RESEARCH PAPER

Repeated trans-Atlantic dispersal catalysed a global songbird radiation

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ABSTRACT

Aim *Turdus* thrushes are one of the most speciose and widespread songbird genera, comprising nearly 70 species that combined have a near-global distribution. Herein, we use molecular phylogenetic, molecular clock and behavioural evidence to examine the historical biogeography of the genus. Ancestral area reconstructions in conjunction with divergence estimates and palaeoclimatogical data are used to test whether the long-standing paradigm of Beringian colonization or trans-Atlantic dispersal best explains modern distributions in the New and Old Worlds.

Location Worldwide, with emphasis on New World–Old World biotic interchange.

Methods Using a molecular phylogenetic hypothesis of *Turdus* thrushes, we reconstructed ancestral area relationships utilizing the five major continental or regional areas occupied by species in the genus. We also examined the evolution of behaviours on the phylogeny, and estimated the timing of major lineage divergences via a molecular clock.

Results *Turdus* originated in Eurasia, and following the colonization of Africa underwent a series of five trans-Atlantic sweepstake dispersals. The data reject the alternative hypothesis that connections between Old and New World *Turdus* species can be attributed to movement through Beringia with subsequent extinction. Divergence estimates indicate that these dispersals all occurred near the Miocene–Pliocene boundary, 5 Ma. A significant phylogenetic correlation between migratory and flocking behaviour is evident in the genus.

Main conclusions The initial divergence of *Turdus* in the Old World was followed by a series of trans-Atlantic sweepstake dispersal events. These dispersals are temporally correlated with a specific palaeoclimatic system, which would have facilitated transport of *Turdus* from the Caribbean to the Old World across the Atlantic. Uplift of the Central American Seaway 4.7 Ma effectively shut down the palaeoclimatic system, and no additional trans-Atlantic dispersals are evident in *Turdus* after this time. Migratory movements by ancestral lineages in flocks, rather than as single individuals, suggest an increased likelihood of successfully colonizing new areas, post-dispersal.

Keywords
Behaviour, dispersal, divergence times, palaeoclimates, Pliocene, sweepstake colonization, vicariance.

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INTRODUCTION

Trans-oceanic dispersal theories can accommodate any distribution or presumed set of relationships; this makes such theories resistant to rejection. Therefore dispersal theories have, rightfully, been regarded as unscientific or at least less parsimonious than vicariance-based theories (Rosen, 1978; Nelson & Platnick, 1981). Well-resolved molecular phylogenies of groups distributed on multiple continents have transformed trans-oceanic dispersal events (and dispersal theories generally) from hypotheses of last

resort into testable alternatives to vicariance as the primary engine of lineage divergence (Raxworthy *et al.*, 2002; de Queiroz, 2005). For example, divergence dates and patterns of relationships within lineages often contradict the timing and sequence of plausible vicariant isolating events, leading to rejection of specific vicariant hypotheses (Bermingham *et al.*, 1992; Klicka & Zink, 1997; Voelker, 1999; Heinicke *et al.*, 2007; Pramuk *et al.*, 2008; Trénel *et al.*, 2007). In such cases, dispersal theories remain viable alternatives. Yet biogeographers have been reluctant to explain global distributions on the basis of trans-oceanic movements between continents because of the presumed rarity of successful sweepstake colonizations (colonization by chance events; Simpson, 1953). This presumption is grounded in two central issues. First is the inherent difficulty that individuals face in surmounting sweepstake barriers such as oceans, deserts or mountain ranges (Simpson, 1953), and second is the improbability that enough individuals can disperse across the barrier to ensure successful colonization (Humphries & Parenti, 1999). This 'successful colonization conundrum' is well reflected in songbird (and many other) lineages that post-date the initial break-up of Laurasia and Gondwanaland: thus far, the distributions of all songbird lineages found in both the Old and New World have been explained by trans-Beringian crossings, rather than trans-Atlantic crossings (Mayr, 1946; Voelker, 1999, 2002; Drovetski *et al.*, 2004).

The continued reluctance of biogeographers to explain avian distributions via oceanic dispersal is confounding for the simple reason that birds fly, and there is abundant evidence of birds colonizing remote volcanic islands. In general, few works have sought to identify extrinsic (e.g. palaeoclimates) or intrinsic (e.g. behaviours) factors that might have made at least some avian groups more capable of overcoming the successful colonization conundrum than others. Such factors need not apply only to oceanic dispersals; indeed, they could apply to any biogeographical distribution that included a sweepstakes barrier for the organism(s) under consideration. Yet, biogeographical studies at various geographical scales (e.g. inter- or intra-continental) of many vertebrate groups have tended to discount the possibility that factors other than shared exposure to single, mainly geologically based, vicariant events might have contributed to common distributions. Pattern-based analyses still dominate historical biogeographical studies, while sweepstake colonization events are almost always trumped by land-based movements at most geographical scales.

Here, we used a molecular phylogeny based on 60 of 65 extant species of *Turdus* thrushes (Voelker *et al.*, 2007) to determine how *Turdus* achieved its modern distribution. Because *Turdus* is almost global in its distribution and because just one recently derived North American species exists, we predicted that sweepstake colonizations might be evident in the history of the group. We employed several methods of ancestral area analysis to reconstruct biogeographical history. We further sought to identify palaeoclimatic events and phylogenetically correlated behavioural traits (here, migratory and flocking behaviour) that might have helped *Turdus*, and by extension other lineages, overcome the successful colonization conundrum.

METHODS

Phylogenetic reconstruction

Our analyses were based on a maximum likelihood molecular phylogeny of the songbird genus *Turdus*, detailed descriptions of which have been previously published (Voelker *et al.*, 2007). This analysis included 60 of 65 extant *Turdus* species, in addition to four species from three genera that were shown to fall within *Turdus*.

Biogeographical reconstructions

Both parsimony and maximum-likelihood (ML) methods were used to infer ancestral areas for the genus. We used weighted ancestral area analysis (WAAA; Hausdorf, 1998), dispersal-vicariance analysis (DIVA; Ronquist, 1997) and ML methods in the Ancestral States module in MESQUITE (Maddison & Maddison, 2004) to determine most likely ancestral areas for *Turdus* at each node. Species were coded in WAAA and MESQUITE as present or absent in the five major distributional areas of the genus: Africa, Caribbean, Central America, Eurasia and South America. The sole North American species was coded as Central American given its phylogenetic position in that clade. Species were coded in DIVA, as well as in MESQUITE, as present or absent in the New and Old Worlds.

Molecular clock dating

Divergence dates were estimated by applying a molecular clock rate to likelihood branch lengths (Sanderson, 2002) generated from cytochrome *b* data as estimated on the phylogeny (Voelker *et al.*, 2007). The Langley–Fitch method was applied under a truncated Newton algorithm in this analysis. The assignment of an internal calibration point to this analysis was not based on fossils or a standard molecular clock. As is typical for many songbird lineages, useful fossil calibration points are generally lacking for *Turdus*; the few existing fossils (late Pliocene of Florida) are not identifiable to extant species (Emslie, 1998). A Miocene *Turdus* humerus was recently used as a calibration point by Nylander *et al.* (2008); however, this humerus cannot be attributed to any extant species, having been simply designated as the 'size of *iliacus*' (Jánossy, 1991) with no supporting osteological description or measurements. Given that European *Turdus* fall in to several clades (Voelker *et al.*, 2007) calibrations relying on this Miocene thrush seem tenuous.

In applying a molecular clock, many avian studies have relied on a 2% sequence divergence per million year value around which most calibrations for cytochrome *b* cluster (Garcia-Moreno, 2004; Ho *et al.*, 2005). The most recent of these studies has supported a generalized 2% divergence rate across a wide range of avian taxa (Weir & Schluter, 2008), but the relevant estimates were all derived using external calibration points (e.g. fossils or geological events). Despite this clustering around 2%, studies (Arbogast & Slowinski, 1998; Garcia-Moreno, 2004) have questioned the validity of the rates even when applied to groups related to lineages initially calibrated (songbirds).

To avoid these issues we assigned an internal calibration point following the lead of Barker *et al.* (2004; see also Weir & Schluter, 2008) who relied on a geological event to apply a calibration date to a passeriform divergence under the assumption that relevant lineages had experienced this event. Our calibration point was based on the palaeoecology of the equatorial tropical forest of Africa. This forest reached its maximum eastward extent (to the Kenyan coast) between 5 and 3 Ma, after which it began to retract rapidly to the west (Hamilton & Taylor, 1991; Feakins *et al.*, 2005; Sepulchre *et al.*, 2006). We used 3 Ma to date the divergence between the sister taxa *Turdus helleri* and *Turdus abyssinicus* (Voelker *et al.*, 2007). *Turdus helleri* is isolated in high-altitude forests in the Eastern Arc Mountains of Kenya, while *abyssinicus* occurs in montane areas north-west of *helleri*'s range and throughout lowland forest areas of the rift system south to southern Malawi (Collar, 2005). Both species are sedentary (Lens *et al.*, 2002), thus it is a reasonable assumption that these two species are the result of vicariant fragmentation of the habitat of their common ancestor and are not much younger than 3 Ma. We avoided applying other ages due to the various issues surrounding ancestral diversity of lineages and relative population sizes.

Phylogenetic-behavioural correlations

Migratory and flocking behaviours were coded as present or absent for each species based on natural history accounts (Clement, 2000; Collar, 2005). Species exhibiting altitudinal migration were considered migratory. Each trait was mapped onto the *Turdus* phylogeny using parsimony methods (Maddison & Maddison, 1992) and the Ancestral States Module in MESQUITE (Maddison & Maddison, 2004), which reconstructs ancestral character states of continuous (via parsimony) and multistate characters (via parsimony or ML) at all nodes of a phylogeny. We used the appropriate model of character evolution (symmetrical versus asymmetrical) as determined by likelihood ratio tests (LRT). We also tested whether these behavioural traits were phylogenetically correlated using DISCRETE (Pagel, 1994), and a concentrated changes test as implemented in MACCLADE (Maddison & Maddison, 1992).

RESULTS AND DISCUSSION

For clarity, biogeographical results and discussion are presented first, alternative phylogenetic and extinction-based hypotheses second and phylogenetic–behavioural correlations third.

Intercontinental movements and trans-Atlantic sweepstake dispersals

Overall, ancestral area reconstructions identify a Eurasian ancestral area for *Turdus* (Fig. 1), but these methods varied in their ability to resolve ancestral distributions at other nodes in the phylogeny. When using the five major distributional regions of *Turdus*, WAAA (Hausdorf, 1998) provided clear indications of ancestral areas at relevant nodes, while ML analysis (Pagel, 1994; Maddison & Maddison, 2004) did not. Using only New World or Old World as area categories, DIVA (Ronquist, 1997) resolved ancestral

areas at most nodes to match the more specific five-region results obtained from WAAA analysis. Movement from the Old World to the New World, with subsequent recolonization of the Old World, is obvious, and five dispersals are required by DIVA to account for current distributions. A similar pattern of movement is evident from ML analysis.

Within Eurasia, a Western Palaearctic origin is most likely, as two of the three oldest extant species are distributed there and the sister genus to *Turdus* (*Psophocichla*) is an African endemic (Klicka *et al.*, 2005; Voelker *et al.*, 2007). Our results show that the early lineage diversification of *Turdus* was achieved by six intercontinental movements, the first having been the colonization of Africa from Eurasia (Figs 1 & 2). Molecular clock dating places this colonization at about 6.6 Ma (Fig. 1). The remaining five intercontinental movements were the result of trans-Atlantic sweepstake dispersals that moved *Turdus* ancestors directly between the Old World and landmasses around the Caribbean basin (Figs 1 & 2).

The trans-Atlantic dispersals we have inferred from the *Turdus* phylogeny are notable for three reasons. First, molecular clock dates indicate that the five trans-Atlantic crossings which produced lineages that survive today occurred early and in a narrow temporal window from 5.7–4.7 Ma (Fig. 1). Second, four of these five trans-Atlantic crossings were recolonizations of the Old World from the New World. Third, none of the inferred dispersals between the New and Old Worlds involved trans-Beringian movement, indicating that North America has not been a stepping-stone that contributed to the large *Turdus* radiations of Eurasia and tropical America (see Fig. 1). Other over-water dispersals have occurred throughout the history of *Turdus* but these are restricted to continent-to-island, or island-to-island, movements (Fig. 2). While populations of three Old World *Turdus* species have colonized Iceland or Greenland, there is no evidence of further direct continent-to-continent ocean crossings similar to those concentrated around 5 Ma (Figs 1 & 2).

Dated near the Miocene–Pliocene boundary 5 Ma (Fig. 1), the five trans-Atlantic dispersal events were temporally associated with the closure of the Central American Seaway which began 4.7 Ma (Haug *et al.*, 2001). We found no palaeoclimatic evidence to explain the initial trans-Atlantic dispersal from Africa to the Caribbean basin, although we note that modern Atlantic storm systems are often of such intensity that dust from the Sahara has been recorded in the New World (see Renner, 2004). The inference of colonization of the Caribbean by dispersal from Africa is a novel result for songbirds. Nearly 100% of vertebrate lineages colonizing Caribbean Islands are from New World areas, with North America being the predominant source area for birds (Hedges, 1996).

Molecular clock and palaeoclimate reconstruction dates suggest that the four trans-Atlantic returns to Eurasia and Africa can be explained by a specific palaeoclimatic regime. Prior to closure of the Central American Seaway, storms formed in the eastern Pacific and Caribbean and moved eastward across the Atlantic (Haug *et al.*, 2001; Zachos *et al.*, 2001; Grodsky *et al.*, 2003; Ravelo *et al.*, 2004; Ravelo & Wara, 2004). This storm pattern would have favoured the transport of *Turdus* from the Caribbean basin to the Old World, but it was effectively eliminated from

A = Africa
B = Central America
C = Caribbean
D = South America
E = Eurasia
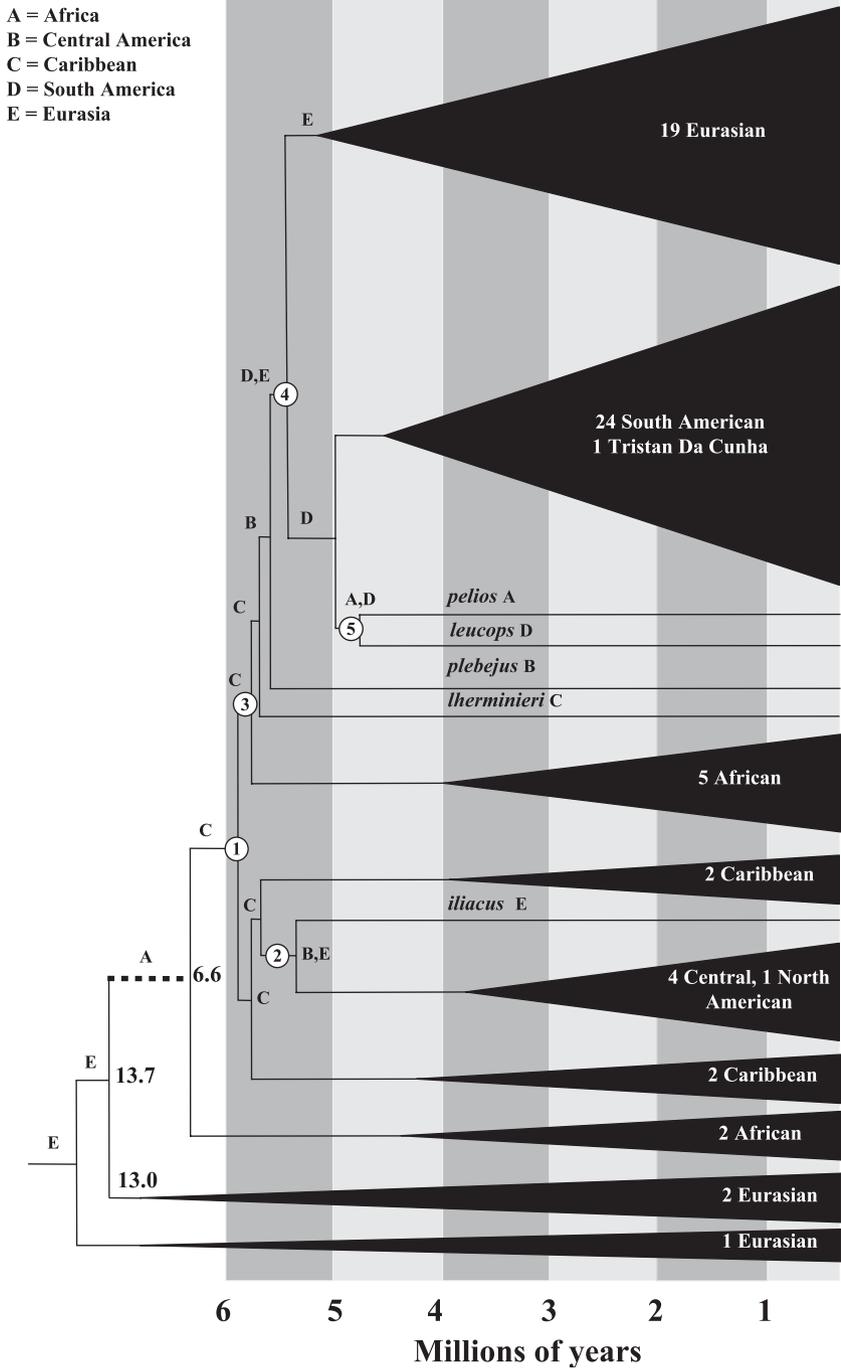
Figure 1 Development of biogeographical patterns in *Turdus* thrushes through time. The tree is a clock enforced maximum-likelihood phylogeny showing the relative timing of lineage divergences. Lineage divergences are based on an assigned calibration date for the *helleri–abyssinicus* divergence of 3 Ma. Geographical distributions are based on the five major distributional areas of the genus. Ancestral area designations for nodes are based on parsimony and maximum-likelihood reconstructions. Numbered nodes indicate nodes where trans-Atlantic dispersals are inferred.

4.7 Ma when the Central American Seaway was closing due to the uplifting of Central America (Haug *et al.*, 2001; Zachos *et al.*, 2001; Grodsky *et al.*, 2003; Ravelo *et al.*, 2004; Ravelo & Wara, 2004). No subsequent trans-Atlantic dispersals or intra-Caribbean lineage diversification occurred in *Turdus* after the closure of the Central American Seaway.

Phylogenetic alternatives

One potential issue with inferring trans-Atlantic dispersals concerns divergences occurring over a relatively short time span; some of these nodes are where dispersals are inferred. Weak support for relationships could indicate fewer dispersals, but this possibility is unlikely. Analysis of *Turdus* systematics (Voelker *et al.*, 2007) included assessments of alternative tree topologies (Shimodaira & Hasegawa, 1999). These assessments rejected the possibility of 'continental' or 'regional' monophyly of Eurasian and Caribbean species in all but one case; in that case (Caribbean clade monophyly; see Fig. 1), the possibility of monophyly was very nearly rejected ($P = 0.056$). This result does not influence our inference of the second trans-Atlantic dispersal.
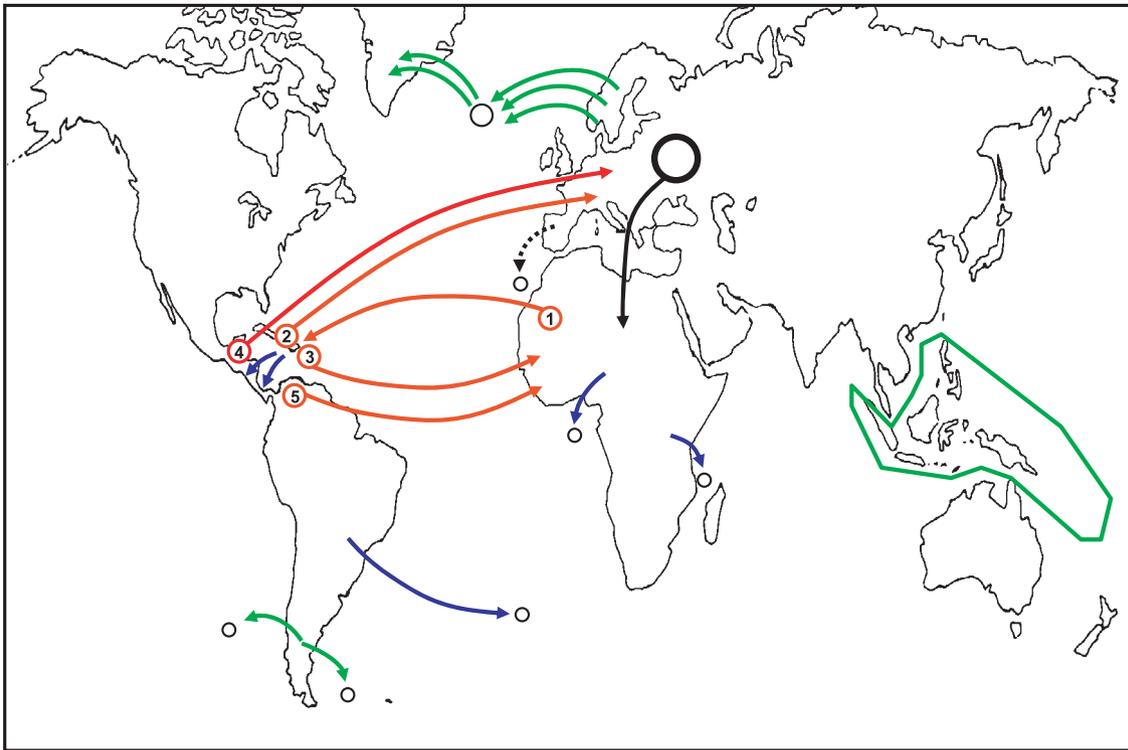
Figure 2 Trans-Atlantic and other over-water dispersals by *Turdus* through time. The black circle indicates the inferred ancestral area of *Turdus*, with the black line indicating the first inferred intercontinental movement. Red arrows indicate trans-Atlantic dispersals near the Miocene–Pliocene boundary, with numbers identifying each dispersal as denoted in Fig. 1. Blue arrows indicate other ancestral over-water dispersal events. Green arrows indicate dispersals by extant taxa, which have broad distributions on the continental land masses from which the arrows emanate, and the solid green line generally delimits the distribution of the island thrush.

Alternative tree topologies reject other placements of African species in the phylogeny (Shimodaira & Hasegawa, 1999; *P* < 0.05), with the exception of placing *pelios* as sister to the African clade of five species (Fig. 1; *P* = 0.59). Forcing all African species to be monophyletic is nearly rejected (*P* = 0.072) as a worse estimate of topology by this very conservative test. Combined, these results would still require three (rather than five) trans-Atlantic sweepstake dispersals to explain distributions (dispersals 1, 2, 4).

This level of uncertainty is not surprising due to long branches and short internodes. The reliability of relationships involving long branches and short internodes is often difficult to assess via node-support measures or alternative topologies. Yet for *Turdus*, accepting alternative relationships of African species requires ignoring the highly supported placement of both *pelios* within the otherwise exclusively South American clade, and of *bewsheri* + *libonyanus* near the base of the phylogeny to the exclusion of other African taxa (Fig. 1; Voelker *et al.*, 2007). Therefore, given the strong support for the placement of African species in the phylogeny, the rejection or near rejection of alternative African species relationships, and that short internodes due to rapid divergence from source populations are expected from sweepstake colonizations (Clegg *et al.*, 2002), our conclusion of five sweepstake dispersals seems reasonable.

Several points are worth making or repeating in the context of phylogenetic structure. First, short internodes are expected if rapid divergence has occurred, and therefore support for those nodes (via bootstrap for example) will be difficult to obtain. Second, mitochondrial genes are the most likely to provide structure at recently diverged nodes (see Zink & Barrowclough, 2008). Coalescent theory clearly argues against a nuclear gene being able to provide support at short internodes, particularly at the relatively recent divergences shown here. Sequencing multiple nuclear genes could possibly provide support (but see Drovetski, 2002), but a large number would need to be sequenced in order to generate the same number of phylogenetically informative sites, and in one striking case 30 nuclear genes provided essentially the same results as a single mitochondrial gene (Jennings & Edwards, 2005). A recent study of *Turdus* relying heavily on nuclear genes (Nylander *et al.*, 2008) supports these points, as that study, like ours (Voelker *et al.*, 2007), failed to achieve strong support values for at least four deep nodes. This would suggest that these deep nodes are in fact a product of rapid speciation, and not simply a case of mtDNA saturation obfuscating relationships. Thus, mitochondrial genes remain a valid choice for phylogenetic analysis of biogeographical patterns (Zink & Barrowclough, 2008). Third, it is apparent that, given the structure of our *Turdus* phylogeny (see also Nylander *et al.*, 2008), the inferred trans-

Atlantic dispersal events remain valid even if the assumption of a molecular clock is rejected.

The ghost of extinction

Biogeographical histories of songbird (and other) lineages distributed in both the Old and New Worlds rely heavily on the inference of interchange via Beringia (Mayr, 1946; Voelker, 1999, 2002; Drovetski *et al.*, 2004). Thus, the lack of evidence that North America served to connect the lineages of *Turdus* in the Old World with those on the land masses surrounding the Caribbean is surprising. Extinction would be the default explanation for North America's absence in *Turdus* distributions, but we think it is generally unlikely to have played a significant role. The first crossing of the Atlantic involved movement of an African ancestor to tropical America. Achieving this distribution without invoking a trans-Atlantic dispersal would have required a recolonization of Eurasia from Africa, followed by colonization of North America via Beringia and then colonization of tropical America. This scenario would require the subsequent extinction of an ancestral lineage both in Eurasia and in North America. Following this initial dispersal from Africa to the New World, four dispersals returned *Turdus* lineages to the Old World from tropical America. Had these distributions instead been accomplished via movement through Beringia, four independent range expansions through North America, followed by colonizations of Asia via Beringia, would have been required. Subsequent extinctions on each continental stepping stone would be required to explain these movements. Further, one of these returns to the Old World (Fig. 2, dispersal 5) requires an additional step from Asia to Africa and an additional extinction in Asia. These simplest-case scenarios assume a minimum number of extinctions; persistence of ancestral lineages in North America or Asia for any length of time would suggest time for speciation, thus increasing the overall number of extinctions that would need to be invoked. Given that several *Turdus* clades are very speciose (Fig. 1), with species occupying diverse habitats, it is probable that intra-North American speciation would have occurred.

A related consideration involves the long-term persistence in central and eastern Eurasia of species in the large Eurasian clade (Fig. 1; Voelker *et al.*, 2007). Cladogenesis in Eurasia has been generally consistent through time, to include speciation during the Pleistocene (not shown). Therefore, this clade persisted despite repeated near-continent-wide climatic perturbations that altered or shifted habitats (Donghuai *et al.*, 1998; Zhisheng *et al.*, 2001; Guo *et al.*, 2002). This makes it difficult to support rampant extinction in North America, where most habitats persisted through similar climatic perturbations (Webb, 1987; Holliday, 1989, and references therein). Indeed other avian songbird genera of a similar age and with multiple-continent distributions similar to *Turdus* do have lineages that survived North American glacial cycles (e.g. Voelker, 1999, 2002). The lack of North American colonization from the Central American–Caribbean clade is also relevant here, in that many regions of southern North America were not substantially affected by glacial cycles. This indicates that colonization and speciation should have been possible for millions

of years, at least in the southern United States. Yet, excepting the very recently derived but distributionally ubiquitous *migratorius*, North American colonization is simply not evident in *Turdus*.

To test the above arguments that extinction is difficult to support, we developed two step matrices in which dispersal and extinction were alternately down-weighted. In the first matrix, extinction was down-weighted four-fold relative to dispersal by forcing a gain of an area to be four times more likely than a loss of an area, while the second matrix down-weights dispersal four-fold by making an area loss four times more likely than a gain. These step-matrices were alternately employed in parsimony-based ancestral character state reconstruction analyses of New World and Old World *Turdus* species distributions using the Ancestral Character States module in MESQUITE (Maddison & Maddison, 2004). When either extinction (a loss of an area) or dispersal (a gain of an area) is down-weighted with respect to the other, seven (rather than five as in other methods) dispersal events are required to explain *Turdus* distributions. Given that this analysis used an over-simplified view of distribution pattern (New versus Old World) our assumptions regarding five sweepstakes dispersals seem conservative.

In sum, the Beringian connection hypothesis requires a minimum of seven continental extinctions to account for the phylogenetic relationships between Old World and New World *Turdus* lineages. Given the success of *Turdus* lineages elsewhere, it is unlikely that some lineage(s) would not have survived in the diverse North American habitats that persisted through glacial periods. Trans-Atlantic dispersals seem far more parsimonious than repeated extinction of lineages across Eurasia and North America, particularly when considered in the context of phylogeny and palaeoclimates.

The role of behaviours in sweepstake dispersal

Vicariance biogeographers have reasonably argued that sweepstake dispersals rarely lead to successful colonizations because they usually involve single, or just a few, individuals (Nelson & Platnick, 1981; Humphries & Parenti, 1999). The most likely post-dispersal fate of these individuals is death without reproduction. We explored this successful colonization conundrum in *Turdus* by examining the association of migratory and flocking behaviour on the *Turdus* phylogeny (Appendix S1 in Supporting Information). Both ML and parsimony-based analyses indicate a significant correlation between the two behaviours in *Turdus* (likelihood ratio test, $P < 0.001$; concentrated changes test, $P = 0.018$). Likelihood results reflect tests of trait dependence versus independence across all species, whereas parsimony results reflect initial gains and losses of traits that preclude large trait-heavy clades from biasing results (e.g. the large Eurasian clade; Figure S1 in Supporting Information). That both analyses are statistically significant suggests that throughout the evolutionary history of *Turdus* there has been a proclivity for movements by flocks, making successful colonizations following sweepstake dispersal more likely. Recent evidence suggests this could still happen in *Turdus* (and probably other lineages): fieldfares (*Turdus pilaris*), which breed almost exclusively in western Eurasia, colonized

Greenland in a flock early in the last century (Salomonsen, 1950). Palaeoclimatic storm patterns, however, are the key factor that allowed the behavioural correlation to be repeatedly relevant to sweepstake dispersals at the Miocene–Pliocene boundary.

These behavioural–palaeoclimate relationships are broadly significant to studies of sweepstake dispersals. Many lineage-specific studies clearly document, via divergence dates, that dispersal is a plausible mechanism to explain distributions (Raxworthy *et al.*, 2002; Filardi & Moyle, 2005; Heinicke *et al.*, 2007). However, most do not simultaneously attempt to explain how lineages might have overcome the successful colonization conundrum. Instead, we are generally left to assume fortuitous events as explanations; the ability to easily invoke such dispersal events is what has led in part to the ascendance of the alternative paradigm of vicariance. A similar point can be made for vicariance-based explanations that use single events to explain multilineage patterns, even when those lineages include diverse vertebrate (or other) taxa with very different behaviours and life histories (e.g. Riddle *et al.*, 2000). The search for pattern still dominates biogeographical inquiry, yet underlying processes can enhance our knowledge of distributional patterns and potentially provide a more realistic view of evolutionary history.

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REFERENCES

Arbogast, B.S. & Slowinski, J.B. (1998) Pleistocene speciation and the mitochondrial DNA clock. *Science*, **282**, 1955a.

Barker, F.K., Cibois, A., Schikler, P., Feinstein, J. & Cracraft, J. (2004) Phylogeny and diversification of the largest avian radiation. *Proceedings of the National Academy of Sciences USA*, **101**, 11040–11045.

Bermingham, E., Rohwer, S., Freeman, S. & Wood, C. (1992) Vicariance biogeography in the Pleistocene and speciation in North American wood warblers: a test of Mengel's model. *Proceedings of the National Academy of Sciences USA*, **89**, 6624–6628.

Clegg, S.M., Degnan, S.M., Kikkawa, J., Moritz, C, Estoup, A. & Owens, I.P.F. (2002) Genetic consequences of sequential founder events by an island-colonizing bird. *Proceedings of the National Academy of Sciences USA*, **99**, 8127–8132.

Clement, P. (2000) *Thrushes*. Princeton University Press, Princeton, NJ.

Collar, N.J. (2005) Family Turdidae (Thrushes). *Handbook of birds of the world,* Vol. 10 (ed. by J. del Hoyo, A. Elliott and D.A. Christie), pp. 514–807. Lynx Edicions, Barcelona.

Donghuai, S., Zhisheng, A., Shaw, J., Bloemendal, J. & Youbin, S. (1998) Magnetostratigraphy and palaeoclimatic significance of Late Tertiary aeolian sequences in the Chinese Loess Plateau. *Geophysical Journal International*, **34**, 207–212.

Drovetski, S. (2002) Molecular phylogeny of grouse: individual and combined performance of w-linked, autosomal, and mitochondrial loci. *Systematics Biology*, **51**, 930–945.

Drovetski, S.V., Zink, R.M., Rohwer, S., Fadeev, I.V., Nesterov, E.V., Karagodin, I, Koblik, E.A. & Red'kin, Y.A. (2004) Complex biogeographic history of a Holarctic passerine. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 545–551.

Emslie, S.D. (1998) Avian community, climate, and sea-level changes in the Plio-Pleistocene of the Florida Peninsula. *Ornithological Monographs,* no. 50. American Ornithologists' Union, Washington, DC.

Feakins, S.J., deMenocal, P.B. & Eglinton, T.I. (2005) Biomarker records of late Neogene changes in northeast African vegetation. *Geology*, **33**, 977–980.

Filardi, C.E. & Moyle, R.G. (2005) Single origin of a pan-Pacific bird group and upstream colonization of Australasia. *Nature*, **438**, 216–219.

Garcia-Moreno, J. (2004) Is there a universal mtDNA clock for birds? *Journal of Avian Biology*, **35**, 465–468.

Grodsky, S.A., Carton, J.A. & Nigam, S. (2003) Near surface westerly wind jet in the Atlantic ITCZ. *Geophysical Research Letters*, **30**, doi:10.1029/2003GL017867.

Guo, Z.T., Ruddiman, W.F., Hao, Q.Z., Wu, H.B., Qiao, Y.S., Zhu, R.X., Peng, S.Z., Wei, J.J., Yuan, B.Y. & Liu, T.S. (2002) Onset of Asian desertification by 22 Myr ago inferred from loess deposits in China. *Nature*, **416**, 159–163.

Hamilton, A.C., & Taylor, D. (1991) History of climate and forests in tropical Africa during the last 8 million years. *Climatic Change*, **19**, 65–78.

Haug, G.H., Tiedemann, R., Zahn, R. & Ravelo, A.C. (2001) Role of Panama uplift on oceanic freshwater balance. *Geology*, **29**, 207–210.

Hausdorf, B. (1998) Weighted ancestral area analysis and a solution of the redundant distribution problem. *Systematics Biology*, **47**, 445–456.

Hedges, S.B. (1996) Historical biogeography of West Indian verte-brates. *Annual Review of Ecology and Systematics*, **27**, 163–196.

Heinicke, M.P, Duellman, W.E. & Hedges, S.B. (2007) Major Caribbean and Central American frog faunas originated by ancient oceanic dispersal. *Proceedings of the National Academy of Sciences USA*, **104**, 10092–10097.

Ho, S.Y.W., Phillips, M.J., Cooper, A. & Drummond, A.J. (2005) Time dependency of molecular rate estimates and systematic overestimation of recent divergence times. *Molecular Biology and Evolution*, **22**, 1561–1568.

Holliday, V.T. (1989) Middle Holocene drought on the southern high plains. *Quaternary Research*, **31**, 74–82.

Humphries, C.J. & Parenti, L.R. (1999) *Cladistic biogeography*, 2nd edn. Oxford University Press, Oxford.

Jánossy, D. (1991) Late Miocene bird remains from Polgárdi (W-Hungary). *Aquila*, **98**, 13–35.

Jennings, W.B. & Edwards, S.V. (2005) Speciational history of Australian grass finches (*Poephila*) inferred from thirty gene trees. *Evolution*, **59**, 2033–2047.

Klicka, J, & Zink, R.M. (1997) The importance of recent ice ages in speciation: a failed paradigm. *Science*, **277**, 1666–1669.

Klicka, J., Voelker, G. & Spellman, G.M. (2005) A molecular systematic revision of the true thrushes (Turdinae). *Molecular Phylogenetics and Evolution*, **34**, 486–500.

Lens, L., Van Dongen, S., Norris, K., Githiru, M. & Matthysen, E. (2002) Avian persistence in fragmented rainforest. *Science*, **298**, 1236–1238.

Maddison, W.P. & Maddison, D.R. (2004) *MESQUITE*, version 1.05. Available from the authors (http://www.mesquiteproject.org/mesquite/mesquite.html).

Maddison, W.P. & Maddison, D.R. (1992) *MACCLADE*, version 3. Sinauer Associates, Sunderland, MA.

Mayr, E. (1946) History of the North American bird fauna. *Wilson Bulletin*, **58**, 1–68.

Nelson, G. & Platnick, N. (1981) *Systematics and biogeography: cladistics and vicariance*. Columbia University Press, New York.

Nylander, J.A.A., Olsson, U., Alström, P. & Sanmartín, I. (2008) Accounting for phylogenetic uncertainty in biogeography: a Bayesian approach to dispersal-vicariance analysis of the thrushes (Aves: *Turdus*). *Systematic Biology*, **57**, 257–268.

Pagel, M. (1994) Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society B: Biological Sciences*, **255**, 37–45.

Pramuk, J.B., Robertson, T., Sites, J.W. Jr. & Noonan, B.P. (2008) Around the world in 10 million years: biogeography of the nearly cosmopolitan true toads (Anura: Bufonidae). *Global Ecology and Biogeography*, **17**, 72–83.

de Queiroz, A. (2005) The resurrection of oceanic dispersal in historical biogeography. *Trends in Ecology and Evolution*, **20**, 68–73.

Ravelo, A.C. & Wara, M.W. (2004) The role of the tropical oceans on global climate during a warm period and major climate transition. *Oceanography*, **17**, 32–41.

Ravelo, A.C., Andreasen, D.H., Lyle, M., Lyle, A.O. & Wara, M.W. (2004) Regional climate shifts caused by gradual global cooling in the Pliocene epoch. *Nature*, **429**, 263–267.

Raxworthy, C.R., Forstner, M.R.J. & Nussbaum, R.A. (2002) Chameleon radiation by oceanic dispersal. *Nature*, **415**, 784–787.

Renner, S. (2004) Plant dispersal across the tropical Atlantic by wind and sea currents. *International Journal of Plant Sciences*, **165** (Suppl.), S23–S33.

Riddle, B.R., Hafner, D.J., Alexander, L.F. & Jaeger, J.R. (2000) Cryptic vicariance in the historical assembly of a Baja California peninsular desert biota. *Proceedings of the National Academy of Sciences USA*, **97**, 14438–14443.

Ronquist, F. (1997) Dispersal-vicariance analysis: a new approach to the quantification of historical biogeography. *Systematic Biology*, **46**, 195–203.

Rosen, D.E. (1978) Vicariant patterns and historical explanation in biogeography. *Systematic Zoology*, **27**, 159–188.

Salomonsen, F. (1950) The immigration and breeding of the fieldfare (*Turdus pilaris* L.) in Greenland. *Proceedings of the International Ornithological Congress*, **10**, 515–526.

Sanderson, M.J. (2002) Estimating absolute rates of molecular evolution and divergence times: a penalized likelihood approach. *Molecular Biology and Evolution*, **19**, 101–109.

Sepulchre, P., Ramstein, G., Fluteau, F., Schuster, M., Tiercelin, J.-J. & Brunet, M. (2006) Tectonic uplift and eastern African aridification. *Science*, **313**, 1419–1423.

Shimodaira, H. & Hasegawa, M. (1999) Multiple comparisons of log-likelihoods with applications to phylogenetic inference. *Molecular Biology and Evolution*, **16**, 1114–1116.

Simpson, G.G. (1953) *The major features of evolution*. University of Colombia Press, New York.

Trénel, P., Gustafsson, M.H.G., Baker, W.J., Asmussen-Lange, C.B., Dransfield, J. & Borchsenius, F. (2007) Mid-Tertiary dispersal, not Gondwanan vicariance explains distribution patterns in the wax palm subfamily (Ceroxyloideae: Arecaceae). *Molecular Phylogenetics and Evolution*, **45**, 272–288.

Voelker, G. (1999) Dispersal, vicariance and clocks: historical biogeography and speciation in a cosmopolitan passerine genus (*Anthus*: Motacillidae). *Evolution*, **53**, 1536–1552.

Voelker, G. (2002) Molecular phylogenetics and the historical biogeography of dippers (*Cinclus*). *Ibis*, **104**, 577–584.

Voelker, G., Rohwer, S., Bowie, R.C.K. & Outlaw, D.C. (2007) Molecular systematics of a speciose, cosmopolitan songbird genus: defining the limits of, and relationships among, the *Turdus* thrushes. *Molecular Phylogenetics and Evolution*, **42**, 422–434.

Webb, T., III (1987) The appearance and disappearance of major vegetational assemblages: long-term vegetational dynamics in eastern North America. *Vegetatio*, **69**, 177–187.

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

Zachos, J., Pagani, M., Sloan, L., Thomas, E. & Billups, K. (2001) Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science*, **292**, 686–693.

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. & Barrowclough, G.F. (2008) Mitochondrial DNA under siege in avian phylogeography. *Molecular Ecology*, **17**, 2107–2121.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Reconstruction of migratory and flocking behaviours on a maximum likelihood phylogeny of *Turdus* thrushes.

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