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REVIEW ARTICLE

Role of Geographical Gaps in the Western Ghats in Shaping Intra- and Interspecific Genetic Diversity

Aritra Biswas* and K. Praveen Karanth

Abstract | Gaps or wide valleys in mountain systems are of much interest to biogeographers and evolutionary biologists since they shape species distributions as well as inter- and intraspecific genetic diversity. The Western Ghats, a hill range that runs parallel to the west coast of India, is one of the biodiversity hotspots with the highest level of endemism in the Indian Subcontinent. This hill range is interrupted by at least three large valleys or gaps, namely Palghat, Shencottah and Goa Gaps. Here, we review studies undertaken in the last two decades that have looked at the role of these gaps in shaping inter and intraspecific genetic diversity in different taxa. Overall, our review suggests that the Palghat gap appears to be a major barrier for a range of taxonomic groups, followed by Shencottah and Goa Gaps to a lesser extent. These patterns are consistent with the depth and width of these gaps, as Palghat gap is the deepest and widest among these gaps. Importantly, all of these divergences across the gaps have occurred long after the formation of these gaps. Therefore, geology-mediated vicariance can be ruled out. Furthermore, in some groups, the ecology, life-history traits, historical biogeography of the taxa in question better explain their distributions.

1 Introduction

Natural discontinuities or gaps in geographical features, such as gaps in a hill/mountain range, have long been of interest to naturalists, biogeographers and evolutionary biologists. Such gaps often shape species distributions, with different species or communities on either side of the gap[23,40,65]. Furthermore, gaps have also been knownto influence intra- and interspecific genetic diversity[34,35,56]. Topographic discontinuities in mountain ranges often create deep and wide valleys with different climatic conditions (microclimate), unsuitable habitats (flowing river), causing discontinuation of species' distribution affecting their genetic diversity as well as evolutionary history[31]. Such barriers can also limit the range and prevent the dispersal of organisms[25,32]. For example, the African montane forest robin shows phylogenetic breaks and genetic clusters corresponding to topographic dips separating different montane habitats[6]. Similarly, Neotropical *Buarremon* brush-finches also show phylogenetic patterns corresponding to major geographical barriers[7]. Voelker et al.[64] have shown that the Congo River acts as a gene flow barrier for four species of Afrotropical understory birds. In this regard, the Western Ghats (WG) hill range is of much interest as it offers a continuous mountain system with deep and wide topological discontinuities.

The WG is one of the world's major biodiversity hot spots. Despite covering less than 6% of the national land area, this region contains over 30% of India's flora and fauna[3]. With 20 national parks, 68 sanctuaries and two biosphere reserves, Western Ghats holds the highest coverage of protected areas (15%) in the mainland of India[3]. According to the IUCN report and "Critical Ecosystem Partnership

[1] Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India.
*aritra110@gmail.com

Fund (CEPF) Western Ghats Hotspot" website, approximately 34% of Western Ghats' biota are endemic. Different groups' percent endemicity is—54% endemicity in plants, 12% endemicity in mammals, 4% endemicity in birds, 65% endemicity in amphibians, 62% in reptiles and 53% in freshwater fishes[38]. With the current rate of new species discovery from this area, these numbers are only likely to increase in the future.

The WG lies almost parallel to India's west coast, extending about 1600 km from Gujarat in North to Kerala in South[54]. There are three significant geological breaks or gaps in this hill range (Fig. 1). The widest of them is the Palghat Gap (PG) at 11° N is about 40 km wide. This gap is situated in the state of Kerala. The average annual rainfall is 1838 mm and average annual highest and lowest temperature are 32.4 °C and 23.2 °C, respectively[14,55]. The average elevation of this gap is approx. 200 m. Although the Palghat Gap's origin is controversial, it is believed to have formed around 500 million years ago (Mya)[48,54]. The PG is a dextral shear zone, and its formation has been attributed to the combined effect of shearing and erosion[11]. The Nilgiri and Annamalai hills form the northern and southern border of the PG and are composed of massive charnockites and associated granulites, which are erosion and weathering-resistant. However, the closely foliated, highly sheared and retrograded gneisses of the PG suffered much greater erosion than the surrounding[11,18]. The Bharathapuzha River originates and flows through PG. Another prominent break is south of the PG and is called the Shencottah Gap (SG) at 9° N, which is the narrowest among these three gaps (7.5 km wide). SG is situated almost 224 km south of PG. It is believed to be as older as of the PG[48,54]. The average elevation of this gap is approx. 300 m. The average annual highest and lowest temperature of this region are, respectively, 31.1 °C and 23.5 °C. This region receives an average annual rainfall of 1312 mm[9]. The Goa Gap (GG) at 15.8° N situated in the Northern part of the Western Ghats is the most recently formed gap (65–80 Mya)[17,57]. It is situated ~ 550 km north of PG. The average elevation of this gap is approx. 600 m. The PG allows the moisture-laden south-west monsoon wind into Tamil Nadu in its western part. Overall, the climatic condition of PG and SG is wet. The climatic condition across GG is intermediate and drier than the other two gaps[44]. Pascal[39] noted that there is a south–north gradient of the dry period length along the WG mountain range. The region belonging to the north of GG experiences an extended dry period (6–7 months) compared to the other two gaps (less than 4 months). The difference in climatic conditions across these regions (PG, SG in south and GG in north) is also reflected by the difference in vegetation patterns between these regions[59]. The PG and SG appear to be physical barriers, given their depth that could potentially restrict the movement of dispersal limited taxa and high-altitude species whereas, GG is more of a climatic barrier. GG does not intersect the WG mountain range as prominently as PG and SG. However, this valley is wide but not very deep. Ramachandran et al.[44] found a clear wet-dry gradient across GG.

These gaps can be a barrier for dispersal of organisms in a continuous hill range like the WG, given that the gap is a wide and of lower elevation than the adjoining areas or with different climatic conditions. Among these gaps, the PG has long been invoked as a major barrier that has shaped species distributions along the WG. For example, there are numerous cases of different species distributed on either side of the gap[12] as well as many cases of turnover of communities across the PG and GG[44]. In the last two decades, many studies have looked at how these gaps might have shaped intra- and interspecific genetic variations across these gaps (review here). These studies fall into four broad categories, (A) species distributed across gaps are expected to exhibit genetic breaks concordant with these gaps due to limited gene flow (Fig. 2A), (B) sister species distributed on either side of the gap due to lack of gene flow among populations across the gap resulting in speciation (Fig. 2B), (C) sister clades distributed on either side of the gap in older groups (Fig. 2C) (D) No/Partial genetic structuring across the gaps. Here, we review various molecular studies undertaken in the last two decades to better understand how gaps in the WG have shaped the distribution of genetic variation in species to higher taxonomic level (clades). Taxonomic groups/clades that are largely endemic to WG are chosen for this review. Broadly, we try to find answers to three questions: (1) Which among the four patterns of genetic diversification (A, B, C, D) is followed by different endemic taxa from WG? (2) Do these endemic species show any spatial concordance of genetic diversification across these gaps? (3) What are the timings of divergence for different taxa and are they congruent across taxa? WG is highly threatened by deforestation and climate change[30,53,58] and identifying biogeographic barriers that are consistent across species is of particular importance as it will help us to identify areas of endemism and determine geographic drivers of species distribution and diversification[10].

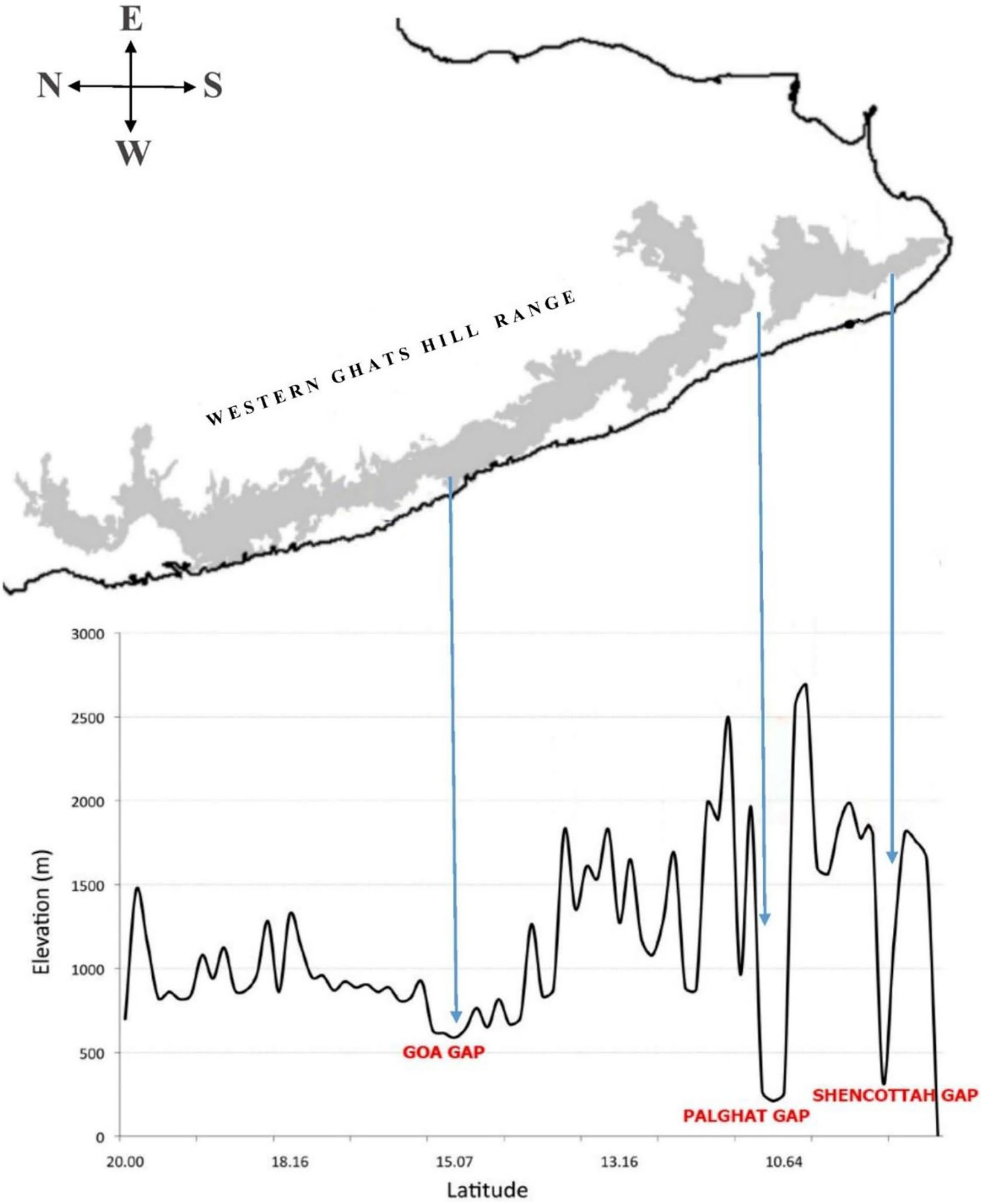

Figure 1: Position and elevational profiles of the three major gaps in the Western Ghats mountain range. Hill range map and elevation profile adapted and modified from[13,45].

2 Patterns of Diversification Across Major Geological Breaks of the Western Ghats in Various Taxa

2.1 Mammals

The most remarkable example among mammals showing genetic differentiation across the PG is the Asian Elephant (*Elephas maximus*). Vidya et al.[62] have sampled all three major populations of the species in Southern India (Nilgiri, Annamalai and Periyar). Six microsatellite loci and 600 bp of mitochondrial Cytochrome-*b* (Cyt-*b*) gene were PCR amplified and sequenced from 243 (224 free-ranging and 19 captive samples) dung samples. The mitochondrial DNA (mtDNA) dataset indicated an absence of shared haplotypes between the population north (Nilgiris) and south (Annamalai, Periyar) of PG. Pairwise F_{ST} and R_{ST} values for microsatellite data

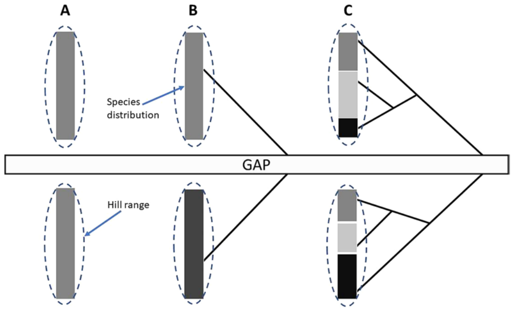

Figure 2: Intra- (A) and interspecific (B, C) genetic variations shaped by a gap in a hill range. See text for details. Filled bars represent distinct species and their distributions.

also showed a similar pattern. Both mtDNA and microsatellite data do not show significant differences among Annamalai and Periyar populations, indicating gene flow between them[62]. Nilgiri is situated at the northern part of the PG and both Annamalai and Periyar are situated at the southern part of the PG.

A study by Kolipakam et al.[28] investigating the population genetic structure of the Bengal Tiger (*Panthera tigris tigris*) across the country has recovered Northern (N) and Southern (S) Western Ghats populations as two different clusters separated by the PG. They have amplified and sequenced 11 microsatellite loci for the analysis from 158 scat samples collected from 34 different populations covering the major tiger landscapes of the country. Surprisingly, the N-WG and S-WG populations' genetic distance is much greater than S-WG and Terai populations[28]. The authors suggest further investigation of this issue using the mitochondrial markers. This genetic differentiation of populations of elephants, tiger across the PG is interesting given that large mammals are known to be vagile and have good dispersal abilities.

The lion-tailed macaque (*Macaca silenus*) is a rainforest-dwelling species endemic to the Western Ghats[29]. Ram et al.[43] have used mtDNA sequence data to examine this endangered macaque's genetic diversity and population structure across its range. The authors have amplified and sequenced partial tRNA-thr, tRNA-pro, partial HVR I (613 bp) and partial mitochondrial Cyt-*b* gene (521 bp) from fresh fecal samples collected throughout the range of the macaque. They have recovered two reciprocally monophyletic groups corresponding to the populations north and south of the PG with high branch support. The average genetic distance between the populations is almost double the genetic distance within populations. According to their analysis, the two populations diverged around 2.11 Mya.

Another important example comes from a phylogeographic study of Nilgiri Thar (*Nilgiritragus hylocrius*) an endangered species endemic to the Western Ghats[41]. Joshi et al.[21] based on analysis of mtDNA data (381 bp of mitochondrial Cyt-*b* gene fragment) sequenced from fecal samples, showed populations north and south of the PG are reciprocally monophyletic. Divergence dating suggests that these populations have diverged from each other around 1.46 Mya.

Thus, published work so far on mammals fall in category A, i.e., these species exhibit genetic break across the PG. However, these studies looked at intraspecific genetic variation across the WG and the number of taxa studied is only four till date. It would be interesting to study mammalian taxa that exhibit high diversity in the WG, such as giant squirrels, to determine if they conform to categories B or C.

2.2 Birds

Birds are one of the well-explored taxa concerning the question being addressed here. Robin et al.[46] have investigated the phylogeographic patterns across the entire community of montane birds (species occurring above 1400 m. from sea level) in the Western Ghats. They have found that the phylogeographic structures of 10 of the 23 species examined are affected by the PG. Two of the ten species are affected by both the PG and SG. The oldest divergence for almost all species was across the PG, followed by the SG and Chaliyar valley. Chaliyar river valley (~ 12° N) is another discontinuity in the WG mountain range separating the Wayanad and Nilgiri mountains. It is a deep river valley that is almost 2–3 km wide. The range of divergence times across the PG for all ten species falls between 6.78 Mya and less than 1 Mya[46]. Thus, in birds, too many species exhibit genetic breaks across the PG (category A). Nevertheless, in birds, one finds two examples of category B (see below).

Studies of two endemic genera from the Western Ghats suggest that these gaps have played an important role in speciation. Robin et al.[47] have sequenced several mitochondrial and nuclear markers for phylogenetic and species delimitations studies on laughingthrushes and shortwings of WG. Western Ghats shortwings are threatened endemic birds, which has undergone major taxonomic revision. First, they were placed in the genus *Brachypteryx* and were moved to *Myiomela* later. Robin et al.[47] have transferred Western Ghats shortwings into a new genus *Sholicola* based on the multi-criteria approach (genetics, song pattern, morphometrics, plumage). *Sholicola* has reciprocally monophyletic groups (*S. major* at the north and *S. albiventris* at the south of PG) that diverged across the PG around 4.33 Mya[47]. Furthermore, the clade south of the PG shows split across the SG around 0.86 Mya. A study investigating the pattern of songs (spectral and syntax variables) in shortwings across six geographically isolated populations has shown that the difference in song patterns across populations corroborates the phylogenetic pattern shown by these populations[42]. The highest level of differentiation is seen across the PG, followed by the SG. The differences across other smaller gaps and recently fragmented populations are much less than those two major gaps[42]. A study of the endemic genus *Montecincla* shows substantial genetic divergence across both the PG and the SG. Based on the multi-criteria approach (song, plumage, morphology, genetic data), the genus *Montecincla* is divided into four species[47]. *M. jerdoni* and *M. cachinnans* are distributed north of the PG and *M. fairbanki* and *M. meridionalis* to the south. *M. fairbanki* and *M. meridionalis* are further separated from each other by SG. The timings of lineage splitting across the gaps are—4.7 Mya across PG and 0.33 Mya across SG. Since the SG is much narrower than the PG, genetic differentiation across this gap is relatively rare. These two genera, *Montecincla* and *Sholicola*, are two crucial examples showing species-level differentiation across the SG.

However, investigation of phylogeographic patterns of the entire community of montane birds from the Western Ghats by Robin et al.[46] has found 14 bird species whose population structures are not affected by the geographical gaps. Details of all these species are given in Table 1.

2.3 Squamates

Taxonomic revision and phylogenetic studies of vine snakes (Genus *Ahaetulla*) from peninsular India by Mallik et al.[33] have identified several morphologically cryptic lineages and assigned them different species based on genetic distance and geographical isolation. They have used three mitochondrial markers (cyt-*b*, 16S and ND4) along with morphometry and geographic distribution data for species delimitation. Many of these species are separated by geological gaps in the Western Ghats. Like, *A. isabellina* (lineage 5, south of PG) and *A. malabarica* (lineage 6, north of PG) are distributed on either side of PG, respectively. Interestingly *A. isabellina* is sister to *A. farnsworthi* (lineage 4) which is found north of the PG. *A. malabarica* is sister to the clade containing *A. isabellina* and *A. farnsworthi*. All these three species form a clade which is sister to *A. borealis* (lineage 3, north of PG). Lineage 3 to 6 are all novel species and they fall within the *A. nasuta* species complex. *A. nasuta* (lineage 2, Sri Lanka) is sister to all the other four Indian species. Another clade which is sister to the *A. nasuta* species complex contains two species separated by SG. *A. disper* (lineage 11) is restricted to the north of SG while its sister species *A. travancorica* (lineage 12) which is also a new species is confined to the south of SG. All these cryptic lineages are restricted by altitude and their distributional ranges are separated by geological gaps like PG and SG. Overall, these patterns conform to category B.

Chaitanya et al.[8] studied the phylogeny of the endemic *Dravidogecko* from the Western Ghats and discovered several new species. They have sequenced both mitochondrial (ND2) and nuclear (PDC, RAG1) markers for species delimitation along with morphometry. Their analysis retrieved three clades, one of which is distributed between PG and SG (clade A), whereas the other two are distributed across PG (clade B2) and SG (clade B1). Thus, the higher-level relationships between these clades were not shaped by the gaps. Nevertheless, at shallower nodes, there are two instances of lineage divergence across gaps, one across PG and the other across SG. Clade B2 in their phylogeny contains two sister species, *D. anamallensis* (south of PG) and *D. septentrionalis* (north of PG). Clade B1 (which is sister to clade B2) is further divided into a sub-clade containing *D. douglasadamsi* and *D. smithi*, both of them are restricted to the south of SG. *D. meghamalaiensis* is found only in the north of SG and is sister to the sub-clade containing *D. douglasadamsi* and *D. smithi*. So, we assign *Dravidogecko* to category B.

2.4 Amphibians

The WG exhibit very high degree of endemism (65%) for amphibians (IUCN TECHNICAL EVALUATION WESTERN GHATS (INDIA) ID No. 1342 Rev). However, very few studies (mostly in frogs) have investigated the effect of these geological gaps on the genetic diversity of these organisms.

Bocxlaer et al.[61] investigated the phylogeography of the endemic genus *Nyctibatrachus* using

Table 1: Studies done on taxa till date and their status concerning the effect of the three major gaps.

Taxa		Genetic structure of populations across the gaps			Category of structuring	Endemic to Western Ghats	Date of divergence (Mya)	References
		Palghat	**Shencottah**	**Goa**				
Mammals	1. *Elephas maximus*	Yes	No	–	A	No	–	Vidya et al.[62]
	2. *Panthera tigris tigris*	Yes	No	–	A	No	–	Kolipakam et al.[28]
	3. *Macaca silenus*	Yes	No	–	A	Yes	PG- 2.11	Ram et al.[43]
	4. *Nilgiritragus hylocrius*	Yes	No	–	A	Yes	PG- 1.46	Joshi et al.[21]
Birds	5. *Iole indica*	Yes	No	–	A	No	–	Robin et al.[46]
	6. *Pomatorhinus horsfieldii*	Yes	No	–	A	No	–	Robin et al.[46]
	7. *Eumyias albicaudatus*	Yes	No	–	A	No	–	Robin et al.[46]
	8. *Alcippe poioicephala*	Yes	No	–	A	No	–	Robin et al.[46]
	9.*Turdus merula*	Yes	No	–	A	No	–	Robin et al.[46]
	10. *Rhopocincla atriceps*	Yes	No	–	A	–	–	Robin et al.[46]
	11. *Zosterops palpebrosus*	Yes	Yes	–	A	No	–	Robin et al.[46]
	12. *Anthus nilghiriensis*	Yes	Yes	–	A	Yes	–	Robin et al.[46]
	13. *Montecincla*	Yes	Yes	–	B	Yes	PG- 4.7, SG- 0.33	Robin et al.[47]
	14. *Sholicola*	Yes	Yes	–	B	Yes	PG- 4.33, SG- 0.86	Robin et al.[47]
	15. *Hypsipetes leucocephalus*	No	No	–	D	No	–	Robin et al.[46]
	16. *Ficedula nigrorufa*	No	No	–	D	Yes	–	Robin et al.[46]
	17. *Schoenicola platyurus*	No	No	–	D	Yes	–	Robin et al.[46]
	18. *Culicicapa ceylonensis*	No	No	–	D	No	–	Robin et al.[46]
	19. *Columba elphinstonii*	No	No	–	D	Yes	–	Robin et al.[46]
	20. *Zoothera citrina*	No	No	–	D	No	–	Robin et al.[46]
	21. *Anthus rufulus*	No	No	–	D	No	–	Robin et al.[46]
	22. *Saxicola caprata*	No	No	–	D	No	–	Robin et al.[46]

Table 1: (continued)

Taxa		Genetic structure of populations across the gaps			Category of structuring	Endemic to Western Ghats	Date of divergence (Mya)	References
		Palghat	Shencottah	Goa				
	23. *Pellorneum ruficeps*	No	No	–	D	No	–	Robin et al.[46]
	24. *Pycnonotus jocosus*	No	No	–	D	No	–	Robin et al.[46]
	25. *Zoothera dauma*	No	No	–	D	No	–	Robin et al.[46]
	26. *Cyornis pallipes*	No	No	–	D	Yes	–	Robin et al.[46]
	27. *Garrulax delesserti*	No	No	–	D	Yes	–	Robin et al.[46]
Squamates	28. *Ahaetulla*	Yes	Yes	–	B	No	–	Mallik et al.[33]
	29. *Dravidogecko*	Yes	Yes	–	B	Yes	–	Chaitanya et al.[8]
Amphibians	30. *Nyctibatrachus*	Yes	No	Yes	C	Yes	PG- 40–50, GG- ~ 16	Bocxlaer et al.[61]
	31. *Indirana cf beddomi*	–	Yes	–	A	Yes	–	Nair et al.[36]
	32. *Raorchestes*	Yes	No	–	C	Yes	PG- 30	Vijayakumar et al.[63]
	33. *Icthyophis bombayensis*	No	No	No	A	Yes	–	Gower et al.[16]
Fishes	34. *Puntius denisonii*	Yes	No	–	C	Yes	PG- 59	John et al.[20]
	35. *Mesonoemacheilus*	Yes	Yes	–	B	Yes		Anoop et al.[1]
	36. *Bhavania*	No	Yes	–	D	Yes	SG- ~ 5	Sidharthan et al.[51]
Centipedes	37. *Digitepes*	No	–	–	D	Yes	–	Joshi and Karanth[22]
Crabs	38. *Vanni*	No	Yes	–	D	Yes	–	Klaus et al.[26]
Butterfly	39. *Mycalesis patnia*	No	No	–	D		–	Sekar and Karanth[50]
Plants	40. *Eurya nitida*	Yes	–	–	A	No	–	Bahulikar et al.[4]
	41. *Dysoxylum malabaricum*	No	No	–	D	Yes	–	Bodare et al.[5]
	42. *Gaultheria fragrantissima*	Yes	–	–	A	No	–	Apte et al.[2]
	43. *Kingiodendron pinnatum*	Yes	–	–	A	Yes	–	Nair et al.[37]

"–" indicates the effect of that gap has not been tested for the taxa. Details of all categories are given in the Sect. 1

both nuclear (tyrosinase) and mitochondrial (16S, tRNA-leu, ND1) markers. They have recovered two large reciprocally monophyletic groups distributed on either side of PG that diverged around 40–50 Mya (Eocene). The northern clade also contains a divergent group across GG. This genus corresponds to category C. Furthermore, the study suggested two dispersal events across the PG, one dispersal event across the GG (mid-Miocene ~ 14 Mya) and four dispersal events across the SG. Their results are consistent with the gaps' hierarchy in that more dispersals have occurred across narrower and shallower SG than PG.

A study by Vijayakumar et al.[63] investigating the diversification of bush frogs (genus *Raorchestes*) in the Western Ghats is one of the most comprehensive studies that elucidate the fine-scale biogeographic patterns across the range of this endemic genus. A concatenated dataset of six genes (16S, 12S, Cyt-*b*, ND1, Tyrosinase and Rhodopsin) was used to build the phylogeny of bush frogs. They have recovered two deeply divergent clades (30Mya) across the PG. Though a few of them dispersed across the gap like *R. flaviventris, R. marki* dispersed from north to south and *R. nerostagona, R. glandulosus* dispersed from south to north. However, compared to other lineages, the number of lineages that dispersed across the gap is significantly less. This example belongs to category C. This study highlights the role of elevations, gradients, past climate and geographic gaps in shaping the diversity within a genus.

An investigation of the population genetic structure of endemic *Indirana cf beddomi* frogs by Nair et al.[36] (using 20 microsatellite loci) has discovered a clear genetic structuring of populations across the SG. The authors have sampled 12 different populations across the distributional range of the frog. Their study has recovered three distinct genetic clusters: Anamalai group (pop 1–5), Periyar group (pop 6–10) and Agasthyamalai group (pop 11, 12). Anamalai and Periyar groups are clustered together and both of them are from north of the SG. Agasthyamalai group is from south of the SG and formed a separate cluster. So, this group corresponds to category A.

Long-tailed unstripped caecilian (*Icthyophis bombayensis*) is a limbless amphibian species endemic to the Western Ghats. Taylor described four different species of *Icthyophis* from the Western Ghats in 1960, but the published keys appeared insufficient for identifying the species[60]. There have been significant confusion and controversy regarding Taylor's four species' taxonomic validity for a long time. Gower et al.[16] investigated the genetic structure of *Icthyophis bombayensis* populations from the Western Ghats using mtDNA sequence. They have shown that all these putative species are genetically homogeneous and appear to be a single, widely distributed species, *Icthyophis bombayensis* or the Bombay caecilian. Phylogenetic analyses of the concatenated dataset (12S and 16S rRNA genes) recovered two clades corresponding to north and south of the PG but with meager bootstrap support (25%). However, the uncorrected p-distance between the north and south populations is higher than within populations and AMOVA analysis suggested significant structuring of populations across the PG. Additional molecular data might resolve this issue. For now, we assign it to category A.

2.5 Fishes

The example of the most ancient divergence across the PG comes from the fishes. Phylogeny of the endemic endangered Red Lined Torpedo Barbs (*Puntius denisonii*) of Western Ghats using mitochondrial Cyt-*b* and Cytochrome oxidase 1 (Cox1) recovered two separate clades on either side of the PG with an estimated divergence date of around 59 Mya[20]. Results from this study are consistent with category C discussed in the introduction. Despite extraordinary diversity and a high degree of endemism, the number of phylogeographic studies of fishes is only a few to date.

Phylogeny of hillstream loach genus *Mesonoemacheilus* from the Western Ghats based on mitochondrial cox1 gene sequence shows sister lineages distributed on either side of these gaps[1]. Species delimitation analysis uncovered multiple lineages and biogeographic analysis suggests multiple dispersals and vicariance events associated with both PG and SG that generated the extant diversity. The gaps have played a significant role in the speciation process within this genus as several sister species can be found on either side of these gaps (category B).

Sidharthan et al.[51] sequenced the mitochondrial Cyt-*b* and Cox1 genes for the phylogeographic study of the endemic mountain loaches of genus *Bhavania*. The authors suggest that well-connected ancient drainage systems can give rise to the observed phylogeographic pattern. Species from the south of the PG are nested within a larger clade composed of species from the north of the PG[51]. This pattern is opposite to that in centipedes of the genus *Digitipes*[22], see below. Interestingly, only one sub-clade representing species below the PG in *Bhavania* phylogeny shows a split across the SG. This subclade consists of *Bhavania australis* populations from Pampa and Achankovil (north of SG) and *Bhavania annandalei* populations from Kallada and Vamanapuram (south of SG). We assign this example to category D since most of the species and the larger phylogeny do not show any concordance with the gaps.

2.6 Centipedes

The study of Biogeography of the endemic centipede genus *Digitipes* by Joshi and Karanth[22] has shown that the PG did not play a significant role in the distribution of centipede lineages. A phylogeny based on 16S rRNA and Cox1 gene sequences shows that species from northern and central Western Ghats are nested within a larger species' clade from southern WG. Nevertheless, their biogeographical analysis suggested an early divergence between southern and northern WG as well as southern and central WG clades followed by dispersal across gaps by some lineages. Based on this overall pattern, we assign it to category D. However, *Digitipes coonoorensis* has two reciprocally monophyletic groups across the PG (Nilgiri and southern WG) and these two groups have diverged around 35 Mya.

2.7 Butterflies

Sekar and Karanth[50] studied the population genetic structure of two butterfly species using the Amplified Fragment Length Polymorphism (AFLP) technique. They sampled one species from the sky island system (*Heteropsis oculus*) and the other from low-altitude habitat (*Mycalesis patnia*). *Heteropsis oculus* is distributed only at the south of PG, but *Mycalesis patina* is distributed across the PG[24,27]. For *Heteropsis oculus*, they have found significant genetic structuring of populations corresponding to the sky island system, but for *Mycalesis patnia*, no such pattern was observed. The population of *Mycalesis patnia* appears to be genetically uniform throughout its range in the Western Ghats.

2.8 Crabs

Freshwater crabs are strongly philopatric[49] and therefore, their relationships are expected to be influenced by barriers. However, the phylogeny of montane freshwater crabs from the southernmost part of Western Ghats based on histone H3 and 16S rRNA gene sequences does not show this expected pattern. Instead, the phylogeny suggests around five independent dispersals into different parts of WG[26]. Thus, the higher-level relationships between these lineages were not shaped by the gaps. This example can be assigned to category D based on the overall pattern shown by the phylogeny. However, one of these lineages has undergone radiation in the S-WG (between PG and SG) and consists of sister species distributed on either side of SG (*Vanni travancoriana* and *Vanni deepta*). In this particular case, SG appeared to have caused diversification between these two species.

2.9 Plants

A phylogeographic study of *Kingiodendron pinnatum*, an endemic, threatened species from the Western Ghats by Nair et al.[37] using *trn*H-*psb*A and *trn*L-*trn*F markers have shown that the PG acts as a biogeographic barrier for this species. Phylogenetic analysis has recovered two divergent haplogroups distributed to north and south of PG with a divergence date of around 14.62 Mya. The haplogroup from the north of the gap contains 13 haplotypes and the haplogroup from the south of the gap contains 12 haplotypes.

Bahulikar et al.[4] investigated the genetic diversity in the populations of *Eurya nitida* using ISSR (inter simple sequence repeat) markers. Though their study was not aimed to test the effect of these geographic barriers on population distribution, their sampling locations spanned well across the PG. Their study recovered three clusters, one confined mainly to central WG (Madikeri, Talakaveri, Kemangundi) and the other two restricted to the north (Nilgiri) and south (Kodaikanal) of PG. Another study by Apte et al.[2] investigated the population genetic structure of *Gaultheria fragrantissima* and recovered results similar to *Eurya nitida.* Populations north of PG (Nilgiri) are clustered together and those south of PG (Munnar, Kodaikanal) form another cluster. From these studies, it is apparent that the PG has shaped the intraspecific variations (category A) in these species.

Bodare et al.[5] investigated the genetic structure of *Dysoxylum malabaricum* from the Western Ghats using both nuclear and chloroplast markers. They found local population genetic structure but these patterns did not correspond to the gaps. The authors suggest that the lack of genetic structuring across the major gaps could be due to frugivore (like hornbills)-mediated seed dispersal. This example belongs to the category D.

3 Discussion

Our literature survey yielded around 24 publications spanning 43 different species where the effect of the major geological barriers has been tested. The majority of the organisms are birds (23 out of 43), followed by mammals and amphibians (4 from each group). At least 21 of these taxa provide evidence of genetic structuring of populations across the Palghat Gap and 7 across the Shencottah Gap. Only two studies have tested the Goa Gap's effect and one of them (*Nyctibatrachus*) shows evidence of lineage splitting across this gap. Palghat gap acts as a biogeographic barrier for the four mammals, ten birds, two amphibians, one reptile, one fish and three plants. Shencottah gap acts as a biogeographic barrier for five birds, one amphibian, one reptile and one fish.

Overall, the PG appears to be a major barrier for a range of taxonomic groups. Importantly, PG has shaped intraspecific genetic diversity (category A) as well as interspecific diversification (category B and C). The other two gaps appear to be less of a barrier for species. If we look at the timings of divergence across the PG for different organisms, it ranges from as old as 59 Mya between clades to less than 1 Mya in case of intraspecific variation. All of these divergences across the gaps have occurred long after the formation of these gaps. Therefore, geology-mediated vicariance can be ruled out. However, climatic conditions across this region have never been consistent, given the complex geological and climatic history of peninsular India[19]. Geological barriers provide a background on which climatic conditions can act to influence species' habitat and, therefore, their distribution[45]. Topographic dips (like PG and SG) can act as a biogeographic barrier depending on the climate[15]. Thus, these gaps might have served as barriers at different time periods for different taxa with changing climatic conditions.

In addition to environmental factors, species-specific attributes, such as life-history traits and habitat specificity etc., might be an important predictor of how these gaps might influence distributions. In this regard, dispersal ability might be important. For example, volant species such as birds, particularly generalists, appear to be less influenced by gaps[46]. Genetic structuring across the gap in large mammals that disperse long distances, like the Asian Elephant and Bengal Tiger, is intriguing. Thus, the ecology and species-specific attributes might be important in governing their distributions. Furthermore, taxa that are confined to freshwater streams, such as crabs[26] and certain fishes[51], do not seem to be affected by these gaps. Also, in some groups, we see contrasting patterns such as south to north diversification in centipedes and vice versa in loaches. These patterns hint at the role of historical biogeography of the group as a whole in shaping their distribution. Thus, to better understand the role of these gaps in shaping the distribution of intraspecific genetic variation and interspecific diversification, one needs to also look into the ecology, life-history traits, historical biogeography of the taxa in question.

However, it must be pointed out that there are several knowledge gaps regarding the role of these gaps as biogeographic barriers. First, it seems like the PG has caught the attention of researchers more compared to the other gaps. Nevertheless, it can be said that PG is a more prominent barrier than SG for the groups investigated in this review, but the number of studies investigating the role of PG and SG in shaping distributions is much higher than GG (from Table 1). Second, GG might be more of a climatic rather than a physical barrier. North of GG, the climatic conditions are very different than central and Southern WG in that this region receives lower rainfall and has a long dry season which in turn has influenced the habitat (see Sect. 1). Third, and most importantly, these studies encapsulate a very small fraction of endemic diversity of WG. Birds are the only taxa that are comparatively well explored. Robin et al.[46] have explored the effect of these gaps (PG, SG and Chaliyar valley but not GG) at the community level in montane birds. However, no such study has been done for other groups. WG has a rich diversity of herpetofauna with a high degree of endemism (65% in amphibians, 62% in reptiles). There are only two examples from squamates and four examples from amphibians. Understanding the community-level patterns among herpetofauna is needed to draw a conclusion regarding the effect of these gaps as a barrier to gene flow. In the case of mammals, the studies are also biased towards large mammals. Investigating the effect of these gaps in small mammals like the giant squirrel, rodents (like *Rattus satare*) and other endemic mammals will help us to understand if category A is prevalent among mammals. There is also a scarcity of studies from invertebrates (only three examples) and plants. Testing the effect of these gaps on endemic tarantulas (like sub-family Thrigmopoeinae) will be interesting as these are ancient taxa and occupy a narrow niche with poor dispersal ability[52].

Thus, for the better understanding of the role of these gaps as barrier to gene flow and species distributions, a wider sampling of taxonomic groups of species with different life-history traits, ecology and biogeography is needed.

Publisher's Note

Author contributions

AB and KPK conceived the paper, AB did the literature search and wrote the first draft, figures jointly prepared by AB and KPK, manuscript vetted and modified by KPK.

Declarations

Conflict of interest

The authors declare that they have no conflict of interest.

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Aritra Biswas Aritra Biswas is a Ph.D. student at the Centre for Ecological Sciences at IISc, Bangalore. His research involves using molecular phylogenetic methods to understand the evolution and biogeography of endemic Indian taxa.

K. Praveen Karanth Praveen Karanth's research area deals with the application of phylogenetic tools in understanding macroevolutionary processes. He is particularly interested in biogeography, character evolution, molecular systematics and conservation genetics.