The global diversification of songbirds (Oscines) and the build-up of the Sino-Himalayan diversity hotspot

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Abstract   Over the last decade, molecular phylogenetic studies have provided the foundation for a comprehensive analysis of the global diversification of songbirds (Oscines), which comprise nearly half of all the birds of the world. By comparing the spatial distribution of species representing basal and terminal root-path groups, this paper provides graphical illustrations of the global pattern of diversification for the major songbird clades. The worldwide expansion of songbirds started as an island radiation in the area where New Guinea is now located, but the mountains of southern China represent a principal center for more recent diversification. The paper suggests priorities and perspectives for further research aiming to understand what determines the variation in biodiversity on different spatial scales.

Keywords   songbirds, Oscines, global diversification, biogeography, Sino-Himalayan biodiversity hotspot

Introduction

Although all organismal groups have a history, evolutionary history was ignored in past correlative studies that aimed to explain the variation in biodiversity on earth (e.g., Rosenzweig, 1995). Today, computer power, distributional databases and molecular data for thousands of species allow a new class of synthetic studies. We can now explicitly document the imprint of history (Jetz et al., 2012). By adding data for ecological traits and community structure at different spatial scales we may finally move towards a mechanistic understanding of what determines the variation of life on earth.

Songbirds (Oscines, which is the main clade of the order Passeriformes) represent an ideal group for such ground-breaking studies. First of all, the global species diversity is well documented and the group is sufficiently large (4700 extant species, or nearly half of all

birds), distributed in all terrestrial habitats around the world, and diversified in terms of feeding adaptations. Unfortunately, earlier studies of adaptational diversity had no reference to phylogenetic relationships, as past systematists, mainly mislead by the recency of the fossil record, viewed this group as being the most "modern" and recently derived of the avian orders, too uniform for a phylogenetic hypothesis to be developed. Because of the diversity of family-level taxa, the Old World tropics were seen as the center of origin. Thus, many odd passerines inhabiting peripheral land areas such as Australasia were long regarded as aberrant members of well-known Old World families. Only ten years ago it became clear that the songbirds has a long history that started in Australia, or East Antarctica (Ericson et al., 2002; Barker et al., 2004), where few suitable deposits with fossil birds are available from the early Tertiary.

With a well-supported songbird phylogeny available we can now reconstruct the world-wide diversification history. This is essential for understanding how the regional species pools were assembled. We can now move towards synthesis where large amounts of spatial and phylogenetic data can be integrated to identify different

modes and shifts in evolutionary and ecological space, and hopefully reach a mechanistic understanding of the structure of avian communities at finer spatial scales.

With a focus on songbird distributions, this paper aims to provide a condensed overview of the biogeographic history of songbirds and more explicitly to place the rich songbird fauna of eastern Asia, and the Sino-Himalayan biodiversity hotspot in particular, in a global context. Rather than testing specific hypotheses I aim to illustrate how histories and patterns vary among the different songbird clades, and reflect over the possible implications of this variation. I will also point out groups of Chinese songbirds that hold particular promise for resolving questions of great generality, and also point out where a broader geographical sampling and international collaboration will be needed.

Materials and methods

This review will be based on knowledge that is currently available, but will be underpinned by original graphical presentations that illustrate global patterns of diversification for six main clades of songbirds. I combined information from a global phylogenetic supertree and a distributional database in a one-degree geographical grid (Holt et al., 2013). The deeper branching of this supertree is close to that presented by Jetz et al. (2012) but further details concerning the terminal branches are added as new phylogenies are published.

This phylogenetic tree is not time calibrated (as a chronogram), and in order to illustrate the different distributions of species representing early and more recent radiation I classify the species according to the length of its "root path", which is the number of phylogenetic nodes from the root of the phylogeny to the species in question. For a simple visual illustration of the diversification history and geographical imbalance in the distribution of phylogenetically basal and terminal species I superimpose the distributions of species representing the 1st root-path quartile (the 25% of species with the shortest root-paths) and the remaining (75%) of more terminal species with different colors, as explained in the legend to Fig. 2. In order to interpret these color patterns I took into account all published biogeographic analyses that identified likely areas of origin at phylogenetic nodes.

Names of biogeographic regions refer to a new global analysis where distributions of 21000 land vertebrate species were analyzed in relation to the phylogenetic relationships among them (Holt et al., 2013). The resulting subdivision of biogeographic realms and regions is somewhat more complex than the traditional biogeographic scheme proposed by Wallace (1876), but is more meaningful in the sense that each region is defined from a clustering analysis of large amounts of data identifying areas with shared evolutionary histories. In this classification, the Palearctic Realm is subdivided in an Eurasian region comprising Europe and the mountain areas of central Asia south to approximately 37 degrees N and extending east to Manchuria and Korea, and an Arctico-Siberian region comprising Siberia, areas around the Bering Strait and the entire circumpolar arctic. Between these vast northern regions and the (tropical) Oriental realm a distinctive Sino-Japanese realm is recognized (encompassing distinct Chinese and Tibetan regions, the latter including the Yunnan-Szechuan mountains). The western Eurasian region is separated from the Afrotropical realm by an arid Saharo-Arabian realm, that includes the Iranian desert.

Results

A concise outline of the songbird radiation

The traditional classification of songbirds (Wetmore, 1957) was based on the recognition of three major complexes of (1) Old World insect-eaters and their relatives, (2) sparrows, finches and New World nine-primaried oscines and (3) crows, birds of paradise and their allies. These were regarded as representing "three broad levels of evolution", from "lower" to "higher". This view was complicated by the fact that crows and some other groups with superior cognitive abilities had a primitive modification of the humerus.

With the advancement of molecular systematics since the 1980s it became apparent that the (expanded) group of crow-like birds (parvorder Corvida; Sibley and Ahlquist, 1990) had its origin in Australasia and had later spread to the north. With development of DNA sequence data and better analytical approaches it became evident that the entire Passeriformes had an austral origin (Ericson et al., 2002; Barker et al., 2004). The suboscines radiated from West Antarctica-South America, and all the true songbirds (Oscines) originated in East Antarctica-Australia and expanded during the upper Tertiary to other continents. This expansion appears to have started 30–40 million years ago, when the Australian plate moved north (Fig. 1), causing an

uplift of coral islands in the shallow epicontinental seas where New Guinea and the southern Moluccan islands are now. The molecular phylogenies suggest rapid radiations centered in this area, followed by multidirectional dispersal and island-hopping in the mobile arc of emerging oceanic islands along the borderline between the Australian, Pacific and Asiatic plates (Hall, 2011). Thus, islands apparently provided the physical setting that triggered the most remarkable increase in diversity of birds (Jønsson et al., 2011).

As a consequence of the new insights it became clear that many of the traditional songbird families (as outlined by Wetmore, 1957) were non-monophyletic and defined by degrees of specialization (grade). Some families, and notably the traditional babbler family (Timaliidae), have long been recognized as being "crap baskets" for species and genera of multiple phylogenetic affinities. Dramatic revisions were needed, at all taxonomic levels, before we can now begin to discuss the evolutionary tendencies by referring to monophyletic groups.

The exodus from Australia and the origin of the oscine fauna of the Old World

Jønsson et al. (2011) provided strong support for two events of dispersal out of the Australian ancestral ar-

eas. The first of these (the "core corvoids" of Barker et al., 2004) is characterized by a number of small clades that mainly inhabit the forest habitats of New Guinea. Embedded among these is a number of subclades that expanded more or less successfully over the surrounding archipelagos (and even back to Australia), with some cases of long-distance expansion to the Old World tropics. The second (provisionally called "transitory oscines") is a smaller group of berrypeckers Melanocharitidae, satinbirds Cnemophilidae, and Australian robins Petroicidae, of Papuan origin, although the petroicids have expanded to much of the Australian realm. This "transitional oscine" radiation gave rise to two presumably independent long-distance dispersals to the Old World: a small clade comprising *Chaetops* and *Picathartes* in Africa and *Eupetes* in Asia (Jønsson et al., 2007) and the monophyletic group Passerida (Johansson et al., 2008) with 3500 species. The main groups will be reviewed below in a concise form.

The radiation of core corvoids

The core corvoids appears to comprise a large polytomy with some small (relic) clades (*Mohoua*, *Daphaenositta*, *Eulacestoma*) and four large radiations (Jønsson et al., 2011). Apparently, these clades diverged within a very short time span, with a pattern of worldwide expansion
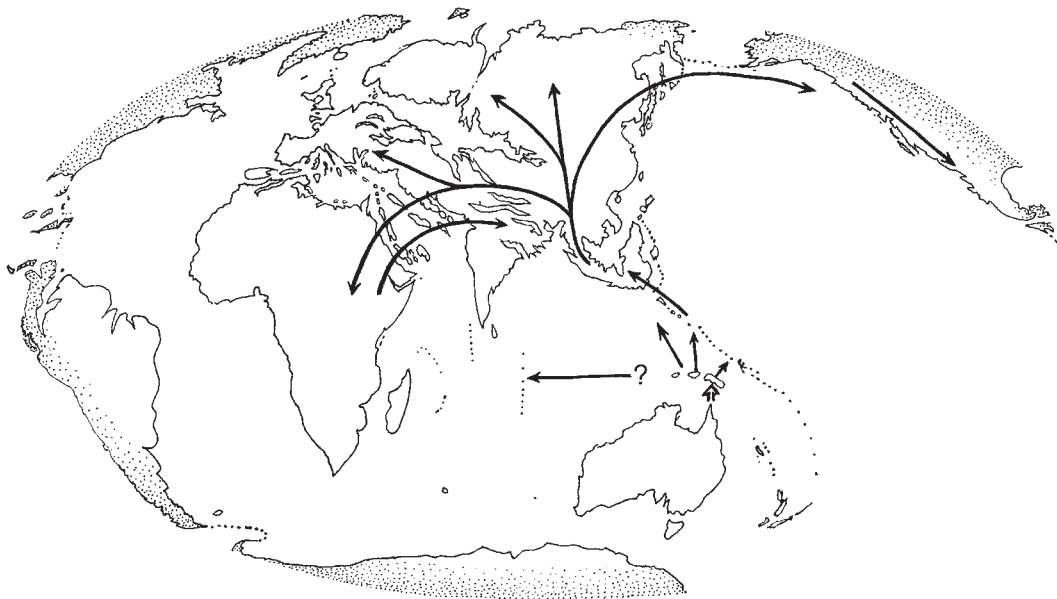

Fig. 1 The distribution of land in the Early Oligocene (34 Mya), corresponding to the time when the expansion of songbirds out of the ancestral area started (as indicated by arrows). Redrawn from www.scotese.com (December 2012). The existence of oceanic islands projecting above sea level is poorly documented for this time period.

as illustrated in Fig. 2.

Clade 1, Campephagidae: The genus *Pericrocotus* represents an early long-distance dispersal to the Oriental realm, where it underwent some expansion and diversification, including some back-colonization to the Indo-Malayan island region (Jønsson et al., 2010a). The core group radiated and expanded in the Papua-Melanesian archipelagos, with two or three independent direct colonizations to Africa, and another to the Oriental realm and to islands in the Indian Ocean (Jønsson et al., 2010b).

Clade 2: This comprises whistlers, orioles, and a number of morphologically quite divergent lineages suggestive of an early adaptive radiation in the Papuan area (*Ptilorrhoa, Cinclosoma, Oreocharis, Paramythia*). As with Clade 1, there was one early dispersal of vireos Vireonidae to the Oriental realm (*Erpornis, Pteruthius*; Reddy, 2008) and then onwards to the Americas. During the late Miocene and Plio-Pleistocene the orioles Oriolidae and whistlers Pachycephalidae underwent multidirectional expansion and diversification, as the whistlers diversified in Australia and archipelagos to the east and west, while orioles did not persist well on smaller islands but underwent phylogenetic expansion in Asia and Africa (Jønsson et al., 2010c, 2010d; Fritz et al., 2011).

Clade 3: This group is also rooted in the Australasian (*Machaerirhinchus*, butcherbirds Cracticidae, wood swallows Artamidae; the latter with some dispersal towards Asia). Fuchs et al. (2012) suggested direct dispersal to Africa but uncertainties about the phylogenetic position of the genera *Rhagologus* (New Guinea), *Pityriasis* (Borneo) and *Aegithina* (Oriental region) imply that an early dispersal through Asia is also possible.

However, some Oriental genera (*Hemipus, Philentoma, Tephrodornis*) have now been confidently placed within the African radiation of helmetshrikes and vangas Vangidae, suggesting back-colonization to Asia. The core group of bush-shrikes Malaconotidae, batises and wattleeyes Platysteiridae are mainly distributed in Africas wooded habitats.

Clade 4: This monophyletic group is very heterogeneous in terms of morphology and dispersal history. The deepest branches comprise fantails Rhipiduridae and drongos Dicruridae. The fantails include *Chaetorhynchus* of New Guinea and *Lamprolia* of Fiji as a basal lineage (Irestedt et al., 2008), and otherwise this family underwent recent multidirectional dispersal from New Guinea to the surrounding archipelagos and mainland areas (Nyári et al., 2009). The drongos diverged after an early dispersal to the Old World tropics, with more recent back-colonization to the archipelagos. The core radiation comprises monarch flycatchers Monarchidae and birds of paradise Paradisaeidae and associated small clades (Corcoracidae, *Ifrita, Melampitta*), which mostly stayed in the Australasian region, except for recent phylogenetic expansions of monarch flycatchers in the Indomalayan and Papua-Melanesian archipelagos (Filardi and Moyle, 2005; Fabre et al., 2012), and with one distinct radiation (*Hypothymis, Terpsiphone*) and expanding and diversifying through the Oriental and Afrotropical realms. Another subclade, established by an early long-distance dispersal to Asia, comprises crows Corvidae and shrikes Laniidae. The most basal taxa (*Platylophus* in Laniidae; *Crypsirina, Dendrocitta, Cissa/Urocissa* and *Temnurus* in Corvidae; Ericson et al., 2005) suggest an origin in the Oriental realm, but *Pyrrhocorax* is widespread in the Old World mountain
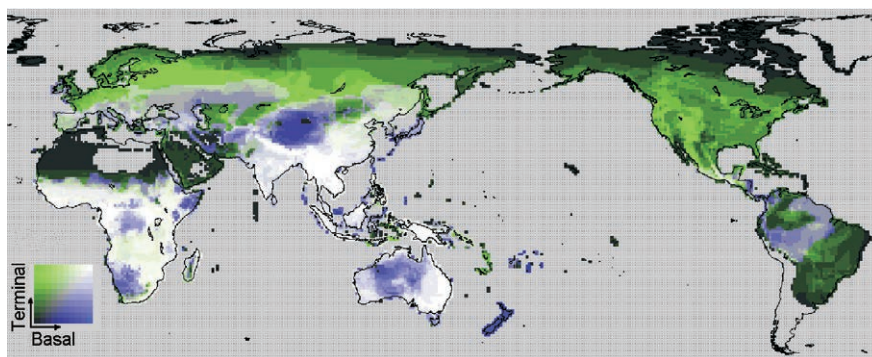

Fig. 2 The worldwide diversification of core corvoid birds (737 species). In this graphical presentatioin, species richness patterns representing the 1st root-path quartile (the 25% of species with the shortest root-paths based on the supertree) are displayed with violet color, and the 75% of more terminal species are displayed in green. A proportionally equal representation of the two groups produces neutral (grey) hues and the total species richness is shown as brightness.

regions. Both families underwent large expansions over a wide latitudinal range, even moving from Asia to North American, and with the American jays proceeding through Central and South America, and the genus *Corvus* colonizing remote oceanic islands (Jønsson et al., 2012b).

The Passerida radiation

Because of conflicting evidence concerning the deepest nodes of the Passerida phylogeny (Johansson et al., 2008; Jetz et al., 2012) I treat this as a soft polytomy, as the major clades (Paroidea, Certhoidea, Sylvoidea, Muscicapoidea and Passeroidea) and some small clades (African *Hyliota*, the African-Oriental Stenostiridae and northern *Regulus* and the bombycilloid group; Fuchs et al., 2006; Fleischer et al., 2008; Fuchs et al., 2009) diverged within a very short time span in the Oligocene period. With some basal taxa in Africa it is unclear whether the initial establishment was in Asia or Africa (Jønsson and Fjeldså, 2006). The ancient African species could represent relict populations since an early stage of expansion. However, the topology and geographical distributions within the main clades illustrate a very rapid expansion across the Old World.

Clade 1, Paroidea, tits and penduline tits (Fig. 3a): The genera *Melanochlora*, *Sylviparus*, *Cephalopyrus*, and *Pseudopodoces* suggest Sino-Himalayan/Oriental origin, but there was an early expansion along the Eurasian mountain ranges to the west and further expansions to Africa (*Anthoscopus* and *Parus*) and to North America.

Clade 2, Certhoidea (Fig. 3b): This group diversified first of all in montane regions. The different distributions of purples and greens in Fig. 3b reflect slow rates of speciation in the Old World subclades (Certhidae, Sittidae, Tichodromidae) compared with the stronger diversification of New World wrens (Troglodytidae, Polioptilidae).

Clade 3, Muscicapoidea (Fig. 3c): The species-poor dipper family Cinclidae is basal. A large subclade comprises Old World starlings Sturnidae (including the Philippine *Rhabdornis*, but the African *Buphagus* now in a separate family) and the American mockingbirds Mimidae. The starlings represent a very dynamic history with a basal radiation in the Oriental realm and secondarily radiations in the Oceanian and Afrotropical realms and in Asian grassland habitats (Lovette and Rubenstein, 2008; Lovette et al., 2008). The other large subclade comprises thrushes (Turdidae) and a mono-

phyletic assemblage of chats and flycatchers (Muscicapidae). The DNA-based systematics reveals a strong complexity in the latter group, with several basal groups of chats and robins (previously placed in the Turdidae) and nested among these are three terminal radiations that correspond to the former perception of flycatchers (Sangster et al., 2010; Zuccon and Ericson, 2010). There were apparently several cases of inter-continental and even trans-oceanic dispersal (Voelker et al., 2009) and the color display (Fig. 3c) suggests deep-rooted diversification centers in many parts of the world, first of all in Africa but also central Siberia, Europe and western North America. The brightest areas in Fig. 3c suggest a continuous high diversification in the mountainous parts of the Old World, with recent phylogenetic expansions into the humid tropical lowlands of the Oriental region and even some terminal radiation in the dry ecoregions.

Clade 4, Sylvoidea (Fig. 3d): The deepest branches are entirely African (African warblers Macrosphenidae and nicators Nicatoridae) or rooted in Africa (larks Alaudidae, cisticolid warblers Cisticolidae, swallows Hirundinidae) (Fregin et al., 2012; Olsson et al., 2013). The bulbuls Pycnonotidae are represented by reciprocally monophyletic radiations in the Africotropics (greenbuls) and the Orient. Grass-warblers (Locustellidae in the broad sense) show an exploded geographical pattern over most of the Eastern Hemisphere and even in the Pacific and Neotropical realms (*Donacobius*), but with strong radiations in eastern Asia (Alström et al., 2011a). Even the large terminal warbler clade may be rooted in Africa (*Hylia/Pholidornis, Erythrocercus*) and the Saharo-Arabian realm (*Scotocerca*), but this was followed by strong radiations centered in Asia (Cettidae, Aegithalidae, Phylloscopidae; Olsson et al., 2005; Päckert et al., 2010; Price, 2010; Alström et al., 2011b; Fregin et al., 2012). The other large terminal radiation, the babblers (Timaliidae in the broad sense; Gelang et al., 2009; Moyle et al., 2012) appear to be rooted in the Oriental montane environments and radiated over the entire south-eastern Asia, with expansions to the Mediterranean region (*Sylvia*) and Africa (mainly *Sylvia* and *Turdoides*). The bright green in the Oriental realm and Chinese region in Fig. 3d is mainly caused by babbler and warbler radiations.

Clade 5, Passeroidea (1603 spp): The very distinctive color pattern in Fig. 3e reflects the imbalance between deep radiations in the Old World and a very large terminal monophyletic radiation in the New World (bun-
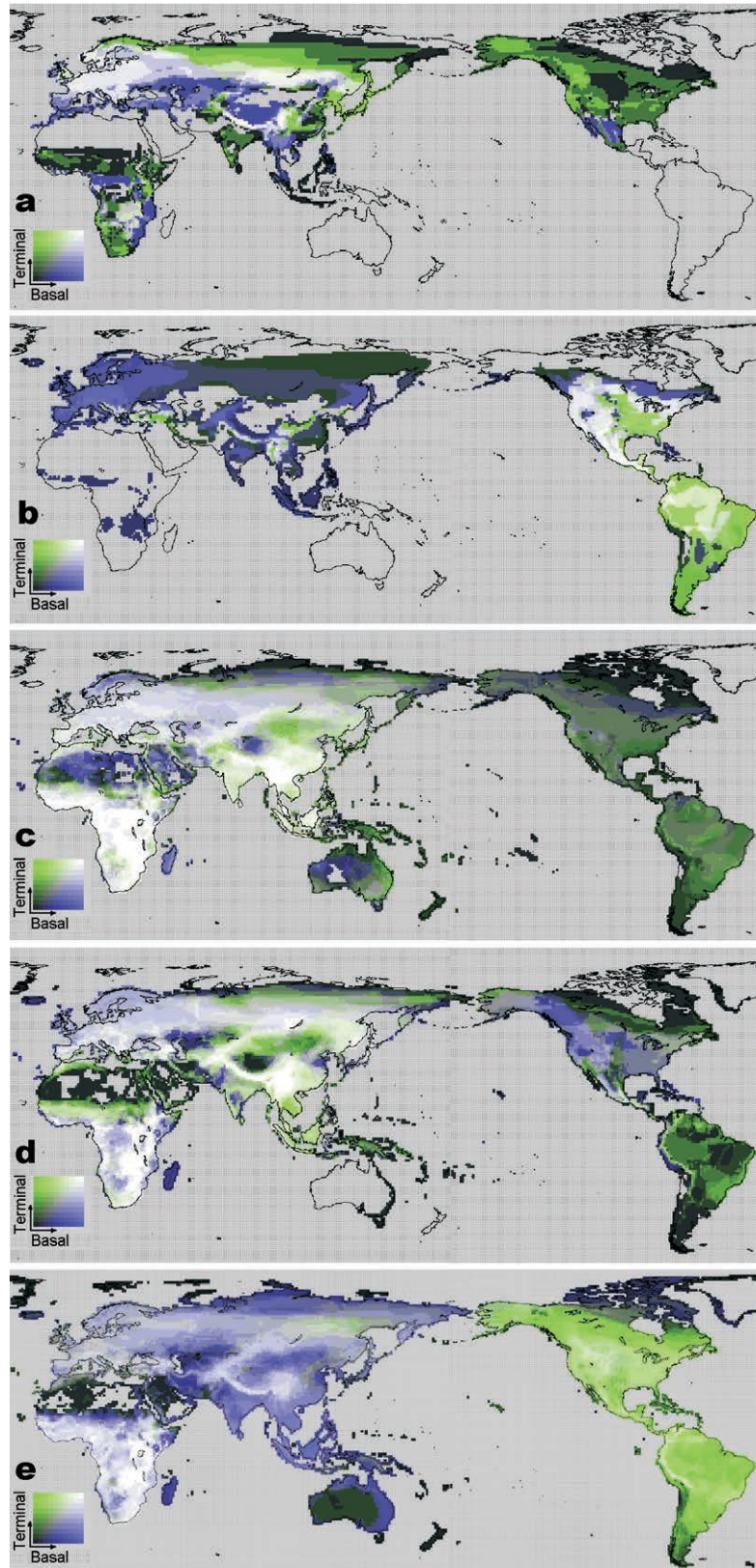
Fig. 3 Worldwide diversification of five large deep Passerida clades. (**a**) Paroidea (72 species); (**b**) Certhoidea (124 species); (**c**) Musci-capoidea (614 species); (**d**) Sylvoidea (1112 species); (**e**) Passeroidea (1603 species). For explanation see the legend to Fig. 2.

tings, Emberizidae in the broad sense, with close to 800 species). Apart from a possibly relictual basal lineage in Africa (*Promerops* and Modulatricidae), the early radiation was in the Oriental Realm (of Nectarinidae, Dicaedae, and basal granivorous groups, with later dispersal and great secondary radiations to Africa (notably weavers Ploceidae and waxbills Estrildidae, and subclades of sunbirds, sparrows Passeridae, pipits Motacillidae and finches Fringillidae. The neutral (grey to white) hues on the map suggest a continued diversification in China and Siberia, Europe and much of Africa (with some back-colonization to the Oriental realm, and even onwards to Australia. Finally, the pipits and finches show phylogenetic expansions in the New World, and in addition the basal group of buntings (Calcariinae and Emberizinae), probably of Siberian origin, colonized the open habitats of the Nearctic, and thus initiated the massive recent radiation New World nine-primaried oscines.

The geographical imbalance of diversification

The purplish color components in the maps (Figs. 2 and 3) represent a predominance of species in clades and subclades that are deeply rooted in the phylogeny. Thus, it appears that the high songbird diversity in the Old World tropics reflects a rapid biotic exchange between the Afrotropical and Oriental realms, and even Eurasia and North America, soon after the colonization from "down under". In addition to the general change towards less diverse and more derived high-latitude communities (Hawkins and Diniz-Filho, 2006), Figs. 2 and 3 also reveal a remarkable variation in color patterns among different clades. Some clades underwent little further radiation (reflected as pure purplish hues) in the tropical rainforest biomes. Others diversified strongly here, especially in ecoregions with a high landscape complexity. A particularly high accumulation of small-ranged species is found in montane regions under the climatic influence from thermally stable seas, presumably because high stability permits locally-adapted populations to persist in the same area for long periods of time (Fjeldså et al., 2012). This provides a long accumulation of species (and bright/greenish colors in Figs. 2 and 3) in much of the Papua-Melanesian, Indo-Malayan, Oriental and Afrotropical regions.

The green hues in Figs. 2 and 3, representing strong terminal radiation, are often caused by a few subclades (and genera in some cases, thus giving phylogenetically clustered communities in some geographic areas). This is particularly characteristic of Asia and the Americas, although with great variation among clades. A detailed scrutiny (e.g., Päckert et al., 2011) revealed that some of the groups that initially evolved in northern Asia had more terminal speciation event in the Chinese region and along various mountain ranges in the interior of Asia, suggesting that groups that had adapted to harsh conditions in the north were forced south during the Pleistocene, through eastern China, and along the Tian-Pamir-Hindu-Kush mountain ranges, to contribute to the build-up of the Sino-Himalayan "biodiversity hotspot" along the borderline between the Tibetan and Oriental regions (see especially Figs. 3a, b, d and e). Here, the well-marked topographic relief allows the geographical overlap (and remarkable beta-diversity) of cold-adapted species on the high mountain ridges and subtropical species in intervening valleys.

Most of the world's dry regions appear dark and deep purple Figs. 2 and 3, suggesting that heavy extirpation lead to phylogenetically overdispersed communities in these areas (with a few unrelated species). Only the old deserts (notably Namibia) have richer avifaunas characterized by phylogenetic clustering with some fairly species-rich groups (cisticolids warblers, chats, and larks) that have had long time to specialize for such conditions (see greenish hues in Figs. 3a, c and d).

Discussion

Dispersal and life strategies

With well supported phylogenetic hypotheses available it is now clear that songbirds originated in Australia but that the world-wide expansion started from the archipelagos that emerged in the Papua-Melanesian area since the mid-Tertiary (Jønsson et al., 2011). Thus islands were not dead ends for evolution, as assumed in classical island biogeography (MacArthur and Wilson, 1967), but apparently offered conditions that favoured dispersive life strategies. The remaining groups of basal songbirds in Australia have been less successful and apparently declined as a consequence of the later aridification in this continent (Byrne et al., 2012). At the same time, the Old World songbird fauna increased and diversified thanks to several colonization waves from the south, followed by dynamic interchange between the Oriental and Afrotropical realms.

Recent studies of the diversification of the Papua-

Melanesian and Indo-Malayan avifaunas suggest two different modes of dispersal: some groups apparently underwent explosive and multidirectional long-distance dispersals while others used stepping-stone islands for a more gradual expansion (Fritz et al., 2011). Both cases are phylogenetic expansions with little ecomorphological change. Presumably, the dispersalists followed a supertramp strategy, as initially described by Diamond (1974). Fabre et al. (2012) illustrated this excellently with phylogeographic data for the *Terpsiphone* monarchs, with a remarkable ability to colonize remote islands, but also established themselves in disturbed scrubby mainland environments (*paradisaea* group in Asia, followed by establishment in Africa), and with a final establishment and diversification within the Congolian rainforest region.

The wide geographical dispersion of basal Passerida lineages, in Africa, the Oriental region and even in the high north, suggests that the supertramp strategy, or nomadism, persisted for some time after the colonization of the Old World. In contrast, adaptive radiation will follow after colonization of an isolated land areas of limited extent (Jønsson et al., 2012).

Ancient and young communities

The largest diversity of songbirds (and highest brightness in Figs. 2 and 3) is found today at low latitudes. The purplish and grey hues, especially in regions with topographically unstructured tropical rainforests, indicate that many lineages that originated long ago (often by rapid interchange between the biogeographic regions and early speciation bursts) could persist as a consequence of the fairly constant warm climate. Areas with this kind of phylogenetically overdispersed communities are often referred to as "museums", in contrast to areas with a continuously high speciation rates, which are referred to as "cradles" of biodiversity. Lack of continued speciation in some lineages and geographical areas could represent competition and saturation of the available niche space (e.g., Raboski and Lovette, 2009) but could also represent late stages of taxon cycles (Ricklefs, 2011).

Adaptive radiation and niche saturation provides a plausible explanation for regions that are bounded by physical barriers (New Guinea or Madagascar; see Jønsson et al., 2012). However, speciation per time plots for some core corvoid groups suggest that a constantly high diversification rate may also be maintained over signifi-

cant time, as these groups undergo geographic expansion and speciation by isolation as they reach new areas (Fritz et al., 2011). Similarly, a large South American suboscine group maintained a constantly high speciation rate as several niche shifts allowed radiations into new habitats and geographical areas (Derryberry et al., 2011). Considering the amount of molecular phylogenetic data that is now available, it should soon be possible to explore the relationships between temporal and spatial growth of songbird diversity for Asia or even on a global scale.

Strong recent radiations take place in young ecoregions, such as grasslands and cold climates, and in the montane regions. However, in spite of a general tendency for young faunas at high latitudes (Hawkins and Diniz-Filho, 2006; Jetz et al., 2012), the variation in color hues in Figs. 2 and 3 suggest idiosyncratic patterns. Unstable conditions, such as draught or large amplitudes of temperature variation may lead to lack of speciation as range dynamics erases local adaptation and speciation (Dynesius and Jansson, 2000). It may also lead to extinction-driven pruning of the phylogenetic trees, and thus shorter root-path patterns, as reflected in dark purple hues in Figs. 2 and 3 in northern Europe and other species-poor regions. Thus, the trend for recent speciation in the north is driven by strong radiation in a few groups, and notably in parts of Siberia and Beringia that remained icefree during the Pleistocene. Similarly, the extraordinarily high rate of diversification in the New World, emphasized by Jetz et al. (2012), is caused by only two songbird groups (Figs. 3b and e) and two groups of endemic suboscine birds (Barker, 2011).

China as opportunity

A number of Chinese species and species groups have already been studied from the viewpoint of understanding phylogeographic patterns and location of refugia within the region. Judging from Figs. 3a and b, the Sino-Himalayan hotspot and the more isolated mountains up to the Great Hingen Mountains and Manchuria offer good prospects for more comprehensive studies of tits, creepers and nuthatches. Also the Chinese-Siberian subclade of thrushes *Turdus*, dunnocks *Prunella*, and somes finches (see Zuccon et al., 2011) of the interior mountain regions offer some prospects. However, we should also look for prospects for more comprehensive studies. The real challenge would be to undertake a comprehensive study of the large sylvoid radiations

(Fig. 3d). Most of the grass- and leaf warblers and babblers are now incorporated in molecular phylogenetic studies, allowing large phylogenies (supermatrices) to be combined with distributional and eco-morphological data to obtain a deeper understanding of how such complex faunas evolved.

The Muscicapoidea radiation also underwent an impressive radiation in the Chinese-Oriental regions (Fig. 3c), but is more difficult to handle because of the complex interchange between different biogeographic realms (Sangster et al., 2010; Zuccon and Ericson, 2010). While some genera (*Phoenicurus, Tarsiger*) show interesting biogeographic patterns within Asia, a more comprehensive analysis requires broad international data collaboration. Similarly, studies of shrikes *Lanius*, pipits *Anthus* and larks Alaudidae make little sense without collaboration between institutions with access to data from much of Asia and the Saharo-Arabian, Eurasian and Afrotropical realms.

Collaboration with institutions in the Oriental realm could allow interesting studies of genera such as *Pericrocotus*, *Eumyias-Niltava-Cyornis*, Cettidae, *Pycnonotus, Chloropsis*. The early phylogenetic branching of the Corvidae needs further attention as the study by Ericson et al. (2005) did not obtain a dense sampling of the basal genera (but the terminal groups of this family are now covered in detail). Some odd species that are still not adequately covered by molecular studies or placed precisely in the global phylogeny comprise fire-capped tit *Cephalopyrus flammiceps* and pink-tailed rosefinch *Urocynchanus pyzlowi*.

Finally, there are some interesting challenges to understand the dispersal of songbirds from the Orient to the New World. Some few groups underwent large phylogenetic expansions there (see notably Fig. 3b and e) but some families are represented there by a single species, mainly in California and Mexico. Because of the enormous expanse of isolating ocean we must assume that these colonization events took place north of the Pacific, as suggested by Chen et al. (2012) for hinge-teeth snakes. We may assume that most dispersal events took place during the mid-Miocene climate optimum. However, for a better understanding, all these cases should be underpinned by time estimates based on molecular phylogenetics data and by niche modeling comparing the climate windows for sister groups (and notably for the most basal species) in Asia and America.

It is important to note that the successful development of collaborative research, which integrates phylogeny and eco-morphological trait data, will require an open policy for collecting and exchange of specimens (notably anatomic material) for global comparative studies.

From regional species pool to local communities

The amount of data that is now available for analyzing the formation of regional species pools open great opportunities for understanding patterns and process also on the local scale. So far, most studies of local avian communities have described a limited assemblage, and often "out of context". Such studies suggest too much contingency to allow the development of general laws. However, with an integrative approach, a well-defined regional species pool, appropriate null models and geographically replicated local studies to determine networks of coexisting species, a synthesis is within reach (Lessard et al., 2012).

There is now a special challenge to study the exceedingly complex patterns of regional and local variation in the avifauna of Indochina and southern China. With field data from large numbers of localities it may be possible to understand the filtering process from regional species pools to formation of contemporary local communities. Figs. 2–3 would suggest phylogenetically overdispersed communities in the Oriental lowlands and mosaics of younger communities in most of China's montane regions, and generally more clustered assemblies towards Manchuria and further north (compare Graham et al., 2009). For a mechanistic understanding of development of local faunas we need to combine the large-scale distributional and phylogenetic data with traits data that describe divergence in functional morphology and diet of individual species. We also need to document their actual coexistence (within study plots), their degree of habitat segregation, and degree of interaction among them. The Paroidea and Certhoidea clades present a special opportunity, since, unlike in the many earlier studies of ecological segregation in these groups, we may now take the phylogenetic structure of local communities into account. Communities of warblers and babblers also provide great opportunities.

Once the evolutionary history of the regional species pool is well understood, data describing the structure of local avian communities can serve to analyze some of the large unresolved questions in community ecology, including the unresolved controversy (Diamond, 1975; Connor and Simberloff, 1979) whether local communi-

ties represent random draws from the regional species pool or is instead controlled by the degree of genomic and phenomic (high-dimensional phenotypic; see Houle et al., 2010) divergence among species.

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鸣禽（鸣禽亚目）的全球多样化及中国-喜马拉雅地区多样性热点的形成

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摘要：鸣禽（鸣禽亚目）鸟类约占世界鸟类种数的一半。过去的十多年里，分子系统发育研究为全面了解鸣禽的全球多样化奠定了良好的基础。通过比较祖裔分支类群代表性鸟种的空间分布，本文以图解法阐述了鸣禽主要分支的全球多样化格局。鸣禽的全球扩散始于现新几内亚所处地域的岛屿辐射，而中国南部的山区则更多地代表了近期多样化的中心。本文建议了进一步了解不同空间尺度上的生物多样性变化影响因素的研究重点。

关键词：鸣禽，鸣禽亚目，全球多样化，生物地理学，中国-喜马拉雅生物多样性热点