Establishing a perimeter position: speciation around the Indian Ocean Basin

G. VOELKER & R. K. OUTLAW
Department of Biology, University of Memphis, Memphis, TN, USA

Introduction

The geological and ecological history of landmasses around the Indian Ocean Basin (IOB) provides evidence with which to test the roles that vicariance and dispersal may have played in the establishment of circum-IOB lineages. Historically, vicariant mechanisms related to the geologically well-documented breakup of Gondwanaland have been invoked to explain present day lineage distributions, several recent studies have instead inferred dispersal across the IOB. This inference is often advanced because lineages under study have species inhabiting IOB islands. Here we examine the roles of continental vicariance vs. trans-IOB dispersal in the distribution of an avian genus found around the perimeter of the IOB. A molecular phylogeny does reveal evidence of a relationship that would require the inference of trans-IOB dispersal between eastern Africa and Sri Lanka. However, molecular clock data, ancestral area analyses and paleoclimatic reconstructions suggest that vicariance related to tropical forest expansion and retraction is more likely to have facilitated African–Asian interchange, with an initial colonization of Africa from Asia quickly followed by a recolonization of Asia. Subsequent dispersal from Asia to Sri Lanka and islands east of the Sunda Shelf are inferred; these latter islands were colonized in a stepping-stone fashion that culminated in colonization of the Sunda Shelf, and a recolonization of mainland Asia. We propose that circum-IOB distributions, which post-date early Gondwanan breakup, are most likely the result of continent-based vicariant events, particularly those events related to large-scale habitat alterations, and not trans-IOB dispersals.

Abstract

Historical biological interactions among peripheral landmasses on the periphery of the Indian Ocean Basin (IOB) are generally poorly understood. While interactions based on early Gondwanan vicariance have been used to explain present day lineage distributions, several recent studies have instead inferred dispersal across the IOB. This inference is often advanced because lineages under study have species inhabiting IOB islands. Here we examine the roles of continental vicariance vs. trans-IOB dispersal in the distribution of an avian genus found around the perimeter of the IOB. A molecular phylogeny does reveal evidence of a relationship that would require the inference of trans-IOB dispersal between eastern Africa and Sri Lanka. However, molecular clock data, ancestral area analyses and paleoclimatic reconstructions suggest that vicariance related to tropical forest expansion and retraction is more likely to have facilitated African–Asian interchange, with an initial colonization of Africa from Asia quickly followed by a recolonization of Asia. Subsequent dispersal from Asia to Sri Lanka and islands east of the Sunda Shelf are inferred; these latter islands were colonized in a stepping-stone fashion that culminated in colonization of the Sunda Shelf, and a recolonization of mainland Asia. We propose that circum-IOB distributions, which post-date early Gondwanan breakup, are most likely the result of continent-based vicariant events, particularly those events related to large-scale habitat alterations, and not trans-IOB dispersals.

Keywords: dispersal; historical ecology; Indian Ocean; thrushes; vicariance.

Correspondence: Gary Voelker, Department of Biology, University of Memphis, 3700 Walker Avenue, Memphis, TN 38152, USA. Tel.: +1 901 678 1386; fax: +1 901 678 4746; e-mail: gvoelker@memphis.edu

mammals (Vrba, 1985, 1993) and plants (Trénel et al., 2007), suggest shifting climatic cycles that post-date Gondwanan breakup drive major ecological changes, and have played a considerable role in driving speciation in vertebrate groups distributed in both Africa and Eurasia.

However, strict vicariance has proven insufficient to explain many present-day IOB distributions. Biogeographic analyses of diverse lineages, from vertebrates to plants, have shown patterns of over-water dispersal within the IOB system (e.g. Vences et al., 2001; Raxworthy et al., 2002; Morley, 2003; Warren et al., 2003, 2005; Yuan et al., 2005; Rocha et al., 2006; Trénel et al., 2007). Increasingly, over-water dispersal has been inferred as a mechanism of colonization and speciation, because molecular clock dates suggest that many lineages diverged too recently to have experienced early Gondwanan rifting, or are not inferred to have dispersed...
during periods ecologically suitable for range expansion. Thus, robust historical biogeographic analyses need to explore the possibility of both scenarios as viable explanations for the observed, often allopatric distributions of lineages around the IOB.

Avian distributions in and around the IOB suggest that dispersal may indeed have played an important role in establishing those distributions; birds fly, making long-distance over-water crossings more plausible than inferring similar sweepstake dispersals for other vertebrate lineages. This is particularly true with respect to highly mobile avian lineages such as seabirds. While songbirds are typically considered less likely to cross large water barriers than are seabirds, numerous songbird lineages have circum-IOB distributions (or nearly so). Although long-distance sweepstake dispersals (Simpson, 1953) across the IOB possibly explain these patterns, an alternative would involve stepping-stone colonizations of land-masses in the IOB. Fuchs et al. (2006) and Jonsson & Fjeldså (2006) have relied on an explicit trans-IOB scenario directly linking avian lineages on the eastern margin of the IOB (southeast Asia and Australia), with avian lineages in Africa. This scenario relies on stepping-stone dispersal across Eocene–Oligocene land bridges, and currently submerged plateaus and seamounts (see also Steenis, 1962), but the scenario is not unique to birds. A similar trans-IOB dispersal pattern connecting southeast Asia and Australia with Madagascar and Africa has been proposed to explain distributions in bees (Fuller et al., 2005), lizards (Rocha et al., 2006) and other lineages (Morley, 2003; Sanmartín & Ronquist, 2004; Trénel et al., 2007).

Elsewhere in the IOB, the Lemurian stepping-stones, which connect India and Sri Lanka to Madagascar via the Seychelles, are considered a likely IOB dispersal channel for animals and plants (Yuan et al., 2005), and there is clear phylogenetic evidence that a variety of lineages have utilized them to some extent (e.g. Raxworthy et al., 2002; Warren et al., 2003, 2005; Rocha et al., 2006).

However, the large number of avian (and other) lineages distributed around the IOB suggests that vicariant events post-dating Gondwanan breakup might better explain many of those distributions. The few phylogeny-based studies that have dealt with this possibility in songbirds (e.g. Voelker, 1999, 2002; Outlaw et al., 2007) have implicated climate change and commensurate habitat alterations as primary vicariant events driving lineage divergence between continents surrounding the IOB. In each case, biogeographic reconstructions and molecular clock data supported continent-based movement in response to major paleocological shifts. Phylogenetic support for the alternative biogeographic scenario of dispersal could have been invoked if species with geographically disjunct IOB distributions (e.g. southern Africa and Southeast Asia) were shown to be sisters. Dispersal could also have been invoked if clock dates indicated that land-based movements occurred when intervening habitats were ecologically unsuitable for the group (i.e. requiring an inference of dispersal over those habitats). Evidence of either dispersal scenario was lacking in those previous studies.

In this paper, we use a molecular phylogeny of a songbird genus in conjunction with ancestral area reconstruction methods and molecular clock and paleoecological data to empirically test vicariance vs. dispersal hypotheses with respect to circum-IOB distributions. Our local genus is currently recognized as a constituent of Zoothera thrushes and has a distributional presence around the margins of the IOB (Fig. 1). Zoothera is a member of the avian family Turdidae, which has a cosmopolitan distribution (Collar, 2005), thereby indicating a tendency for inter-continental movements that is reflected in both inter- and intra-generic biogeographic patterns. Many species within several Turdidae genera (particularly Myadestes and Turdus) have proven very successful in achieving over-water dispersal to islands and across the Atlantic (Collar, 2005; G. Voelker, S. Rohwer, D.C. Outlaw & R.C.K. Bowie, unpublished data), and Zoothera has clearly dispersed to Southeast Asian islands (see below). Therefore, while many songbird lineages are geographically restricted to single continents and as such are unlikely to cross ocean barriers, members of Turdidae appear far more likely to disperse across such barriers.

Furthermore, Zoothera thrushes and their close relatives are too young to have experienced initial Gondwanaland rifting (Klicka et al., 2005; and below), phylogenetic relationships directly linking species in Africa with those in India, Sri Lanka or the islands of Southeast Asia would strongly support trans-IOB dispersal events (e.g. Raxworthy et al., 2002; Fuchs et al., 2006). This is true even if the modern-day absence of Zoothera on major IOB islands is interpreted as an indication that IOB islands were never colonized by this lineage. However, the absence of distributions could be a function of extinction. While we are unaware of fossil evidence of Zoothera species from IOB islands, it is clear that larger songbirds can quickly go extinct after human colonization (Steadman, 2006). Regardless, if Zoothera historically utilized or dispersed over IOB islands such that they established distributions on multiple continents, evidence of this should still be reflected in the phylogeny and dispersal could again be supported. Specifically, this historical utilization would directly link species in Africa with those in India or the islands of Southeast Asia.

Narrow ranges of species divergences, as reflected by very short internode distances, can also be indicative of dispersal events. In such instances, barring repeated long-term migration of genes, colonists (dispersers) to new areas will rapidly differentiate from source populations given their reduced genetic variability (Clegg et al., 2002). Such a pattern would not generally be expected in response to vicariant events, which typically affect
population divergences over longer evolutionary periods, thus resulting in longer internode distances.

Alternatively, the absence of Zoothera species on IOB islands could suggest that continental vicariant events are equally plausible alternatives that might better explain circum-IOB distributions. In this instance, we would expect that phylogenetic relationships would show a pattern of movement between adjacent areas of Africa and Asia indicative of range expansion (biotic dispersion) rather than dispersal between distant areas (e.g. Voelker, 1999, 2002; Outlaw et al., 2007). Using molecular clock data and ancestral area reconstruction methods, we examined the roles that vicariance and dispersal have played in the development of Zoothera distributions around the IOB.

Materials and methods

Taxon sampling and molecular methods

We sampled 40 taxa comprising 29 species of Eurasian and African Zoothera, based on previously published taxonomy (Sibley & Monroe, 1990). These taxa formed two distinct clades (see below), with 18 taxa forming a clade (the sibirica clade) that is distributed around the IOB (Table S1; Collar, 2005). We focus on this clade here. In general, we did not use multiple samples from species, as detecting genetic breaks within species was not the focus of the study. The major exception is citrina, which has a broad distribution, several major allopatric populations and significant morphological diversity across those populations (Collar, 2005). We therefore sampled from major citrina distributions to test for monophyly (Table S1). We extracted whole genomic DNA from each sample using DNeasy (Qiagen, Valencia, CA, USA) based on the manufacturer’s protocols for tissue and blood.

The NADH subunit 2 (ND2) and cytochrome b (cyt b) mitochondrial genes were isolated and amplified using standard PCR protocols. Gene amplification and sequencing were performed using primers designed for other thrushes (Voelker & Spellman, 2004; Outlaw et al., 2007) and the following thermocycling parameters were used: an initial 2-min denaturation at 94 °C followed by 35–40 cycles of: 94 °C for 45 s (denature), 50–54 °C for 45 s
We performed 20-μL cycle-sequencing reactions on purified PCR products using BigDye dye-labelled terminators (ABI, Foster City, California, USA) according to standard protocols. Reactions were purified and target DNA precipitated with isopropanol. Cycle-sequencing reactions were conducted on an ABI3777-automated sequencer using acrylamide gels. Each sample was sequenced for light and heavy strands.

All sequence data (1041 bp ND2 and 998 bp cyt b) were aligned using Sequencher v. 4.5 (Gene Codes, Ann Arbor, MI, USA) and by eye. For toepad samples, no fewer than two separate DNA extractions and sequencing reactions were performed, at intervals of up to several months apart. Repeated toepad extractions yielded identical sequences. Relevant sequences (Table S1) are deposited in GenBank under the following accession numbers: EU874398-EU874429.

**Phylogenetic analysis**

Several initial analyses were conducted on the combined ND2 and cyt b dataset. Zoothera has previously been suggested to be a polyphyletic genus based on limited sampling (Klicka et al., 2005). Therefore, our first analysis determined to which clade each species belonged. We did this by including previously published sequence data (Klicka et al., 2005; Voelker et al., 2007) from most other Turdidae genera in a maximum likelihood (ML) search. **modelfit** 3.04 (Posada & Crandall, 1998) was used to select the most appropriate model of sequence evolution. Hierarchical likelihood ratio tests (LRTs) and the Akaike Information Criterion identified GTR + I + G as the best fit model for our data. **paup*** (Swofford, 2000) was used for all ML searches.

An initial ML search was started from a HKY-85 neighbour-joining topology using **modelfit** parameters. After 5000 rearrangements without a change in likelihood score, parameters were re-estimated on the resulting topology, and a subsequent search was initiated using this topology and the re-estimated parameters. This process was repeated a second time, running 10 000 rearrangements without a change in likelihood score or parameters.

Bayesian inference was implemented using **MrBayes** 3.0 (Huelsenbeck & Ronquist, 2001) to assess nodal support. We used the GTR + I + G model of sequence evolution, and each gene was allowed to vary in parameter estimates. Three Bayesian analyses were initiated from random starting trees, with four MCMC chains running for two million generations and sampled every 100 generations, yielding 20 000 trees. The first 5000 trees from each analysis were discarded to ensure chain stationarity. Remaining trees were combined yielding a total of 45 000 topologies from which a 50% majority rule consensus tree was reconstructed. Nodes having posterior probability values of 95% or greater were deemed significantly supported. We further assessed node support using ML bootstrap analysis in **treefinder** (Jomb, 2005), using the GTR + I + G model with 500 pseudoreplicates.

Subsequent analyses focused on the ‘sibirica’ clade (see below); *sibirica* was identified in the above analyses as the basal (albeit distantly related) member of the focal clade, and it was used as an outgroup. This clade is distributed around the perimeter of the IOB (Fig. 1). In assessing relationships within this clade, we again used the GTR + I + G for ML searches, based on new **modelfit** (Posada & Crandall, 1998) results. All ML and support analyses for this clade followed the protocols described above.

**Molecular clock**

In applying a molecular clock, many avian studies utilize a 2% sequence divergence per million year value, around which most calibrations for cyt b cluster (García-Moreno, 2004; Ho et al., 2005). Despite this, studies (Arbogast & Slowinski, 1998; García-Moreno, 2004) have questioned the validity of this rate even when applied to lineages related to those initially calibrated (songbirds). An additional problem is that most songbird lineages, including *Zoothera*, do not have a deep fossil record to aid in applying temporal calibration points to phylogenies. In the absence of fossils, Barker et al. (2004) applied a calibration date from a geological event to the basal passeriform divergence, with the assumption that one divergent lineage was present on New Zealand during its rift from Antarctica. This method eliminates some of the issues surrounding the application of a DNA-based molecular clock.

We employed this concept, relying on the historical ecology of the equatorial tropical forest of Africa, which reached its maximum eastward extent (to the Kenyan coast) about 3 Mya (Hamilton & Taylor, 1991; Feakins et al., 2005; Sepulchre et al., 2006). Subsequent forest retraction to the west from 3 Mya was rapid, as indicated by the loss of east African equatorial high forest mammalian fauna from the fossil record 2.95–2.52 Mya (Wesselman, 1995). This would suggest that the establishment of east African montane refugia to the south was also rapid. We therefore used 3 My to date the divergence between *gurneyi* and its sister clade (see below), all of which occupy montane areas around the East African Rift system (Collar, 2005). This assumes niche conservatism of species through time. Calibrating this same node using a standard rate applied to songbirds (2% divergence per My; García-Moreno, 2004; Ho et al., 2005) provides a congruent date of 3.2 My.

Divergence times were estimated by incorporating the calibration date into a nonparametric rate-smoothing analysis (Sanderson, 2002) using likelihood branch
lengths estimated from our cyt b dataset. The Langley–Fitch method was applied under a truncated Newton algorithm for this analysis.

Ancestral area reconstruction

For biogeographic analysis, we used both dispersal–vicariance analysis (DIVA; Ronquist, 1997) and weighted ancestral area analysis (WAAA; Hausdorf, 1998). Our focus was to determine the most likely ancestral area(s) for the sibirica clade and to infer movement patterns between major areas. Movements at finer scales are more readily interpreted from distributions mapped on the phylogeny. In both analyses, we coded each species as present or absent in each of four major areas: Asia, India + Sri Lanka (India), Africa and Southeast Asian Islands (Islands). To minimize the number of areas recovered as potentially ancestral, we set the maximum areas allowed at any node to two (the lowest possible setting) in DIVA, and the minimum Probability Index threshold in WAAA to 0.2.

Results

Phylogenetic analyses and taxonomic considerations

Klicka et al. (2005) have suggested that Zoothera comprises up to three distinct lineages. Our results, which incorporated additional species sampling, confirm Zoothera polyphyly, with all species sampled falling into two distinctly related (nonsister) clades (not shown). ML analyses identified 18 species as belonging unambiguously to a derived clade of Afro-Asian ‘Zoothera’, and we focus on this clade here.

Initial ML analyses identified sibirica as the basal extant taxon in the focal clade, with wardii being the next to diverge (not shown). Subsequent analysis with sibirica as an outgroup confirms the position of wardii (Fig. 2). Bayesian analysis indicates posterior probabilities of 1.0 for the position of these taxa relative to the remaining species, and ML bootstrap support is similarly high (Fig. 2).

Results of ML analyses indicate that the next divergence resulted in two distinct clades to which all remaining focal ‘Zoothera’ belong (Fig. 2). The first of these clades (cameronensis–gurneyi) comprises the African spot-winged thrushes, all of which have distributions that include the East African Rift system. Our results confirm a prediction from morphology (Klicka et al., 2005) that crossleyi and oberlaenderi are members of this clade (Fig. 2). The phylogenetic placement of oberlaenderi suggests that it is best recognized as a distinct species; it has previously been recognized as a race of both piaggiae and gurneyi. The ML topology further indicates that crossleyi is not a race of gurneyi, where it has been placed in the past despite substantial plumage differences (Collar, 2005).

The second major clade (guttata–cinerea) is comprised of a plumage-diverse assemblage of species that are distributed around the IOB (Figs 1 and 2). Although nodal support for the placement of guttata and spiloptera is lacking (Fig. 2), all ML analyses placed them at the base of this clade. These species are clearly not part of the African spot-winged thrush clade or of the clade to which they are basal (the cinerea clade); both of these clades are well-supported (Fig. 2).

‘Zoothera’ cinerea diverged early from a common ancestor with other Southeast Asian species (Fig. 2). The cinerea clade is sister to cinerea and comprises at least six species, all of which occur primarily on Southeast Asian Islands (Figs 1 and 2). Although support is lacking for three nodes in this clade, molecular clock dates (and distributions; see below) suggest rapid, and thus difficult to support, divergences.

Our analyses concur with the previous suggestion (Klicka et al., 2005) that Zoothera is polyphyletic, and the type (Zoothera monticola) falls in an assemblage of Austral-Asian species that is not sister to our focal clade (see Klicka et al., 2005; Voelker & Klicka, 2008). Following taxonomic priority for Zoothera (see Mayr & Pyntner, 1964), the next available genus name is Geokichla. The type, by original designation, is Turdus citrinus, which is included in our focal clade (Geokichla cinerea; Müller, 1835, in Mayr & Pyntner, 1964). We therefore recognize Geokichla as the valid taxonomic designation for all members of the sibirica clade, and apply it below.

Biogeography

Both methods of ancestral area reconstruction identify Asia as the most likely area for the origin of Geokichla (Fig. 2, Table S2). Geokichla sibirica and wardii are distributed in Asia and both are inferred to have arisen in the late Miocene (Fig. 2). The sister clade to Geokichla comprises the genera Psophiocichla (monotypic) and Turdus (65 species) (Voelker et al., 2007). While the former is distributed in Africa, the ancestral area for Turdus is clearly Asia, and several purely Eurasian species are the basal members of this genus (Voelker et al., 2007). Therefore Asia would remain the most likely ancestral area for Geokichla in a broader multi-genus analysis.

Despite arising approximately 8.5 Ma, just two speciation events appear to have occurred in Asia over the next 4.5 Ma (Fig. 2). From 4–3.4 Ma, lineage diversification increased, following the colonization of Africa (Figs 1 and 2). Most African species form a single clade, the spot-winged thrushes, and their diversity is centred around the East African Rift system (Collar, 2005). As all have distributions including the Rift system, this is the most likely ancestral area for this clade. Additional sampling of races and isolated populations in the Rift system is necessary to resolve taxonomic
affinities and biogeographic reconstructions of the spot-winged thrushes.

Although *guttata* is distributed in Africa, it is clearly sister to an Asian clade, and not to the African spot-winged thrushes (Fig. 2). Thus, we infer from ancestral area analysis a recolonization of Asia, via India (Figs 1 and 2; Table S2), which accounts for the presence of *spiloptera* on Sri Lanka, and *citrina* throughout much of Southeast Asia. Two movements to Southeast Asian Islands follow. One of these movements can explain the distribution of *citrina aurata* on Borneo, while a second movement would explain the distribution of the *cinerea* clade throughout Southeast Asian Islands (Fig. 2).

Within the *cinerea* clade, most species distributions reflect a high degree of island endemism (or nearly so if small satellite islands are considered; Figs 1 and 2; Table S2), which accounts for the presence of *spiloptera* on Sri Lanka, and *citrina* throughout much of Southeast Asia. Two movements to Southeast Asian Islands follow. One of these movements can explain the distribution of *citrina aenata* on Borneo, while a second movement would explain the distribution of the *cinerea* clade throughout Southeast Asian Islands (Fig. 2).

Discussion

Which process, dispersal or vicariance, explains more of the variance in *Geokichla* distribution? Recalling the ability of Turdidae (and other) lineages to disperse over water barriers, and more specifically the distribution of some *Geokichla* species on oceanic islands (Fig. 2), it is impracticable to *a priori* hypothesize an inability to disperse across the IOB. Indeed, we note that barring any correlation between divergence dates, paleoecology and habitat adaptation, the structure of the phylogeny (Fig. 2, left) would clearly support a dispersal event between southeastern Africa (*guttata*) and Sri Lanka (*spiloptera*).

Despite phylogenetic structure, the most parsimonious explanation for African–Asian interchange in *Geokichla* is
vicariance. The colonization of Africa is dated at 4.1 Mya, and recolonization of Asia occurred almost simultaneously (Fig. 2). From 5–3 Mya, African tropical forests extended to coastal Kenya and through Ethiopia (Hamilton & Taylor, 1991; Feakins et al., 2005; Sepulchre et al., 2006). Divergence dates suggest that ancestral movements between Asia and Africa occurred during this period, when forest connectivity was high. Virtually all Geokichla are (now) forest adapted, making intercontinental movements during periods of forest expansion a likely event. Similar ‘suitable paleoecology’ arguments have, when temporally associated with lineage divergences, been used to explain African–Asian interchange in lizards (Amer & Kumazawa, 2005), and nonforest-adapted birds (Voelker, 1999, 2002) and mammals (Vrba, 1985, 1993).

Following intercontinental movements by Geokichla, African tropical forests began to rapidly retract westward between 3–2.5 Mya (Hamilton & Taylor, 1991; Feakins et al., 2005; Sepulchre et al., 2006). This retraction served as a driving vicariant event that eliminated Asian–African forest connectivity, and montane forest connectivity in Eastern Africa. The resulting retraction greatly impacted small mammal distributions (Wesselman, 1995), and vicariance-driven speciation in forest refugia would explain the major radiation of African thrushes, in which most speciation events occurred after 3.0 Mya. This pattern of lineage diversification via forest fragmentation has been proposed for other thrushes, which, like most African Geokichla, are isolated in montane forest refugia around the African Rift system (Bowie et al., 2005).

Although a vicariant explanation is plausible to explain divergence between Asian and African lineages, the ranges of guttata (southeast coast of Africa), spiloptera (Sri Lanka) and the cinerea clade (southeast Asian islands) require exploring the possibility of dispersal across the IOB. Avian lineages have clearly used the Lemurian stepping-stones to colonize IOB islands from both India and Africa (Warren et al., 2003, 2005), and lineages far less mobile than birds, such as chameleons, have dispersed from Madagascar to India (Raxworthy et al., 2002). The trans-IOB distributions of bees (Fuller et al., 2005), Cryptoblepharus lizards (Rocha et al., 2006) and plants (Morley, 2003; Sanmartín & Ronquist, 2004; Trénéel et al., 2007) have been explained by dispersal, often times with molecular clock support for that conclusion, rather than by land-based vicariant explanations.

Although there is clear evidence that diverse lineages have dispersed across the IOB, there is no evidence to support trans-IOB dispersal by Geokichla from Africa to either southern Asia or Southeast Asian Islands. No Geokichla species are distributed on Madagascar or other potential Africa-to-Asia stepping-stone islands; phylogenetic evidence suggests no relationships that might have required utilization of these islands. Further, evidence is lacking that submerged plateaus and seamount formations formed aerial land-masses (Fuchs et al., 2006; Jønnson & Fjeldså, 2006) at temporal intervals consistent with Geokichla evolution. Finally, the lineage divergence dates inferred in connection with these potential plateau-facilitated dispersals are far older (ca. 45 Mya) than those we consider here (Fuchs et al., 2006; Jønnson & Fjeldså, 2006). We therefore conclude that trans-IOB dispersal by Geokichla is unlikely to have taken place, and that vicariant mechanisms better explain IOB perimeter distributions in Africa and continental Asia.

Dispersal can, however, explain Geokichla distributions on islands located on the IOB perimeter. Geokichla spiloptera, endemic to Sri Lanka, diverged from its sister clade of derived Asian Geokichla in the early Pliocene. During this period, it appears that northern Sri Lanka had subsided below sea level, isolating southern Sri Lanka from India (Jacob, 1949). Dispersal may therefore account for the distribution of spiloptera.

Dispersal is inferred to explain the distributions of Geokichla species on the northern Philippines, Sulawesi, Tanimbar and the Lesser Sunda Islands. These islands are not part of the Sunda Shelf system, which precludes the possibility of historical movements across the exposed shelf during periods of low sea level. Most Southeast Asian Islands have been in their current geographical position for 10 My (Hall, 1998), which, when considered with molecular clock dates, eliminates the possibility of Geokichla distributions resulting from tectonic rifting. The distribution of interpres on Sunda Shelf islands and mainland Asia (Figs 1 and 2), and a race of citrina on Borneo, is likely due to vicariant isolation following movement onto the islands during periods of low sea level. Short-range dispersal is necessary to account for the interpres–dohertyi sister relationship; dohertyi is distributed east of the Sunda Shelf. A similar pattern of dispersal across nonshelf islands, followed by recolonization of the mainland or Sunda Shelf islands, has also been documented in the avian genus Ficedula (Outlaw & Voelker, 2008). The question of why Geokichla skipped over the Sunda Shelf islands early in its biogeographic history remains. Given that Geokichla subsequently and rapidly established distributions on Sunda Shelf islands, extinction of ancestral Sunda Shelf lineages seems unlikely.

The narrow range of divergence dates (ca. 0.75 My) across the cinerea clade suggests rapid island colonizations. The initial divergence of this clade from its sister (citrina) is coincident with the closing of the Indonesian seaway 3–4 Mya (Cane & Molnar, 2001); associated regional climate and habitat changes might explain rapid colonization of islands. These alterations positively impacted the ability of vertebrates to expand from Asia onto Sunda Shelf islands and beyond (Tedford, 1985; Voelker, 1999; Gorog et al., 2004). Divergence dates between members of the cinerea clade also imply rapid speciation, which is expected unless continued dispersal from source areas maintains gene flow (Clegg et al.,
Species relationships within the clade suggest that distributions were achieved by a series of stepping-stone movements, beginning with colonization of the Philippines, and ending with colonization of islands on the eastern perimeter of the IOB (Figs 1 and 2). Relationships and distributions within the *citrina* clade indicate a complex pattern of mainland–Sunda Shelf–nonshelf eastern perimeter of the IOB (Figs 1 and 2). Relationships and distributions were achieved by a series of stepping-stone 2002). Species relationships within the clade suggest that ecological associations. Similar temporal ecological associations, driven by repeated climatic shifts (Hamilton & Kikkawa, 1991; Feakins et al., 2005; Sepulchre et al., 2006), have also proven important to the establishment of inter- and intra-continental distributions in other vertebrate lineages (Vrba, 1985, 1993; Wesselman, 1995; Amer & Kumazawa, 2005).

Such ecological associations allow a general temporal prediction for African–Asian interchange of lineages: forest-adapted species (e.g. sunbirds; R.C.K. Bowie, unpublished data) and thrushes (this study) should colonize during periods of forest expansion (5–3 My), whereas nonforest-adapted species (e.g. pipits, Voelker, 1999; wagtails, Voelker, 2002; rock-thrushes, Outlaw et al., 2007) should colonize during periods of forest retraction. Further, forest-adapted lineages should experience increased cladogenesis during periods of forest retraction, and arid species should do the same during periods of forest expansion. Thus far, these predictions seem to hold for songbird lineages and fossil mammal lineages; analyses of other lineages are clearly necessary to test whether this prediction applies more broadly across other vertebrate lineages. Another potential vicariant signature is evident late in *Geokichla* evolution as well, but is limited to a few movements presumably linked to low sea levels across the Sunda Shelf.

By comparison, dispersal has played a predominant role in establishing distributions at the northern and eastern margin of the IOB, and through the islands of Wallacea. The possibility of derived Asian lineages having stemmed from a single trans-IOB dispersal, or via stepping-stone movements across the IOB for *Geokichla*, seems unlikely. Yet, it is clear from studies of a variety of lineages (Raxworthy et al., 2002; Morley, 2003; Warren et al., 2003, 2005; Sanmartín & Ronquist, 2004; Fuller et al., 2005; Yuan et al., 2005; Rocha et al., 2006; Trénel et al., 2007) that such dispersal events cannot be discounted out of hand. Despite evidence of IOB dispersal patterns, we suggest that, barring extant or fossil taxa on IOB islands or future evidence of seamount exposure that is temporally relevant, vicariant speciation related to continental paleoecological shifts should be considered the null hypothesis for any nonseagoing lineage distributed around the perimeter of the IOB.

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**References**


**Supporting information**

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

**Table S1** Specimens used, sample sources and locality information for species in the *sibirica* clade.

**Table S2** Results of weighted ancestral-area analysis.

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