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Functional variations in spider communities across different land-use categories along an elevational gradient in North-Western Indian Himalaya

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Abstract

1. Land-use change and elevational gradients jointly influence biodiversity and species distribution, yet their concurrent effects on arthropods in the Indian Himalayan Region remain largely undocumented.
2. Using spiders as a model taxon, this study assesses the parallel influences of elevation (1500–4500-m at 500-m intervals) and land-use categories *viz.* forests, agricultural lands and human-dominated regions on spider functional diversity in a North-Western Himalayan landscape.
3. The results show non-general patterns, with significant discrepancies in managed habitats compared to forests, and a higher abundance of synanthropic species in human-dominated regions.
4. Directional shifts in functional traits are associated with elevational change, with the transition between 3000 and 3500 m emerging as a critical functional and community threshold for Himalayan spider assemblages.
5. The findings highlight functional variability under simultaneous natural and anthropogenic pressures and raise concerns about habitat homogenization driven by large-scale agro-production in climate-vulnerable Himalayan regions, potentially shifting biodiversity towards new functional regimes.

KEYWORDS
Araneae, Community Ecology, Environmental gradient, Functional Trait, Indian Western Himalaya

INTRODUCTION

Land-use changes across mountain ecosystems of the global south remain distinct and pervasive. Contemporary threats to these landscapes, especially in the Himalaya, emerge from anthropogenic activities, particularly agricultural expansion (Batar et al., 2017; Mondal & Zhang, 2018; Nandy et al., 2015). The conversion of complex natural landscapes to simplified ecosystems leads to changes in ecological structures, often resulting in taxonomic and functional homogenization (Cadotte & Tucker, 2017; Ibáñez-Álamo et al., 2017; Penjor et al., 2022). This is evidenced by reduced species diversity and ecosystem functionality across different trophic scales (Grab et al., 2019; Le Provost et al., 2020; Shahabuddin et al., 2021; Thakur & Chawla, 2019). While responses of mammals and birds to changing land-use and climate are well documented (e.g., Dar et al., 2021; Girish & Srinivasan, 2020; Penjor et al., 2021; Srinivasan et al., 2019), our understanding of how ectothermic fauna respond to these changes remains currently limited (Mungee & Athreya, 2019, 2021). Changing climate and land-use regimes have been identified as primary drivers of widespread loss of arthropod diversity globally (Martínez-Núñez et al., 2024; Outhwaite et al., 2022; Raven & Wagner, 2021). Research has also demonstrated spillover, that is., dispersal of species across habitat borders, of arthropods across variably managed habitats (Gallé et al., 2020; Madeira et al., 2016; Opatovsky & Lubin, 2012). While this can potentially affect ecosystem functioning and ecological interactions (Schneider et al., 2013; Tscharntke et al., 2012), its extent of occurrence in Himalayan ecosystems is scarcely understood.

Although diversity has traditionally been measured as taxonomic diversity (TD), the concept alone fails to explain fluctuations in functional strategies that influence ecosystem functioning (Swenson, 2014; Violle et al., 2014). Several research has indicated stability in TD in response to shifting land-use patterns (Ernst et al., 2006; Spaak et al., 2017) despite functional homogenization and possible redundancy (Aguirre-Gutiérrez et al., 2017; Petchey et al., 2007). This allows for functional diversity (FD) to serve as a robust currency for quantifying community resilience to natural and anthropogenic perturbations. Trait-based metrics such as Functional Diversity Index (FDI) and Functional Redundancy (FunRed) provide insights into uniqueness and composition of traits within communities and can be used to inform community resilience (de Bello et al., 2007; Laliberté & Legendre, 2010; Pillar et al., 2013; Villéger et al., 2008).

Arthropods represent an excellent group for taxonomic and trait-based studies, including those assessing FD, owing to their wide distribution throughout the terrestrial biosphere (Stork, 2018). Within the hyperdiverse group, spiders (Arthropoda, Arachnida, Araneae), can provide powerful tests of multifaceted diversity patterns owing to their high diversity, integral role within terrestrial trophic webs and demonstrated ecosystem services (Cardoso et al., 2011; Fernández et al., 2018; Macías-Hernández et al., 2020; Pekár et al., 2021). This is furthered by their sensitivity to small changes in habitat structures, including vegetation complexity, litter depth and microclimate characteristics (e.g., Cardoso et al., 2010). Furthermore, several studies have corroborated that different land-use and management practices introduce variable environmental and species compositions, consequently influencing functional variations (Gallé et al., 2018; Mazzia et al., 2015; Pinto et al., 2021; Potapov et al., 2020). Similar implications have also been reported from India, albeit along gradients of habitat disturbances (De et al., 2023; Sharma et al., 2024). Although research assessing functional variabilities of Indian Himalayan fauna are limited, some have reported a decline in functional attributes with elevational increase (Chakravarty et al., 2021), while others have reported functional randomness (Mungee & Athreya, 2019). However, investigations into functional variations in Himalayan spider communities remain hitherto unknown, across both elevation and land-use gradients (Sarkar et al., 2023).

The current study addresses a significant knowledge gap by conducting the first assessment of functional variations in spider assemblages in the North-Western Himalaya. Particularly, we compare FD variations across three land-use classes (forests [FR], agricultural lands [AG] and human dominated regions [HD]) along a common elevational gradient of 1500-4500 m. The primary objective is to understand how functional properties vary across different land management strategies when a constant elevational gradient is maintained. The study provides insights into how Himalayan spider communities respond to simultaneous effects of elevational changes and land management practices. The overarching goal is to provide evidence for the influence of land-use variabilities (and management) in shaping spider FD. Understanding these dynamics is vital for informed conservation strategies that need to consider both elevation and land management practices as factors in predicting future implications of rapidly changing environments in the Indian Himalayas.

MATERIALS AND METHODS

Study area and sampling design

The study was conducted in the Himalayan State of Himachal Pradesh (HP), India. Covering an area of 55,673 sq. km., HP accounts for 1.69% of the national geographic area, 10.54% of the Indian Himalayan landmass and 17% of the North-Western Himalayan area (FSI, 2019; Sharma & Sidhu, 2016). The geomorphological relief features of the State comprise of massive peaks, hills, valleys, spurs and mountains, with an elevational gradient of 248 m–6500 m (Upgupta et al., 2015). The state harbours one of the most diverse bioreservoirs in the world, with eight classified forest groups, further subdivided into 39 forest types. Broadly, coniferous and broad-leaved forests are distributed along the elevational gradient of the state with the lowest and highest zones are represented by dry scrub forests and alpine pastures, respectively, with distinct bands of mixed deciduous forests.

Field work was conducted across an elevational gradient of 1500-4500 m in two districts of HP, Kullu and Lahaul-Spiti (LS) (Figure 1), encompassing two protected areas and their respective buffer zones: Great Himalayan National Park Conservation Area, Kullu (GHNPCA: 1500 m–2500 m) (hereafter represented as E1500–E2500) and Kibber Wildlife Sanctuary, Spiti (E4000–E4500), and two Reserve Forests (RFs), Lahaul (E3000–E3500). GHNPCA, situated at the convergence of the Indomalayan and the Palearctic realms, supports 25 forest types, including temperate broadleaved, conifer, scrub, sub-alpine and alpine vegetation (Singh & Rawat, 1999). It serves as a core conservation area within the North-Western Himalayan landscape and is recognized as a UNESCO World Heritage Site for its biodiversity significance (UNESCO, 2014). Here you can add some line regarding selecting the two study area depicting the fact that at GHNPCA other land-use areas are not there.

Lahaul-Spiti, constitutes the largest district in HP, situated between the mountain chains of Pir Panjal of the Greater and Trans Himalaya (Aswal & Mehrotra, 1994; Joshi et al., 2020). Lahaul consists of glacial valleys with high mountain ranges, while Spiti is a comparatively drier valley located in the rain-shadow area of the Great Himalayan range, and includes the Kibber Wildlife Sanctuary (WLS), an integral part of the Cold Desert Biosphere Reserve (CDBR). This extremely arid and high-altitude terrain, with its challenging environmental conditions, shelters a diverse array of unique and endemic species (Kala, 2000, 2005; Sharma & Samant, 2019).

Systematic elevational sampling was conducted in intervals of 500 ± 100 m, resulting in seven sampling bands. Within each

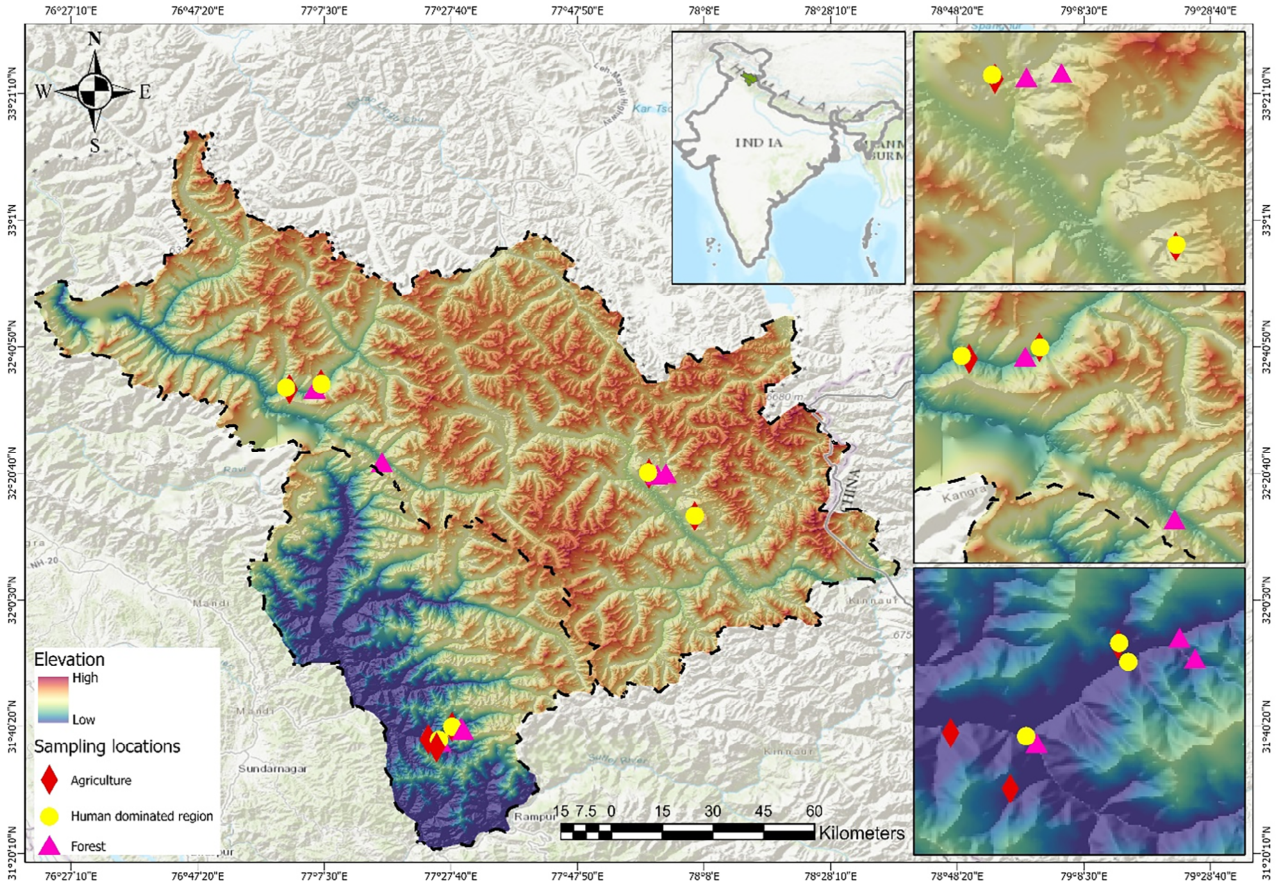

FIGURE 1 Digital Elevation Map (DEM) of study area detailing sampling locations across the study landscapes within each elevational site and independent land-use class. Map insets from bottom to top: sampling within Kullu (E1500–E2500), sampling within Lahaul (E3000–E3500), sampling within Spiti (E4000–E4500).

TABLE 1 Elevational and locality details of sampling sites assessed for the study across independent land-use classes.

Elevation	Sampled Site: Forests (FR)	Sampled Site: Agricultural Lands (AG)	Sampled Site: Human-dominated Regions (HD)
E1500	Gushaini, GHNPCA Eco-zone (Oak and Pine)	Nagni, GHNPCA Eco-zone (Apple Orchard)	Gushaini, GHNPCA Eco-zone (Residential built-up area)
E2000	Rolla Camp, GHNPCA (Pine and Cedar)	Jamala, GHNPCA Eco-zone (Apple Orchard)	Darakhali, GHNPCA Eco-zone (Residential built-up area)
E2500	Kholipoi Nursery, GHNPCA (Silver Fir and Horse Chestnut)	Daran, GHNPCA Eco-zone (Apple Orchard)	Daran, GHNPCA Eco-zone (Residential built-up area)
E3000	Dorni Reserve Forest (Himalaya Birch)	Lower Keylong (Vegetable crop field)	Lower Keylong, Lahaul (Residential built-up area)
E3500	Pangrang Reserve Forest (Pine)	Kwaring (Vegetable crop field)	Kwaring, Lahaul (Residential built-up area)
E4000	Kibber WLS (Shrubs)	Chicham (Vegetable crop field)	Chicham, Spiti (Residential built-up area)
E4500	Kibber WLS (Shrubs)	Komic (Vegetable crop field)	Komic, Spiti (Residential built-up area)

Note: Elevations E1500–E2500 represents Kullu landscape, E3000–E4500 represents Lahaul-Spiti landscape.

elevational zone, we accounted for three broad land-use (LU) categories, totalling to 21 sampling sites (Table 1): Forests (FR) represented protected areas that hosted natural vegetation with minimal interference and no anthropogenic management; AG included fruit/crop fields that were agro-chemically managed for agro-production; HD included the infrastructural habitation zones for local residence. Quadrat-based sampling was adopted, with 25 quadrats, each measuring 1 m*1 m randomly sampled within each site resulting in 525 sampling points. Each quadrat was sampled for 20 min by two individuals simultaneously and independently, to

TABLE 2 Overview of functional traits used for assessing functional diversity and their validity as a justifiable indicator of species fitness.

Trait	Ecological Role	Categorization of values with their ecological roles
Feeding guild	Feeding guild influence access to prey and microhabitat resources, shaping species' foraging strategies and resource sharing, which in turn affects growth, reproduction and survival (Cardoso et al., 2011).	1. Space web builders 2. Orb web builder 3. Sheet web builders 4. Sensing web builders 5. Ambush hunters 6. Ground hunters 7. Other hunters 8. Specialists
Circadian Activity	Body size along with circadian activity dictates partitioning of resources, range of prey and hunting affinities (Cardoso et al., 2011).	1. Diurnal 2. Nocturnal 3. Cathemeral
Prey range	Diet breadth of species dictates trophic specialization and adaptation to new trophic zones by driving physiological efficiency, competition, coevolutionary interactions and use of enemy-free space (Cardoso et al., 2011; Pekár et al., 2012).	1. Euryphagous 2. Stenophagous
Ballooning	Dictates dispersal abilities, since dispersal by ballooning allows spiders to rapidly colonize remote habitats across large distance (Cardoso et al., 2011; Langlands et al., 2011).	1. Capable of efficient ballooning 2. Incapable of efficient ballooning/ballooning restricted over growth phase
Hunting Strata	Vertical stratification of hunting strategies dictates feeding guilds and strategies along with prey range and resource utilization (Cardoso et al., 2011).	1. Ground strata 2. Vegetational strata 3. Both ground and vegetation

ensure swift detection and reduce sample loss, particularly for fast-moving species such as ground-dwellers and active hunters, contributing to a total sampling effort of 175 h per observer, resulting in 350 total sampling hours across all sites. A consistent distance of 3–5 m between each quadrat was maintained to ensure spatial independency. Field sampling was carried out from March to September, 2021.

Spider sampling followed established protocols (Coddington et al., 1996) and involved a combination of active sampling methods such as aerial and ground hand collection along with bush beating. Due to logistical and financial constraints, nocturnal sampling was not conducted, and sampling was standardized across the elevational and land-use gradient to ensure comparability. The methods aimed to sample spiders across different microhabitat and guild preferences. Collected specimens were preserved in 70% ethanol and identified under a Carton DSZ-45 T stereo-microscope, using various keys, catalogues and established literature sources from the World Spider Catalog (WSC, 2023). Species identification was further confirmed through dissection of copulatory organs for taxonomic verification. Sub-adult specimens were identified as morphospecies and later assigned genus-level classification aligning with key identifiable features. Juvenile specimens were excluded from the dataset due to ambiguity of their identification.

Functional traits

Species traits were selected to assess functional variations in species communities as abundance-based data at both overall elevational and LU specific scales. While a combination of morphological, behavioural and life history traits best represent sensitivity to stressors and ecosystem processes (Moretti et al., 2017), we could not determine morphological variations due to a significant proportion of sub-adult specimens. Three ecological (circadian activity, hunting strata, ballooning) and two predational traits (hunting guild and prey range) were selected that directly relate to feeding and dispersal success, consequently dictating overall ecological roles and influence resource partitioning within communities (Table 2). These traits are established predictors of ecological strategies and filtering in ecosystems and values of each were derived from literature (Cardoso et al., 2011; de la Delgado Flor et al., 2020; Gobbi et al., 2017; Lowe et al., 2020; Schirmel et al., 2012).

Data analysis

Taxonomic species diversity was assessed for each elevational-LU site, measured as observed richness and extrapolated using non-parametric estimators (Jacknife, ACE and Chao) (Chao & Chiu, 2016). A rarefaction/extrapolation (R/E) approach was used to estimate both observed and estimated richness, along with sampling completeness through Hill numbers, accounting for both species' abundance and evenness, using the function *iNEXT()* within package *iNEXT* (Hsieh et al., 2016). Species richness estimates can be influenced by sample size and effort. To account for this, we applied a R/E approach, which allows for standardized comparisons of observed and estimated richness while minimizing data loss (Chao & Jost, 2012; Colwell et al., 2012; Hsieh et al., 2016). Sample completeness was assessed through sample coverage, representing the proportion of total individuals belonging to detected species (Hsieh et al., 2016).

Quantification of various FD metrics was achieved through a distance-based multidimensional framework, specifically designed to assess FD using a Gower dissimilarity matrix derived from trait data (Laliberté et al., 2014). Each metric was assessed at two scales, overall elevational and elevational-LU gradients. The former combined data from all sampled sites without accounting for LU differences. The latter assessed each LU as an independent dataset (along a common elevational gradient) to quantify FD. Functional Richness (FRic) quantifies the variety of functional traits present within a community, higher values indicating more diverse capacities to perform ecological roles. Functional Evenness (FEve) measures the evenness of trait distribution within a community, representing the balance of ecological functions. Functional Divergence (FDiv) evaluates the degree of (dis) similarity among species in terms of the traits they possess. Functional Dispersion (FDis) reflects the average trait dissimilarity among co-occurring species (Laliberté & Legendre, 2010), while Rao's Quadratic Entropy (RaoQ) accounts for both species' abundances and trait differences, thereby providing a measure of diversity and community trait heterogeneity (Rao, 1982; Swenson, 2014). FunRed quantifies functional similarities among species within a community and can be used to inform community resilience (de Bello et al., 2007; Pillar et al., 2013). FunRed was calculated using the function *rao.diversity()* in package *SYNCSA* (Debastiani & Pillar, 2012), while all other functional metrics were computed using function *dbFD()* within package *FD* (Laliberté et al., 2014). All FD metrics were regressed against elevational turnovers for each LU class to assess independent elevational relationships and graphically represented.

We conducted Tukey's post hoc tests within each land-use type to identify significant differences in FD metrics (FRic, FEve, FDiv, FDis, RaoQ and FunRed) across immediately adjacent elevation bands (E1500–E2000, E2000–E2500 and so on) to identify key transitional zones of changing species adaptabilities. This approach assessed whether specific elevation bands exhibited distinct shifts in functional structuring while minimizing the confounding effects of comparing extreme elevations (e.g., E1500–E4000).

While Mason et al. (2005) and Villéger et al. (2008) developed several indices to quantify FD, others (Garnier et al., 2004; Lavorel et al., 2008; Ricotta & Moretti, 2010) argued that the range and distribution of individual trait values offer more suitable insights into assessing relationships between community structure and ecological dynamics. Thus, to assess the influence of elevation on individual traits characteristics, we calculated the Community Weighted Means (CWM) of each quantified trait at each site using *functcomp()* function within package *FD* (Laliberté et al., 2014). This metric calculates the average value of a particular trait within each specific elevational-LU unit, considering the relative abundance of each trait value within that unit (Bricca et al., 2019; Garnier et al., 2004). This essentially indicates how trait properties shift in their independent characters to accommodate for changing habitat gradients. Additionally, to account for hierarchical sampling and uneven temporal coverage, we additionally fitted generalized linear mixed-effects models (GLMMs) with site identity (defined as elevation band and land-use type) and sampling month included as random intercepts, while elevation was treated as a continuous fixed effect. All analysis was performed in R version 4.2.1 (R Core Team, 2013) using packages *SYNCSA* (Debastiani & Pillar, 2012), *vegan* (Oksanen, 2010), *FD* (Laliberté et al., 2014), *BAT* (Cardoso et al., 2015), *iNEXT* (Hsieh et al., 2016), *ggplot2* (Wickham et al., 2016), *glmmTMB* (Magnusson et al., 2017) and *cowplot* (Wilke et al., 2019).

RESULTS

Taxonomic diversity

The study recorded a total of 2936 adult and sub-adult individuals representing 126 species across 65 genera and 26 families from the study area (Supplementary Annexure 1). Along independent land-use (LU) classes, we recorded 85 species across 49 genera from 21 families from FR, 43 species across 29 genera and 15 families from AG and 73 species across 45 genera and 22 families from HD (Table 3). Taxonomic diversity, measured as observed species richness and richness estimators, generally declined with increasing elevation although the magnitude differed across LU categories. With a few exceptions within LUs (e.g., E3500-FR and E1500-AG), sample-size and coverage-based rarefaction/extrapolation (R/E) and sample completeness curves indicated adequate (>95%) sampling efforts and accurate diversity representation from resident species pool across each LU (Figure 2a–l). Additionally, GLMMs accounting for site identity and sampling month indicated no significant effect of elevation on total spider abundance ($\beta = -0.06 \pm 0.05$ SE, $z = -1.27$, $p = 0.20$), suggesting that observed FD patterns are unlikely to be driven primarily by changes in overall abundance (Supplementary Annexure 2).

Variabilities in FD

We observed a general trend of decreasing FD across both overall elevational and LU gradients, albeit with idiosyncrasies across the latter (Figure 3a–f; Table 4). Significant declines in all FD metrics were observed across overall, FR and HD scales with increasing elevation. Contrastingly, AG sites across the gradient exhibited minimal variations with no statistical significance. We also observed considerable convergence of trends between forested areas and the overall patterns, particularly evident for FEve, FDis and RaoQ, suggesting a stronger influence of forest habitats in shaping elevational-FD patterns. Additionally, barring FunRed, all metrics across LUs approached near-zero values at the highest elevational sites (E4000 and E4500).

Tukey's post hoc tests revealed significant shifts in FD metrics across multiple elevational transitions, with notable differences across LUs (Supplementary Annexure 3). Within FR sites, all functional metrics except FRic exhibited significant differences at E3000–E3500. Additionally, E2000–E2500 showed significant differences in FDiv and FunRed, while E2500–E3000 exhibited significant variation in FDis, RaoQ and FunRed. At the highest elevation band, 4000–4500 m, both FDis and FunRed showed significant differences.

In AG sites, the E2500–E3000 transition exhibited significant differences in FEve, FDis and RaoQ, while E3000–E3500m showed significant variation in RaoQ alone. Within HD sites, E2000–E2500 exhibited significant differences in FEve, whereas E2500–E3000 showed significant variation across all FD metrics barring FunRed. The E3000–E3500 transition exhibited significant differences in FEve and FDiv, while E3500–E4000 and E4000–E4500 both exhibited significant shifts in FunRed.

TABLE 3 Elevational variation in taxonomic alpha diversity (observed and estimated species richness) across forest, agricultural and human-dominated land-use types.

Land-Use	Sites	Observed Species	Chao	Ace	Jack1	Jack2
Forests (FR)	E1500FR	26	44.82	47.52	39.44	47.91
	E2000FR	37	49.00	47.99	51.4	57.27
	E2500FR	15	19.00	19.78	19.8	21.76
	E3000FR	13	33.16	22.53	19.72	26.16
	E3500FR	8	20.00	13.71	12.8	16.52
	E4000FR	8	11.84	8.41	11.84	13.76
	E4500FR	3	3.00	3.00	3	2.12
Agricultural lands (AG)	E1500AG	17	33	28.24	26.6	33.16
	E2000AG	11	13.56	16.44	14.84	15.88
	E2500AG	4	4.48	4.69	4.96	5.00
	E3000AG	9	21	20.64	13.8	17.52
	E3500AG	7	8.92	10.66	8.92	9.88
	E4000AG	7	14.68	9.58	10.84	13.64
	E4500AG	5	6.92	8.22	6.92	7.88
Human-dominated regions (HD)	E1500HD	39	45	46.95	48.60	3.34
	E2000HD	29	31	31.71	33.80	2.91
	E2500HD	29	35	36.45	38.60	3.34
	E3000HD	15	19	19.84	19.80	2.15
	E3500HD	4	4	4.00	4.00	0.00
	E4000HD	7	14.68	9.57	10.84	2.37
	E4500HD	4	4	4.00	4.00	0.00

Variabilities in Community Weighted Means

CWM highlighted broad, directional patterns in dominant functional traits across elevations and LU types (Figure 4a–e). CWM of prey ranges (Figure 4a) and dispersal capabilities (Figure 4b) did not exhibit drastic fluctuations across elevations and LUs. However, certain elevational sites hosted specialist species such as *Tropizodium* sp. and *Trachelas* spp. (e.g., E3500). The discrepancy in dispersal ability patterns coincides with the presence of Coelotinae species at E3000–E3500 that have limited ballooning tendencies in their adult stage (Quasin et al., 2017). Variation in circadian patterns also highlighted the predominance of cathemeral species across all LU and elevational sites, particularly within FR and AG sites (Figure 4c). However, lower elevational HD sites also hosted considerable abundance of nocturnal species, particularly *Tamgrinia palpator* and *Makdiops montigenus*.

Variations in hunting strata and feeding guilds showed prominent patterns across elevational gradients, influenced by LU types (Figure 4d–e). Low to upper-intermediate sites (E1500–E3500) where foliage was abundant, mixed communities of both ground and vegetation hunters were observed for overall, FR and HD communities. We observed an increase in ambush hunters at E3500 within FR sites, while analogous HD sites retained orb-web building guilds, abundantly hosting *Araneus marmoreus* and *Neoscona xishanensis*. However, AG communities deviated notably from this pattern. Ground hunters were more prevalent in lower elevational orchards (E2000–E25000), transitioning to ambush hunting and web-building groups at E3000–E3500, where agro-production was characterized by vegetable crops. Furthermore, despite similarities in foliage and landscape composition at E4000 and E4500, we observed notable differences in guild compositions. The former hosted an abundance of opportunistic sensing web-weavers (*Titanoeca asimilis*), especially within FR and HD sites. Contrastingly, AG sites at the same elevation were dominated by *Cambalida* sp. nov.1., an obligate ground-hunter. At the highest elevation (E4500), ground hunters were commonly prevalent across all LUs.

DISCUSSION

The current study addresses a significant knowledge gap by providing one of the first insights into functional variations of North-Western Himalayan spider communities across different land-use (LU) types over a wide elevational gradient. Our findings underscore how differences in land management influence functional properties of spiders within closely spaced regions, at comparable elevational turnovers. It also highlights unprecedented influences of long-term habitat alterations such as agriculture and infrastructural built-up on natural patterns. The findings emphasize the need for investigating functional dynamics in ground arthropod assemblages in mountain ecosystems to assess impacts of climate, environmental and anthropogenic perturbations.

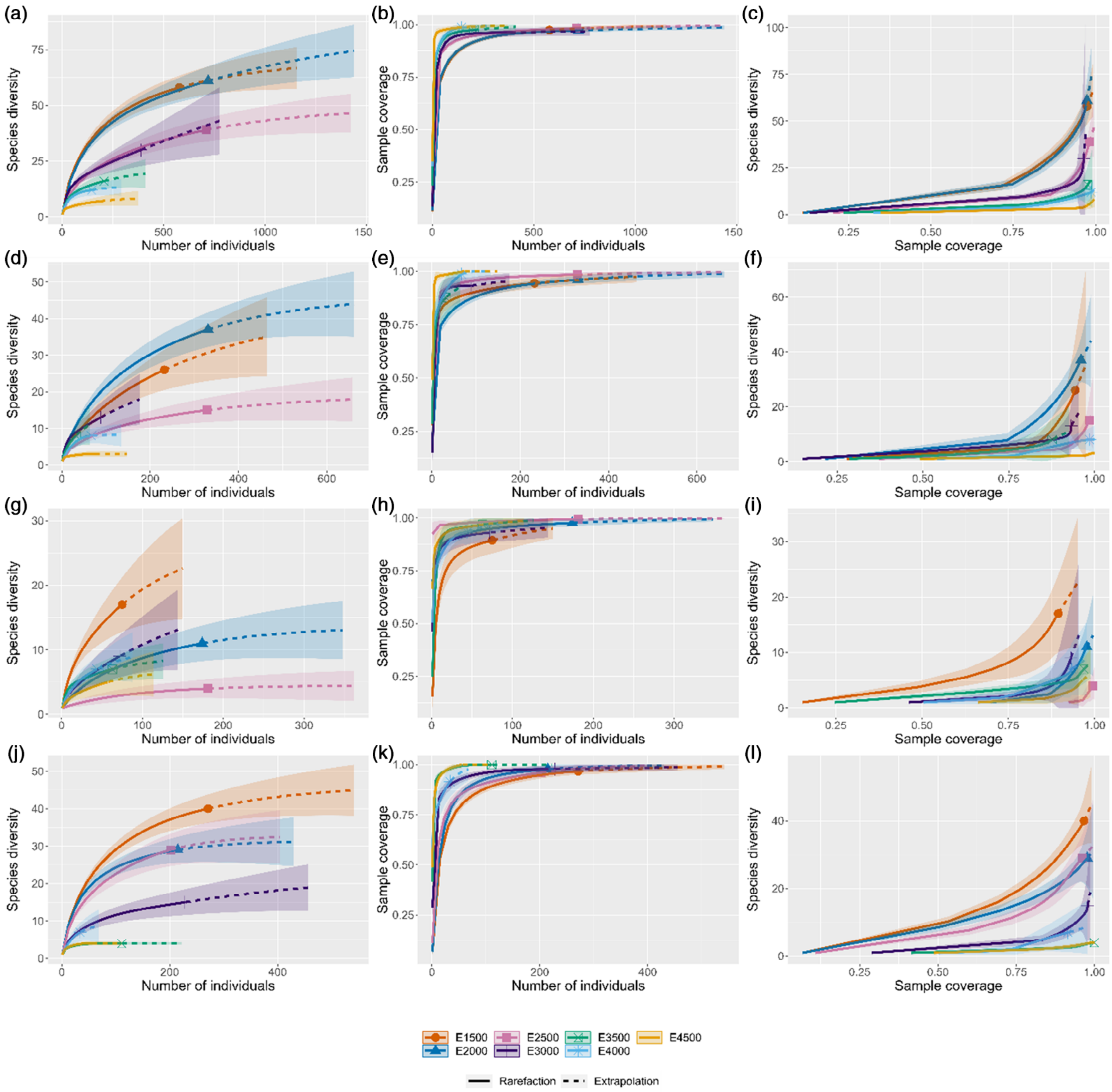

FIGURE 2 Sample-based (a, d, g, j) and Coverage-based (c, f, i, l) Rarefaction (solid line segment) and Extrapolation (dotted line segments) curves, linked to represent Sample completeness (b, e, h, k) with 95% confidence intervals (shaded areas) for overall and independent land-use gradients (a–c: Overall; d–f: Forests (FR); g–i: Agriculture lands (AG); j–l: Human Dominated regions (HD)).

Our findings support significant yet variable influences levied by LU modifications on spider FD. Although species richness declined with elevation across LU types, taxonomic patterns did not fully mirror changes in FD, indicating that functional restructuring reflects shifts in trait composition rather than simple species loss. Responses in most metrics along overall, FR and HD elevational turnovers supports distinct directional shifts in functional properties within these communities, emphasizing trait uniqueness within independent sites in an otherwise contiguous gradient. Observed declines in FRic and RaoQ with elevational gains indicate more diverse trait associations in heterogenous ecosystems that remains consistent with previous findings (Bovo et al., 2018; Ibarra & Martin, 2015; Liu et al., 2022; Thakur & Chawla, 2019; Vollstädt et al., 2017). Additionally, the higher trait richness observed in relatively disturbed sites (HD) underpins the presence of more diverse and specialised roles fulfilled by synanthropic species co-habiting anthropogenic spaces. This pattern aligns with findings by Leroy et al. (2014) and Kaltsas et al. (2019), supporting the notion of comparatively higher FD in sites of heightened disturbances resultant from colonization by more resilient species with distinct functional characters. Further, the stronger association of trait diversity (RaoQ) within such disturbed sites also supports the intermediate disturbance hypothesis, suggesting a trade-off

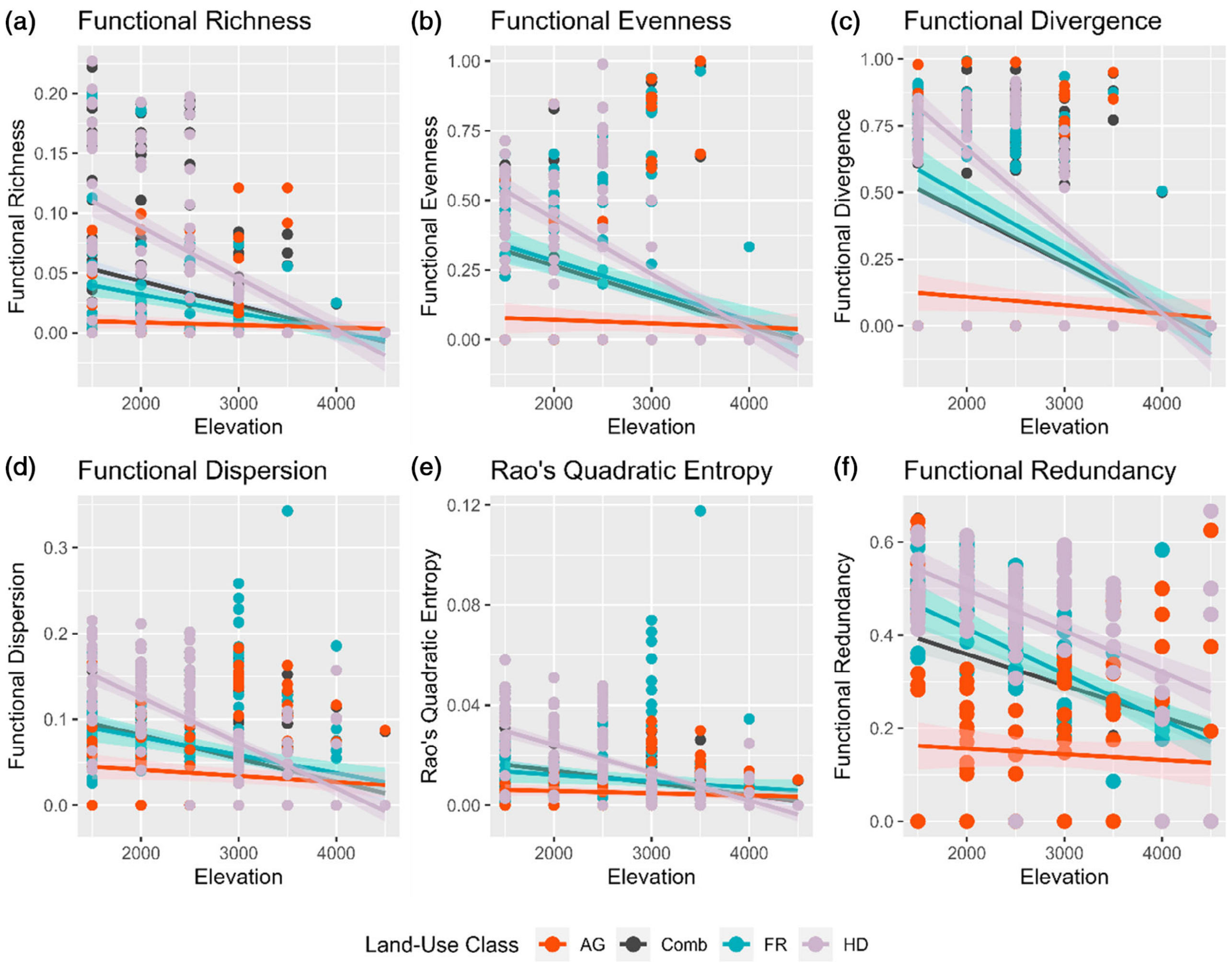

FIGURE 3 Elevational patterns of Functional Diversity metrics across overall and land-use gradients, representing variabilities in Functional richness (FRic: a), Functional evenness (FEve: b), Functional divergence (FDiv: c), Functional dispersion (FDis: d), Rao's Quadratic Entropy (RaoQ: e) and Functional Redundancy (FunRed: f). AG, agricultural lands; FR, forests; HD, human dominated regions.

between species' competitive ability and tolerance to disturbance, averting dominant species from excluding others with more adaptable traits (Sasaki et al., 2009). Additionally, the reduction in FDis within HD communities along elevation supports previous findings of anthropogenic stressors leading to trait homogenization (Ao et al., 2022; Barnum et al., 2017; de Castro et al., 2018; Laliberté & Legendre, 2010). The infrastructural consistency of human settlements across the landscapes reinforces modified habitat similarities conducive for early and sustained colonization by synanthropes and dominant species from proximate natural habitats. Similarly, FDis in AG sites remains largely consistent across elevation, showing no significant variation, suggesting potential trait homogenization, consistent with the effects of agricultural intensification (Gámez-Virués et al., 2015). While several studies have negated elevational associations of FEve and/or Functional Divergence (FDiv) within natural systems (Apaza-Quevedo et al., 2015; Butterfield & Suding, 2013; Thakur & Chawla, 2019), our study establishes their strong relationships with changing elevations. Significant declines in FEve from lower to higher elevations may reflect shifts in resource use dynamics, either due to reductions in resource availability or changes in community functional structuring. This aligns with observations from Eastern Qinghai-Tibetan plateau (Liu et al., 2022). This may indicate an even use of available niches with low probability of invaders being established to disrupt overall functioning (Mason et al., 2005). Similarly, patterns of FDiv and FDis hint towards lowered abundance of functionally specialist species at higher elevations. This implies that functionally similar species are more likely to co-exist at higher elevational sites, possibly due to reduced competition, limited availability of resources and harsher climatic conditions. Moreover, as FDiv captures the interplay between biotic and abiotic factors, it becomes evident that the balance between competitive interactions and environmental filtering experiences significant shifts across higher elevational gradients.

Declining FunRed trends with increasing elevation in overall, FR and HD communities support the notion that as elevation increases, the breadth of ecological roles performed by species become

TABLE 4 Linear regression analysis of functional diversity metrics across elevations and land-use types.

Land-Use	Functional diversity metric	Multiple R^2	F-Stat	*p*
Combined Elevational Gradient	FRic	0.18	112.1	**<0.001**
	FEve	0.18	107.4	**<0.001**
	FDiv	0.26	178.2	**<0.001**
	FDis	0.18	113.7	**<0.001**
	RaoQ	0.12	68.2	**<0.001**
	FunRed	0.09	53.02	**<0.001**
Forests (FR)	FRic	0.17	34.82	**<0.001**
	FEve	0.17	35.4	**<0.001**
	FDiv	0.32	78.62	**<0.001**
	FDis	0.11	21.09	**<0.001**
	RaoQ	0.02	4.25	**0.041**
	FunRed	0.24	52.84	**<0.001**
Agricultural lands (AG)	FRic	0.01	1.36	0.245
	FEve	0.00	0.69	0.408
	FDiv	0.02	2.63	0.107
	FDis	0.02	2.91	0.090
	RaoQ	0.01	1.73	0.191
	FunRed	0.00	0.68	0.412
Human-dominated regions (HD)	FRic	0.44	131.2	**<0.001**
	FEve	0.53	187.5	**<0.001**
	FDiv	0.64	294.2	**<0.001**
	FDis	0.61	261.2	**<0.001**
	RaoQ	0.55	208.6	**<0.001**
	FunRed	0.25	56.07	**<0.001**

Note: Bold figures signify statistically significant values.
Abbreviations: FDis, Functional Dispersion; FDiv, Functional Divergence; FEve, Functional Evenness; FRic, Functional Richness; FunRed, Functional Redundancy; RaoQ, Rao's Quadratic Entropy.

narrower and specialised, with minimal overlap (Monge-González et al., 2021). Although this may be speculative under the assumption that only the quantified traits play absolute roles in ecosystem functioning, general consensus dictates that communities with low FunRed could have dramatic consequences from loss of few species (Flynn et al., 2009). Consequently, it also foreshadows a potential loss in overall functioning in a scenario of species losses, due to deliberate or stochastic factors, as there are no redundant species to compensate for functions (Bruno et al., 2016; Mori et al., 2013, 2015). This further strengthens the vulnerability of temperate high-altitude communities to external stressors, rendering them vulnerable to loss of ecosystem functions and functional collapse (Martin et al., 2021; Pigot et al., 2016). These findings also align with the hypothesis proposed by Cornwell and Ackerly (2009), which suggests that regions experiencing strong environmental filtering tend to exhibit lower FD compared to regions with weaker filtering effects and communities characterized by stronger competitive interactions (Chakravarty et al., 2021; Monge-González et al., 2021). This may be derivative of select traits acting as a determinant of species' coping capabilities under stressful conditions, particularly those found at higher elevations (Hoiss et al., 2012). Importantly, accounting for site-level and seasonal heterogeneity did not reveal a significant elevational trend in overall spider abundance, indicating that the documented shifts in FD may reflect community reorganisation rather than simple abundance gradients.

Corroborating prior Himalayan research (Chakravarty et al., 2021; Thakur & Chawla, 2019), our study highlights the transition between E3000–E3500 within FR as an ecologically crucial site of changing species adaptabilities and niche partitioning. Coinciding with the ecotonal treeline in HP (Singh et al., 2021), this transitionary zone witnessed strong shifts in trait properties, potentially highlighting functional underdispersion and specialization. These changes align with documented vegetation transitions beyond this site, which may also contribute to the observed significant uptick in ground-dwelling spiders. This is unsurprising given that the onset of harsher environmental conditions at higher altitudes allows environmental filtering to be the deterministic driver of community assemblages, especially for ectotherms (Zhao et al., 2023). The clear convergence of shifting treeline zones and functional properties of spider assemblages can be integrated for better informed monitoring of climatic responses in ectothermic communities.

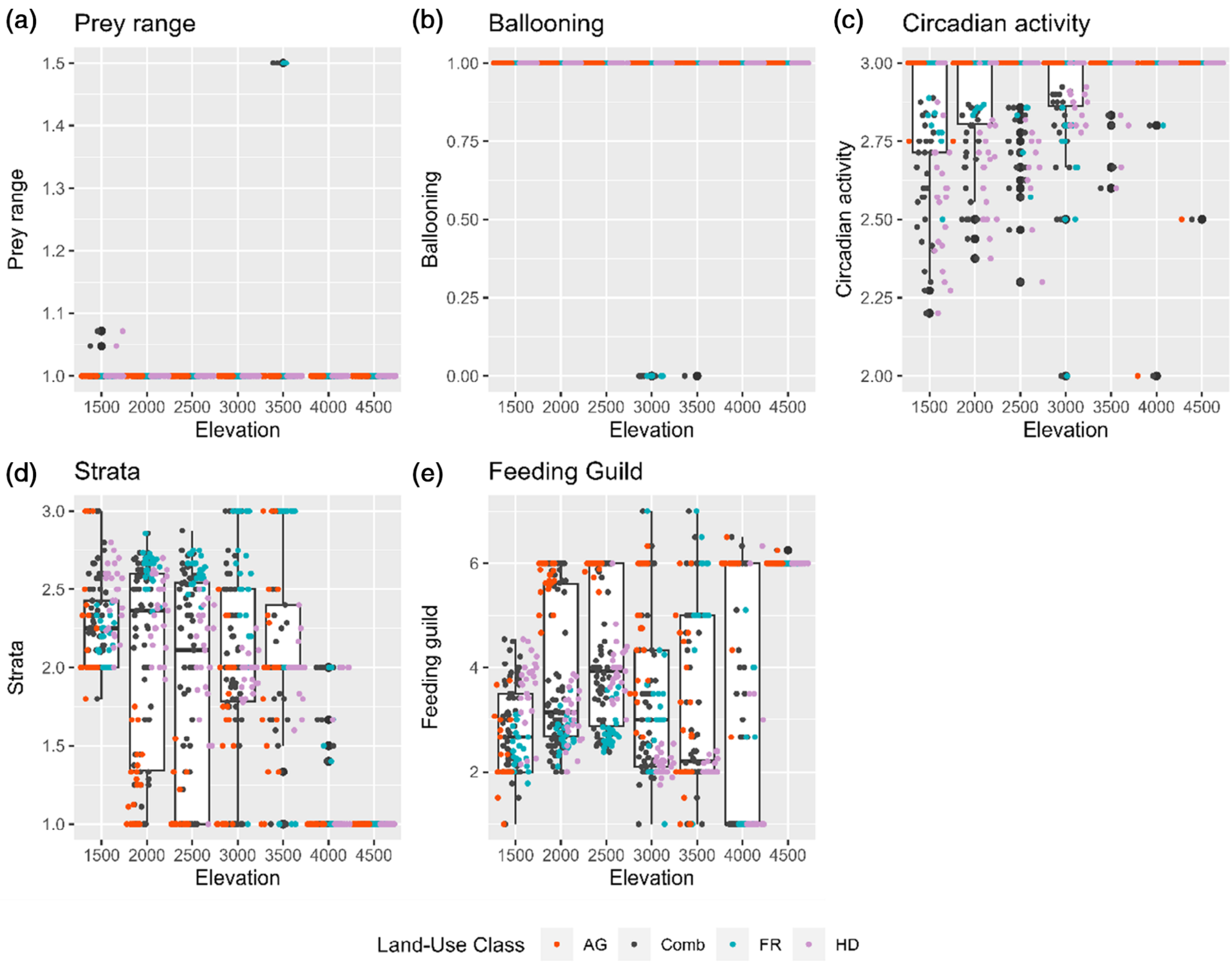

FIGURE 4 Community Weighted Means quantifying typical trait values across overall and land-use gradients, representing variabilities in Prey Ranges (a), Dispersal Abilities (b), Circadian Patterns (c), Hunting Strata (d) and Functional Feeding Guilds (e). AG, agricultural lands; FR, forests; HD, human dominated regions.

Agricultural intensification has been widely linked to disruptions in arthropod FD (Edwards et al., 2014; Jonason et al., 2017; Tscharntke et al., 2008), and the same remains corroborated by our study. The non-significance of all metrics with elevational gains (against other LUs) indicates higher functional specialization in agro-elevational communities (Davies et al., 2020; Jonason et al., 2017; Monge et al., 2022). While such alterations have previously been directly linked to ecological inefficiency (Clavel et al., 2011; Frishkoff et al., 2014), the observed stability in FD metrics across elevation may highlight fulfilment of roles by specific species, conferring functional stability. One potential explanation for this stability may be the presence of FunRed among species. This means that despite changes in species compositions and/or a decline in species richness with increasing elevation, the key ecological functions are maintained across the gradient. However, the stark deviations of agro-communities from overall and natural trends also parallels previous findings (Grab et al., 2019; Ibáñez-Álamo et al., 2017; Penjor et al., 2022). While this may be attributed to systematic habitat homogenization for sustaining commercial produce, it results at the cost of stark reduction of functional groups (e.g., web-builders in lower elevational classes). This raises concerns regarding functional resilience, especially under the ongoing crop/fruit production adversities driven by climate crisis in HP (Gautam et al., 2014; Sahu et al., 2020; Sen et al., 2015; Singh et al., 2016). Lowered resilience in these sites, coupled with eroding taxonomic and functional properties may cause severe deficiencies in ecosystem functioning if not appropriately and sustainably mitigated.

Our findings also support the generalist and voracious feeding capabilities exhibited by spiders, while maintaining variable hunting strategies and wide dispersal abilities (Bell et al., 2005; Cardoso et al., 2011; Michalko et al., 2019; Nyffeler & Birkhofer, 2017). Circadian activity is inherently linked to the natural day-night rhythm, which is influenced by environmental factors like light and humidity, shaping circadian rhythms (Krumpalova & Tuf, 2013). While habitat specialization in spiders plays a deterministic role, Schoener (1974) suggests that these rhythms could have an even greater impact since temporal stratification has been proposed as a mechanism to reduce competition among congeners (Breymeyer, 1966; Łuczak, 1959). This holds true even for high-altitude communities, where habitat conditions, food availability and reproductive trade-offs play significant roles in driving circadian activities under extreme environmental conditions (Mann et al., 1980). While our study does not definitively conclude acute activity partitioning, certain findings remain nuanced. FR and AG communities across the elevational gradient seem to be comprised of predominantly cathemeral species, although the typical activity within HD communities, especially lower sites, tend to include a higher proportion of nocturnal species. However, it remains difficult to derive conclusions from these patterns since species in the former classes are known to exhibit inter-specific variabilities in activity peaks (Flatz, 1987; Krumpalova & Tuf, 2013; Nyffeler & Benz, 1988).

Variabilities in hunting strata and guild variations remain closely associated with floral complexity within sites, a pattern widely established for spider communities (Barton et al., 2017; Carvalho et al., 2011; Chatzaki et al., 2005; Gallé et al., 2018; Hore & Uniyal, 2008; Lafage et al., 2019; Malumbres-Olarte et al., 2013). In habitats with greater vegetation complexity, both ground-dwelling and foliage-dwelling species co-occur, likely benefiting from increased structural diversity and resource availability. However, agricultural communities deviate significantly from this pattern, exhibiting a shift towards predominantly ground-dwelling species. While this departure from the expected trend is pronounced, it aligns with established research on habitat simplification and its effects on arthropod communities (Corcuera et al., 2010; Ibarra-Núñez, 2014). Notably, studies documenting spider diversities from temperate apple orchards in the Western Himalaya have reported a mix of web-builders and ground dwellers (Khan, 2009, 2011, 2012). However, our study reports an over-abundance of ground obligates, particularly Lycosidae species, aligning partially with aforementioned and other findings (see Marshall et al., 2002). This may raise alarms of a general unquantified decline in arthropod diversity in heavily manipulated agro-ecosystems of the North-Western Himalaya, that may lead to/be resultant of substantial alterations in overall functioning in contiguous habitats.

While both Gnaphosids and Lycosids were abundant in areas of significant guild transitions from foliage to substratum dependency, the overlap in their preferred habitats remains quite distinct. While this can be primarily attributed to different hunting strategies, their common grouping (as ground hunters) remains debated (Cardoso et al., 2011; Cardoso et al., 2015; Höfer & Brescovit, 2001). Research has also shown that "sit-and-wait" strategies work particularly well towards capturing highly mobile prey, while pursuing spiders are more adept at capturing sedentary prey (Kuusk & Ekbom, 2012; Sweeney et al., 2013). As a result, variations in strategies may allow spiders within communities to utilize similar types of prey, but in varying proportions (Birkhofer & Wolters, 2012; Michalko et al., 2019; Michalko & Pekár, 2016). A similar debate over the trade-off of guild clustering and actual resource-microhabitat utilization exists over generalization of various web-building categories, especially sheet builders (Cardoso et al., 2015).

Marked shifts in guild composition of FR communities supports a higher abundance of ground dwellers in drier ecosystems of E3500 (Chatzaki et al., 2005). However, for other LUs, this shift was less pronounced. Contrary to our expected results, despite similar habitats in E4000 and E4500, the former supported high abundance of space web-builders. While limited studies have attempted to explore this theory within alpine habitats, findings of Wirta et al. (2015) supports the occurrence of opportunistic web-builders from similar habitats in high-arctic ecosystems, a finding common across all LUs except AG fields.

Overall, the use of guild offers several advantages in understanding FD shifts, trophic relationships and competition or coexistence among similar species. However, as pointed out by one of the pioneers of the contemporary guild classification (Cardoso et al., 2011), using "taxonomic family" as a surrogate for guilds may have some exceptions. A similar limitation applies to the circadian activity trait, which is also commonly assigned at the taxonomic family level, based on literature. While this provides a functional approximation, species-level variations in activity patterns may exist, highlighting the need for finer-resolution behavioural assessments to improve accuracy. These could become more prevalent as we gain further knowledge about the individual species' ecology. While we agree more comprehensive and quantitative traits are needed to support our findings, which currently remain speculative at best, we believe that the results can serve as early warning systems for functional losses in Himalayan communities driven by drastic and uncontrolled changes in connective ecosystems.

Overall, the study highlights predominantly significant patterns in spider FD across land-use types and elevational gradients, without attempting to disentangle the independent effects of site and distance. In addition to understanding how functional properties vary across different LUs, it provides evidence of consistent and significant deviations from natural patterns in agricultural communities. This remains indicative of potential disruptions in community and functional attributes that caution managerial interventions. We identify transitions between 3000 and 3500 m as key zones where shifts in FD suggest potential changes in trait distributions. While our findings indicate variation in functional attributes, further research incorporating species-specific adaptive traits is needed to explicitly assess niche partitioning and conservation priorities in these regions. The study also confirms broad feeding and dispersal capabilities of spiders, similarly influenced by elevational-LU idiosyncrasies. The findings also corroborate the association of hunting strategies and guild variations with vegetation strata. In conclusion, findings from the study emphasize the need to further investigate functional dynamics in other ground arthropod assemblages to better understand ecological impacts of LU-mediated changes and environmental disturbances in mountain ecosystems—a field of research that hitherto remains scarcely documented. It also serves as an early warning system for potential functional losses in Himalayan spider communities due to drastic environmental changes in connected ecosystems. These insights can better inform conservation strategies aimed at preserving the functional integrity of Himalayan spider and overall ecological communities amidst ongoing environmental challenges.

STUDY LIMITATIONS

This study offers key insights into how FD patterns vary across elevation and land-use gradients in Himalayan spider assemblages, but several limitations merit acknowledgment.

First, our analysis focused on FD metrics without incorporating taxonomic turnover. While FD captures trait-level community variation, parallel evaluation of species turnover would help determine whether functional shifts are driven by species replacement or intraspecific trait variation. Although a separate taxonomic analysis has been submitted elsewhere, integrating both dimensions would yield a more holistic view of community restructuring along environmental gradients.

Second, while our design targeted FD variation across elevation and land use, the inclusion of two distinct regions, Kullu and Lahaul-Spiti, introduces biogeographic heterogeneity. These districts differ in climate, vegetation and evolutionary history, which may influence trait distributions. Although comparable land-use types were sampled within each district to minimize confounding, residual biogeographic variation cannot be entirely excluded. We addressed this by incorporating site identity (defined by elevation band and land-use type) and sampling month as random effects in a generalized linear mixed-effects framework, thereby accounting for hierarchical spatial structure and uneven seasonal sampling. Future studies could further refine this approach by integrating explicit spatial distance measures or spatially explicit models to disentangle the relative roles of dispersal limitation and spatial autocorrelation in shaping functional patterns.

Third, due to logistical constraints, we used relatively small (1 m × 1 m) quadrats across 525 sampling units. While effective in previous studies, larger sampling areas may have better captured habitat heterogeneity and rare species.

Trait assignments, especially for circadian activity and feeding guilds, were derived from literature rather than direct field observations. Activity patterns were assigned at the family level, despite potential species-level variation. While feeding guilds offer a useful ecological lens, they may overlook behavioral plasticity. Overall, FD metrics provide an estimate of functional composition but are not direct indicators of ecological function. Future studies with finer-resolution trait data and direct behavioral observations could improve trait-function inference.

Seasonal variation is another consideration. Although sampling occurred between March and September 2021, not all sites were visited each month. As spider abundance and traits may shift seasonally, year-round sampling would yield more temporally robust patterns.

Lastly, while we interpret elevation as a proxy for forest-type transitions, an approach supported by prior literature, we acknowledge that vegetation composition and resource availability were not directly measured. Controlled studies incorporating habitat variables and experimental validation would strengthen causal interpretations of environmental filtering or competition.

Despite these constraints, this study establishes a foundational understanding of how elevation and land use shape spider FD in the Himalayas. Future work integrating species turnover, finer trait data and expanded spatial–temporal sampling will build upon these insights.

AUTHOR CONTRIBUTIONS

Irina Das Sarkar: Conceptualization; investigation; funding acquisition; writing – original draft; methodology; writing – review and editing; formal analysis; data curation; visualization. **Manju Siliwal:** Conceptualization; validation; supervision; writing – review and editing; resources. **Soumya Dasgupta:** Writing – review and editing; conceptualization. **Virendra Prasad Uniyal:** Conceptualization; funding acquisition; writing – review and editing; supervision; project administration; resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest regarding the publication of this paper.

DATA AVAILABILITY STATEMENT

The authors confirm that the data supporting the findings of this study, specifically abundance-based species records and Tukey's HSD Post-hoc results for pairwise elevational comparisons are openly available in Figshare as supplementary materials and can be accessed at https://doi.org/10.6084/m9.figshare.29094170.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting Information.

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