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Deep and wide valleys drive nested phylogeographic patterns across a montane bird community

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Montane species distributions interrupted by valleys can lead to range fragmentation, differentiation and ultimately speciation. Paleoclimatic fluctuations may accentuate or reduce such diversification by temporally altering the extent of montane habitat and may affect species differently. We examined how an entire montane bird community of the Western Ghats—a linear, coastal tropical mountain range—responds to topographic valleys that host different habitats. Using genetic data from 23 species (356 individuals) collected across nine locations, we examined if different species in the community reveal spatial concordance in population differentiation, and whether the timing of these divergences correlate with climatic events. Our results reveal a nested effect of valleys, with several species (10 of 23) demonstrating the oldest divergences associated with the widest and deepest valley in the mountain range, the Palghat Gap. Further, a subset of these 10 species revealed younger divergences across shallower, narrower valleys. We recovered discordant divergence times for all valley-affected montane birds, mostly in the Pleistocene, supporting the Pliestocene-pump hypotheses and highlighting the role of climatic fluctuations during this period in driving species evolution. A majority of species remain unaffected by valleys, perhaps owing to geneflow or extinction–recolonization dynamics. Studying almost the entire community allowed us to uncover a range of species' responses, including some generalizable and other unpredicted patterns.

1. Introduction

Montane habitats harbour high biodiversity and serve as excellent laboratories to study evolution and diversification [1]. Montane or sky island systems are characterized by specific environmental conditions, limiting species that occur there. Topographic dips in mountain ranges, which lead to valleys of unsuitable habitat and micro-climate, cause discontinuities in species' distributions, thereby affecting their genetic structure and evolutionary trajectories [2]. Understanding evolution and diversification in montane habitats is particularly important as these habitats are disproportionately threatened by climate change [3] and anthropogenic deforestation [4].

Biogeographic barriers, like the Makassar Strait of Wallace's line, or the Isthmuses of Tehuantepec and Panama (which separate South and North America), correlate with genetic divergences across several species inhabiting these regions (reviewed in [5]). Identifying biogeographic barriers that are consistent across taxa elucidates the geographic drivers of species' distribution and biodiversity, and helps to delineate areas of endemism [6].

Topographic dips in mountain ranges function as biogeographic barriers for montane taxa, with some affecting species concordantly (e.g. Africa [7] and Americas [8]), while others create discordant divergences (e.g. Africa [9]). But mountain valleys can act as bridges or barriers, depending on the climatic conditions. Climatic fluctuations can change montane habitat distributions [10,11], enhancing the effects of biogeographic barriers [12]. Empirical evidence for the effects of climatic fluctuations comes from several montane regions where phylogenetic

divergence correlates with the Pliocene in African forest robins [13] and in a Western Ghat sky island insectivore [14], Pleistocene in Australasian sky island species [15] and older Miocene events for South American Tanagers [16]. However, species may respond differentially to topography and climate. Comparative phylogeographic analyses have thus far been conducted on subsets of bird communities; studies from the Americas [17–19], Africa [12,20,21], Australia [22] and southeast Asia [2] exhibit varied patterns among the species sampled. Such studies include species pairs that are often picked to make specific, often extreme, comparisons like wet/humid species versus dry [17,23]. Joseph *et al.* [24] found higher genetic divergences among rainforest species than in co-distributed generalist species. While comparing extremely ecologically divergent species pairs is interesting, it is possible that examining phylogeographic patterns in an entire montane bird community might reveal more generalizable insights and reveal a gradient of genetic effects.

The Indian subcontinent hosts the highest global oscine (songbird) diversity [25] and includes the biodiverse Western Ghats. The sky islands of the Western Ghats host Tropical Montane Cloud Forests [26], or *Sholas* as they are known locally, spread across a 700 km range (figure 1) with 17 endemic bird species. Unlike the Andes, where recent topographic changes led to diversification of montane species (for example flycatchers [27] and hummingbirds [28]), the Western Ghats' topography is relatively older (ca 50 Myr, arising owing to a series of uplifts during the Indian plate movement between 160 and 50 Ma [29]), and perhaps existed when songbirds (or oscines) arrived in India (ca 34 Ma) [25].

We investigate comparative phylogeographic patterns in an almost entire community of songbirds in the montane *Shola* habitat across the sky islands of Western Ghats, India. We attempted to capture as many species as possible (with mist-nets) from the community in order to recover a differential impact of generalists and specialists in the community. Although all species examined here are found in these montane habitats, some species occur all the way to the lowest elevations (coastal, sea level), with no (or less) allopatry, and we expect such species to exhibit less genetic divergence than purely montane species. This would result in varied species responses in the community. Specifically, we use genetic data from 22 of 25 oscine birds and one non-passerine in the Shola community from across the Western Ghats to ask: (i) if there is spatial concordance of genetic differentiation across valleys in the Western Ghats between species, and (ii) when genetic divergence across these valleys took place and if there is temporal concordance across the bird community. Together, answering these questions will allow us to investigate the dominant biogeographic paradigm for this region, specifically exploring vicariant events resulting in temporal concordance across species.

2. Material and methods

Field sampling was conducted at nine locations across the Western Ghats sky islands, hereafter Shola Sky Islands. We planned our sampling such that we had samples from at least four major island groups (A, B, C and D; figure 1) divided by the three deepest valleys in this region: Chaliyar River valley between A (Wayanad and northern hills) and B (Nilgiri mountains), Palghat Gap between B and C (Anamalai–Palani–Highwavies Hills) and Shenkottah Gap between C and D (Agasthyamalai).

We defined the montane bird community of the Western Ghats as species occurring above 1400 m.a.s.l. assessed from our 5-year ringing data and further supported by independent auditory and visual point-count data from other studies (electronic supplementary material, S1). We sampled 22 oscine species (including two species complexes with two species each) and one columbiform (Wood Pigeon) comprising 30 races in all, with 11 endemic species from both forests and grasslands. We were unable to sample two canopy species, *Nectarina minima* and *Dicaeum concolor*. Eight species were exclusively found in the high elevations (more than 1000 m) where the highest mountains range between 1700 and 2600 m (figure 1). Our data consist of sequences from two nuclear (fifth intron of nuclear b-fibrinogen (FIB) and the third intron of the muscle-specific kinase gene (MUSK)) and two mitochondrial (Cytochrome-b (Cyt-b) and NADH dehydrogenase 3 (ND3)) genes from blood samples of 356 individuals belonging to 23 species. Field and laboratory methods are detailed in electronic supplementary material, S2.

(a) Phylogenetic methods

We built maximum-likelihood and Bayesian phylogenetic trees (details in electronic supplementary material, S2). We considered that a phylogeographic break was recovered for a species if we observed reciprocal monophyly (within the species across the four sampling localities). Final Bayesian trees with posterior support and maximum-likelihood bootstrap values at the nodes of divergence are presented in electronic supplementary material, S3. We also assessed divergence dates using Bayesian methods (electronic supplementary material, S2). The time to most recent common ancestor (TMRCA) of the internal node in the phylogenetic tree was considered as the divergence time corresponding to the biogeographic barrier (figure 1).

(b) Temporal concordance in divergences

We explicitly tested for simultaneous divergence in the 10 taxa using MTML-msBayes, a hierarchical approximate Bayesian computation method that permits across-species demographic variation, inter-gene variability in coalescent times and DNA mutation rate heterogeneity [30]. This implementation allows us to estimate the hyper-parameter PSI: the number of different divergent times across the 10 species pairs in our study. PSI was allowed to vary from 1 (concordant divergence) to 10 (incongruent divergence). Several iterations of divergence time (τ) prior were examined to explore the parameter space adequately (details in electronic supplementary material, S2). As MsBayes is considered to show a bias towards inferring a concordant divergence largely owing to broad uninformative prior distributions used [31], we also analysed the data with DPP-msBayes [32], which allows for more flexible priors and uses a non-parametric approach—Drichlet-process priors on divergence models [32].

3. Results

(a) Where do spatially concordant divergences occur in montane birds of the Western Ghats?

Ten of the 23 species examined showed genetic divergences (see the phylogenetic trees in electronic supplementary material, S3, and summary table in electronic supplementary material, S2) that were spatially concordant with valleys, while a majority [13] showed no such effects across the distribution examined. While the distributions of four of these species extend to lower elevations, potentially enabling gene-flow, the exceptions included the small, high-elevation
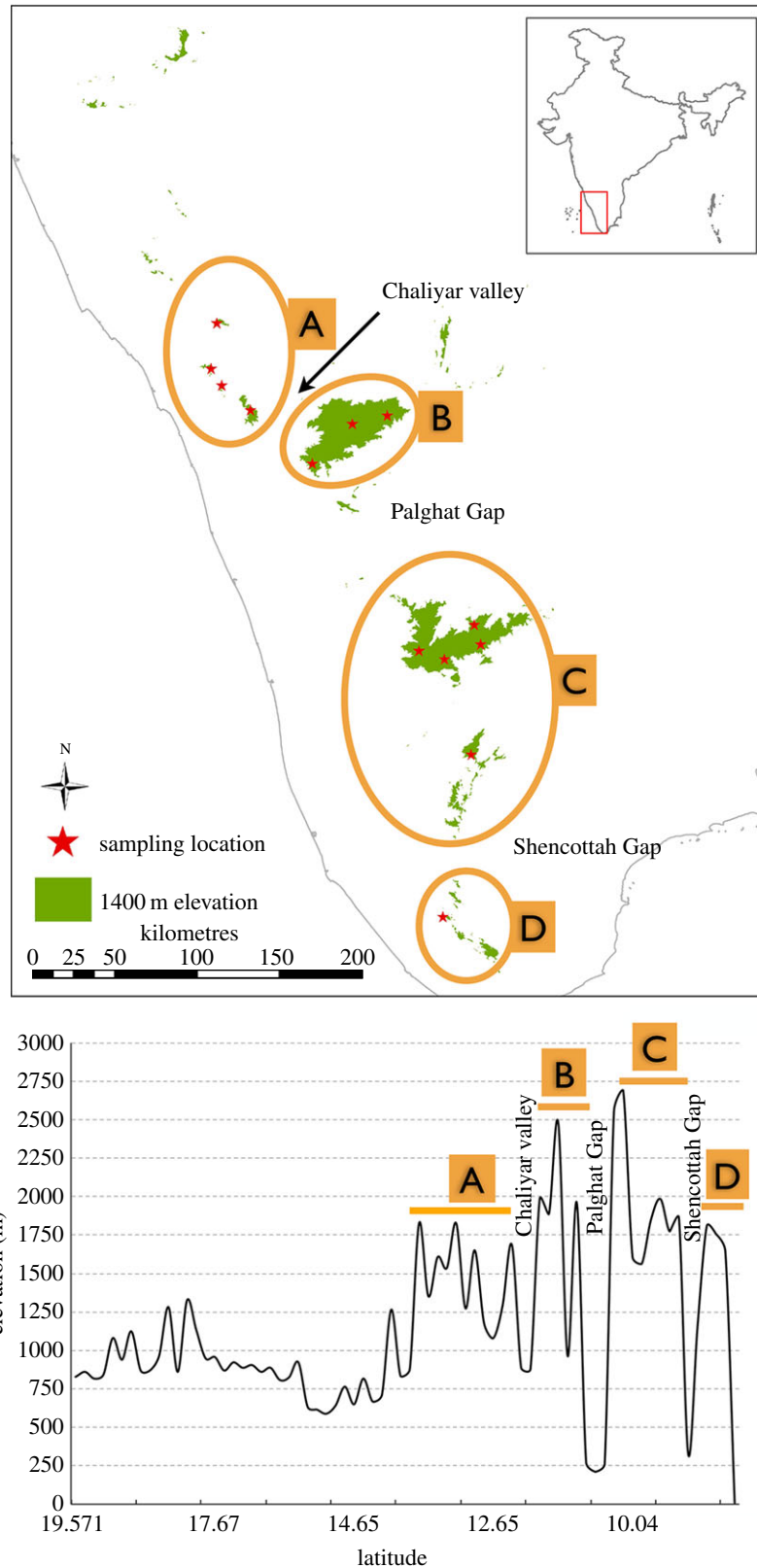
Figure 1. Western Ghat sky islands: (*a*) sampling locations, (*b*) elevation profile (adapted from [14]). (Online version in colour.)

restricted endemic flycatcher *Ficedula nigrorufa* and other high-elevation birds like the *Hypsipetes*, *Columba* and *Zoothera dauma*, which showed no genetic divergence (figure 2). We recovered phylogenetic divergence that correlated with the Palghat Gap in 10 species, of which half were high-elevation (more than 1000 m) restricted while others are thought to be elevationally widespread in the Western Ghats (figure 2). The laughing thrush *Strophocincla* spp. complex was affected by all three

valleys examined, while *Myiomela* spp. and *Zosterops palpebrosus* were affected only by Palghat Gap and Shenkottah Gap. Although the *Zosterops* distribution extends well below the valleys, we recovered unexpected phylogenetic divergence in the montane populations. We found the grassland endemic, Nilgiri Pipit *Anthus nilghiriensis*, to be genetically distinct across the only two highest mountain-tops that it occurs in, the Nilgiris and the Anamalai–Palni Hills (regions B and C in figure 1).
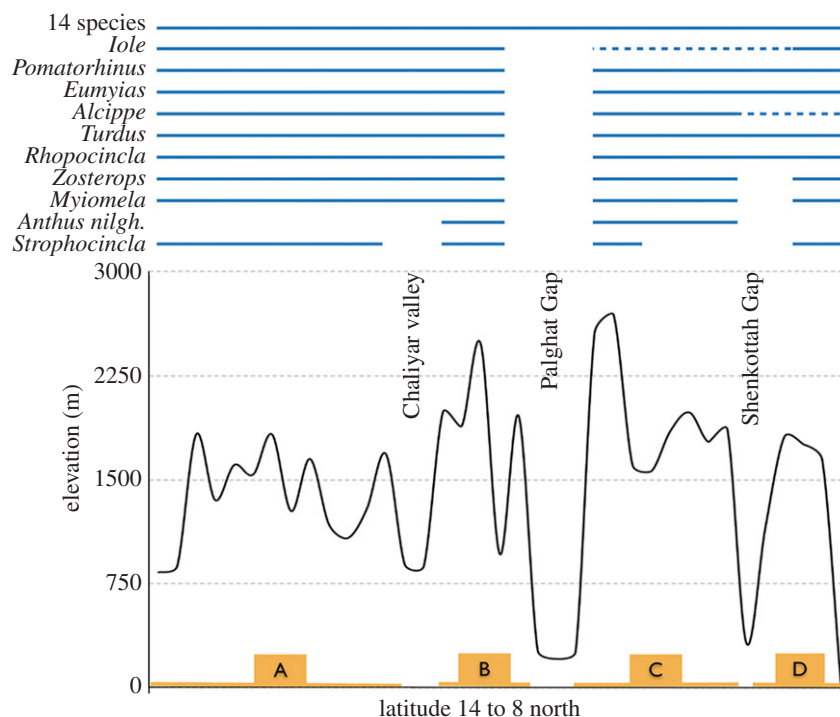
Figure 2. Phylogenetic effect of valleys on montane bird community in the Western Ghats. Bottom half indicates the elevational profile of the sampled region and the upper half represents the phylogenetic data for each species. The break in the horizontal lines (blue online) in the upper half indicates phylogenetic division (inferred from phylogenetic trees; electronic supplementary material, S3); dashed lines (blue online): no data. Note that *Anthus* sp. distribution extends only to mountains B and C. (Online version in colour.)

(b) Is there temporal concordance among phylogenetic divergences in the Shola Sky Islands?

For almost all species, the oldest divergence was across the Palghat Gap. The oldest divergences were for two species complexes, *Strophocincla* and *Myiomela*, with a mean TMRCA of 6.78 (95% highest posterior density (hpd): 5.04–8.66) and 4.84 (95% hpd: 3.8–6.06) Ma, respectively. Of the other eight species that showed genetic differentiation, the mean divergence time for five species were between 2.5 and 1 Ma, while for all other species, the mean TMRCA was less than a million years (figure 3). The populations of the other 13 species that did not show any genetic divergence were also very young, with mean TMRCA less than a million years (electronic supplementary material, S4). Our examination of temporal concordance revealed that the two old divergences of *Strophocincla* and *Myiomela* were concordant when analysed with msBayes ($\psi = 1$, narrow and low Ω) but were discordant with DPP-msBayes (approximate posterior probability of two divergences = 0.997, GLM-adjusted posterior probability = 1). The eight younger divergences in the Pleistocene were also recovered to be discordant by both MTML-msBayes ($\psi = 8$, broad and high Ω) and DPP-msBayes (approximate posterior probability of eight divergences = 0.999, GLM-adjusted posterior probability = 1). As DPP-msBayes permits specification of more flexible priors while msBayes tends towards concordance [31,32], here we interpret all our study taxa to have discordant divergences.

(c) Nested effect of valleys

The montane birds of the Western Ghats are impacted by valleys in a nested pattern, with the Palghat Gap (between B and C) being the most important biogeographic divide, impacting most species (all 10 species that showed any genetic differentiation) followed by the Shenkottah Gap (between C and D) and then by the Chaliyar river valley (between A and B; figure 2). Species that were affected by two barriers were additionally affected by the Shenkottah Gap and then finally by the Chaliyar river, in a nested pattern. A similar nested pattern in age of divergences was observed, with those at Palghat Gap being older than at the Shenkottah Gap, followed by the Chaliyar River (figure 4).

4. Discussion

We assessed the impact of habitat valleys and topographical dips on patterns of genetic differentiation in an entire montane bird community. Our results reveal that (i) not all species are affected to a similar extent and (ii) species are affected by topographic valleys in a nested pattern: the deepest gaps impact more species than do shallower gaps. Correspondingly, divergences across deeper gaps are older than those across shallower gaps. We suggest that climate-driven habitat shifts may accentuate genetic differentiation between locations concordant with deep and wide valleys, resulting in this nested pattern.

(a) Nested patterns of divergences in time and space

The relative impact of different topographic features revealed a consistent hierarchy or nestedness in the importance of different gaps, with the Palghat Gap affecting more species and creating more ancient divergences, followed by the impacts of the Shenkottah Gap and the Chaliyar river valley. We suggest that the relatively greater impact of the Palghat Gap may be owing to it being a wider (40 km wide compared with 10 km Shenkottah and 2–3 km wide Chaliyar valley) and deeper gap than the other two. Although no
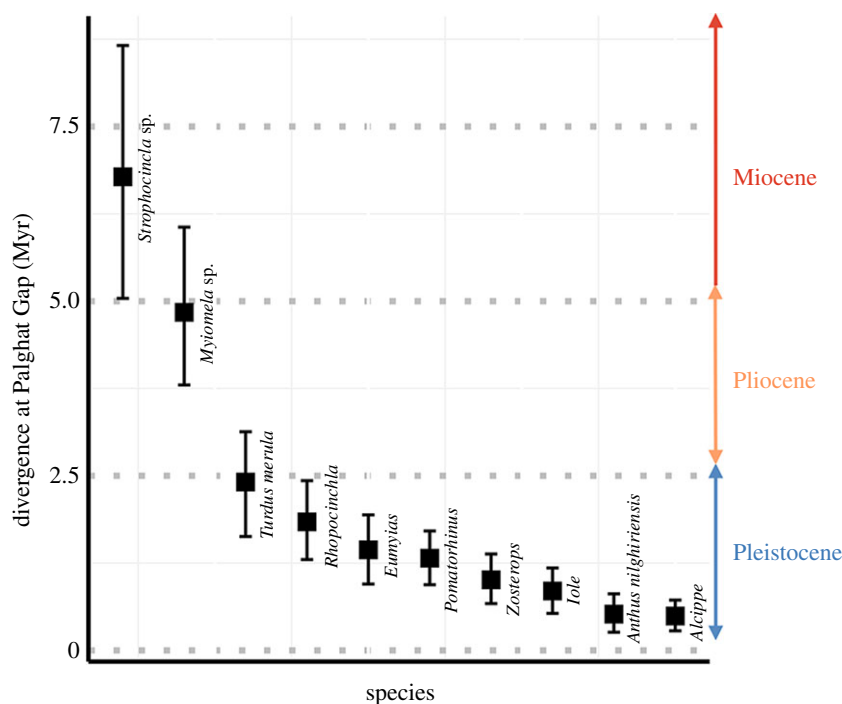
Figure 3. Molecular divergence time estimates (TMRCA—in Myr ± hpd) at the Palghat Gap (largest valley) for species that showed any genetic divergence. (Online version in colour.)
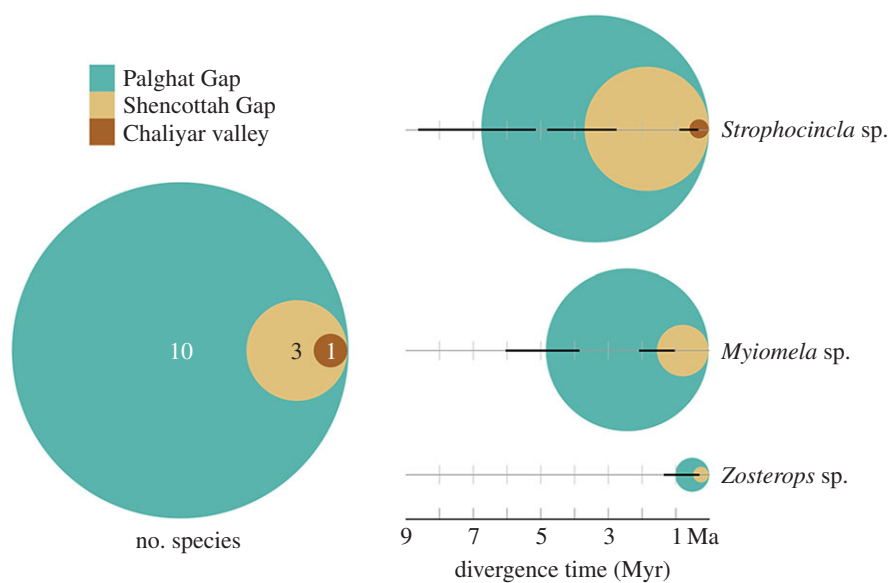

Figure 4. Nested effect of valleys on bird community. The panel on the left indicates the number of species showing genetic impacts—smaller, nested circles indicate a subset of species impacted by the respective valleys. The panel on the right indicates the age of divergence of three study taxa, with the older divergences always at Palghat Gap and younger divergences at smaller valleys. (Online version in colour.)

systematic studies have been conducted comparing species of differing ecologies and dispersal abilities, an impact of this Gap has also been found in small, restricted species like frogs [33] and some plants [34] and even in large-bodied, wide-ranging species like elephants [35]. However, certain older taxa like centipedes [36] and some long-lived trees [37] do not appear to be affected by this Gap.

Although the Shenkottah and the Palghat Gaps are geologically very old (pre-Cambrian), the impact on recent and relatively vagile colonizers like birds, especially those with small ranges, is likely to be through more recent climatic effects [38]. However, we indicate that in scenarios where climate-mediated habitat shifts lead to genetic structure in

species, topography provides the background for climate to act upon. Species are thus more affected by the deeper, wider valleys than narrower, shallow ones—a probable paradigm for montane species. Such patterns, including nestedness, may not be apparent in other mountain ranges with many parallel ranges and complex topography. It is possible that this clear effect was recovered here possibly owing to the very linear Shola Sky Island system of the Western Ghats with relatively simple topography. Specifically, in the Western Ghats, our results suggest the Palghat Gap to be the most significant biogeographic barrier, possibly affecting patterns of diversity and distribution across varied taxa.

(b) Pleistocene divergences of montane bird community

Recent examination of montane bird diversification revealed that most African montane birds diverged from their sister taxa in the Pliocene–Miocene boundary and not in the Pleistocene [12]. However, in this study, the examination of the entire bird community reveals that all species diverged discordantly, with a majority of the species in the Pleistocene, while the only two older divergences are *Myiomela* and *Strophocincla* in the Pliocene–Miocene. The Pleistocene period is known to have had dramatic fluctuations in dry and wet periods driving the extent of wet evergreen habitats in India (reviewed in [39]) and in southeast Asia (e.g. [40]) and our dating of the phylogenetic divergences are consistent with the 'Pleistocene-pump' ([16], review in [41]), which suggests enhanced divergence during this period.

(c) Why are some montane species not impacted by valleys?

Some montane-restricted endemic species (*F. nigrorufa* and *Schoenicola platyura*) that we expected to respond to valleys like other specialists, did not show any population divergence across their range, and had young TMRCA. Such patterns could be caused (non-exclusively) as follows. (i) Species could actively disperse across these barriers, though current information does not support this. (ii) Extinction recolonization responses to paleoclimatic cycles are well documented in montane taxa [11,40] and have been proposed as an explanation for a similar lack of genetic structure in a high-altitude specialist bird in Australian sky islands [24]. (iii) Incomplete lineage sorting owing to recent divergence has been implicated in other bird species that do not indicate apparent divergence (see review in [42]). We suggest that some of these factors together with recolonization during inter-glacials may be responsible for the apparent lack of phylogeographic pattern in some species. Future studies could attempt to differentiate between these hypotheses.

(d) Insights from examining an entire community

Montane species in the Western Ghats revealed differing responses to topographic (and habitat) valleys. The highest genetic differentiation was observed in montane-restricted species (such as in [18,22]), while widespread generalists such as *Pycnonotus jocosus*, grassland generalists like *Anthus rufulus*, open country birds such as *Saxicola caprata* and

large-bodied species like *Columba elphinstonii* and *Z. dauma* were not genetically differentiated. Both of these patterns are expected based on existing data on other species (e.g. [43]). However, our study also revealed cryptic structure in some species, such as *Z. palpebrosus*, a widespread species that extends to lower elevations.

While our study supports the role of climate in species diversification as suggested in the literature [12], we propose the additional importance of the physical structure of barriers, such as depth and width of valleys. Topography provides the canvas for climate-mediated habitat shifts to occur. Deeper, wider valleys allow greater climatic effect, resulting in greater genetic differentiation.

Finally, we emphasize that studying the entire community allowed us to uncover these varied, and often species-specific responses. An examination of species traits that affect genetic divergence may provide insights into diversification patterns. That species were differentially impacted in the evolutionary past emphasizes that changing climate may elicit idiosyncratic responses from species in such hotspots of biodiversity.

References

1. Graham CH *et al.* 2014 The origin and maintenance of montane diversity: integrating evolutionary and ecological processes. *Ecography* **37**, 711–719. (doi:10.1111/ecog.00578)

2. Lim HC, Rahman MA, Lim SL, Moyle RG, Sheldon FH. 2011 Revisiting Wallace's haunt: coalescent simulations and comparative niche modeling reveal historical mechanisms that promoted avian population divergence in the Malay Archipelago. *Evolution* **65**, 321–334. (doi:10.1111/j.1558-5646.2010.01105.x)

3. La Sorte FA, Jetz W. 2010 Projected range contractions of montane biodiversity under global warming. *Proc. R. Soc. B* **277**, 3401–3410. (doi:10.1098/rspb.2010.0612)

4. Soh MC, Sodhi NS, Lim SL. 2006 High sensitivity of montane bird communities to habitat disturbance in Peninsular Malaysia. *Biol. Conserv.* **129**, 149–166. (doi:10.1016/j.biocon.2005.10.030)

5. Woodburne MO. 2010 The Great American biotic interchange: dispersals, tectonics, climate, sea level and holding pens.

J. Mammal. Evol. **17**, 245–264. (doi:10.1007/s10914-010-9144-8)

6. Cracraft J. 1985 Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. *Ornithol. Monogr.* **6**, 49–84. (doi:10.2307/40168278)

7. Bowie R, Fjeldså J, Hackett S, Bates J, Crowe T. 2006 Coalescent models reveal the relative roles of ancestral polymorphism, vicariance, and dispersal in shaping phylogeographical structure of an African montane forest robin.

Mol. Phylogenet. Evol. **38**, 171–188. (doi:10.1016/j.ympev.2005.06.001)

8. Cadena CD, Klicka J, Ricklefs RE. 2007 Evolutionary differentiation in the Neotropical montane region: molecular phylogenetics and phylogeography of *Buarremon* brush-finches (Aves, Emberizidae). *Mol. Phylogenet. Evol.* **44**, 993–1016. (doi:10.1016/j.ympev.2006.12.012)

9. Fjeldså J, Bowie R. 2008 New perspectives on the origin and diversification of Africa's forest avifauna. *Afr. J. Ecol.* **46**, 235–247. (doi:10.1111/j.1365-2028.2008.00992.x)

10. Sukumar R, Suresh HS, Ramesh R. 1995 Climate change and its impact on tropical montane ecosystems in southern India. *J. Biogeogr.* **22**, 533–536. (doi:10.2307/2845951)

11. Knowles L. 2001 Did the Pleistocene glaciations promote divergence? Tests of explicit refugial models in montane grasshoppers. *Mol. Ecol.* **10**, 691–701. (doi:10.1046/j.1365-294x.2001.01206.x)

12. Fjeldså J, Bowie RC, Rahbek C. 2012 The role of mountain ranges in the diversification of birds. *Annu. Rev. Ecol. Evol. Syst.* **43**, 249–265. (doi:10.1146/annurev-ecolsys-102710-145113)

13. Voelker G, Outlaw RK, Bowie RCK. 2010 Pliocene forest dynamics as a primary driver of African bird speciation. *Glob. Ecol. Biogeogr.* **19**, 111–121. (doi:10.1111/j.1466-8238.2009.00500.x).

14. Robin VV, Sinha A, Ramakrishnan U. 2010 Ancient geographical gaps and paleo-climate shape the phylogeography of an endemic bird in the sky islands of southern India. *PLoS ONE* **5**, e13321. (doi:10.1371/journal.pone.0013321)

15. Toussaint EF, Sagata K, Surbakti S, Hendrich L, Balke M. 2013 Australasian sky islands act as a diversity pump facilitating peripheral speciation and complex reversal from narrow endemic to widespread ecological supertramp. *Ecol. Evol.* **3**, 1031–1049. (doi:10.1002/ece3.517)

16. Fjeldså J, Rahbek C. 2006 Diversification of tanagers, a species rich bird group, from lowlands to montane regions of South America. *Integr. Comp. Biol.* **46**, 72–81. (doi:10.1093/icb/icj009)

17. Weir JT, Bermingham E, Schluter D. 2009 The great American biotic interchange in birds. *Proc. Natl Acad. Sci. USA* **106**, 21 737–21 742. (doi:10.1073/pnas.0903811106)

18. Amei A, Smith BT. 2014 Robust estimates of divergence times and selection with a Poisson random field model: a case study of comparative phylogeographic data. *Genetics* **196**, 225–233. (doi:10.153/genetics.113.157776)

19. Burney CW, Brumfield RT. 2009 Ecology predicts levels of genetic differentiation in Neotropical birds. *Am. Nat.* **174**, 358–368. (doi:10.1086/603613)

20. Voelker G *et al*. 2013 River barriers and cryptic biodiversity in an evolutionary museum. *Ecol. Evol.* **3**, 536–545. (doi:10.1002/ece3.482)

21. Bowie RCK. 2011 The utility of contemporary and historical estimates of dispersal in determining response to habitat fragmentation in a tropical forest-dependent bird community. *Mol. Ecol.* **20**, 1799–1802. (doi:10.1111/j.1365-294X.2011.05032.x)

22. Dolman G, Joseph L. 2012 A species assemblage approach to comparative phylogeography of birds in southern Australia. *Ecol. Evol.* **2**, 354–369. (doi:10.1002/ece3.87)

23. Moritz C, Hoskin CJ, MacKenzie JB, Phillips BL, Tonione M, Silva N, VanDerWal J, Williams SE, Graham CH. 2009 Identification and dynamics of a cryptic suture zone in tropical rainforest. *Proc. R. Soc. B* **276**, 1235–1244. (doi:10.1098/rspb.2008.1622)

24. Joseph L, Moritz C, Hugall A. 1995 Molecular support for vicariance as a source of diversity in rainforest. *Proc. R. Soc. Lond. B* **260**, 177–182. (doi:10.1098/rspb.1995.0077)

25. Price TD *et al*. 2014 Niche filling slows the diversification of Himalayan songbirds. *Nature* **509**, 222–225. (doi:10.1038/nature13272)

26. Bunyan M, Bardhan S, Jose S. 2012 The Shola (Tropical Montane Forest)-grassland ecosystem mosaic of Peninsular India: a review. *Am. J. Plant Sci.* **3**, 1632–1639. (doi:10.4236/ajps.2012.311198)

27. Bates JM, Zink RM. 1994 Evolution into the Andes: molecular evidence for species relationships in the genus *Leptopogon*. *Auk* **111**, 507–515.

28. Chaves JA, Weir JT, Smith TB. 2011 Diversification in *Adelomyia* hummingbirds follows Andean uplift. *Mol. Ecol.* **20**, 4564–4576. (doi:10.1111/j.1365-294X.2011.05304.x)

29. Chatterjee S, Goswami A, Scotese CR. 2013 The longest voyage: tectonic, magmatic, and paleoclimatic evolution of the Indian plate during its northward flight from Gondwana to Asia. *Gondwana Res.* **23**, 238–267. (doi:10.1016/j.gr.2012.07.001)

30. Hickerson MJ, Stahl E, Takebayashi N. 2007 msBayes: pipeline for testing comparative phylogeographic histories using hierarchical approximate Bayesian computation. *BMC Bioinform.* **8**, 268. (doi:10.1186/1471-2105-8-268)

31. Oaks JR, Sukumaran J, Esselstyn JA, Linkem CW, Siler CD, Holder MT, Brown RM. 2013 Evidence for climate-driven diversification? A caution for interpreting ABC inferences of simultaneous historical events. *Evolution* **67**, 991–1010. (doi:10.1111/j.1558-5646.2012.01840.x)

32. Oaks JR. 2014 An improved approximate-Bayesian model-choice method for estimating shared evolutionary history. *BMC Evol. Biol.* **14**, 150. (doi:10.1186/1471-2148-14-150)

33. Nair A, Gopalan SV, George S, Kumar KS, Shikano T, Merilä J. 2012 Genetic variation and differentiation in *Indirana beddomii* frogs endemic to the Western Ghats biodiversity hotspot. *Conserv. Genet.* **13**, 1459–1467. (doi:10.1007/s10592-012-0389-z)

34. Deshpande AU *et al*. 2001 Genetic diversity across natural populations of three montane plant species from the Western Ghats, India revealed by intersimple sequence repeats. *Mol. Ecol.* **10**, 2397–2408. (doi:10.1046/j.0962-1083.2001.01379.x)

35. Vidya T, Fernando P, Melnick D, Sukumar R. 2005 Population differentiation within and among Asian elephant (*Elephas maximus*) populations in southern India. *Heredity* **94**, 71–80. (doi:10.1038/sj.hdy.6800568)

36. Joshi J, Karanth P. 2013 Did southern Western Ghats of peninsular India serve as refugia for its endemic biota during the Cretaceous volcanism? *Ecol. Evol.* **3**, 3275–3282. (doi:10.1002/ece3.603)

37. Bodare S. 2013 *Conservation genetics and speciation in Asian forest trees*. Uppsala, Sweden: Uppsala University.

38. Smith BT *et al*. 2014 The drivers of tropical speciation. *Nature* **515**, 406–409. (doi:10.1038/nature13687)

39. Karanth KP. 2003 Evolution of disjunct distributions among wet-zone species of the Indian subcontinent: testing various hypotheses using a phylogenetic approach. *Curr. Sci.* **85**, 1276–1283.

40. Cannon CH, Morley RJ, Bush AB. 2009 The current refugial rainforests of Sundaland are unrepresentative of their biogeographic past and highly vulnerable to disturbance. *Proc. Natl Acad. Sci. USA* **106**, 11 188–11 193. (doi:10.1073/pnas.0809865106)

41. Rull V. 2011 Neotropical biodiversity: timing and potential drivers. *Trends Ecol. Evol.* **26**, 508–513. (doi:10.1016/j.tree.2011.05.011)

42. McKay BD, Zink RM. 2010 The causes of mitochondrial DNA gene tree paraphyly in birds. *Mol. Phylogenet. Evol.* **54**, 647–650. (doi:10.1016/j.ympev.2009.08.024)

43. Stuart-Fox DM, Schneider CJ, Moritz C, Couper PJ. 2001 Comparative phylogeography of three rainforest-restricted lizards from mid-east Queensland. *Aust. J. Zool.* **49**, 119–127. (doi:10.1071/ZO00092)