monophyletic subclade of the Timaliidae tree (Gelang *et al.*, 2009) and was consequently ranked as a family of its own by some authorities (Leiotrichidae: Gill & Donsker, 2011). The monophyly of the subgenera *Trochalopteron* and *Ianthocincla* received good support from molecular data analyses by Luo *et al.* (2008). The Timaliidae data set also included cyt *b* sequences of Sino-Himalayan wren babblers of the genus *Pnoepyga*: a taxon that was recently shown to be not closely related to Timaliidae (Gelang *et al.*, 2009).

With respect to taxonomy and nomenclature, we adhere largely to Dickinson (2003), except for laughing-thrushes (*sensu* Collar & Robson, 2007) and for some species splits in Paridae (see Päckert & Martens, 2008) and Phylloscopidae (see Martens *et al.*, 2011).

Biogeographic regions – horizontal pattern

The key forest regions for Southeast Asian bird taxa investigated here are shown in Fig. 1a. The map is slightly modified from that of BirdLife International (Collar *et al.*, 2001, p. 22). Forest regions are as follows: F01, north Palaearctic boreal and temperate forests: Siberian taiga belt southwards to forested areas of Mongolia; F02, Japanese temperate forests (for ancestral range reconstruction subsumed under F01, Palaearctic bioregion); F03, south Chinese (sub)tropical forests: south-eastern continental China, forest regions east of the Sichuan Basin to the eastern Pacific coast, southwards to the border of Guangxi and north-eastern Vietnam, including Taiwan (F03T); F04, Sino-Himalayan mountain forests: the term 'Sino-Himalayas' is frequently used in the sense of a biogeographic/zoogeographic region of its own. However, because several of our target species (groups) show a strong phylogeographic structure, we further subdivided F04 (*sensu* Collar *et al.*, 2001) as follows: F04a, western and central Himalayas: western Himalayas from around the Arun Valley (eastern Nepal) westwards to Hindukush; F04b, eastern Himalayas: from the Arun Valley eastwards to the mountains of the Indo-Burmese region including Chin Hills and parts of south Yunnan; F04c, central and south-western China: mountainous and forested areas of central/northern Yunnan, Sichuan, south Gansu, parts of Shaanxi, Qinghai and forested regions of Tibet; F04d, north-eastern China: mountainous forests of Hebei, Nei Mongol and adjacent forested provinces; F05, Indian peninsula and Sri Lankan forests; F06, continental Southeast Asian lowland forests: forested Thailand, Vietnam, Laos, Cambodia and parts of southern Yunnan, Hainan; F07, F08, F09, Sundaland forests, Wallacea and Philippine tropical forests (for ancestral range reconstructions treated as a single bioregion); Central Asia: the Tien Shan-Altai mountain system, including parts of Pamir (not included in Collar *et al.*, 2001).

Terrestrial ecoregions of Sino-Himalayan mountain forests – elevational pattern

For inter-species comparison, we distinguish three categories of mountain forest ecoregions in the Himalayas embracing different elevational belts characterized by climate, vegetation and avian communities (following Wikramanayake *et al.*, 2001; details at http://www.worldwildlife.org). Species ranges can largely overlap between ecozones and therefore the affiliation of a species to its respective ecozone refers to the maximum elevational extent of its breeding area. Data on the elevational extent of breeding ranges in the Himalayas and Chinese mountain ranges were inferred from the literature (Appendix S1) and from field trip databases (J. Martens: tissue samples collected and sound documents recorded from 1970 to 2010; Appendix S1). Georeferenced data points and locality data were inferred from the field and collection databases of J. Martens at the Institute of Zoology, University of Mainz (e.g. 307 records for Paridae, 232 for Phylloscopidae).

The three ecoregions are:

Himalayan Subalpine Conifer Forests (ecoregions 28 and 29 according to Wikramanayake *et al.*, 2001, pp. 340–345). Forests of this ecoregion are dominated by spruce (*Picea smithiana*), firs (three *Abies* species), junipers (*Juniperus indica*, *J. recurva*) and other evergreens, about 30 *Rhododendron* species grow in the rich understorey. The subalpine conifer belt reaches up to the tree line at 3000–4000 m; however, the breeding areas of some typical subalpine passerine species extend even up to the higher elevations of the Himalayan and Tibetan Plateau alpine steppe above the tree line.

Himalayan Broadleaf Forests (ecoregions 26 and 27 according to Wikramanayake *et al.*, 2001, pp. 335–340). The Himalayan evergreen and deciduous broadleaf forests of median and lower elevations (above 2000–3000 m; overlapping with mixed coniferous forests up to 3500 m) are dominated by oak (*Quercus*) species and have a dense understorey of mosses and ferns. Maples (*Acer campbellii*), Nepal alders (*Alnus nepalensis*) and common walnuts (*Juglans regia*) dominate the deciduous forests at these elevations. Only occasionally, the typical passerine character species of that ecoregion are found above 4000 m. In our study, the corresponding conifer belts of upper and median elevations from two Indo-Burmese forest regions are subsumed under ecoregion B: northern Triangle temperate forests and north-east India–Myanmar pine forests (ecoregions 76 and 77 according to Wikramanayake *et al.*, 2001).

Himalayan Subtropical Broadleaf and Pine Forests (ecoregions 25 and 31 according to Wikramanayake *et al.*, 2001, pp. 332–335, 347–349). The subtropical Himalayan broadleaf forests include a number of different forest types, such as dry evergreen stands of *Olea cuspidata*, dry Siwalik sal (*Shorea robusta*), and moist mixed deciduous and wet broadleaf hill forests. Subtropical pine forests extend from the dry western Kali Gandaki valley in western to central Nepal and wetter forests of the eastern Himalayas. They are dominated by chir pines (*Pinus roxburghii*) and range between 1000 and 2000 m in central Nepal. South China–Vietnam subtropical evergreen forests (ecoregion 75 according to Wikramanayake *et al.*, 2001) represent a transitional zone between Southeast Asian tropical forests and subtropical/mixed forests of southern China.

Inference of phylogeny and molecular dating

For this study, the time to the most recent common ancestor (TMRCA) was estimated for Sino-Himalayan sister taxa and for their closest relatives from adjacent biogeographic regions using a relaxed uncorrelated lognormal clock approach as implemented in BEAST v. 1.4.8 (Drummond & Rambaut, 2007). Molecular dating for our seven study groups was carried out using three independent approaches, as follows.

1. In order to provide a rough estimate of divergence times between mitochondrial lineages, we applied a fixed mean substitution rate of 0.0105 substitutions per site per lineage per million years to the cyt *b* data sets – this estimate resulted from a re-evaluation by Weir & Schluter (2008) of more than 90 different avian clock calibrations.

2. Taking into account that substitution rates might differ substantially among mitochondrial and nuclear genes, and might even differ in the same gene among closely related avian taxa (Ruokonen & Kvist, 2002), we carried out independent runs using one to five fixed age constraints assigned to given nodes of the phylogenies in each independent run with each data set (see below and Table 1).

3. Because inference of phylogeny from mitochondrial and nuclear data might result in conflicting topologies (Bensch *et al.*, 2006), we ran a third independent analysis using the same fixed node ages as under the second approach with multi-gene sequence data sets for six species groups.

We chose a lognormal relaxed clock model (see Drummond *et al.*, 2006) for all sequence data sets. TMRCA was estimated for several subsets of taxa defined with BEAUTI v. 1.4.8. For the runs with BEAST, the length of the Markov chain was set to 10,000,000 generations and log parameters were sampled every 1000th generation. In each run with BEAST, the 'auto-optimize' option was activated. Linearized consensus trees, including posterior probabilities, were inferred from the tree output files (concatenated sequence data sets) using TREEANNOTATOR v. 1.4.8 (as implemented in BEAST) with the burn-in parameter set to 3000 and node heights set to 'mean heights'. Time estimates of lineage splits and mean substitution rates were inferred from the log output files using TRACER v. 1.4 (Rambaut & Drummond, 2007). For analysis of the cyt *b* sequence data, we additionally applied to the data best-fit model parameters, as estimated with MRMODELTEST 2.3 (Nylander, 2004), by setting the initial values of prior distributions accordingly for each parameter. For concatenated data sets, the input sequence data were partitioned manually according to the different gene fragments in the XML file generated with BEAUTI. The GTR and HKY models, respectively, were *a priori* assigned to each partition according to the estimates with MRMODELTEST. Model settings for the different gene partitions are provided for each passerine study group in Appendix S2.

Time constraints and fixed node ages

Several key nodes of the molecular input trees (TMRCA of taxon subsets in BEAST) were constrained to age estimates for palaeogeographic events that should correspond roughly to lineage splits between genetic lineages: ages of volcanic islands, submergence or emergence of land bridges, etc. (cf. Fleischer *et al.*, 2006; Päckert *et al.*, 2007; Rheindt *et al.*, 2009). As time estimates for most events comprise time ranges such as between oldest and youngest lava flows (available for all Canary Islands and Azores), rather than a single fixed age, several nodes of input trees were constrained to a minimum

Table 1 Time constraints applied as upper and lower bound of time to most recent common ancestor priors for molecular age dating with BEAST for different genera of forest passerines.

Event	Split	Genus	Upper	Lower	Reference
LB	Nearctic/Palaearctic	*Regulus* *Pinicola* *Certhia* *Aegithalos* *Poecile*	10.0 (14.0)	4.8	Hopkins (1967) Gladenkov *et al.* (2002)
ISL	Continent/Canary Islands	*Regulus* *Cyanistes* *Phylloscopus* *Fringilla*	5.96	1.22	Ancochea *et al.* (1990) Krijgsman *et al.* (1999)
ISL	East/West Canary Islands	*Regulus*			
	to La Palma	*Cyanistes*	1.77	–	Ancochea *et al.* (1990)
	to El Hierro	*Cyanistes*	1.22	–	Ancochea *et al.* (1990)
ISL	Continent/Azores	*Regulus*			
		Pyrrhula	0.88	–	Johnson *et al.* (1998)
ISL	East/West Azores	*Regulus*	0.20	–	Johnson *et al.* (1998) Chovellon (1982)
LB	Europe/North Africa	*Certhia*	5.96	–	Krijgsman *et al.* (1999) ('Messinian crisis')
CONT	East/West Palaearctic	*Phylloscopus*	2.4	0.18	West (1988) (Pleistocene)

Concerned nodes correspond to major geographic lineage splits.

Age estimates for palaeogeographic events (ISL, volcanic island formation; LB, opening and closing of land bridges; CONT, continental events) given in Ma.

The split among Nearctic and Palearctic sister clades was assigned to different upper bounds in comparative independent runs in Aegithalidae only.

and a maximum age. Time estimates for those palaeogeographic events used as calibration points shown in Table 1 roughly follow Päckert *et al.* (2007). However, time constraints for a presumed faunal interchange via land bridges were set to broader time intervals than those of the earlier studies. We broadened these time intervals because all former calibrations based on a time interval for the Pliocene opening of the Bering Strait of 4.8–7.4 Ma (Gladenkov *et al.*, 2002) always dated splits between Palaearctic and Nearctic sister taxa to the upper bound of this time constraint (cf. Päckert *et al.*, 2007, 2009). Thus, mitochondrial lineages of these Eurasian/North American sister taxa might not have segregated through allopatric disjunction of a formerly Holarctic species, as assumed in former studies, but through intercontinental dispersal via the Bering land bridge during a rather long time of faunal interchange. We therefore set the time constraint for the Palaearctic/Nearctic faunal interchange to a broad interval from 10 Ma (beginning of a major faunal interchange via Beringia; Hopkins, 1967) to 4.8 Ma (lower bound of Pliocene opening of Bering Strait; Gladenkov *et al.*, 2002). In order to control for unexpectedly high cyt *b* substitution rate estimates for our Aegithalidae data set, we carried out further runs with an even larger time constraint for the Nearctic–Palaearctic split, setting the upper TMRCA prior bound to 14 Ma (assuming possible faunal interchange via a continuous coniferous forest belt across Beringia until the Pliocene Opening of the Bering Strait; cf. Sanmartín *et al.*, 2001).

We also expanded the time constraint for the invasion of Palaearctic faunal elements to the Canary Islands (in this study, *Phylloscopus canariensis*, *Regulus regulus teneriffae*, *Cyanistes teneriffae*) from 5.96 Ma (beginning of the Messinian crisis; Krijgsman *et al.*, 1999) to 1.22 Ma (last phase of volcanic eruptions on El Hierro; Ancochea *et al.*, 1990; but see Fernández-Palacios *et al.*, 2011 for slightly younger ages). Volcanic ages of islands used as upper and/or lower TMRCA bounds are given in Table 1. For molecular dating of the leaf-warbler tree we added a further constraint to two nodes uniting different allopatric taxa of the former chiffchaff complex, which, according to their extant distribution patterns and former dating approaches separated through glacial forest range fragmentation (in this study: *Phylloscopus collybita collybita* versus *P. c. tristis* and *P. sindianus sindianus* versus *P. s. lorenzi*). We therefore set the upper and lower TMRCA bounds to the maximum estimate range for the beginning and end of the Pleistocene (2.4–0.18 Ma; West, 1988; see Table 1).

Historical biogeography

We inferred ancestral distributions of the clades in each of our study groups using the ancestral states reconstruction package as implemented in MESQUITE v. 2.5 (Maddison & Maddison, 2008). As the best and most robust phylogenetic hypotheses we used Bayesian trees resulting from Bayesian inference of phylogeny with MRBAYES v. 3.1.2. (Huelsenbeck & Ronquist, 2001) based on multi-gene data sets. Bayesian trees were incorporated into the corresponding MESQUITE files and slightly adjusted in the tree window: clades with posterior probability support lower than 0.95 were collapsed in all topologies. Biogeographic regions were coded in a character matrix by successive numbers (character states = bioregions F01–F09). In addition to the Asian key forest regions we added a few further distribution areas to the character matrix, e.g. 'Nearctic', 'Macaronesia/North Africa' and 'Central Asia'. The Indo-Malayan key forest regions F07–F09 were treated as one major region and were thus subsumed under the same character state and so were the two north Palaearctic forest regions F01 and F02 (encoded as 'Palaearctic'). Distribution of taxa could encompass more than one bioregion – in these cases the character state was polymorphic (all bioregions were encoded in the matrix for the corresponding taxon). Ancestral states of distribution areas were reconstructed using the parsimony reconstruction method under two default models ('unordered' and 'ordered') and under a user-defined step-matrix model. The step-matrix model allows for the definition of 'costs of *i* to *j* transitions', i.e. the cost of immigration/dispersal from one bioregion to another. As an *a priori* assumption, faunal interchange among neighbouring bioregions is common and likely to occur, while faunal interchange among two regions becomes less probable with increasing distance and the increasing number of connecting regions (in our case, forest areas) in between. The step-matrix model applied to all passerine groups is provided in Appendix S3.

RESULTS

Node age estimates

In most study groups, age estimates based on cyt *b* sequence data did not differ much from calibrations based on either fixed mean substitution rates or fixed node ages. The 95% highest posterior density (95% HPD) intervals of rate estimates largely overlap among all taxa except for the considerably higher rate estimates for the Aegithalidae data set. The relative divergence rate among mitochondrial lineages of this Aegithalidae tree exceeds the empirical 2% rule-of-thumb by about three times. This effect is certainly due to the time constraint assigned to the node uniting Eurasian *Aegithalos* and North American *Psaltriparus*. For four out of five genera, 95% HPD intervals of age estimates for the Nearctic–Palaearctic clade split (inferred from runs based on fixed mean rates) lie well or partly within the assumed time interval for TMRCA constraints of this node. In these runs, only the split between *Aegithalos* and *Psaltriparus* was dated as being much older than the upper bound of 10 Ma. In BEAST runs with a uniform TMRCA prior distribution at constraint nodes, time estimates and HPD intervals for lineage splits within Aegithalidae did not differ considerably whether a broad or a narrow time constraint was assigned to the *Aegithalos*/*Psaltriparus* split (upper bound set to 10.0 or 14.0 Ma). In general, age estimates based on fixed node ages dated lineage splits to slightly more recent times and the 95% HPD were slightly larger, but overlapped with 95% HPD based on fixed mean rates.

Rate-smoothed trees inferred from multilocus data sets were dated using from one to five fixed node ages per group and, in general, this dating approach yielded slightly (except for *Aegithalos*) more recent time estimates for lineage splits. These would thus represent minimum time estimates. One should therefore keep in mind that the mean estimates based on cyt *b* data, using a fixed substitution rate, yielded slightly older ages (most strikingly in long-tailed tits and leaf-warblers).

Congruent phylogeographic pattern

The general phylogeographic pattern sketched in Fig. 1b was found at least once in all seven passerine phylogenies. One boreal species of the north Palaearctic Taiga belt (in a few genera with distinct genetic lineages in north-east Chinese mountain forests; F04d) is sister to at least one subalpine Sino-Himalayan species. The entire boreal clade contrasts with a sister group of Sino-Himalayan species from the foothills of the mountain range and (sub)tropical relatives from Chinese and/or Southeast Asian lowland forests (in a few groups comprising distinct genetic lineages from the Indo-Malayan Realm; Fig. 1b). This phylogeographic pattern is perfectly reflected in the genera *Certhia*, *Aegithalos* and *Pyrrhula*, but intraspecific phylogenetic relationships between genetic lineages of the coal tit (*Periparus ater*) are not well resolved. On the leaf-warbler tree, this pattern has evolved independently in several subclades (*Phylloscopus* and *Seicercus*; Fig. 2). The basal split separates two leaf-warbler clades with different phylogeographic structure (see 'Continental horizontal patterns'). However, the general boreal phylogeographic pattern (Fig. 1b) is well reflected in three subclades of boreal clade B and two subclades of the subtropical Clade A (Fig. 2, A1, A2, B1–B3), while several other subclades correspond to the general subtropical branching pattern (Fig. 2, A3–A7). Branching patterns in the laughing-thrush tree do not include Palaearctic or Central Asian lineages at all. All Sino-Himalayan laughing-thrush species form a clade with sister taxa from adjacent Southeast Asian regions including four endemic taxa from Taiwan (Fig. 3).

Continental horizontal patterns

Historical biogeography

Although phylogeographic patterns of our study groups are highly similar, parsimony-based ancestral state reconstructions suggest some differences with respect to their biogeographic origin (Figs 2–4). The kinglets represent the only study group for which a Nearctic centre of origin was reconstructed with MESQUITE (Fig. 4b). The whole family Aegithalidae was suggested to be of East Palaearctic origin (equally F01 and F04d), although the genus *Aegithalos* was equally likely to have a subtropical Indo-Burmese or north Chinese ancestral range (F04b, F04d; Fig. 4c). Even the coal tit and its allies (*Periparus*), which include mainly boreal species, were suggested to be of subtropical East Asian origin (F04/F03), as they feature a basal split that separates Philippine and south Chinese species from a Sino-Himalayan/Palaearctic clade

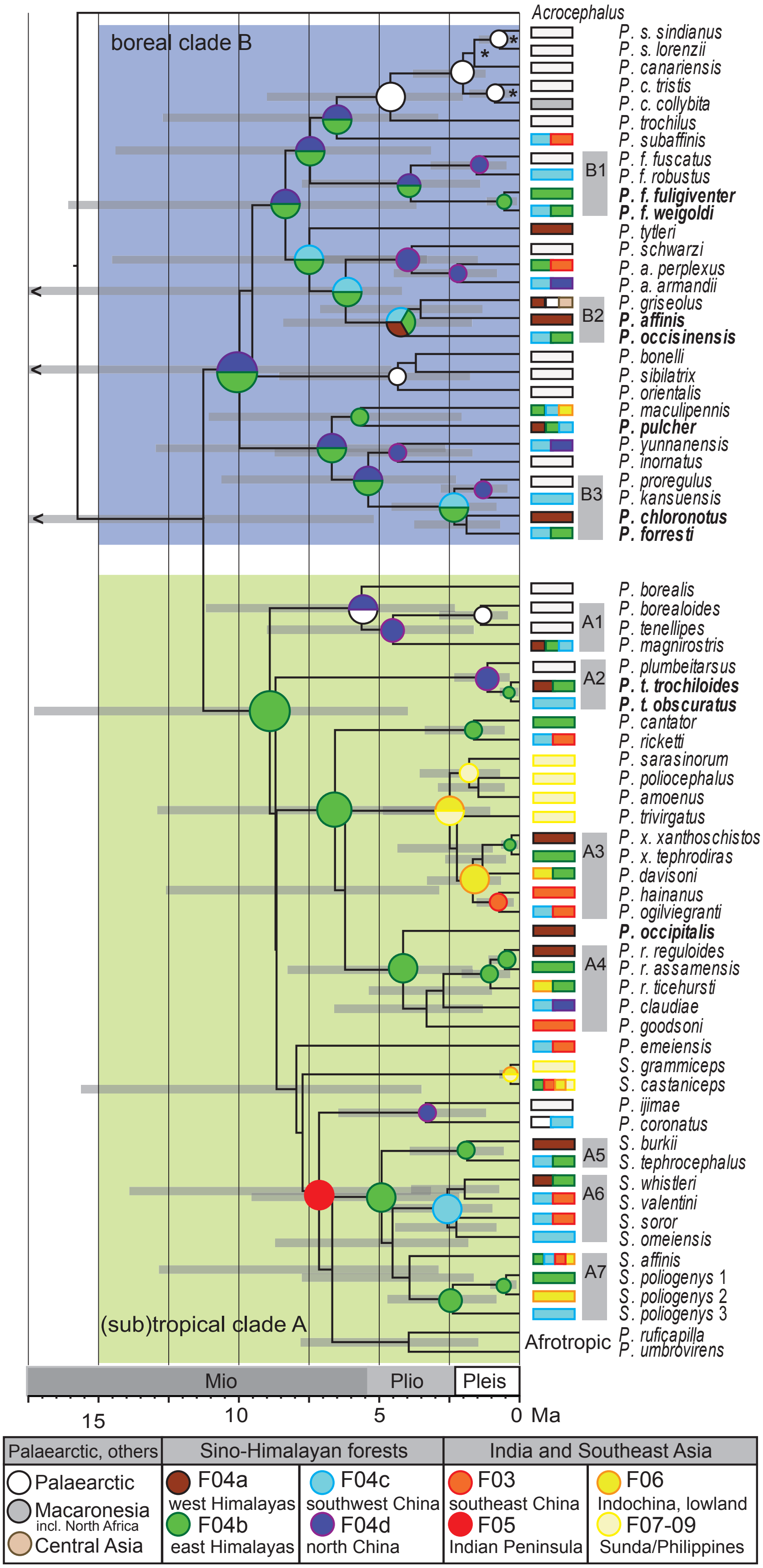

Figure 2 Biogeographic history for leaf-warblers of genera *Phylloscopus* and *Seicercus*. Rate-smoothed tree inferred from concatenated cytochrome *b*, 12S rDNA and myoglobin intron 2 sequences (1899 bp) with BEAST 1.4.8, Markov chain length = 10,000,000 generations, tree prior = speciation (Yule process), relaxed uncorrelated lognormal clock model; * = uniform time to most recent common ancestor (TRMCA) prior distribution (Canary Islands; Pleistocene); grey bars indicate 95% highest posterior density (HPD) intervals (< = upper HPD extends beyond time scale); ancestral areas reconstructed with MESQUITE 2.5 (maximum parsimony, step-matrix model) indicated at nodes with posterior probabilities > 0.95 only (nodes with lower values were collapsed in MESQUITE analysis), extant distribution indicated at terminal clades (bars). Key forest regions (areas) encoded by colours; east Himalaya including Indo-Burmese mountain forests; vertical distribution in the Sino-Himalayas: subalpine, high-elevation species in bold; subclades A3–A7 = (sub)tropical general branching pattern; subclades B1–B3, A1, A2 = boreal general branching pattern.

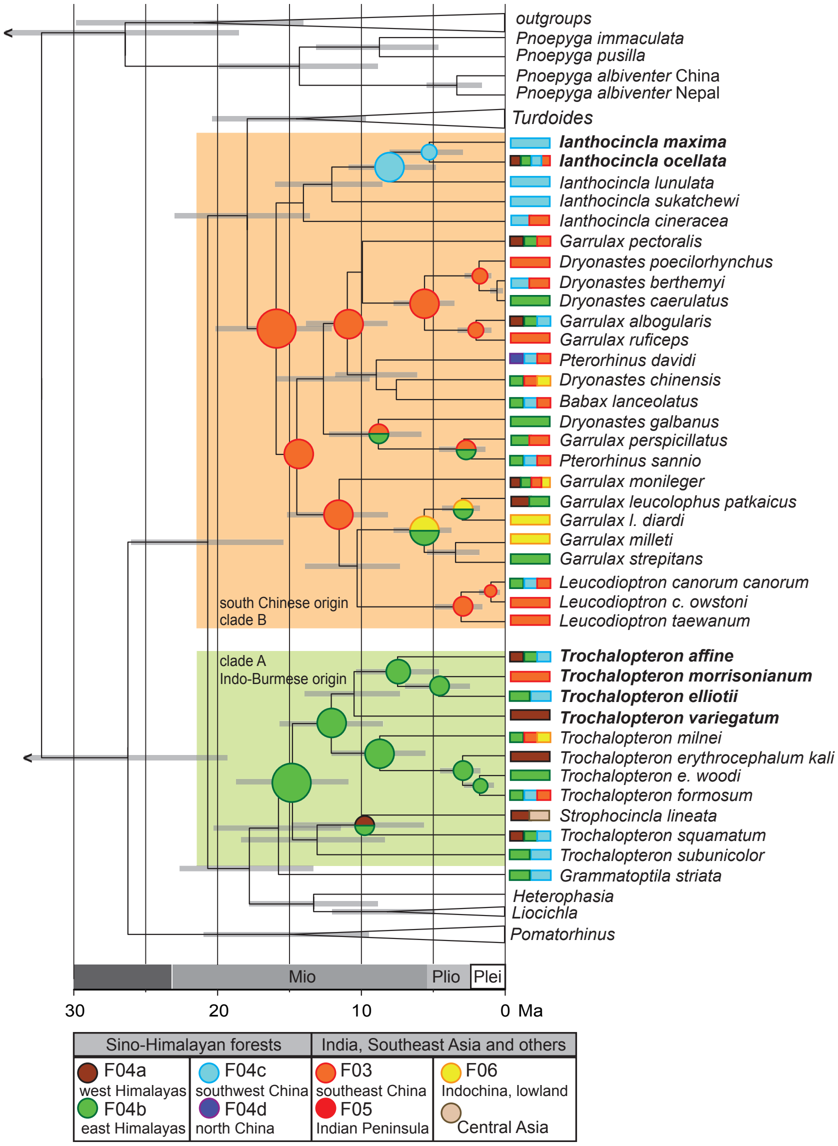

Figure 3 Biogeographic history for (sub)tropical laughing-thrushes (Timaliidae: *Garrulax* and allies; genera as re-established by Collar & Robson, 2007). Rate-smoothed tree inferred from cytochrome *b* sequence data with BEAST 1.4.8, Markov chain length = 10,000,000 generations, tree prior = speciation (Yule process), relaxed uncorrelated lognormal clock model, rate fixed at 0.0105; grey bars indicate 95% highest posterior density (HPD) intervals (< = upper HPD extends beyond time scale); ancestral areas reconstructed with MESQUITE 2.5 (maximum parsimony, step-matrix model) for two major clades indicated at nodes with posterior probabilities > 0.95 only (nodes with lower values were collapsed in MESQUITE analysis except basal nodes of clades A and B, which had received strong support from multi-locus data by Luo *et al.*, 2008), extant distribution indicated at terminal clades (bars). Key forest regions (areas) encoded by colours; east Himalaya including Indo-Burmese mountain forests; vertical distribution in the Sino-Himalayas: subalpine, high-elevation species in bold.

(Fig. 4a). The ancestral distributions of both treecreepers and bullfinches presumably comprised the southern subtropical regions of the Sino-Himalayas (F04b in both, plus F04a and F04c in *Pyrrhula*; Fig. 4d,e). Each of the two species-rich groups of leaf-warblers and laughing-thrushes was divided into two major clades and in both groups the Indo-Burmese mountain region (F04b) was inferred to be the ancestral distribution area for one of these clades (clade A in both groups, Figs 2 & 3). Several extant Himalayan species emerged from these Southeast Asian ancestors in both groups, and among these, extant breeding ranges of two leaf-warbler species only and of four laughing-thrush species are restricted or extend to the subalpine zone. The ancestral distribution area of the boreal leaf-warbler species clade B was equally likely to have been in the eastern Himalayas and/or north China (F04b, F04d) and all of the six extant Himalayan species of clade B inhabit the subalpine or temperate forest belt (no species from the Himalayan foothills is nested in this clade; Fig. 2). The second major laughing-thrush clade B (Fig. 3) comprises species from south-eastern and central China (F03, F04c) and also a few from the Indo-Chinese region (F06). Five extant Himalayan species emerged from these ancestors; two of them breed up to the temperate and subalpine forest belt. South-eastern China (F03) was inferred to be the ancestral distribution centre of the entire clade and two subclades (Fig. 3).

Time estimates

Most of the basal splits between tropical and boreal clades in each of the passerine study groups were dated to the Miocene with the oldest separation events occurring in *Phylloscopus*/*Seicercus*, *Garrulax* and *Certhia* (*c.* 17–12 Ma; Figs 2, 3 & 4e). The younger intrageneric separation events among subtropical and boreal lineages were dated to the late Miocene/early Pliocene (6–8 Ma) in *Periparus*, *Aegithalos* and *Pyrrhula* (Fig. 4a,c,d). Mean ages for those splits between Palaearctic

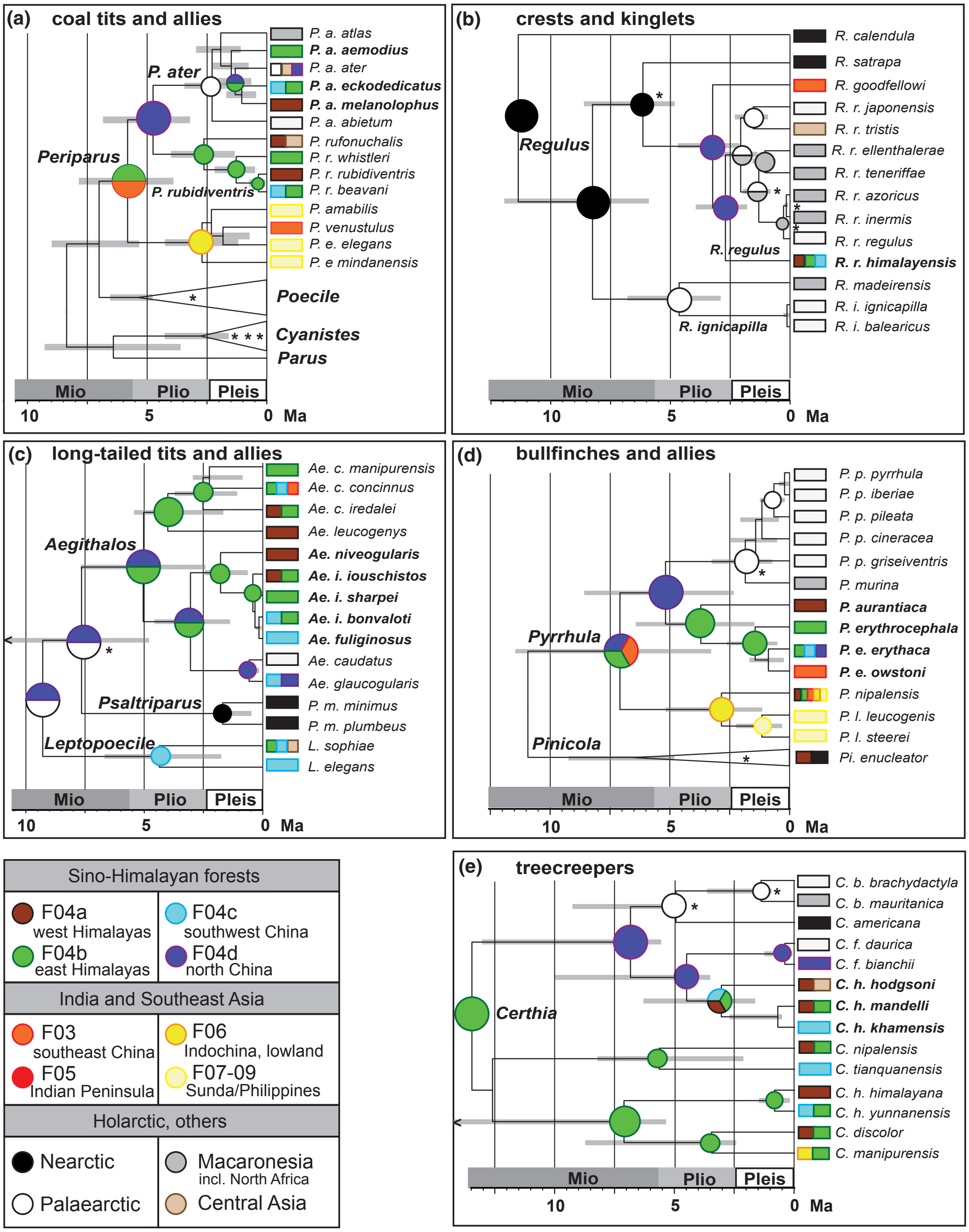

Figure 4 Biogeographic histories of five passerine study groups; boreal-subalpine taxa: (a) coal tits and allies [Paridae: *Periparus* spp., 2527 bp cytochrome *b* (cyt *b*), 16S rDNA (16S), control region (CR) and fibrinogen intron 7 (fib7)]; (b) crests and kinglets [Regulidae: *Regulus* spp., 3332 bp cyt *b*, 16S, CR, myoglobin intron 2 (myo2) and glyceraldehyde-3-phosphate dehydrogenase intron 11 (GAPDH11)]; (c) long-tailed tits and allies [Aegithalidae, 3995 bp cyt *b*, 16S, NADH dehydrogenase, subunit 2 (ND2), fib7, GAPDH11, ornithine decarboxylase introns 6-7 (ODC6) and transforming growth factor beta intron 2 (TGFB2)]; (d) bullfinches (Fringillidae: *Pyrrhula* spp., 2357 bp cyt *b*, 16S, fib7 and GAPDH11); (e) treecreepers (Certhiidae: *Certhia* spp., 2019 bp cyt *b*, 16S, myo2 and GAPDH11). Rate-smoothed trees inferred from concatenated sequence data sets with BEAST 1.4.8, Markov chain length = 10,000,000 generations, tree prior = speciation (Yule process), relaxed uncorrelated lognormal clock model, no rate fixed, bars indicate 95% highest posterior density (HPD) intervals (< = upper HPD extends beyond time scale); * = uniform TMRCA prior distribution assigned to node; ancestral areas as reconstructed with MESQUITE 2.5 (maximum parsimony, step-matrix model) indicated at nodes with posterior probabilities > 0.95 only (nodes with lower values were collapsed in MESQUITE analysis), extant distribution indicated at terminal clades (bars). Key forest regions (areas) encoded by colours, east Himalaya including Indo-Burmese mountain forests; distribution ranges in the Sino-Himalayas: subalpine, high-elevation species in bold.

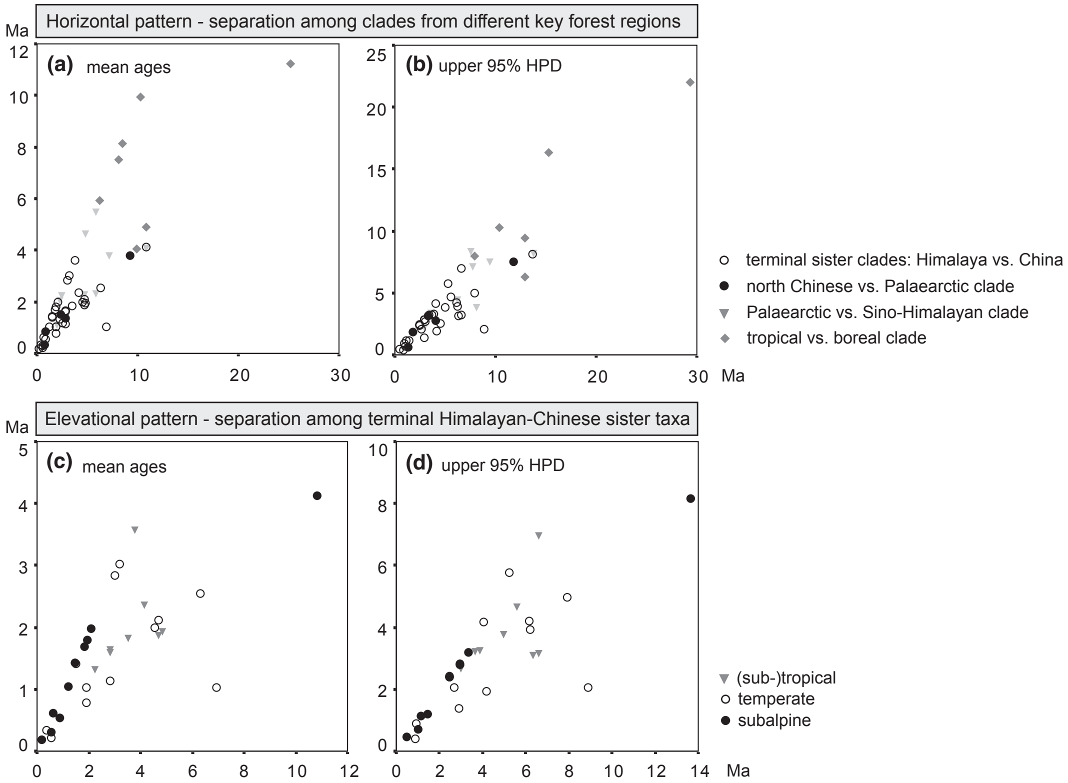

Figure 5 Time estimates for genetic lineage splits of forest passerines in Eurasia and Southeast Asia [(sub)tropical laughing-thrushes excluded], means and upper bounds of 95% highest posterior density (HPD) intervals. (a,b) Horizontal pattern, time to most recent common ancestor (TMRCA) estimates for splits among clades from different adjacent key forest regions, indicated by symbols. (c,d) Elevational pattern, TMRCA estimates for splits among terminal Himalayan and Chinese sister taxa, assignment of a taxon pair to one of the three ecoregions [subalpine, temperate and (sub)tropical] was based on the upper distributional limit of the Himalayan sister taxon; *x*-axis: estimates based on a fixed mean substitution rate (cytochrome *b*: $r = 0.0105$, single gene data set), *y*-axis: estimates based on uniform TMRCA priors (fixed node ages, concatenated data sets).

and subalpine Sino-Himalayan clades were generally dated to the Pliocene (even approaching the Pleistocene boundary, Fig. 5a,b) but 95% HPD intervals were large for some nodes. The youngest subalpine immigrant to the Sino-Himalayas is the coal tit (*Periparus ater*). Three larger separation events among biogeographic regions were dated to the Pleistocene era in most genera: (1) separation among subalpine Himalayan and Chinese (Indo-Burmese) sister taxa (Fig. 5a,b); (2) separation of eastern and western genetic lineages within the Himalayas; and (3) separation of Palaearctic species and geographically isolated north Chinese sister taxa (Fig. 5a,b; *Phylloscopus kansuensis* and *P. fuscatus robustus*, Fig. 2; *Aegithalos glaucogularis*, Fig. 4c; *Certhia familiaris bianchii*, Fig. 4e). The goldcrest (*Regulus regulus*) is the only study species that shows no particular phylogeographic pattern within the entire Sino-Himalayan breeding range of the species, and only the endemic species from Taiwan, *Regulus goodfellowi*, represents a second Southeast Asian lineage, being sister to *R. regulus* (Fig. 4b). Ancestors of the flamecrest (*R. goodfellowi*) were among the earliest arrivals on the island (along with vinaceous rosefinches, *Carpodacus vinaceus formosanus*), but there were also some relatively recent late Pleistocene invasions of Taiwan by coal tits and two Asian bullfinch species (*Periparus ater*, *Pyrrhula erythaca*, *Pyrrhula nipalensis*). In all calibrations the origins of all extant passerine populations from Taiwan were dated to the Pliocene and younger (Fig. 6b).

Elevational pattern

Historical biogeography

According to the parsimony-based ancestral-states reconstruction, subalpine and subtropical species of the Sino-Himalayan region (F04 and subgroups) are of a different biogeographic origin in almost all passerine genera investigated. Most northern Palaearctic–Sino-Himalayan sister clades have their ancestral distribution areas either in the Palaearctic (*Periparus ater*) or in north China (F04d for *Regulus regulus*, *Phylloscopus* clades A1/A2 and for the entire boreal group of both *Certhia* (*C. familiaris*, *C. hodgsoni*) and *Pyrrhula* (*P. pyrrhula*/*P. murina* and Asian sister clade; Figs 2 & 4a,b,d,e). In *Periparus*, the second subalpine clade has no clear phylogenetic affiliation to the Palaearctic and presumably originated from an ancestral area in

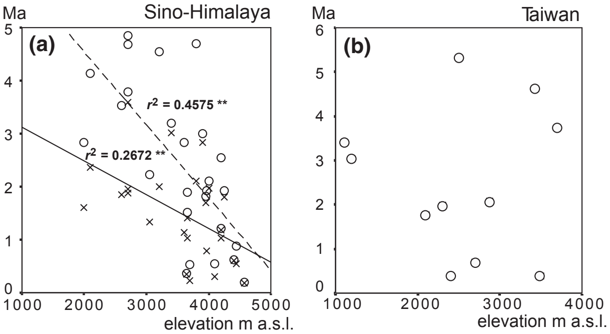

Figure 6 Scatterplot of mean age estimates for lineage splits (*y*-axis) against upper elevational limit of breeding area ('elevation', *x*-axis) for forest passerines in the Himalayas and on Taiwan (in m a.s.l.). (a) Terminal Himalayan and Chinese sister taxa, molecular dating based on fixed node ages, crosses and continuous line; molecular dating based on fixed substitution rate, circles and dotted line; r^2 is indicated at regression lines. (b) Taiwan endemics and their continental Southeast Asian sister taxa [(sub)tropical laughing-thrushes included].

the Indo-Burmese mountain region (*Periparus rubidiventris* and *P. rufonuchalis*: F04b; Fig. 4a). An ancestral distribution east and south-east of the Himalayas was inferred for three subalpine Sino-Himalayan leaf-warbler clades (Fig. 2: B1, F04b/d; B2, F04a-c; B3, F04b/c). Uniquely, in *Aegithalos*, both subclades from the subalpine forest belt and from the foothills of the Sino-Himalayan region were assigned to a subtropical ancestral distribution area (F04b; Fig. 4c). Like these two *Aegithalos* lineages, several other species from the Himalayan foothills have their ancestral distribution area in subtropical regions of Southeast Asian mountain ranges: (1) Indo-Burmese origin (F04b) was inferred for all treecreeper species from the Sino-Himalayan foothills and the temperate forest belt (*Certhia discolor*, *C. manipurensis*, *C. himalayana*, *C. nipalensis*, *C. tianquanensis*; Fig. 4e) and for four subclades of the subtropical leaf-warbler clade (Fig. 2: Phylloscopidae, clades A4, A5, A6 and the *Phylloscopus cantator*/*P. ricketti* sister species pair); (2) a south-eastern Chinese origin (F03) was inferred for most Sino-Himalayan species groups of laughing-thrushes of clade B (Fig. 3: Timaliidae, *Garrulax* and allies; but strikingly F04c for three *Ianthocincla* species).

Time estimates

Most of these extant species from the Himalayan foothills (and some from the temperate belt at mid-elevations) represent relatively old splits from their closest relatives from (sub)tropical Southeast Asia, and their origin was in some cases even dated back to the late Miocene (Fig. 5c,d). In contrast, the separations of almost all subalpine and several temperate Himalayan species from their Chinese sister taxa were dated back to Pleistocene times or at least to the Pliocene/Pleistocene boundary (Fig. 5c,d). Most time estimates for temperate forest taxon pairs that pre-date the Pliocene/Pleistocene boundary represent sister taxa with closest relatives in subtropical Southeast Asia (all laughing-thrushes and three *Phylloscopus* species). Typically, mean age estimates of separation events among sister taxa tend to be younger as the upper elevational limit of breeding distribution of the allopatric Himalayan (sub)species increases (Fig. 6a). This bivariate correlation was significant for age estimates inferred from molecular dating using a fixed (cyt *b*) substitution rate (Spearman's rank correlation test: $\rho = -0.655$, $P < 0.01$, Pearson's $r = -0.636$, $P < 0.01$) and using fixed node ages (Spearman's rank correlation test: $\rho = -0.529$, $P < 0.01$, Pearson's $r = -0.517$, $P < 0.01$), respectively. It is noteworthy that the latter correlation tests were carried out under exclusion of one outlier corresponding to one leaf-warbler species pair (*Phylloscopus affinis*/*P. occisinensis*). In contrast to all other terminal taxon pairs, these two leaf-warblers are not true arboreal species, but inhabit the open shrub- and bush-steppe above the timber line. However, when including this species pair in the data set, the correlation of separation age and elevational distribution remained significant for molecular dating based on a fixed substitution rate (Spearman's rank correlation test: $\rho = -0.484$, $P < 0.01$; plot not shown). Unlike in the Himalayas, on Taiwan we do not find a similar successive colonization pattern with early (sub)tropical arrivals and late boreal arrivals (Spearman's rank correlation test, not significant; Fig. 6b).

DISCUSSION

Despite other evidence from molecular systematic studies, present-day taxonomy and systematics tend to unite clearly paraphyletic taxonomic units under their traditional genus names (for laughing-thrushes compare Luo *et al.*, 2008 with Collar & Robson, 2007; for leaf-warblers cf. Johansson *et al.*, 2007) and to accept species limits at significantly different levels of genetic differentiation even within the same genus (for Paridae see Päckert & Martens, 2008; for Phylloscopidae see Martens *et al.*, 2011). However, regardless of taxonomic levels, the phylogeographic patterns of Eurasian passerines are largely congruent and suggest a common origin and timeline. Based on our molecular dating results, we sketch three major phases of genetic lineage separation among different bioregions and/or ecoregions during which extant patterns of large-range vicariance and local elevational parapatry were established.

First phase: Miocene and Pliocene (sub)tropical radiation

This first phase is characterized by the first basal phylogenetic splits in all our study families separating ancestral lineages of extant subtropical from boreal species groups. Presumably during these times these ancestors acquired ecological and behavioural adaptations to different climate regimes and habitats that later on might have determined the elevational niche occupied by their descendants in the Sino-Himalayas.

With respect to palaeoclimate changes, there is an ongoing debate on the dating of orogenesis and the onset of Indian and

Southeast Asian monsoons linked to the Himalayan-Tibetan Uplift at 9–8 Ma (Zhisheng *et al.*, 2001; Zheng *et al.*, 2004; for an alternative scenario of first middle Miocene monsoon phases at 15–13 Ma see Sun & Wang, 2005; Ganjoo & Shaker, 2006). Nevertheless, regardless of the date when the first monsoon phases actually occurred, the Miocene must have been a period of severe climatic changes in Southeast Asia, with (1) northward extension of a humid belt over large parts of the Indian subcontinent and the Himalayas towards the Early Miocene, and (2) a considerable drying of Central Asia at the same time (Guo *et al.*, 2008). As a consequence, the drier western Himalayan region apparently experienced a considerable turnover of the mammal fauna between 9.5 and 7 Ma due to the northward migration of e.g. grazing herbivores from the Indian subcontinent and adjacent Southeast Asia (Barry *et al.*, 2002; Badgley *et al.*, 2008).

The reconstruction of a similar scenario for the Asian passerine avifauna is hardly practical because, in general, the fossil record for Palaearctic passerines from the early Oligocene onwards is poor and best studied for Europe (Manegold *et al.*, 2004; Mayr, 2005), while data are even more scarce for fossil Asian passerines (Rich *et al.*, 1986). However, according to our molecular dating results, Southeast Asia was a mid- to late Miocene centre of origin for a huge passerine diversification, particularly in the species-rich leaf-warblers and laughing-thrushes (in accordance with the results by Johansson *et al.*, 2007; Luo *et al.*, 2008). There is further evidence of multifold passerine intra- and intergeneric diversification of largely Australasian passerine genera even later, towards the Miocene/Pliocene boundary, including a subsequent influx of Indo-Pacific faunal elements to mainland Asia (core Campephagidae: Jønsson *et al.*, 2010a; Pachycephalidae: Jønsson *et al.*, 2010b; *Pteruthius*: Reddy, 2008). In continental Southeast Asia during that time, first (sub)tropical avian faunal elements must have invaded the foothills and medium elevations of the Himalayas and Chinese mountain system either from the Indo-Burmese and Indo-Chinese region in the south or from south-east China in the east. Even then, at the very beginning of their Miocene radiation, a large ecological variation of Southeast Asian leaf-warblers was presumably already associated with body size and beak proportions (Price, 2010).

At the same time, towards the end of the Miocene, further passerine invasions originated from the Sino-Himalayas moving mainly towards two adjacent biogeographic regions. In a westward direction, towards the Central Asian Hindukush, the Pamir-Altai region and the Tien Shan, several local endemic faunal elements emerged from western Himalayan ancestors (cf. Johansson *et al.*, 2007). In a southward direction, there was an apparently continuous influx of continental Southeast Asian faunal elements to the island of Taiwan from the early Pliocene onwards. In accordance with palaeogeographic data, our mean TMRCA estimates for sister clades from Taiwan and the continent never pre-dated the time estimate for the major uplift phase of the central mountain ridge during the Penglai Orogeny of Taiwan (starting at 4–5 Ma according to Liu *et al.*, 2000).

Second phase: boreal radiations towards the Pliocene/Pleistocene boundary

In all of our study families, this phase coincides with the separation among clades of extant subalpine Sino-Himalayan taxa from their closest north Palaearctic relatives. According to our dating results, the radiation of boreal avian faunal elements was strongly connected to climate cooling and the emergence of temperate forests in the subalpine elevational belt towards the end of the Pliocene. Corridors that might have enhanced the boreal faunal interchange between the northern Palaearctic and the Southeast Asian mountain systems were postulated by some authors (Kitamura, 1955: westward range expansion of Sino-Japanese vascular plants via a Himalayan temperate forest belt; Wang *et al.*, 2006: two major Pliocene vegetation shifts on the central Loess Plateau from dry steppe first to a temperate more humid forest ecosystem and successively to dry grassland and desert steppe until 3.7 Ma).

The true (sub)tropical passerine species assemblages inhabiting the foothills of the Sino-Himalayan mountain systems were obviously the first to diversify towards the late Pliocene and to establish the allopatric distribution patterns still found today. At roughly the same time, local parapatry of congeneric species across an elevational gradient became firmly established due to the occupation of the high-elevation Sino-Himalayan forests by the immigrant boreal avifaunal elements from the north-east. Different ecological preadaptations acquired by the ancestors of extant congeners during early Miocene radiation might have enhanced the formation of elevational parapatry in that region, as found in three high-elevation leaf-warbler clades from west Himalayan coniferous versus birch and rhododendron habitats (Price, 2010), and in three muscicapid clades from different elevations within the semi-open (and open) alpine zone of the central Himalayas (Landmann & Winding, 1993). In contrast, among those species of (sub)tropical origin, only a few apparently adapted successfully to temperate habitat conditions and were not successively displaced by boreal close congeners to lower elevations (e.g. *Certhia himalayana*, *Pyrrhula nipalensis*, *Trochalopteron elliotii*, *Pnoepyga albiventer*). These species inhabit a very broad breeding range from elevations of about 1500 m to above 3500 m to the temperate ecozone, and might thus be less limited with respect to their elevational niche than the true subtropical foothill species. Different patterns of species diversification at different elevations were also found in Neotropical forest ecosystems: the highland avifauna of the Andes is characterized by increased diversification rates throughout the Pliocene and Pleistocene, while diversification rates in the lowland ecosystems slowed significantly through time (Weir, 2006).

Beyond the Sino-Himalayan chain, our data suggest further faunal interchange among the Philippines and the adjacent continental bioregions towards the Pliocene/Pleistocene boundary in three of our study groups: bullfinches, tits and leaf-warblers (in accordance with molecular dating for Philippine populations of *Copsychus saularis*; Sheldon *et al.*, 2010).

In all three genera, the ancestral range of each of the three continental-Philippine sister clades was suggested to be the continental Southeast Asian lowland forests (F06). However, because the very diverse Philippine avifauna also encompasses Indo-Papuan and Australasian faunal elements, different possible colonization routes and different times of origin (including multiple colonization events) were reconstructed for several Philippine endemics (Jones & Kennedy, 2008; Lohman *et al.*, 2010; Oliveros & Moyle, 2010; Sheldon *et al.*, 2010). For instance, in the complex biogeographic history of the Philippines, the island of Palawan was suggested to be both a 'springboard to diversification' of terrestrial vertebrates (Esselstyn *et al.*, 2010) and a barrier enhancing isolation of early Philippine colonizers through exclusion from Palawan by a congener occupying the same ecological niche (Sheldon *et al.*, 2010). Among our study groups, the phylogeographic pattern among the Palawan tit (*Periparus amabilis*) and the possibly paraphyletic elegant tit (*P. elegans*) tends to support the springboard hypothesis.

Third phase: Pleistocene range fragmentation and vicariance

Competing viewpoints in the long-running debate on the late Pleistocene origin of bird species largely depend on a number of general assumptions for molecular dating, such as the species concept applied (Johnson & Cicero, 2004; Zink *et al.*, 2004). Nevertheless, despite this controversy, there is some good evidence for Pleistocene speciation events (in terms of genetic lineage splits), for the boreal New World avifauna (Weir & Schluter, 2004), for Southeast Asian forest-dwelling passerines (Päckert *et al.*, 2009), and some Asian mammals such as flying squirrels (Sciuridae of the genera *Eothenomys*, *Eupetaurus* and *Dremomys*; Luo *et al.*, 2004; Yu *et al.*, 2004; Li *et al.*, 2008) and langurs of the genera *Trachypithecus* and *Semnopithecus* (Wangchuk *et al.*, 2008). In the New World, speciation rate estimates were found to increase, while species ages decreased with increasing latitude (Weir & Schluter, 2007; cf. also Mittelbach *et al.*, 2007), and although Pleistocene speciation seems to have occurred most often in the boreal avifauna, it has occasionally been documented in tropical birds, too (Zosteropidae: Moyle *et al.*, 2009).

According to our data, in this third phase of East Asian passerine radiation only true boreal faunal elements were affected by Pleistocene impact. Their extant allopatric and parapatric distribution patterns correspond well to forest refuges where isolated ancestral populations survived glacial cycles (mainly reconstructed for the Last Glacial Maximum: Nazarenko, 1990; Qiu *et al.*, 2011). Regarding those refuges, there was recent evidence from palaeolake sediments in south-western Yunnan for the persistence of forest vegetation throughout the Pleistocene, including shifts of elevational belts among glacial and interglacial periods (Xiao *et al.*, 2007). In the light of our molecular dating, several extant phylogeographic disjunctions of the East Asian forest avifauna emerged during these times.

East–west Himalayan disjunction (F04a versus F04b)

The existence of a western forest refuge was already hypothesized by de Lattin (1957). Ancestors of at least 36 bird species are thought to have survived the LGM there; among these 14 are Himalayan endemics or near endemics, including two of high taxonomic level, *Catreus wallichii* and *Callacanthis burtoni* (Nazarenko, 1985; Martens & Eck, 1995, pp. 39–41). Twenty-one taxa from that region are ranked as sister to distinct conspecific (or in some cases congeneric) populations from the eastern Himalayas or south-western China (Nazarenko, 1985). Thus, 'speciation' *in situ*, and maybe regional extinctions, evidently took place even within the Himalayas, followed by Late Glacial/Holocene establishment of secondary contact including hybridization.

East Himalayan/Burmese–south Chinese disjunction (F04a/b versus F04c, F03)

Throughout the whole Sino-Himalayan belt of practically continuous forest environment, a fundamental replacement of forest bird taxa can be observed between 85° and 115° E (62% of 366 species surveyed; Nazarenko, 2002). Most of these sister taxa are distributed east and west of the Mekong–Salween Divide (Kingdon Ward, 1921), which was occasionally described as a biogeographic barrier promoting population differentiation of plants and vertebrates (Geissmann *et al.*, 2011; Li *et al.*, 2011; Qiu *et al.*, 2011). In a wide context, this zoogeographic pattern matches the centres of dispersal (*Ausbreitungszentren*) for terrestrial animals in that region reconstructed by de Lattin (1957). The emergence of allopatry (parapatry), including large zones of overlap and cases of hybridization between boreal passerine sister taxa across this divide, was reliably dated back to Pleistocene times – subtropical sister clades east and west of the divide apparently diverged earlier (see above).

Taiwan–continental Southeast Asian disjunction (F03T versus others)

According to our TMRCA estimates, some late invasions of boreal faunal elements from continental Southeast Asia also reached Taiwan. A disjunction across a divide up to 2000 km between Taiwan bird populations and their closest continental relatives can be found in at least 21 forest-dwelling species of the upper subalpine fir and spruce forests.

Palaearctic–Chinese disjunction (F01 versus F04d)

The northern Chinese avifauna contrasts with considerably greater species diversity in south China (Lei *et al.*, 2003, 2006), which in the latter key forest region (F03) presumably originated from the repeated influx of immigrants from both the north Palaearctic region and the Oriental region. Emergence of four locally endemic bird taxa of the north Chinese forests (F04d) was unambiguously dated back to the Pleistocene and assigned to an ancestral range in the same region. Their glacial refuges of the 'Sino-Japanese Forest Subkingdom' were dominated by temperate character tree species of north Chinese forests, for example extant *Pinus tabulaeformis*, which during the LGM had retreated southward due to eastward expansion of steppe and desert vegetation (Li *et al.*, 2011).

Tibetan Plateau

Pleistocene habitat fragmentation apparently triggered not only increased genetic diversity of forest-dwelling birds, but also that of the endemic species from open habitats on the Tibetan Plateau. There is recent evidence that even some Tibetan birds (including endemics) have undergone severe changes in population size, past range fragmentation of habitats and a post-Pleistocene re-colonization of the plateau (Yang *et al.*, 2009; Qu *et al.*, 2010).

Synthesis – origin of faunal transition zones in Southeast Asian birds

A number of so called 'transition zones' between zoogeographic regions have been described for East Asia, for example, the Isthmus of Kra was shown to represent a transition zone among Indo-Chinese and Sundaic faunal elements in mammals and birds (Hughes *et al.*, 2003; Woodruff & Turner, 2009). Similarly, transitions of Palaearctic and Oriental faunal elements are apparent throughout large parts of China and the Himalayas (Vaurie, 1972; Martens, 1984). Even across narrow ranges within the Himalayan mountain range itself, Martens & Eck (1995, p. 51) identified suture zones of local contact between eastern and western subspecies in Nepal and defined four of them: Karnali catchment transition zone, Dhaulagiri transition zone, Kathmandu transition zone, and the Arun catchment transition zone. More than 50 species were analysed, demonstrating that the Himalayan system harbours populations that differentiated in that area or immigrated at various periods. Moreover, we find a clear faunal transition from lower to higher elevations in the Himalayas, suggesting that the subalpine conifer forest ecoregion 'straddles the transition from the southern Indo-Malayan to the northern Palaearctic fauna' (Wikramanayake *et al.*, 2001, p. 341). Belik (2006) found strong faunal similarities among the Himalayan alpine and subalpine mountain forests and the boreal forests of northern Eurasia, and the Tibetan Plateau was even suggested to be ranked as a subregion of the Palaearctic based on the distribution patterns of terrestrial mammals (Xiang *et al.*, 2004). The dating results for the lineage splits within our seven target families (Aegithalidae, Certhiidae, Fringillidae, Paridae, Phylloscopidae, Regulidae and Timaliidae) provide a rough timeline for the emergence of extant biogeographic patterns and faunal transitions. Particularly in the Sino-Himalayan mountain forests, transition zones among Southeast Asian and north Palaearctic forest-dwelling passerines seem to be relatively young and might have formed largely during the Pliocene invasion of north Palaearctic faunal elements into the subalpine ecozone.

ACKNOWLEDGEMENTS

A large part of the sequences used for this study were inferred from genetic material collected during regular field trips in Central Europe and a number of expeditions to the Himalayan region (results of the Himalaya Expedition of J. Martens, No. 275; for No. 274 see *Genus, Wrocław*, 2011, **22,** 181–190). Travel and research funds were granted by the Deutsche Ornithologen-Gesellschaft (various, including travel grants for China and Taiwan to J.M. and M.P.), the Gesellschaft für Tropenornithologie (travel grants to M.P. and J.M.), SYNTHESYS (D.T.T., T.T.), Evangelisches Studienwerk Villigst (D.T.T.), Feldbausch-Stiftung and Wagner-Stiftung (J.M.), Deutsche Forschungsgemeinschaft to D.T.T. (Ti 679/1-1) and the National Natural Science Foundation of China to Y.-H.S. (30620130110). Many friends and colleagues assisted during fieldwork on several expeditions; Y. Fang, C. Fischer, M. Kaiser and O. Valchuk provided samples. We finally thank M. Patten and two anonymous referees for their constructive critique. The present study was financially supported by the research funding programme 'LOEWE – Landes-Offensive zur Entwicklung Wissenschaftlich-ökonomischer Exzellenz' of Hesse's Ministry of Higher Education, Research and the Arts.

REFERENCES

Alström, P. (2006) Species concepts and their application: insights from the genera *Phylloscopus* and *Seicercus*. *Acta Zoologica Sinica*, **52**(Suppl.)**,** 429–434.

Alström, P., Davidson, P., Duckworth, J.W., Eames, J.C., Le, T.T., Nguyen, C., Olsson, U., Robson, C. & Timmins, R. (2010) Description of a new species of *Phylloscopus* warbler from Vietnam and Laos. *Ibis*, **152,** 145–168.

Ancochea, E., Fuster, J.M., Ibarrola, E., Cendero, A., Coello, J., Hernan, F., Cantagrel, J.M. & Jamond, C. (1990) Volcanic evolution of the island of Tenerife (Canary Islands) in the light of new K-Ar data. *Journal of Volcanology and Geothermal Research*, **44,** 231–249.

Badgley, C., Barry, J.C., Morgan, M.E., Nelson, S.V., Behrensmeyer, A.K., Cerling, T.E. & Pilbeam, D. (2008) Ecological changes in Miocene mammalian record show impact of prolonged climatic forcing. *Proceedings of the National Academy of Sciences USA*, **105,** 12145–12149.

Barry, J.C., Morgan, M.E., Flynn, L.J., Pilbeam, D., Behrensmeyer, A.K., Raza, S.M., Khan, I.A., Badgley, C., Hicks, J. & Kelley, J. (2002) Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan. *Paleobiology*, **28,** 1–71.

Belik, V.P. (2006) Faunogenetic structure of the Palaearctic avifauna. *Entomological Review*, **86,** 15–31.

Bensch, S., Irwin, D.E., Irwin, J.H., Kvist, L. & Åkesson, S. (2006) Conflicting patterns of mitochondrial and nuclear DNA diversity in *Phylloscopus* warblers. *Molecular Ecology*, **15,** 161–171.

Chovellon, P. (1982) *Évolution volcanotectonique des îles de Faial et de Pico, Archipel des Açores – Atlantique Nord*. Thèse de docteur 3ème cycle, Université de Paris-Sud, Centre d'Orsay, Paris.

Collar, N.J. & Robson, C. (2007) Babblers (Timaliidae). *Handbook of the birds of the world*, Vol. 12 (ed. by J. del Hoyo, A. Elliott and D.A. Christie), pp. 70–291. Lynx Edicions, Barcelona.

Collar, N.J., Andreev, A.V., Chan, S., Crosby, M.J., Subramanya, S. & Tobias, J.A. (eds) (2001) *Threatened birds of Asia: the BirdLife International Red Data book*. BirdLife International, Cambridge.

Dickinson, E. (ed.) (2003) *The Howard & Moore complete checklist of birds of the world*, 3rd edn. Christopher Helm, Princeton University Press, Princeton, NJ.

Drummond, A.J. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, **7,** 214.

Drummond, A.J., Ho, S.Y.W., Phillips, M.J. & Rambaut, A. (2006) Relaxed phylogenetics and dating with confidence. *PLoS Biology*, **4,** e88.

Esselstyn, J.A., Oliveros, C.H., Moyle, R.M., Peterson, A.T., McGuire, J.A. & Brown, R.M. (2010) Integrating phylogenetic and taxonomic evidence illuminates complex biogeographic patterns along Huxley's modification of Wallace's Line. *Journal of Biogeography*, **11,** 2054–2066.

Fernández-Palacios, J.M., de Nascimento, L., Otto, R., Delgado, J.D., García del Rey, E., Arévalo, J.R. & Whittaker, R.J. (2011) A reconstruction of Palaeo-Macaronesia with particular reference to the long-term biogeography of the Atlantic island laurel forests. *Journal of Biogeography*, **38,** 226–246.

Fleischer, R.C., Kirchman, J.J., Dumbacher, J.P., Bevier, L., Dove, C., Rotzel, N.C., Edwards, S.C., Lammertink, M., Miglia, K.J. & Moore, W.S. (2006) Mid-Pleistocene divergence of Cuban and North American ivory-billed woodpeckers. *Biology Letters*, **2,** 466–469.

Ganjoo, R.K. & Shaker, S. (2006) Middle Miocene pedological record of monsoonal climate from Northwest Himalaya (Jammu & Kashmir State), India. *Journal of Asian Earth Sciences*, **29,** 704–714.

Geissmann, T., Lwin, N., Aung, S.S., Aung, T.N., Aung, Z.M., Hla, T.H., Grindley, M. & Momberg, F. (2011) A new species of snub-nosed monkey, genus *Rhinopithecus* Milne-Edwards, 1872 (Primates, Colobinae) from northern Kachin State, northeastern Myanmar. *American Journal of Primatology*, **73,** 96–107.

Gelang, M., Cibois, A., Pasquet, E., Olsson, U., Alström, P. & Ericson, P.G.P. (2009) Phylogeny of babblers (Aves, Passeriformes): major lineages, family limits and classification. *Zoologica Scripta*, **38,** 225–236.

Gill, F. & Donsker, D. (eds) (2011) *IOC World Bird Names (version 2.8)*. Available at: http://www.worldbirdnames.org.

Gladenkov, A.Y., Oleinik, A.E., Marincovich, L., Jr & Barinov, K.B. (2002) A refined age for the earliest opening of Bering Strait. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **183,** 321–328.

Guo, Z.T., Sun, B., Zhang, Z.S., Peng, S.Z., Xiao, G.Q., Ge, J.Y., Hao, Q.Z., Qiao, Y.S., Liang, M.Y., Liu, J.F., Yin, Q.Z. & Wie, J.J. (2008) A major reorganization of Asian climate regime by the early Miocene. *Climate of the Past*, **4,** 153–174.

Hopkins, D.M. (1967) The Cenozoic history of Beringia – a synthesis. *The Bering Land Bridge* (ed. by D.M. Hopkins), pp. 451–484. Stanford University Press, Stanford, CA.

Huelsenbeck, J.P. & Ronquist, F. (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, **17,** 754–755.

Hughes, J.B., Round, P.D. & Woodruff, D.S. (2003) The Indochinese–Sundaic faunal transition at the Isthmus of Kra: an analysis of resident forest bird species distributions. *Journal of Biogeography*, **30,** 569–580.

Johansson, U.S., Alström, P., Olsson, U., Ericson, P.G.P., Sundberg, P. & Price, T.D. (2007) Build-up of the Himalayan avifauna through immigration: a biogeographical analysis of the *Phylloscopus* and *Seicercus* warblers. *Evolution*, **61,** 324–333.

Johnson, N.K. & Cicero, C. (2004) New mitochondrial DNA data affirm the importance of Pleistocene speciation in North American birds. *Evolution*, **58,** 1122–1130.

Johnson, C.L., Wijbrans, J.R., Constable, C.G., Gee, J., Staudigel, H., Tauxe, L., Forjaz, V.H. & Salgueiro, M. (1998) ^{40}Ar/^{39}Ar ages and paleomagnetism of São Miguel lavas, Azores. *Earth and Planetary Science Letters*, **160,** 637–649.

Jones, A.W. & Kennedy, R.S. (2008) Evolution in a tropical archipelago: comparative phylogeography of Philippine fauna and flora reveals complex patterns of colonization and diversification. *Biological Journal of the Linnean Society*, **95,** 620–639.

Jønsson, K.A., Bowie, R.C.K., Nylander, J.A.A., Christidis, L., Norman, J.A. & Fjeldså, J. (2010a) Biogeographical history of cuckoo-shrikes (Aves: Passeriformes): transoceanic colonization of Africa from Australo-Papua. *Journal of Biogeography*, **37,** 1767–1781.

Jønsson, K.A., Bowie, R.C.K., Moyle, R.G., Christidis, L., Norman, J.A., Benz, B.W. & Fjeldså, J. (2010b) Historical biogeography of an Indo-Pacific passerine bird family (Pachycephalidae): different colonization patterns in the Indonesian and Melanesian archipelago. *Journal of Biogeography*, **37,** 245–257.

Kingdon Ward, F. (1921) The Mekong–Salween Divide as a geographical barrier. *The Geographical Journal*, **58,** 49–56.

Kitamura, S. (1955) Flowering plants and ferns. *Fauna and flora of Nepal Himalaya* (ed. by H. Kihara), pp. 73–290. Fauna and Flora Research Society, Kyoto.

Krijgsman, W., Hilgen, F.J., Raffi, I., Sierro, F.J. & Wilson, D.S. (1999) Chronology, causes and progression of the Messinian salinity crisis. *Nature*, **400,** 652–655.

Landmann, A. & Winding, N. (1993) Niche segregation in high-altitude Himalayan chats (Aves, Turdidae): does morphology match ecology? *Oecologica*, **95,** 506–519.

de Lattin, G. (1957) Die Ausbreitungszentren der holarktischen Landtierwelt. *Verhandlungen der Deutschen Zoologischen Gesellschaft* (1956), 380–410.

Lei, F.-M., Qu, Y.-H., Lu, J.-L., Liu, Y. & Yin, Z.-H. (2003) Conservation on diversity and distribution patterns of endemic birds in China. *Biodiversity and Conservation*, **12,** 239–254.

Lei, F., Zhao, H. & Yin, Z. (2006) Distribution pattern of endangered bird species in China. *Integrative Zoology*, **1,** 162–169.

Li, S., Yu, F., Yang, S., Wang, Y., Jiang, X., McGuire, P.M., Feng, Q. & Yang, J. (2008) Molecular phylogeny of five species of *Dremomys* (Rodentia: Sciuridae), inferred from cytochrome *b* gene sequences. *Zoologica Scripta*, **37,** 349–354.

Li, Y., Zhai, S.-N., Qiu, Y.-X., Guo, Y.P., Ge, X.-H. & Comes, H.P. (2011) Glacial survival east and west of the 'Mekong–Salween Divide' in the Himalaya–Hengduan Mountains region as revealed by AFLP and cpDNA sequence variation in *Sinopodophyllum hexandrum* (Berberidaceae). *Molecular Phylogenetics and Evolution*, **59,** 412–424.

Liu, T.K., Chen, Y.G., Chen, W.S. & Jiang, S.H. (2000) Rates of cooling and denudation of the Early Penglai Orogeny, Taiwan, as assessed by fission-track constraints. *Tectonophysics*, **320,** 69–82.

Lohman, D.J., Ingram, K.K., Prawiradilaga, D.M., Winker, K., Sheldon, F.H., Moyle, R.G., Ng, P.K.L., Ong, P.S., Wang, L.K., Braile, T.M., Astuti, D. & Meier, R. (2010) Cryptic genetic diversity in 'widespread' Southeast Asian bird species suggests that Philippine avian endemism is gravely underestimated. *Biological Conservation*, **143,** 1885–1890.

Luo, J., Yang, D., Suzuki, H., Wang, Y., Chen, W.-J., Campbell, K.L. & Zhang, Y.-P. (2004) Molecular phylogeny and biogeography of Oriental voles: genus *Eothenomys* (Muridae, Mammalia). *Molecular Phylogenetics and Evolution*, **33,** 349–362.

Luo, X., Qu, Y.H., Han, L.X., Li, S.H. & Lei, F.M. (2008) A phylogenetic analysis of laughing-thrushes (Timaliidae: *Garrulax*) and allies based on mitochondrial and nuclear DNA sequences. *Zoologica Scripta*, **38,** 9–22.

Maddison, W.P. & Maddison, D.R. (2008) *Mesquite: a modular system for evolutionary analysis*. Version 2.5. Available at: http://mesquiteproject.org.

Manegold, A., Mayr, G. & Mourer-Chauvire, C. (2004) Miocene songbirds and the composition of the European passeriform avifauna. *The Auk*, **121,** 1155–1160.

Martens, J. (1984) Vertical distribution of Palaearctic and Oriental faunal components in the Nepal Himalayas. *Erdwissenschaftliche Forschung*, **18,** 323–336.

Martens, J. & Eck, S. (1995) Towards an ornithology of the Himalayas: systematics, ecology and vocalizations of Nepal birds. *Bonner Zoologische Monographien*, **38,** 1–445.

Martens, J., Sun, Y.-H. & Päckert, M. (2008) Intraspecific differentiation of Sino-Himalayan bush-dwelling *Phylloscopus* leaf-warblers, with description of two new taxa (*P. fuscatus*, *P. fuligiventer*, *P. affinis*, *P. armandii*, *P. subaffinis*). *Vertebrate Zoology*, **58,** 233–265.

Martens, J., Tietze, D.T. & Päckert, M. (2011) Phylogeny, biodiversity, and species limits of passerine birds in the Sino-Himalayan region – a critical review. *Ornithological Monographs*, **70,** 64–94.

Mayr, G. (2005) The Paleogene fossil record of birds in Europe. *Biological Reviews*, **80,** 515–542.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V. *et al.* (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10,** 315–331.

Moyle, R.G., Filardi, C.E., Smith, C.E. & Diamond, J. (2009) Explosive Pleistocene diversification and hemispheric expansion of a 'great speciator'. *Proceedings of the National Academy of Sciences USA*, **106,** 1863–1868.

Nazarenko, A.A. (1985) Some historic–biogeographic problems connected with the Himalayas (with special reference to the dendrophilous avifauna. *Zhurnal Obshchei Biologii*, **46,** 41–54 (in Russian with English summary).

Nazarenko, A.A. (1990) Recent history of the east Palearctic avifauna: transzonal interchange of the forest elements between south and north Asia since the last 35 000 years. *Proceedings of the International 100th Deutsche Ornithologen-Gesellschaft meeting, Bonn 1988 – Current Topics in Avian Biology* (ed. by R. van den Elzen, K.-L. Schuchmann and K. Schmidt-Koenig), pp. 81–87. Verlag der Deutschen Ornithologen-Gesellschaft, Bonn.

Nazarenko, A.A. (2002) The east Himalayan versus south Chinese speciation 'hot spot': diverse patterns of allopatry and replacement in forest birds. *23rd International Ornithological Congress, Abstract Volume*, pp. 182–183. China Zoological Society, Beijing.

Nylander, J.A.A. (2004) *MrModeltest ver. 2*. Program distributed by the author. Evolutionary Biology Centre, Uppsala University, Uppsala.

Oliveros, C.H. & Moyle, R.G. (2010) Origin and diversification of Philippine bulbuls. *Molecular Phylogenetics and Evolution*, **54,** 822–832.

Päckert, M. & Martens, J. (2008) Taxonomic pitfalls in tits – comments on the Paridae chapter of the handbook of the birds of the world. *Ibis*, **150,** 629–631.

Päckert, M., Martens, J., Tietze, D.T., Dietzen, C., Wink, M. & Kvist, L. (2007) Calibration of a molecular clock in tits (Paridae) – do nucleotide substitution rates of mitochondrial genes deviate from the 2% rule? *Molecular Phylogenetics and Evolution*, **44,** 1–14.

Päckert, M., Martens, J., Sun, Y.-H. & Tietze, D.T. (2009) Phylogeography and the evolutionary time-scale of passerine radiations in the Sino-Himalaya. *Biodiversity and natural heritage of the Himalaya,* Vol. III (ed. by M. Hartmann and J. Weipert), pp. 71–80. Verein der Freunde und Förderer des Naturkundemuseums Erfurt, Erfurt, Germany.

Päckert, M., Martens, J. & Sun, Y.H. (2010) Phylogeny of long-tailed tits and allies inferred from mitochondrial and nuclear markers (Aves: Passeriformes, Aegithalidae). *Molecular Phylogenetics and Evolution*, **55,** 952–967.

Price, T. (2010) The roles of time and ecology in the continental radiation of the Old World leaf-warblers (*Phylloscopus* and *Seicercus*). *Philosophical Transactions of the Royal Society B: Biological Sciences*, **365,** 1749–1762.

Price, T. & Gross, S. (2005) Correlated evolution of ecological differences among the Old World leaf-warblers in the breeding and nonbreeding seasons. *Birds of two worlds: the ecology and evolution of migration* (ed. by R. Greenberg and P. Marra), pp. 359–372. Johns Hopkins University Press, Baltimore, MD.

Qiu, Y.-X., Fu, C.-X. & Comes, H.P. (2011) Plant molecular phylogeography in China and adjacent regions: tracing the genetic imprints of Quaternary climate and environmental change in the world's most diverse temperate flora. *Molecular Phylogenetics and Evolution*, **59,** 225–244.

Qu, Y., Lei, F., Zhang, R. & Lu, X. (2010) Comparative phylogeography of five avian species: implications for Pleistocene evolutionary history in the Qinghai–Tibetan plateau. *Molecular Ecology*, **19,** 338–351.

Rambaut, A. & Drummond, A.J. (2007) *Tracer v1.4*. Available at: http://beast.bio.ed.ac.uk/Tracer.

Reddy, S. (2008) Systematics and biogeography of the shrike-babblers (*Pteruthius*): species limits, molecular phylogenetics, and diversification patterns across southern Asia. *Molecular Phylogenetics and Evolution*, **47,** 54–72.

Renner, S.C. & Rappole, J.H. (2011) Bird diversity, biogeographic patterns and endemism of the eastern Himalayas and southeastern sub-Himalayan mountains. *Ornithological Monographs*, **70,** 153–166.

Rheindt, F.E. (2006) Splits galore: the revolution in Asian leaf-warbler systematics. *BirdingASIA*, **5,** 25–39.

Rheindt, F.E., Christidis, L., Cabanne, G.S., Miyaki, C. & Norman, J.A. (2009) The timing of Neotropical speciation dynamics: a reconstruction of *Myiopagis* flycatcher diversification using phylogenetic and paleogeographic data. *Molecular Phylogenetics and Evolution*, **53,** 961–971.

Rich, P.V., Hou, L.H., Ono, K. & Baird, R.F. (1986) A review of the fossil birds of China, Japan and Southeast Asia. *Geobios*, **19,** 755–772.

Roselaar, C.S., Sluys, R., Aliabadian, M. & Mekenkamp, P.G.M. (2007) Geographic patterns in the distribution of Palaearctic songbirds. *Journal of Ornithology*, **148,** 271–280.

Ruokonen, M. & Kvist, L. (2002) Structure and evolution of the avian mitochondrial control region. *Molecular Phylogenetics and Evolution*, **23,** 422–432.

Sangster, G. (2009) Increasing numbers of bird species result from taxonomic progress, not taxonomic inflation. *Proceedings of the Royal Society B: Biological Sciences*, **276,** 3185–3191.

Sanmartín, I., Enghoff, H. & Ronquist, F. (2001) Patterns of animal dispersal, vicariance and diversification in the Holarctic. *Biological Journal of the Linnean Society*, **73,** 345–390.

Sheldon, F.H., Lohman, D.J., Lim, H.C., Zou, F., Goodman, S.M., Prawiradilaga, D.M., Winker, K., Braile, T.M. & Moyle, R.G. (2010) Phylogeography of the magpie-robin species complex (Aves: Turdidae: *Copsychus*) reveals a Philippine species, an interesting isolating barrier and unusual dispersal patterns in the Indian Ocean and Southeast Asia. *Journal of Biogeography*, **36,** 1070–1083.

Stattersfield, A.J., Crosby, M.J., Long, A.J. & Wege, D.C. (eds) (1998) *Endemic Bird Areas of the world: priorities for biodiversity conservation*. BirdLife International, Cambridge.

Sun, X. & Wang, P. (2005) How old is the Asian monsoon system? – Palaeobotanical records from China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **222,** 181–222.

Vaurie, C. (1972) *Tibet and its birds*. H.F. & G. Witherby, London.

Wang, L., Lü, H.Y., Wu, N.Q., Li, J., Pei, Y.P., Tong, G.B. & Peng, S.Z. (2006) Palynological evidence for late Miocene–Pliocene vegetation evolution recorded in the red clay sequence of the central Chinese Loess Plateau and implication for palaeoenvironmental change. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **241,** 118–128.

Wangchuk, T., Inouye, D.W. & Hare, M.P. (2008) The emergence of an endangered species: evolution and phylogeny of the *Trachypithecus geei* of Bhutan. *International Journal of Primatology*, **29,** 565–582.

Weir, J.T. (2006) Divergent timing and patterns of species accumulation in lowland and highland neotropical birds. *Evolution*, **60,** 842–855.

Weir, J.T. & Schluter, D. (2004) Ice sheets promote speciation in boreal birds. *Proceedings of the Royal Society B: Biological Sciences*, **271,** 1881–1887.

Weir, J.T. & Schluter, D. (2007) The latitudinal gradient in recent speciation and extinction rates in birds and mammals. *Science*, **315,** 1574–1576.

Weir, J.T. & Schluter, D. (2008) Calibrating the avian molecular clock. *Molecular Ecology*, **17,** 2321–2328.

West, R.G. (1988) The record of the cold stage. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **318,** 505–522.

Wikramanayake, E., Dinerstein, E., Loucks, C.J. & Primm, S. (eds) (2001) *Terrestrial ecoregions of the Indo-Pacific: a conservation assessment (World Wildlife Fund Ecoregion Assessments)*. Island Press, Washington, DC.

Woodruff, D.S. & Turner, L.M. (2009) The Indochinese–Sundaic zoogeographic transition: a description and analysis of terrestrial mammal species distributions. *Journal of Biogeography*, **36,** 803–821.

Xiang, Z.-F., Liang, X.-C., Huo, S. & Ma, S.-L. (2004) Quantitative analysis of land mammal zoogeographical regions in China and adjacent regions. *Zoological Studies*, **43,** 142–160.

Xiao, X.Y., Shen, J., Wang, S.M., Xiao, H.F. & Tong, G.B. (2007) Palynological evidence for vegetational and climatic changes from the HQ deep drilling core in Yunnan Province, China. *Science in China, Series D – Earth Sciences*, **50,** 1189–1201.

Yang, S., Dong, H. & Lei, F.M. (2009) Phylogeography of the regional fauna on the Tibetan Plateau: a review. *Progress in Natural Science*, **19,** 789–799.

Yu, F., Yu, F., McGuire, P.M., Kilpatrick, C.W., Pang, J., Wang, Y., Lu, S. & Woods, C.A. (2004) Molecular phylogeny and biogeography of woolly flying squirrels (Rodentia: Sciuridae) inferred from mitochondrial cytochrome *b* gene sequences. *Molecular Phylogenetics and Evolution*, **33,** 735–744.

Zheng, H., Powell, C. McA., Rea, D.K., Wang, J. & Wang, P. (2004) Late Miocene and mid-Pliocene enhancement of the

East Asian monsoon as viewed from the land and sea. *Global and Planetary Change*, **41,** 147–155.

Zhisheng, A., Kutzbach, J.E., Prell, W.L. & Porter, S.C. (2001) Evolution of Asian monsoons and phased uplift of the Himalaya–Tibetan plateau since late Miocene times. *Nature*, **411,** 62–66.

Zink, R.M., Klicka, J. & Barber, B.R. (2004) The tempo of avian diversification during the Quaternary. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **359,** 215–220.

Zuxiang, W. (1982) On the vertical distribution of birds in the Himalayan region. *Zoological Research*, **3,** 260–292.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Taxon sampling for each group of forest passerines.
Appendix S2 Model settings for molecular data sets.
Appendix S3 Stepmatrix as used in ancestral range reconstructions with MESQUITE.

BIOSKETCH

Martin Päckert is the Curator of Birds at Senckenberg Natural History Collections Dresden, Germany. His research interests are the molecular systematics and bioacoustics of Eurasian passerines.

Author contributions: M.P. designed the study, conducted molecular dating and ancestral states reconstructions, and largely wrote the manuscript. J.M. collected and provided most of the material and co-wrote the manuscript. Y.-H.S. organized field trips in China from 1999 to 2009. L.L.S. organized field trips in Taiwan and supervised the lab work at Biodiversity Research Center, Taipei. A.A.N. collected samples from east Palaearctic species and co-wrote parts of the discussion. J.T. produced the molecular data set and carried out phylogenetic reconstructions for laughing-thrushes; T.T. did the same for bullfinches. D.T.T. carried out all molecular analyses and phylogenetic reconstructions for coal tits and cyt *b* data for treecreepers; he also provided samples collected on his own field trips and designed the databases for samples and recordings.

Editor: Michael Patten