

Tectonic activities shape the spatial patchiness in the distribution of global biological diversity

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The most well-recognized pattern in the global distribution of biological diversity is that the tropics at lower latitudes harbour relatively more species per unit area than the temperate zones at higher latitudes¹⁻¹⁰ and several arguments are forwarded to explain this pattern^{6-8,11-13}. However within the tropics, the biological diversity does not exhibit any distinctly recognizable patterns. Rather it exhibits a very patchy distribution and we do not as yet understand the factors and processes driving such patchiness. In this paper, we demonstrate a strong spatial association between tectonic activities (TA) and the areas of high biological diversity (HBD), especially in the tropics. We argue that TAs over long geological time periods bring about altitude variations in their surrounding areas, contribute to volcanic and magma mineral nutrients and bring about climatic changes, all of which translate into habitat heterogeneity, facilitating a high species packaging in such areas. Thus, we propose that within the biologically-rich tropical belt, spatial distribution of biological diversity is brought about by the tectonic activities.

BIOLOGICAL diversity on our planet is concentrated in the tropical belt, but our understanding of any patterns in its

distribution within the tropics is very limited; less so of the factors driving such patterns. It has been suggested that the existing biologically-rich patches of the planet could be viewed as Holocene refugia¹³, akin to Pleistocene refugia. Accordingly, just as certain pockets of the planet served as refugia for biological diversity in the Pleistocene era¹⁴⁻²⁰, in the present human-dominated world, a few areas inaccessible to human activities have remained as less or undisturbed islands amidst an ocean of human habitation, retaining a high level of biological diversity. One common feature of most of these biologically-rich areas is high altitude variation associated with habitat diversity^{13,21}. Most of the hot spots and areas of high biological diversity are concentrated in hilly and mountainous ranges that harbour diverse habitats. While the habitat diversity associated with the altitude variations facilitates a high species package, the altitude variation per se renders these areas relatively inaccessible, with the net effect that they harbour high diversity¹³. Large-scale altitude variations over vast areas are created mostly due to recurring tectonic activities (TA) over long geological periods. Thus it is likely that recurrent TA over long geological time periods facilitates the concentration of the biological diversity in certain areas. TA may also result in high biodiversity in several other ways (see later in the article). In other words, the patchy distribution of biological diversity within the tropics might be predominantly determined by the distribution of tectonic activity in this zone. We tested this relation by analysing the spatial association between the global tectonic activities and the distribution of biological diversity.

We used two data sets to represent areas of HBD: (a) Hot spot (HS) maps^{13,22,23}, and (b) areas of the world with more than 1500 vascular plant species per 10,000 sq km representing high plant diversity (HPD), from the maps prepared by Barthlott *et al.*²⁴ Cologne (scale 1 : 130,000,000). The areas with 200-1500 species

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and < 200 species per 10,000 sq km in these maps were used to represent medium plant diversity (MPD) and low plant diversity (LPD), respectively. We obtained TA maps from Lowman *et al.*²⁵. The maps were digitized onto a common projection (Robinson projection), GIS format and overlaid for further analysis.

TA maps depicting the centres of concentration of volcanoes for the last one million years, and of the epicentres of 200,855 earthquake events (for the period 1963–1998) and, faults – both reverse and major, were obtained from Lowman *et al.*²⁵. For biological diversity, two data sets were used: (a) the HS map prepared by the Conservation International, which incorporates distribution of animal and plant species richness, and their endemism. Hot spots represent species-rich and highly endemic areas that are also under severe threat due to anthropogenic pressures^{13,22}, thus they do not necessarily represent all the areas that are biologically rich. Hence we used another independent data set on plant richness. (b) Plant species richness map: This data set which captures the gradients of the vascular plant species richness has been prepared by Barthlott *et al.*²⁴. Among the ten gradients of plant species richness in this map, the first five (i.e. areas with > 1500 species per 10,000 sq km) were used as areas of HPD. The other five categories were grouped as MPD (those with 200 to 1500 species per 10,000 sq km) and LPD (those with < 200 species per 10,000 sq km) area. Though this data set pertains only to plants, it is generally known that at a global scale, plant and animal diversities are correlated¹⁰. HS and HPD were digitized as independent data sets to represent areas of high biological diversity (HBD). MPD and LPD were also used for spatial analysis as areas of low and moderate diversity. In this paper we refer to HS and HPD as HBD areas.

Centres of volcanic activities were digitized as points and faults as lines, and buffers of varying width (25, 50, 100, 200, 400, 800 km) were drawn around them to represent areas impacted by the TA. These buffers were overlaid on maps of biological diversity and the areas of the land mass, HS and different gradients of plant diversity covered within these buffers were measured. Proportion of land mass in buffers that are occupied by HS, HPD, MPD and LPD was computed. The spatial association between the TA and the areas of HBD was tested in two different ways:

(1) Spatial correlation and or correspondence between TA and biological diversity: The entire globe was divided into 5° × 5° grids, and a two-way contingency table was set-up for the presence (or absence) of TA and of HBD. The strength of the association between them was measured as the phi-coefficient and the level of its significance by chi-square test²⁶. Pearson's product moment correlation was computed between the land mass areas in the buffers associated with TA and that with HS, HPD, MPD and LPD in the respective grids. Analysis was repeated for grid sizes 50, 100 and 200 km.

(2) Comparison of the observed and expected areas of different biodiversity categories covered in the buffers around TA: The globe was divided into 5° latitude zones, and the total area of the land mass (LM), HS, HPD, MPD and LPD in each zone was measured. Areas of these covered within the buffers drawn around the tectonic activities (observed) were also measured. If the TA and the HBD areas are independently distributed on the land mass, then the proportion of the latter covered within the buffers should be equal to that of the land mass covered within the buffers. Accordingly, the expected area of HS

Table 1. Probability levels of significance of *t*-test between the expected and observed areas of biodiversity categories

Buffer size (km)	HS	HPD	MPD	LPD
25	+ 0.0045; <i>n</i> = 36 (0.0036; <i>n</i> = 20)	+ 0.0083; <i>n</i> = 36 (0.0071; <i>n</i> = 19)	- 0.0207; <i>n</i> = 36 (0.0204; <i>n</i> = 27)	- 0.1637; <i>n</i> = 36 (0.1649; <i>n</i> = 27)
50	+ 0.004; <i>n</i> = 36 (0.0031; <i>n</i> = 20)	+ 0.0069; <i>n</i> = 36 (0.0057; <i>n</i> = 19)	- 0.0156; <i>n</i> = 36 (0.0152; <i>n</i> = 27)	- 0.1794; <i>n</i> = 36 (0.1806; <i>n</i> = 27)
100	+ 0.0012; <i>n</i> = 36 (0.0007; <i>n</i> = 20)	+ 0.0047; <i>n</i> = 36 (0.0037; <i>n</i> = 19)	- 0.0078; <i>n</i> = 36 (0.0074; <i>n</i> = 27)	- 0.2125; <i>n</i> = 36 (0.2136; <i>n</i> = 28)
200	+ 0.0013; <i>n</i> = 36 (0.0008; <i>n</i> = 20)	+ 0.0122; <i>n</i> = 36 (0.011; <i>n</i> = 19)	- 0.0351; <i>n</i> = 36 (0.035; <i>n</i> = 27)	- 0.1487; <i>n</i> = 36 (0.1497; <i>n</i> = 28)
400	+ 0.0211; <i>n</i> = 36 (0.0202; <i>n</i> = 20)	+ 0.0227; <i>n</i> = 36 (0.0218; <i>n</i> = 19)	- 0.0718; <i>n</i> = 36 (0.0722; <i>n</i> = 27)	- 0.1688; <i>n</i> = 36 (0.1698; <i>n</i> = 28)
800	- 0.2442; <i>n</i> = 36 (0.2474; <i>n</i> = 20)	+ 0.1128; <i>n</i> = 36 (0.1144; <i>n</i> = 19)	- 0.1076; <i>n</i> = 36 (0.1084; <i>n</i> = 27)	+ 0.3194; <i>n</i> = 36 (0.32; <i>n</i> = 28)

'+' indicates observed > expected; '-' indicates observed < expected.

Since several of the 36 zones of 5° latitude did not have the expected areas *t*-test was repeated only for those zones which did have biodiversity covering them. These are given in parentheses.

and other categories of plant diversity was computed as

$$\text{Expected area for HS} = \text{LM within buffer} * \text{HS/LM}, \tag{1}$$

for each of the 5° latitudes and compared with that observed for these categories using a one-tailed *t*-test (the 5° latitude zones were used as the replicates). The analysis was carried out for the buffer sizes 25, 50, 100, 200, 400 and 800 km.

The proportion of the area with HBD (i.e. of HS or HPD) covered within the buffers drawn around the TA was always higher than that predicted for independent distribution of the TA and HBD zones (see below and Table 1 for test of this). The other categories (MPD and LPD) were equal to, or, less than that predicted (Figure 1; inset). This was true for a range of buffer sizes from 25 to 800 km, though the deviations were higher for buffers of the size 100 to 200 km (Figure 1; inset). If the HBD is distributed independent of the TA, then the proportion of the buffer areas covered by HS and HPD should remain the same, irrespective of the buffer size drawn around the TA. But these proportions decreased significantly with the buffer sizes (Figure 1). Thus HBD areas appear to be concentrated around TA, while MPD and LPD areas are located away or independent of the TA.

The areas of HBD included in the buffers around TA in each of the 5° latitudinal zones were compared with those expected for an independent distribution of the two events (Figure 2 *a* and *b*). Three conclusions emerged: (a) As expected, the areas of HBD are concentrated in the zones between 45°N and 30°S (Figure 2 *a* and *b*); (b) The observed area of HBD covered within the buffers around the TA was significantly higher than that expected for an independent distribution of the two events (Figure 2 *a* and *b* and Table 1). This was true for a range of buffer sizes

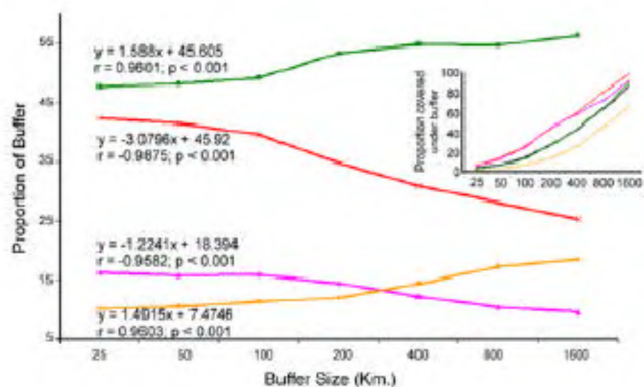


Figure 1. Proportion of buffer land mass area covered by hot spots (pink line), high (red line), medium (green line) and low (yellow line) plant diversity zones with increasing size of the buffers. (Inset) Proportion of the total land mass (black line), hot spots (pink line), high (red line), moderate (green line) and low (yellow line) plant diversity covered within the buffers of increasing sizes around the TA.

from 25 to 400 km; for buffer size of 800 km, the expected and observed areas of HBD did not differ; (c) On the other hand, the observed areas of MPD were significantly less than expected; observed areas of LPD did not differ from the expected. Thus HBD appears to be concentrated in and around tectonic zones, while MPD and LPD are distributed away from or, independent of, the TA.

Since most of the biological diversity was concentrated in the tropical zones (30°N and 30°S), we assessed the spatial correlation between the TA and the HBD only for these zones, using the grid size of 5° (longitude) × 5° (latitude). There was a strong and significant association (correspondence) between the occurrence of the TA with that of the HBD in the grids (r_{ϕ} , Table 2). This association was true for buffer sizes 50, 100 and 200 km (we did not attempt for buffer sizes with 400 km and more, because such buffers were likely to spread into adjacent grids). The areas of land masses within the buffers around the TA in a 5° × 5° grid were also strongly and positively correlated with those of HS and HPD (*r*; Table 2). Thus, besides a mere spatially qualitative association, there

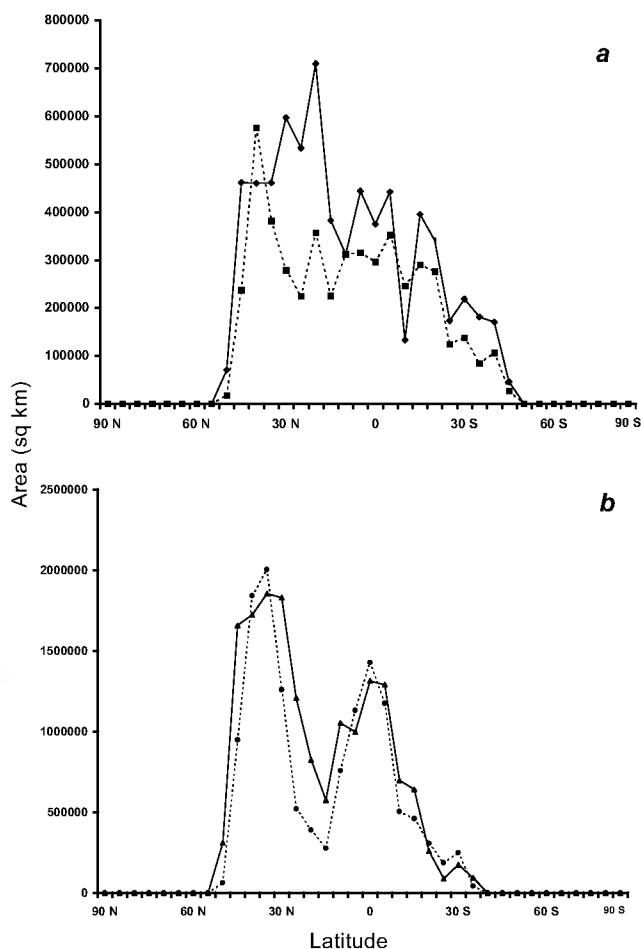


Figure 2. *a*, Expected (dotted line) and observed (solid line) areas of hot spots in the buffer sizes of 200 km in 5° latitude zones. *b*, Expected (dotted line) and observed (solid line) areas of high plant diversity in the buffer sizes of 200 km in 5° latitude zones.

appears to be a quantitative relation between the spread of TA in a grid and the HBD areas.

Thus globally, biological diversity is concentrated mostly in the tectonically active areas of the tropics. Several factors may lead to this relationship:

(a) TA zones are associated with altitude variations. In fact, the tectonic fault lines are inferred from the profile patterns of altitudes²⁵. Altitude variations are most likely to be associated with habitat diversity²², which in turn favours high species packing.

(b) Volcanism and magmatism that provide high nutrients (metallic elements, Fe, Mn, Zn, Se, etc. N, Cl, I, carbon and sulphur compounds and so on) which can encourage biodiversity²⁷.

(c) The climatic changes brought about by elevation that can modify the rainfall rates favourably to one half and adversely to the other half. For example, the rise of the Himalayas has polarized the climate on either side²⁷.

(d) High variations in the altitude are associated with steep slopes and mountain ranges that are not easily accessible and hence these areas retain their biological diversity relatively unaffected.

Admittedly, some of these processes are destructive as well, for example, volcanism; but the long aftermath of favourable nutrient supply and other favourable factors may outweigh the destructive consequences. In fact, the frequent disturbances in the geological and climatic conditions of the areas are known to favour HBD. At least one of HS zones, the Amazon, is attributed to the frequent perturbations due to flooding of the area¹⁴ and this is one among the few HS areas that does not appear to be associated with the TA (Figure 3). It is also likely that all these processes might act synergistically causing accumulation of biological diversity along the areas of the TA. Understanding the influence of these conditions on the HBD might be a challenging task per se.

Of the 28 hot spots, a few, viz. the Amazon, Western Ghats and certain areas of Africa did not appear to be spatially associated with the TA (Figure 3). This could be because, factors other than TA could be causing packing of HBD¹⁴ (as in the Amazon) or, the data sets of the TA might be incomplete on these areas. Further, tectonic belts in the near past can imbibe a critical level of biodiversity that grows with time, under stable regimes. Perhaps the Western Ghats exemplifies this possibility. About 65

Table 2. Phi coefficient of association (r_ϕ) and Pearson's product moment correlation (r) between tectonic activity and biological diversity zones in the tropical belt

	HPD	HS	MPD	LPD [#]
r_ϕ				
Buffer 50 km	0.23; $P < 0.001$; $n = 467$	0.13; $P < 0.01$; $n = 467$	0.11 [@] ; $P < 0.02$; $n = 467$	0.12; $P < 0.02$; $n = 467$; (0.02 [@] ; NS; $n = 467$)
Buffer 100 km	0.24; $P < 0.001$; $n = 467$	0.12; $P < 0.02$; $n = 467$	0.15 [@] ; $P < 0.01$; $n = 467$	0.14; $P < 0.01$; $n = 467$; (0.05 [@] ; NS; $n = 467$)
Buffer 200 km	0.19; $P < 0.001$; $n = 467$	0.13; $P < 0.01$; $n = 467$	0.14 [@] ; $P < 0.01$; $n = 467$	0.11; $P < 0.02$; $n = 467$; (0.06 [@] ; NS; $n = 467$)
r				
Buffer 50 km	0.33; $P < 0.001$; $n = 467$; (0.45; $P < 0.001$; $n = 177$)	0.13; $P < 0.001$; $n = 467$; (0.16; NS; $n = 177$)	0.14; NS; $n = 467$; (0.30; $P < 0.01$; $n = 177$)	-0.08; NS; $n = 467$; (-0.12; NS; $n = 177$)
Buffer 100 km	0.35; $P < 0.001$; $n = 467$; (0.46; $P < 0.001$; $n = 205$)	0.18; $P < 0.05$; $n = 467$; (0.27; $P < 0.01$; $n = 205$)	0.13; NS; $n = 467$; (0.29; $P < 0.01$; $n = 205$)	-0.06; NS; $n = 467$; (-0.10; NS; $n = 205$)
Buffer 200km	0.39; $P < 0.001$; $n = 467$; (0.52; $P < 0.001$; $n = 259$)	0.23; $P < 0.02$; $n = 467$; (0.34; $P < 0.001$; $n = 259$)	0.16; NS; $n = 467$; (0.29; $P < 0.01$; $n = 259$)	-0.02; NS; $n = 467$; (-0.07; NS; $n = 259$)

r_ϕ coefficient was computed from 2×2 contingency table of tectonic activity (present or absent) and biodiversity of given category (present or absent) in grids of $5^\circ \times 5^\circ$. The significance of r_ϕ was determined by computing χ^2 for the table.

[@]The contingency table showed that the number of grids where both TA and MPD co-occur was less than that expected for an independent distribution of the two events.

[#]Only about 15% of the tropical land mass had LPD and hence when the contingency table is set-up for presence or absence of LPD, there were more grids of its absence corresponding to HBD and MPD, confounding the analysis and resulting in a positive association. Therefore the MPD and LPD were clubbed and analysed. These results are shown in parentheses.

r , the Pearson's product moment correlation was computed for the land mass area of the buffer around the tectonic activity and area of biodiversity of the given category in each of the $5^\circ \times 5^\circ$ grids. This association r was computed using only those grids where tectonic activity was recorded. These values are given in parentheses.

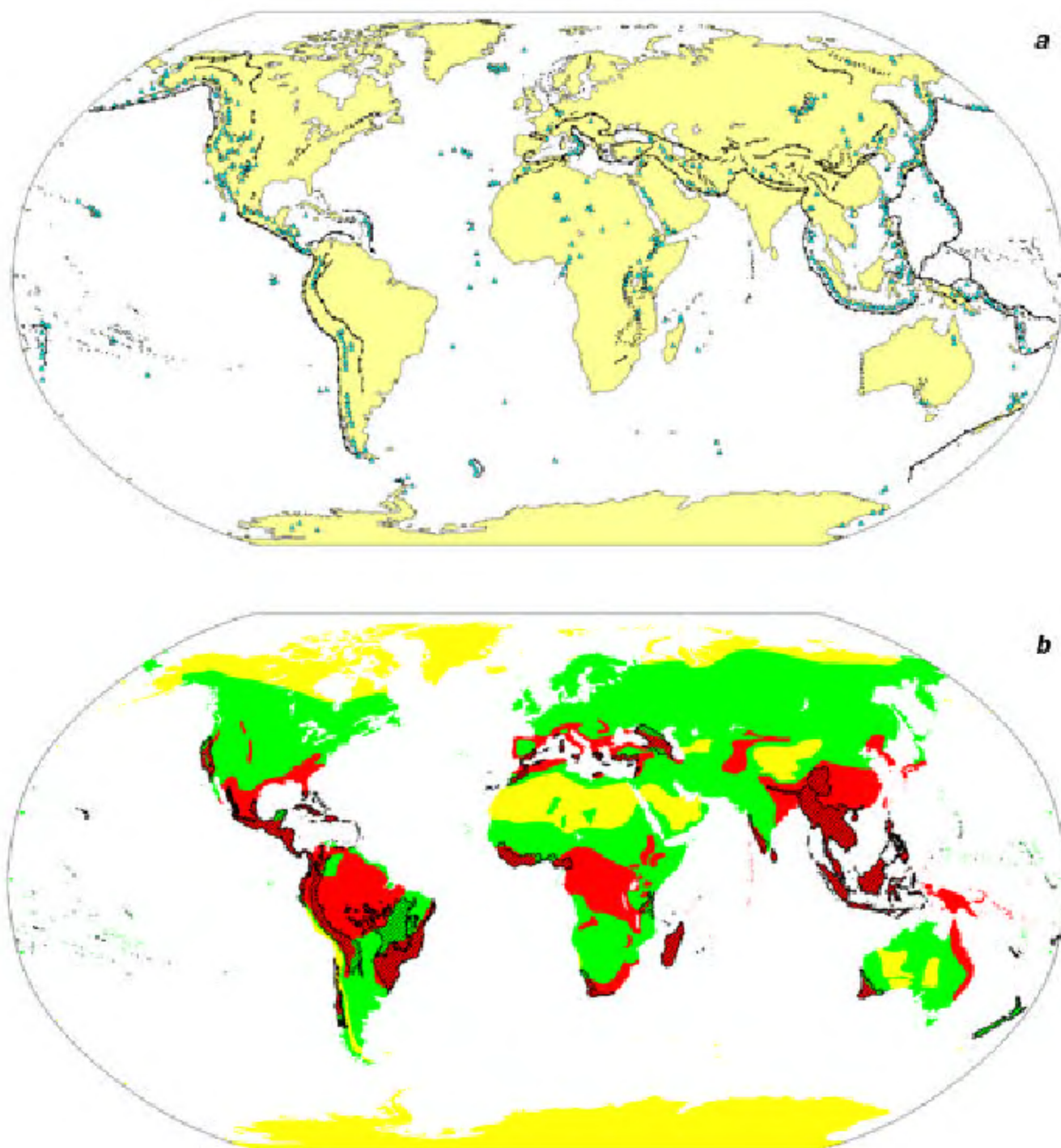


Figure 3. *a*, Digitized map of the tectonic activities (source: Lowman *et al.*²⁵). Reverse faults (hashed line), major faults (solid line), other faults (broken line) and centres of earthquakes (red triangles); *b*, Plant richness and hotspot map (source: Myers *et al.*²² and Barthlott *et al.*²⁴). High plant richness (red area), medium plant richness (green area), low plant richness (yellow area) and hot spots (black shaded area).

million years ago the Western Ghats was the western collar of a rift believed to have been standing over a 'geological hot spot'²³ that ushered in the extensive Deccan volcanism. The western collar of the rift was underplated and uplifted²⁷. In fact, the Western Ghats is known to be tectonically active^{28,29} and it is an uplifted

region. The high biodiversity of this region, therefore may be due to large nutrients the volcanism brought in, the relatively higher thermal gradients along this belt, widely varying elevations and a long period of stability following the 65 million year aftermath of volcanism. In this sense the association between the TA and HBD might be much

more stronger than depicted through our analysis²⁷. All these suggest a possibly greater significance of these below-ground tectonic processes in shaping the otherwise patchy distribution of biological diversity in the tropics.

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ACKNOWLEDGEMENTS. We thank Dr P. Lowman for providing the tectonic activity maps and relevant papers, Dr Barthlott for the map of the vascular plant distribution and Conservation International for maps and data on hot spots. We also thank Dr R. Uma Shaanker, Prof. K. S. Valdiya, Dr N. V. Joshi, Dr Chandrashekara and Dr A. R. V. Kumar for their help in developing the idea. We thank DBT, New Delhi for financial help.

Received 30 August 2001; revised accepted 15 November 2001