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## **Valley forests as ecological bottlenecks: Topography and resource concentration structure herbivore use in the Western Ghats**

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The full-length article is available in Kannada and Sanskrit languages in the Supporting section S1 and S2.

## Abstract

Large-herbivore distributions in the Western Ghats are often interpreted through the perspective of protected areas, forest loss, and human disturbance. This perspective can undermine the ecological role of valley forests and riparian lowlands in steep, human-modified landscapes. Evidence from Asian elephants and other large herbivores indicates that habitat use is shaped by interacting filters of topography, water, forage, and human pressure, with valley systems frequently concentrating accessible resources and movement pathways. In the Western Ghats, dry-season elephant occurrence is strongly associated with rivers and forest cover, while assemblage-level studies show multiple herbivores responding similarly to forest cover, reserve proximity, and human density. These findings support the hypothesis that low-lying forests act as ecological bottlenecks; constrained areas with abundant resources due to topographic conditions. Degradation of valley forests is likely to redistribute herbivore activity toward adjacent agricultural and settlement areas, rather than simply reducing habitat use. We suggest that valley forests and riparian lowlands should be treated as explicit management units in conservation planning and conflict mitigation, while targeted tests using movement data, occupancy models and spatial conflict records are needed to evaluate this mechanism more directly.

**Keywords:** Western Ghats; large herbivores; valley forests; habitat use; human-wildlife conflict; landscape connectivity

## Main text

Large-herbivore distributions in the Western Ghats region of India are structured less by protected-area boundaries than by the interaction of topography, resource availability, and human disturbance (Karanth 2016). In this context, valley forests and riparian habitats warrant explicit attention. These habitats function as disproportionately important zones where multiple limiting resources converge due to topographic conditions. Valley forests and riparian lowlands occupy an awkward position in this planning landscape: they are rarely large enough to qualify as priority conservation units under area-based criteria, yet they are disproportionately exposed to encroachment, hydrological alteration, and invasive plant spread precisely because they sit at the interface of forest and agricultural land (Richardson et al. 2007). This positional vulnerability, combined with their functional importance for large herbivores, makes them a category of habitat that current frameworks consistently undervalue (Jelil et al. 2021). Degradation of these critical habitats is likely to redistribute, rather than simply reduce, herbivore use across the landscape (Lakshminarayanan et al. 2016; Neupane et al. 2019). This argument is strongest for elephants but is supported more broadly by patterns across other large herbivores in the region (Karanth 2016).

The Western Ghats combine steep elevational gradients, dissected terrain, and fine-scale land-use heterogeneity over short distances (Pascal 1988; Pascal & Pelissier 1996; Harbor & Gunnell 2007; Das et al. 2015). The range extends approximately 1,600 km along the western coast of peninsular India, with elevations rising sharply from coastal lowlands to peaks exceeding 2,500 m, creating one of the steepest and most biologically diverse escarpments in tropical Asia (Myers et al. 2000; Gunawardene et al. 2007). Valley bottoms and riparian corridors in this system sit within a matrix of smallholder agriculture, plantation crops, and settlements that interrupt forest cover at fine spatial scales, placing large herbivores in frequent proximity to human land use (Jha et al. 2000; Raman et al. 2009). In such landscapes, movement is not equally feasible across space, and large herbivores must balance forage acquisition, water access, and the energetic and risk costs of moving through rugged or disturbed areas (Lakshminarayanan et al. 2016). Under these conditions, habitats that offer relatively gentle terrain, reliable water, and productive vegetation are expected to play a key role in structuring movement and habitat use. Valley forests and riparian corridors frequently meet these conditions and thus emerge as candidate ecological bottlenecks that organise movement and occurrence across the wider landscape matrix (Lakshminarayanan et al. 2016; Neupane et al. 2019). We use the term 'ecological bottleneck' here to refer to habitats where topographic constraints simultaneously funnel animal movement and concentrate access to multiple limiting resources such as

water, forage, and gentle terrain - such that changes in these areas have disproportionate effects on space use across the surrounding landscape.

Asian elephants (*Elephas maximus*) provide the clearest support for this perspective. Across tropical Asia, elephant habitat use is strongly influenced by water availability, vegetation structure, food reserves, slope, and elevation, with anthropogenic pressure further constraining space use (Neupane et al. 2019). In the Western Ghats, dry-season elephant habitat use is best predicted by distance to rivers and forest cover, underscoring the importance of riparian and associated lowland habitats during periods of resource limitation (Lakshminarayanan et al. 2016). Elephants are capable of wide movements, but they are not indifferent to terrain: steep slopes and high elevations restrict use, whereas accessible, vegetated lowlands with water support higher probabilities of occurrence (Lakshminarayanan et al. 2016; Neupane et al. 2019). Recent work from the Western Ghats also shows that seasonal habitat use reflects a balance between resource distribution and human disturbance, with elephants shifting space use between seasons in response to both ecological and anthropogenic drivers (Anoop et al. 2023). Together, these studies suggest that valley forests function as integrated resource zones and movement pathways rather than incidental low-elevation habitats.

The importance of valley forests and riparian corridors extends beyond elephants, although in a more context-dependent way. Gaur (*Bos gaurus*) habitat use is shaped by forage quality, vegetation structure, water availability, and human disturbance, with some populations making substantial use of productive lowland and transition habitats when these concentrate resources (Sankar et al. 2013; Poudel et al. 2024). Sambar (*Rusa unicolor*) show more variable responses across landscapes: habitat selection is influenced by canopy cover, vegetation density, elevation, and proximity to water, but the relative importance of these factors differs among sites (Haleem & Ilyas 2023). This variation indicates that valley forests are not universally preferred or sufficient habitats for all species; rather, they exert their influence through general constraints - access to water, forage, and traversable terrain - expressed differently across species and settings.

More generally, research from Karnataka state shows that elephants, gaur, sambar, chital (*Axis axis*), and wild pig (*Sus scrofa*) all respond to forest cover, distance to reserves, and human density (Karanth 2016). A comparable pattern has been documented in the steep terrain of the Tenasserim-Dawna Mountains, Thailand, where ungulate assemblage abundance, including gaur herds, muntjac, sambar, and wild pig groups was significantly higher in lowland forest (600–1,100 m) than in montane forest (1,100–1,800 m) across four dry seasons, with the lowland concentration attributed to the convergence of grass, bamboo, mineral licks, and water sources that are scarce at higher elevations (Steinmetz et al. 2008). Notably, elephants in that system were concentrated in montane forest, reflecting human-compelled displacement from heavily hunted lowlands rather than intrinsic habitat preference, underscoring that anthropogenic pressure can override topographically expected distributions. A parallel pattern emerges across a very different tropical system: in the Serengeti, Africa, large-bodied herbivores including elephants and buffalo were significantly more concentrated near rivers than smaller-bodied species, with proximity to riverine and woodland habitats emerging as a strong predictor of occupancy for the largest members of the herbivore guild (Anderson et al. 2016). Taken together, these results point to multiple interacting filters shaping herbivore distributions and situate valley forests as one class of habitat where several of these filters converge. Valley and riparian systems are often forested, relatively less steep, and close to surface water, and they frequently occur near or across reserve boundaries; together, these attributes increase their potential to structure occurrence across the broader mosaic (Steinmetz et al. 2008; Anderson et al. 2016; Karanth 2016; Lakshminarayanan et al. 2016).

The implications of framing valley and riparian areas as critical habitats become most pronounced when connected to human-wildlife interactions. If valley forests function as concentrated resource zones under topographic constraints, then their degradation is unlikely to manifest as a simple contraction of herbivore ranges. Instead, declines in forage quality, water persistence, or connectivity within these habitats are expected to redistribute herbivore activity, increasing the likelihood that animals use adjacent croplands and settlement edges where crops provide predictable, high-quality food (Karanth 2016; Ramesh et al. 2022). This redistribution is expected because large herbivores facing resource loss in a concentrated habitat must seek alternatives rather than cease foraging; where valley forests are degraded, the nearest alternative is often the crop mosaic at the forest edge, which offers both accessibility and reliable forage. In southern

India, occupancy-based work has shown that elephants and other herbivores frequently occur outside protected areas and that their distributions are influenced by forest cover, reserve proximity, and human density (Karanth 2016). Additional studies across the Eastern and Western Ghats demonstrate that terrain, water distribution, and crop configuration influence where human-megaherbivore interactions and damages occur (Ramesh et al. 2022). Together, these findings make it ecologically plausible that degradation of valley forests and riparian lowlands would displace herbivore use toward human-dominated lands, even if direct causal pathways remain to be tested.

Recognising valley forests as ecologically strategic habitats helps integrate insights from habitat-use studies, landscape ecology, and conflict research that are often treated separately. Habitat-use analyses emphasise the importance of water, slope, and forest structure, while work on herbivore occurrence in human-dominated matrices highlights persistence and movement outside reserves and sensitivity to human density and land-cover configuration (Karanth 2016; Lakshminarayanan et al. 2016). Conflict studies, in turn, document how megaherbivore interactions with people vary with terrain and the spatial configuration of crops and water (Ramesh et al. 2022). A valley-focused lens provides a unifying framework by identifying where these ecological and social constraints intersect in space. Yet no study in the Western Ghats has been designed to evaluate valley and riparian habitats as the spatial intersection where habitat-use constraints, landscape connectivity, and conflict risk converge simultaneously – leaving a conceptual gap between what existing studies collectively imply and what has been explicitly tested.

The management implications of recognising the importance of valley forests are direct. Conservation planning in the Western Ghats has often prioritised aggregate forest cover and protected-area networks (Das et al. 2006; Athira et al. 2017). This remains essential, but it is unlikely to be sufficient if valley forests and riparian corridors act as functional nodes that disproportionately influence herbivore distribution and conflict risk. Maintaining and restoring lowland forest strips, riparian vegetation, and connected foraging habitats may be as important as protecting upland blocks for sustaining populations and moderating conflict (Karanth 2016; Lakshminarayanan et al. 2016). Conversely, degradation of these habitats through encroachment, hydrological alteration, or invasive plant spread may have cascading effects that extend beyond their limited spatial extent.

At the same time, the argument for special recognition of valley and riparian forests must be supported with further empirical research. Current studies in the Western Ghats identify correlates of herbivore occurrence and conflict (Ramesh et al. 2022; Pavithra et al. 2025), but few are designed to evaluate whether valley habitats mediate the relationship between resource decline and animal redistribution (Karanth 2016; Ramesh et al. 2022). Addressing this gap will require integrating occupancy models, movement data, fine-scale measures of forage and water persistence, and spatial records of damage or encounters, with valley and riparian systems treated as explicit hypotheses rather than background categories (Lakshminarayanan et al. 2016; Anoop et al. 2023). Promising study designs would include before-after comparisons of herbivore space use following documented valley forest degradation events, such as encroachment, invasive plant spread, or hydrological alteration, to test whether redistribution toward cropland edges follows detectable loss of valley resources. Paired occupancy models that explicitly contrast habitat use within and adjacent to valley networks, linked to fine-scale maps of forage quality, water persistence, and spatially explicit records of conflict incidence georeferenced relative to valley and riparian networks, would allow direct evaluation of whether valley systems mediate the broader relationship between forest condition and human-wildlife interaction risk.

Valley forests are not universally preferred habitats for all large herbivores across the Western Ghats, and their influence will always be filtered through species traits, local land use, and historical contingencies (Sankar et al. 2013; Haleem & Ilyas 2023). However, where these habitats concentrate accessible forage, water, and movement pathways within a steep and human-modified landscape, they are likely to exert a disproportionate influence on herbivore distribution and on the spatial pattern of human-wildlife interactions (Karanth 2016; Lakshminarayanan et al. 2016; Neupane et al. 2019). Treating valley forests as functional nodes rather than incidental lowlands offers a more mechanistic and testable way to think about herbivore ecology and conservation in the Western Ghats.

## **Supplementary Data**

Supplementary Data D1: Sanskrit language version of the manuscript.

Supplementary Data D2: Kannada language version of the manuscript.

## **Author contribution**

NA and RT conceived the research. RT and NA wrote the manuscript. All co-authors contributed to manuscript revision and approved the final version for submission.

## **Conflict of interest**

The authors declare no conflict of interests.

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