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# Within-Habitat β Diversity Increases With Elevation in Tropical Forest Spider Assemblages

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## ABSTRACT

While between-habitat comparisons are commonplace in ecology, we know very little about the changes among species assemblages within habitats. Here we aimed to examine within-habitat processes in spider assemblages across three elevations in tropical forests, using a design tailored both geographically and methodologically for this purpose. We hypothesised greater within-habitat βTD (caused by lower connectivity), decreasing body sizes (because of lower temperatures) and less frequent ballooning (due to greater isolation) with increasing elevation. We collected spiders at five within-habitat (horizontal) distances at each elevation in the Udzungwa Mountains, Tanzania, applying standardised protocols. We assessed differences among assemblages using taxonomic and functional β-diversity measures and their components. We applied PerMANOVAs to test for different β between elevations, PERMDISP to evaluate within-habitat variability, exponential and power-law models to examine within-habitat distance-decay, and community weighted values of traits to capture functional patterns for each trait. As predicted, within-habitat βTD was greater at higher elevations, with stronger distance-decay relationships (taxonomic and functional). Also, as predicted, high elevation assemblages appeared to show smaller body sizes and lower ballooning frequency. Our results demonstrate the uniqueness of mountain assemblages and that the Udzungwa Mountains, as well as other mountainous areas, should receive increasing conservation attention, as they provide unmissable opportunities to conserve, through small additions or connections, countless small-range or habitat-restricted endemic species.

## 1 | Introduction

Mountainous regions have long been considered suitable for testing the effects of environmental variation and geographic distances on the changes in species communities—the decay of similarity between them (Nekola and White 1999; Soininen et al. 2007)—as proxies to study niche-based deterministic processes and dispersal-related neutral processes (Hubbell 2001), respectively, behind community assembly (Körner 2007; Nogués-Bravo et al. 2008; Sanders and Rahbek 2012; Graham et al. 2014). As most studies focus on regional-large spatial scales, very little is still known about the changes among assemblages within the same habitat, that is, from localities that share similar environmental and biotic characteristics and are spatially connected (but see Noguerales et al. 2023; Trujillo et al. 2019), and in relation to geographic distance (distance-decay).

Comparing connected assemblages within habitats provides insights into the effects of small-scale environmental variability or the role of neutral processes. When extended to areas with different habitats, this approach may help to test how environmental variability shapes geographic patterns (Draper et al. 2018). This question has implications for designing and adapting conservation strategies (Morlon et al. 2008; Socolar et al. 2016), particularly in tropical habitats, where assemblages may change composition at smaller scales than at higher latitudes due to narrower physiological tolerances and/or lower dispersal rates of species (Montaño-Centellas et al. 2021).

The effects of environmental changes on geographic patterns in assemblages may be multiple. On one hand, harsher conditions (at higher elevations) may act as environmental filters, reducing the number of species and functional differences (lower alpha and gamma diversity, functional evenness and dispersion) and potentially also reducing the differences between assemblages (taxonomic β diversity, βTD) (Cooper et al. 2023; Henriques et al. 2022; Kraft et al. 2011; Mouchet et al. 2010; Myers et al. 2013). On the other hand, topographic changes—an increase in the slope and a reduction in the available area—may cause high elevation habitats to occupy smaller areas and to be more isolated, reducing the movement of organisms between them and increasing βTD. Assuming similar environmental conditions, carrying capacity and a strong niche effect, βTD at the same elevation should be mainly driven by the changes in the identity of the species (the replacement component, $\beta TD_{Rep}$), with very little contribution of the changes in the number of species (richness component, $\beta TD_{Ric}$) (Podani and Schmera 2011; Carvalho, Cardoso, and Gomes 2012; Cardoso et al. 2014). While the taxonomic structure may be expected to vary within each elevational band, one may hypothesize that their functional characteristics (including functional β diversity, βFD) will not be as variable, if niche processes act similarly (Cardoso et al. 2014). In other words, at high elevations βTD may be higher due to dispersal limitation while βFD may be lower due to environmental filtering, with both patterns being, in turn, mediated by dispersal ability.

For spider species assembly, environmental filtering appears to prevail over geographic/spatial limitations (Carvalho, Cardoso, Crespo, et al. 2012; Baldissera et al. 2012; Rodriguez-Artigas et al. 2016; Zhang et al. 2018). However, the relative effects of niche-related processes may vary with the spatial scales (Carvalho, Cardoso, Crespo, et al. 2012), with habitat-related factors dominating at the metacommunity/local scale (Malumbres-Olarte et al. 2013; Gonçalves-Souza et al. 2015; Ávila et al. 2017; De Ávila et al. 2020) and climate exerting a stronger filtering at broader scales (Jimenez-Valverde and Lobo 2007; Finch et al. 2008; Jiménez-Valverde et al. 2010; Miller et al. 2014; Rodriguez-Artigas et al. 2016; Malumbres-Olarte et al. 2021). In addition, the dispersal ability of species (often indicated by ballooning frequency) may also condition or interact with the effects of geographic distances at regional scales (Carvalho, Cardoso, Crespo, et al. 2012; Rodriguez-Artigas et al. 2016; Malumbres-Olarte et al. 2020).

Although niche processes may determine changes in spider assemblages across elevations (Chatzaki et al. 2005; Foord and Dippenaar-Schoeman 2016), as with other taxa, it is unknown how they change within habitats. Furthermore, the functional perspective is seldom applied, and we lack information on how the structure of the assembly changes and how niche (e.g., body-size, web-using adaptations) and dispersal-related (ballooning frequency) traits vary accordingly. Indeed, spiders provide measurable and assignable characteristics that reflect their ecological adaptability and can be used as physiological and functional traits (Whittaker et al. 2014; Pekár et al. 2021).

Here we aim to elucidate how environmental changes condition geographic patterns in tropical rainforest spider assemblages, through a study designed specifically for the task. We aimed to test four sets of hypotheses: (1) βTD between the spider assemblages at higher elevations (within each elevation) will be greater due to greater isolation and possibly smaller available areas with suitable climatic conditions, compared to lower elevations, with this difference increasing with horizontal distance—greater within-elevation distance decay at higher elevations; (2) conversely, βFD (and the distance-decay) will remain similar across elevations as the physical structure of the habitat varies little, despite decreases in functional α diversity metrics with elevation; (3) within each of the three elevations, the replacement component of βTD is greater than that of richness as the environmental conditions remain similar and, therefore, the environmental filter is weak; and, as with total βTD, the replacement component of βTD will be greater at higher elevations; and (4) with increasing elevation, spider body size (a niche-related ecological trait) decreases constrained by lower temperatures (Entling et al. 2010), and ballooning (a dispersal-related trait) becomes less frequent as higher elevation areas are more isolated and, therefore, ballooning may mean a greater risk of landing in a non-suitable habitat.

## 2 | Methods

### 2.1 | Study Area and Sampling

We conducted our study on the eastern slopes of the Udzungwa Mountains National Park (UMNP) and the Uzungwa Scarp Nature Forest Reserve (USNFR), both of which are located in the Udzungwa Mountains (7.82° S, 36.70° E) in the southern part of the Eastern Arc Mountains, Tanzania, and a priority area for the conservation of regional and local biodiversity (Lovett and Thomas 1986; Lovett et al. 1988; Dinesen et al. 2001), and a biodiversity hotspot (Myers et al. 2000). With an average annual rainfall of 2000 mm (Mumbi et al. 2008), these mountains go annually through a heavy rainy season (March–May), a lighter rainy season (November–February) (Lovett 1996) and a dry season (June–October), although the areas at the highest elevations receive constant high levels of precipitation caused by mist condensation. Habitats change from deciduous miombo woodlands (*Brachystegia* spp.) at the lowest elevations (300 m a.s.l.) to evergreen montane rainforests before reaching the mosaics of bamboo (*Oldeania alpina*

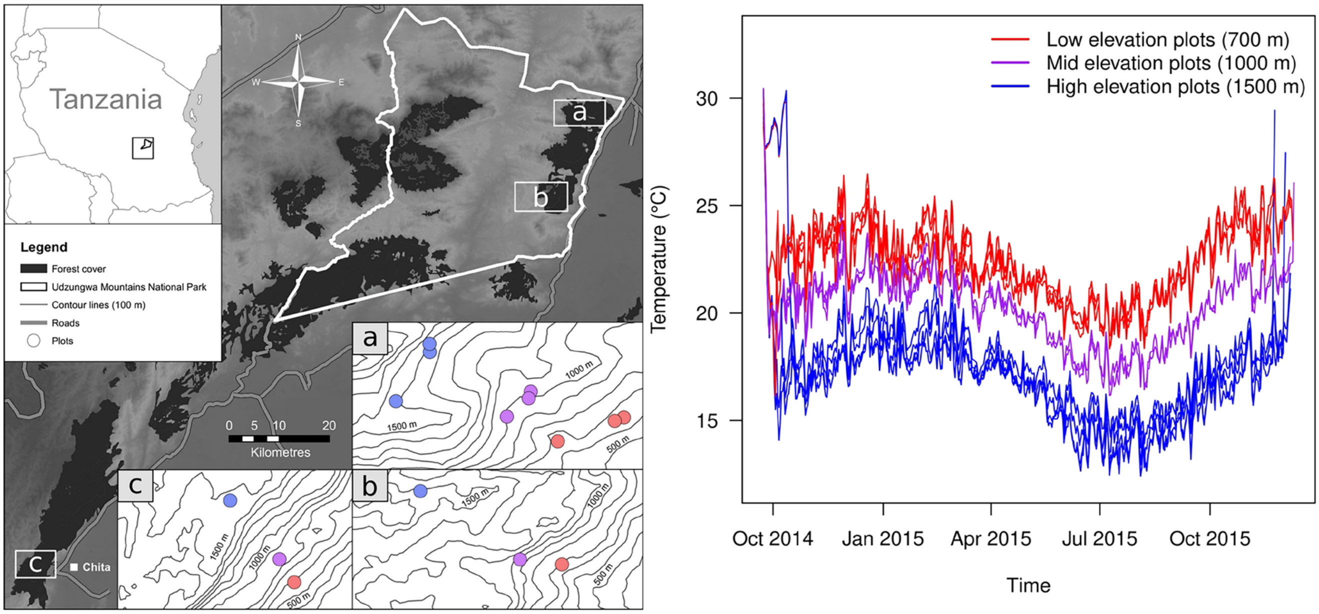

**FIGURE 1** | Locations of the sampling plots (represented by circles in areas a, b, and c, left) and mean daily temperatures across the studied plots, each represented by a line (right). Individual lines at the same elevation may not be distinguishable as they show very similar values, and they overlap.

(K. Schum.) Stapleton) and *Hagenia abyssinica* (Bruce) J.F. Gmel. woodlands (Lovett et al. 2006; Rovero et al. 2017) at the highest peaks (2400 m a.s.l.).

We set up three longitudinal/horizontal transects, each at a different elevation (between 650–708, 908–1006 and 1448–1552 m a.s.l.) corresponding to three types of forest (lowland forest, submontane forest and montane forest, respectively) (Lovett and Wasser 1993; Lovett 1999). Each transect had five sampling plots (representing the assemblages and the sampling unit for our tests), 50 m × 50 m squares (0.25 ha), separated by 0.1 (the minimum), 1, 20 and 175 km (Figure 1, see coordinates in Malumbres-Olarte et al. 2018). To test whether plots at the same elevation had similar climatic conditions, we measured their temperature and humidity throughout a year with LASCAR EasyLoc EL-USB-2 dataloggers (Figure 1).

We sampled the spider fauna in October–November 2014 by applying the COBRA-TF sampling protocol for spiders (Malumbres-Olarte et al. 2017). In brief, the COBRA-TF protocol (Conservation Oriented Biodiversity Rapid Assessment for Tropical Forests) samples different microhabitats (vegetation strata) with optimised collecting methods to maximise the number of species to use in between-site species assemblage comparisons (Cardoso 2009; Cardoso, Guillerme, et al. 2024; Cardoso, Arnedo, et al. 2024). In each plot, we collected 36 samples: 8 samples of nocturnal aerial hand collecting, 6 samples of diurnal vegetation beating, 2 samples of nocturnal vegetation beating, 2 samples of diurnal ground hand collecting, 2 samples of nocturnal ground hand collecting, 2 samples of diurnal sweep netting, 2 samples of nocturnal sweep netting and 12 pitfall samples (each sample consisting of four pitfall traps running for 14 days). Each sample, except for the pitfall ones, consisted of 1 h of continuous collecting (using one method) by one person moving within the plot to cover as much area as possible. Each method targeted a specific microhabitat (or stratum/height of vegetation): ground (ground hand collecting and pitfall trapping), herbaceous vegetation (sweep netting) or low canopy (aerial hand collecting and vegetation beating). All spider specimens are currently stored in 70% ethanol in the Natural History Museum of Denmark.

## 2.2 | Taxonomic and Functional Data

We counted all specimens (including juveniles) and identified all adults to the lowest possible taxonomic level (minimum family), assigning a morphospecies name when species-level identification was not possible. The functional data were based on 16 traits or measurements (see individual descriptions further down the text): prosoma width, prosoma height, length of tibia I, cheliceral fang length, habitat verticality, nocturnality, eight predatory/foraging features (capture web builder, sensing web builder, tube web builder, sheet web builder, space web builder, orb web builder, ambush hunter and active hunter), ballooning frequency and stenophagy (as described in Macías-Hernández et al. 2020) (see Appendix S1 for details).

Using our trait data, we computed a matrix of dissimilarity between all the species using the Gower distance, which can handle different types of variables/traits (e.g., numerical, categorical, ordinal, etc.) as individual or groups of associated variables. The Gower distance was implemented using the gawdis function (gawdis R package, de Bello et al. 2021), which is an extension of the gowdis function from the R package FD (Laliberté et al. 2014) that allows us to find the best weights to equalise the contribution of the traits to the global dissimilarity matrix. For our analysis, we grouped our variables according to their type and ecological meaning: (1) morphologic measurements as numerical variables (prosoma width, proportional prosoma height, proportional length of tibia I and proportional fang length); (2) habitat verticality as a numerical variable; (3) nocturnality as a numerical variable; (4) eight predatory/foraging features (capture web builder, sensing web builder, tube web builder, sheet web builder, space web builder, orb web builder, ambush hunter and active hunter) as fuzzy variables (i.e., the eight binary variables define a single trait); (5) ballooning frequency as an ordinal variable; and (6) stenophagy as a binary variable. Prior to this analysis, we log-transformed prosoma width, proportional length of the tibia of leg I and proportional fang length to normalise the data. We then applied a hierarchical cluster analysis with the neighbour-joining method to create the functional tree that we used in the subsequent analyses. The neighbour-joining method provides a tree with the same quality as most multidimensional hypervolume representations, while being more robust to outliers (Cardoso, Guillerme, et al. 2024; Cardoso, Arnedo, et al. 2024).

To investigate which morphological traits that may cause the differences in functional diversity between assemblages across elevations, we calculated the Community Weighted Means (CWM) (representing the average or 'typical' values in a given assemblage) of the three uncorrelated morphologic traits—prosoma width, the proportional length of tibia I and the proportional length of fangs—weighted by incidence and abundance (to consider both the features of the species that form the assemblages and the effects of relative abundances on them) using the corresponding function of the BAT package (Cardoso et al. 2015). We also computed CWM for the ordinal classification of ballooning frequency (1 = low; 2 = occasional and 3 = frequent).

## 2.3 | Data Analyses

As a general exploration of functional patterns, we first calculated sampling completeness using the Chao 1 species estimator (Scharff et al. 2003; Magurran and McGill 2011) and then we computed three α diversity functional measures for each spider assemblage: rarefied richness, dispersion and evenness (see Hypothesis 2) as defined in the R package BAT (Cardoso et al. 2015). We also tested if the number and percentage of quantitatively rare species (species whose total abundance was either one [singleton] or two [doubletons]) and if the species that were unique to each assemblage differed across elevations by applying ANOVAs (count data) and beta regressions (percentages). We tested the effects of elevation on the differences in each of the functional α diversity measures between the assemblages through a series of ANOVAs.

To evaluate how functionally different each assemblage was (and compare the differences between elevations), we built a series of null models for the six functional α diversity measures. For each assemblage, we randomly sampled species from the overall functional tree (with the species from all assemblages), while keeping the number of species and relative abundances constant in each assemblage and computed each of the six α diversity functional metrics in 1000 iterations. For each of the six metrics, we tested whether the observed values fell below the 0.025 and 0.005 or above the 0.975 and 0.995 percentiles (as a two-sided test) of the 1000 values obtained from the null models.

We visualised general differences between assemblages across elevations through non-metric multidimensional scaling (NMDS; McCune and Grace 2002) using the abundance-based Jaccard index (Jaccard 1912), which is equivalent to a Bray–Curtis—to obtain a more complete view on the assemblages by considering relative abundances of the species. We also computed the Jaccard index for the partitioning of both taxonomic and functional β diversities as βtotal = βreplacement ($\beta_{Rep}$) + βrichness ($\beta_{Ric}$) (Carvalho, Cardoso, and Gomes 2012; Cardoso et al. 2014) to measure the differences among the five assemblages at each elevation (for Hypotheses 1, 2 and 3). We considered this partitioning approach more suitable to answer our questions (Carvalho et al. 2013; Schmera et al. 2020), as the species replacement and the differences in richness (loss/gain) are the basic processes behind β diversity, making them conceptually and mathematically appropriate (Legendre 2014).

To test for the differences in the total taxonomic (Hypothesis 1) and functional (Hypothesis 2) β diversities across elevations, we carried out non-parametric permutational multivariate analyses of variance (PerMANOVA) by using permutation tests with 9999 iterations (Anderson 2001). We also tested the within-habitat variability of assemblages (measured by the taxonomic and functional $\beta_{Rep}$ values) across elevations by implementing a permutational analysis of multivariate dispersions (PERMDISP, Anderson et al. 2006), which applies a permutation test (1000 permutations) on the average distances of sampling units (i.e., assemblages) to the centroid of their group (i.e., elevation) in the euclidean space, defined by a principal coordinate analysis. Subsequently, we ran Tukey's honest significant differences tests (Tukey HSD) for pairwise comparisons. We looked into the functional redundancy in each plot through the Ricotta's (Ricotta et al. 2016) and Pavoine and Ricotta's (Pavoine and Ricotta 2019) redundancy coefficients (R and $R_{star}$, respectively) using the R package adiv.

We tested whether there were any correlations between horizontal geographic distance (within each elevation) and the six measures of beta diversity (taxonomic and functional $\beta_{Tot}$, $\beta_{Rep}$ and $\beta_{Ric}$)—the distance-decay tests of Hypotheses 1 and 2—using two distinct approaches: (1) simple Mantel tests (non-parametric Spearman correlations) between beta and geographical distances; and (2) a series of exponential and power-law models (with 1000 permutations) for each elevation separately. In each model, the response variable was one of the six β diversity measures (pairwise), whereas the explanatory variable was the geographic distance between the assemblages at the same elevation. We then compared the exponential and power-law models using the values of AIC and pseudo-$R^2$ (as the goodness of fit of each curve) with the function model.decay of the package betapart (Baselga et al. 2021). This approach has been presented as an appropriate and effective alternative for non-linear parametric models (Gómez-Rodríguez and Baselga 2018; Martínez-Santalla et al. 2022). We favoured the power-law models as they showed lower values of AIC and greater values of pseudo-$R^2$. From these 18 final models (three elevations by six β diversity measures), we also extracted their significance and slope—a higher slope representing faster rates of β diversity change with geographic distance (Montaño-Centellas et al. 2021). We then tested for differences between the slopes of the distance-decay models from the different elevations using the method proposed by Martín-Devasa et al. (2022), which uses a statistic that

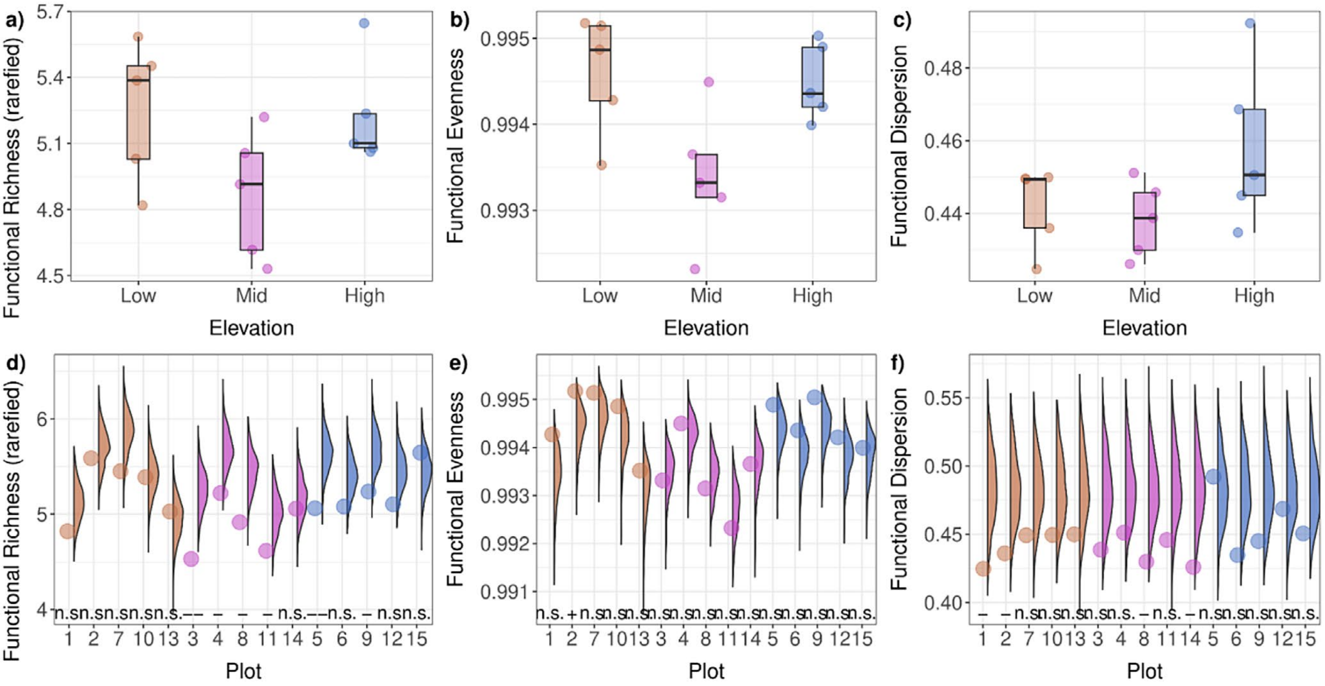

**FIGURE 2** | Observed (a–c) and estimated (d–f) values of the α functional measures (rarefied richness, evenness, and dispersion) of spider assemblages according to elevation. In the graphs showing the results of the null models (d–f), circles represent observed values. Symbols above the plot numbers/names represent non-significant (ns) tests and tests that showed greater than expected (+ for > 0.975 percentiles, ++ for > 0.995 percentiles) and smaller than expected (– for < 0.025 percentiles, – for < 0.005 percentiles) observed values.

accounts for pairwise dependence and uses a site-block resampling procedure to estimate the variance of model parameters. We used both incidence and abundance data to evaluate the effects of species' relative abundances on the distance-decay patterns.

To test the differences in the replacement and richness components of the taxonomic β diversity within and across elevations (Hypothesis 3) we applied another set of PerMANOVAs. For our fourth hypothesis, we evaluated the differences in the CWM of the three morphologic traits and ballooning frequency between elevations by applying Kruskal–Wallis tests. When the overall Kruskal–Wallis was statistically significant, post hoc Wilcoxon rank sum exact tests were used to identify statistically significant pairwise differences between elevations. Following Zelený's recommendations for hypotheses such as ours that assume a link between species composition and sample features (Zelený 2018), we applied random trait sorting through another series of null models. We built these models using the same approach as for the α FD measures—randomly sampling species traits for each assemblage, obtaining 1000 values for each metric, and testing if the observed values fell below the 0.025 and 0.005 or above the 0.975 and 0.995 percentiles.

## 3 | Results

The 40,613 individuals that we collected represent 631 species (including morphospecies) from 52 families. Sampling completeness ranged between 59% and 83% in all plots (Malumbres-Olarte et al. 2018), and the number and percentage of quantitatively rare and unique species were not different across elevations ($p > 0.05$, Figure S4). However, when excluding an outlier (plot 15, high elevation assemblage in USNFR, with disproportionately more rare species), we found greater percentages of rare species at low elevation (Low elevation, Coeff: −1.53, $p < 0.001$; Mid elevation, Coeff: −0.45, $p < 0.01$; High elevation, Coeff: −0.54, $p < 0.01$; phi = 114.98, $p < 0.01$) and near-differences for their number ($F_{2,12} = 3.78$, $p = 0.056$). Although according to our ANOVAs, there were no differences in rarefied functional richness ($F_{2,12} = 2$, $p = 0.1$) and functional dispersion ($F_{2,12} = 2.24$, $p = 0.15$) between plots according to elevation, there were differences in functional evenness ($F_{2,12} = 5.1$, $p = 0.025$) (Figure 2). Four out of the five mid-elevation plots showed functional richness values significantly lower than expected (Figure 2). The values of the two functional redundancy coefficients varied across plots and elevations, but they remained similar, with ranges of $R = 0.71–0.72$ and $R_{star} = 0.987–0.99$.

Across the three elevations, for both taxonomic and functional β, and when partitioning $\beta_{Tot}$, $\beta_{Rep}$ was usually much greater than $\beta_{Ric}$ (Figure 3). The values of taxonomic $\beta_{Rep}$ were between 0.37–0.8, 0.41–0.8 and 0.36–0.89, and the ones of $\beta_{Ric}$ were 0.05–0.37, 0.03–0.46 and 0.01–0.22. Functional $\beta_{Ric}$ was greater than $\beta_{Rep}$ at low (0.07–0.45, 0.09–0.37) and mid elevations (0.03–0.55, 0.14–0.27) and the opposite at high elevations (0.01–0.28, 0.11–0.4).

All PerMANOVA tests showed differences: $\beta_{Tot}$ ($F_{2,12} = 2.91$, $p = 0.001$; $F = 4.14$, $p = 0.001$, for taxonomic and functional, respectively), $\beta_{Rep}$ ($F_{2,12} = 2.35$, $p = 0.01$; $F_{2,12} = 3.5$, $p = 0.02$) and $\beta_{Ric}$ ($F_{2,12} = 6.02$, $p = 0.02$; $F_{2,12} = 6.25$, $p = 0.01$) (Figure 3). The PERMDIST tests did not show any significant differences in the taxonomic and functional dispersion of assemblages within

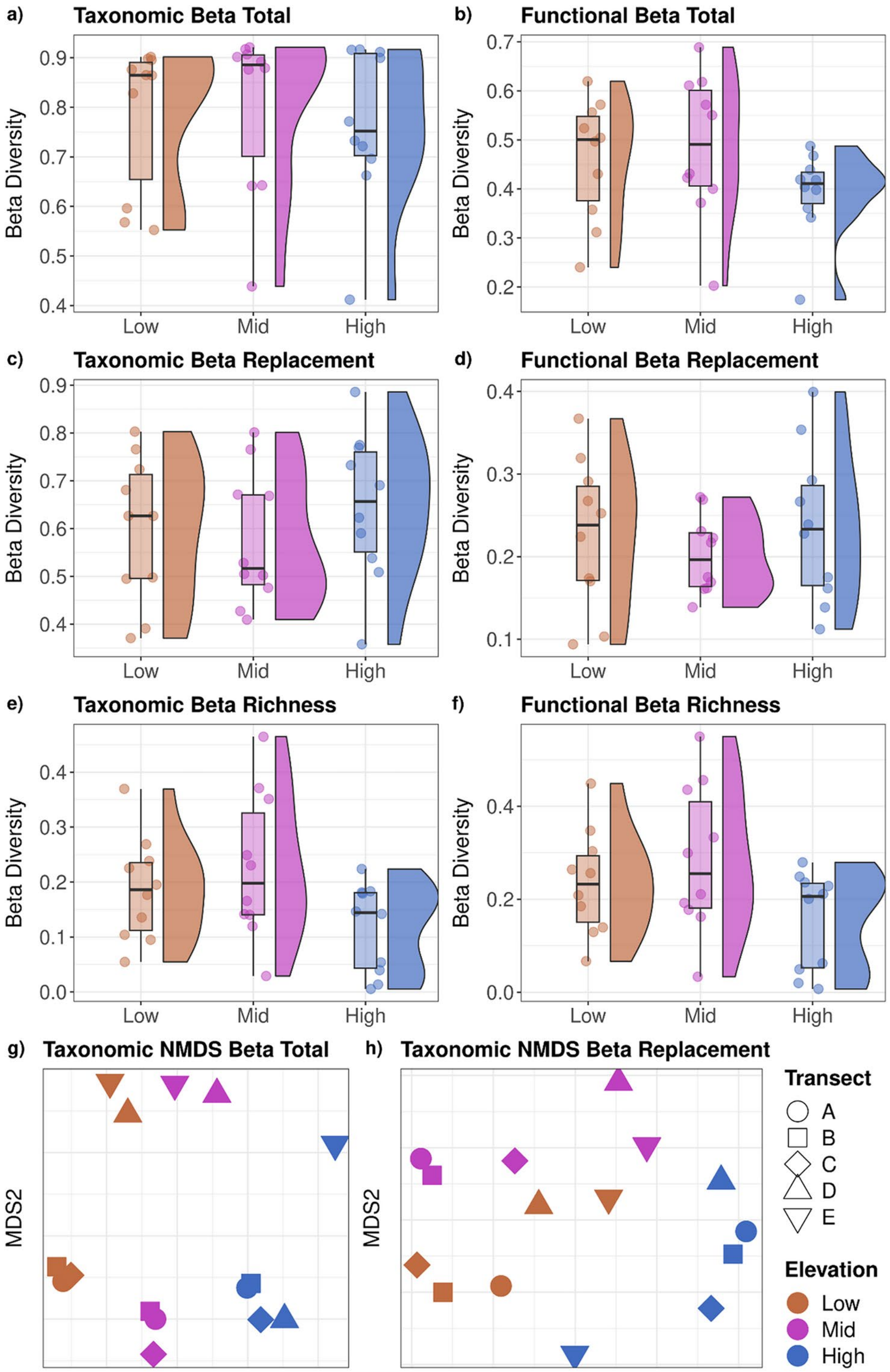

**FIGURE 3** | Taxonomic and functional β diversity values ($\beta_{Tot}$, $\beta_{Rep}$ and $\beta_{Ric}$) for each elevation and NMDS ($\beta_{Tot}$, $\beta_{Rep}$) according to elevation. The shapes in the NMDS represent horizontal distances, with A being the community of the plot at point 0, B the one at 100 m, C the one at 1 km, and so on.

habitats across elevations ($F=0.16$, $p=0.8$; $F=0.31$, $p=0.73$, respectively).

Although distance-decay power-law models showed a general increase in β diversity with geographic distance (Figure 4, Figure S5, Table 1, Table S2), there was some variability. Incidence-based taxonomic and functional $\beta_{Tot}$ and $\beta_{Rep}$ increased, whereas some $\beta_{Ric}$ values decreased slightly with horizontal distance—with only five out of the 18 models (taxonomic and functional * three β measures * three elevations) providing $p$ values higher than 0.05, all of which corresponded to taxonomic $\beta_{Ric}$. The slopes of the taxonomic and functional $\beta_{Tot}$ and taxonomic $\beta_{Rep}$ models increased with elevation (high elevation > mid elevation > low elevation), and in the case of the functional $\beta_{Rep}$ models, the slope was the greatest at mid elevation, followed by high elevation (Table 1). The slopes of

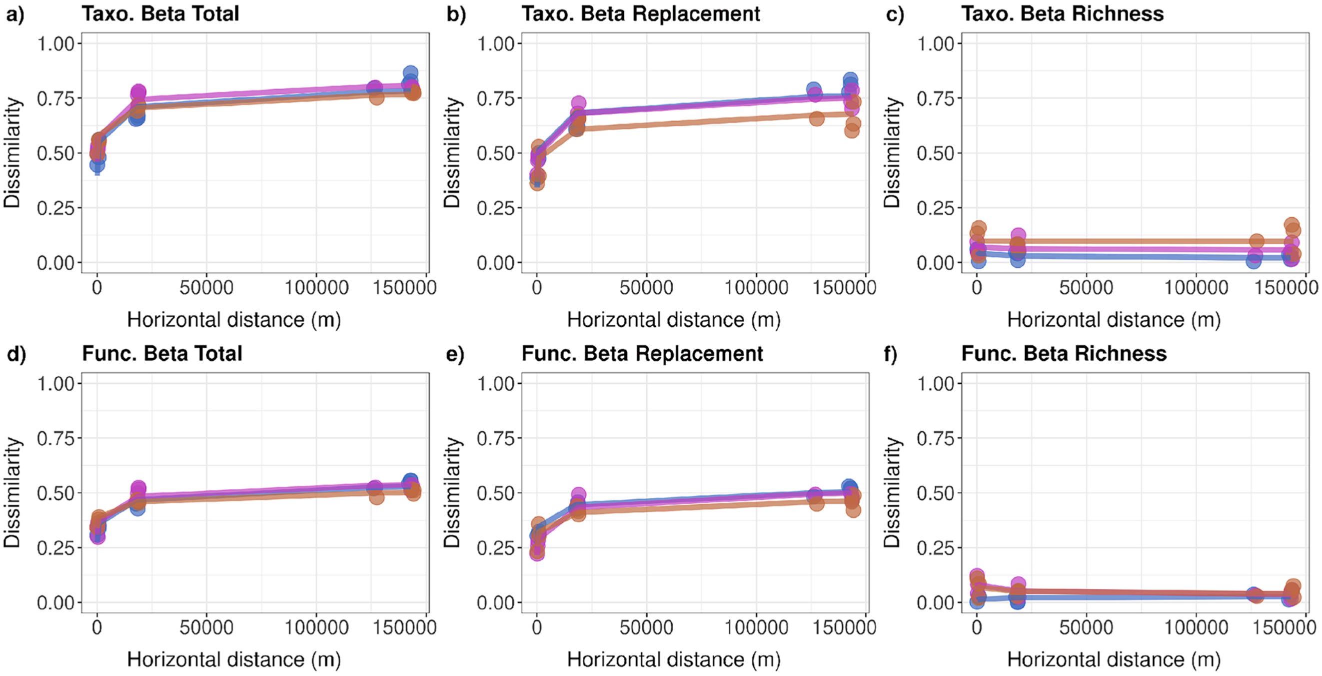

**FIGURE 4** | Distance-decay power-law models for $\beta_{Tot}$, $\beta_{Rep}$ and $\beta_{Ric}$ for the three target elevations (low, mid and high in red purple and blue, respectively) for incidence data.

taxonomic $\beta_{Tot}$ and $\beta_{Rep}$ diversity models were also greater than those of corresponding functional $\beta_{Tot}$ and $\beta_{Rep}$.

As for the abundance-based indices, nine out of the 18 models, five of the $\beta_{Rep}$ models and four of the $\beta_{Ric}$ models, showed $p<0.05$ (Figure S5, Table S2). Although the slope was positive for almost all models, the mid-elevation plots were the ones with the greatest slope for $\beta_{Tot}$ and $\beta_{Ric}$, for both taxonomic and functional data. Despite these results, our tests of the differences between the slopes (of the models at different elevations) did not provide $p$ values lower than 0.05, which might require a greater number of plots. The within-habitat Mantel tests provided different results at each elevation (Table S3), but with a general pattern indicating correlations between taxonomic changes between assemblages and geographic distance, mainly driven by the replacement component of β diversity.

Prosoma width did not change with elevation when using incidence-based data ($\chi^2=5.18$, $p=0.07$) but did so with the abundance-based data ($\chi^2=9.14$, $p=0.01$; being lower in the high-elevation assemblages than in the low ($p=0.016$) and mid ($p=0.008$) elevation ones) (Figure 5). The CWM of the relative length of tibia I varied according to incidence data ($\chi^2=7.62$, $p=0.022$), being longer at mid than at high elevations ($p=0.008$). The incidence-based CWM of relative fang length changed across elevations ($\chi^2=9.92$, $p=0.007$; being greater at high elevation than at mid ($p=0.016$) and low ($p=0.008$) elevations). The abundance-based data also indicated longer average fangs at high-elevation communities ($\chi^2=6.14$, $p=0.046$), compared to the ones at mid-elevations ($p=0.008$) (Figure 5).

Our tests of the effects of elevation on CWM of ballooning were different for abundance data ($\chi^2=1.5$, $p=0.47$) and incidence data ($\chi^2=7.58$, $p=0.02$) (Figure 5d,h). According to the incidence data, low elevation assemblages contained species with greater frequencies of ballooning than those at high elevation ($p=0.008$) (Figure 5d). As for the null models, patterns varied depending on the metric and the data used (Figure S6), with the clearest and most relevant findings being the lower-than-expected values of CWM for prosoma width at all higher elevation assemblages ($p<0.01$) and at two low elevation assemblages (CWM, $p<0.05$) (all for abundance data).

## 4 | Discussion

Two measures of α diversity changed with elevation: functional evenness and dispersion. As the relationship between these two indices and elevation was not linear, with lowest values found for mid elevation, it remains to be explained exactly how climatic differences (gradients) may affect the traits on which our measures are based. Regardless of whether or not climate exerts a measurable effect on our functional measures, it is also plausible that habitat-related physical features, such as the three-dimensional structure of vegetation, condition them (i.e., a greater structural heterogeneity in mid-elevation forests may provide more niches and microhabitats, which may lead to a greater partitioning of resources (Tews et al. 2004, Carrasco et al. 2018, Cooper et al. 2023) and to spider assemblages with more regular or dispersed distribution of functional traits).

### 4.1 | Taxonomic Beta Diversity Across Elevations

The differences between spider assemblages (within-habitat β diversity) were greater at higher elevations than at lower elevations, and, furthermore, these differences increased more with geographic distance (more pronounced distance decay) at higher elevations. Our findings match the idea that the distances between the localities and dispersal-related processes may be more

**TABLE 1** | Pseudo $R^2$, $p$ value, and slope of distance-decay power-law models for taxonomic and functional $\beta_{Tot}$, $\beta_{Rep}$, and $\beta_{Ric}$ for the three target elevations for incidence data.

| Model | Pseudo $R^2$ | $p$ | Slope |
|---|---|---|---|
| $\beta_{Tot}$ | | | |
| Taxonomic | | | |
| Low elevation | 0.978 | 0.007 | 0.117 |
| Mid elevation | 0.95 | 0.001 | 0.14 |
| High elevation | 0.879 | 0.001 | 0.142 |
| Functional | | | |
| Low elevation | 0.97 | 0.001 | 0.04 |
| Mid elevation | 0.877 | 0.04 | 0.054 |
| High elevation | 0.937 | 0.001 | 0.06 |
| $\beta_{Rep}$ | | | |
| Taxonomic | | | |
| Low elevation | 0.793 | 0.01 | 0.095 |
| Mid elevation | 0.955 | 0.001 | 0.122 |
| High elevation | 0.901 | 0.001 | 0.14 |
| Functional | | | |
| Low elevation | 0.889 | 0.003 | 0.046 |
| Mid elevation | 0.946 | 0.001 | 0.061 |
| High elevation | 0.929 | 0.001 | 0.054 |
| $\beta_{Ric}$ | | | |
| Taxonomic | | | |
| Low elevation | 0 | 0.944 | 0 |
| Mid elevation | 0.038 | 0.593 | −0.003 |
| High elevation | 0.224 | 0.12 | −0.004 |
| Functional | | | |
| Low elevation | 0.234 | 0.097 | −0.006 |
| Mid elevation | 0.409 | 0.013 | −0.008 |
| High elevation | 0.152 | 0.131 | 0.002 |

determinant for within-habitat species assembly, which was particularly evident when focusing on the distance-decay of species/functional composition (incidence data). These processes may be driven partly by the lower connectivity among localities (greater habitat fragmentation) at higher elevations (Bjorholm et al. 2008; Bertuzzo et al. 2016; Arellano et al. 2017). The effects of mountains as islands for organisms, increasing the rates of endemism through speciation, is well known across the world (Steinbauer et al. 2016). Alternatively, these patterns may be caused by greater habitat heterogeneity or uneven human disturbance. The few studies that have looked into changes in within-habitat β diversity have also related them to local scale environmental/habitat changes (unmeasured heterogeneity), spatial effects (topographic features/connectivity) and species interactions (Jankowski et al. 2009; Burrascano et al. 2013).

Although geographic distance and topography may limit the homogenising effect of dispersal on assemblages (Gianuca et al. 2013; Liu et al. 2018), habitat structure can also contribute to it (Dantas De Miranda et al. 2019; Hořák et al. 2019; Barczyk et al. 2023). Thus, habitats with denser vegetation (which, in our case, may be mid or high elevation forests) may act as stronger barriers for the movement of spiders—which often use ballooning for dispersal (Bell et al. 2005; Reynolds et al. 2007)—and affect species assembly (Carvalho and Cardoso 2014; Wu et al. 2017). This hypothesis remains, however, untested, and it will require detailed and complex three-dimensional data.

In summary, differences in spider assemblies between locations at similar elevations may be determined first by habitat type (along the elevational/climatic gradient) at a sub-regional scale, and then by habitat structure (conditioned by vegetation) and/or the microclimatic conditions of the specific locality, and the within-habitat dispersal limitations posed by local geography/topography (larger scale dispersal may occur before any other process).

### 4.2 | Functional Beta Diversity Across Elevations

The increase in functional β diversity with geographic distance (at the same elevation) was greater for higher elevations, just like taxonomic β diversity. Both patterns may be explained in part by dispersal limitations. Like for the latter, dispersal limitation may explain, in part, the pattern in the former. Another potential explanation could have been low species densities in higher elevations—which may lead to unsaturated ecological spaces and gaps in functional distribution that increase functional differences between assemblages (Hořák et al. 2019). However, we may discard it in our case since we detected very high levels of saturation (redundancy) in all assemblages, perhaps as the result of large niche overlaps, as has been found in other tropical areas of high diversity (Arellano et al. 2017). One could have also invoked the effects of environmental filtering—α functional diversity may decrease with elevation (due to harsher conditions, like at higher latitudes, Stevens et al. 2003; Lamanna et al. 2014), assembling species that have a combination of traits adapted to the conditions at higher elevations (Bishop et al. 2015; Mammola et al. 2024), and thus decreasing the differences (β) between high elevation assemblages. Although hypothesised, we found a consistent decrease in neither α nor β functional diversity, so we may also not consider this explanation. Our results open the door to the questions of whether (greater) small-scale habitat heterogeneity increases within-habitat β functional diversity as climate may at larger scales (Måsviken et al. 2023). Indeed, when it comes to spiders, vegetation/habitat structure may be a major driver behind the variation in the functional structure of assemblages, with habitat connectivity also being a variable correlated with functional (β) diversity (Schirmel et al. 2016; Delgado De La Flor et al. 2020; Korányi et al. 2023).

### 4.3 | Partitioning of Beta Diversity Across Elevations

As expected, $\beta_{Rep}$ was always greater than $\beta_{Ric}$ (taxonomic and functional) and, within each habitat, it increased with elevation,

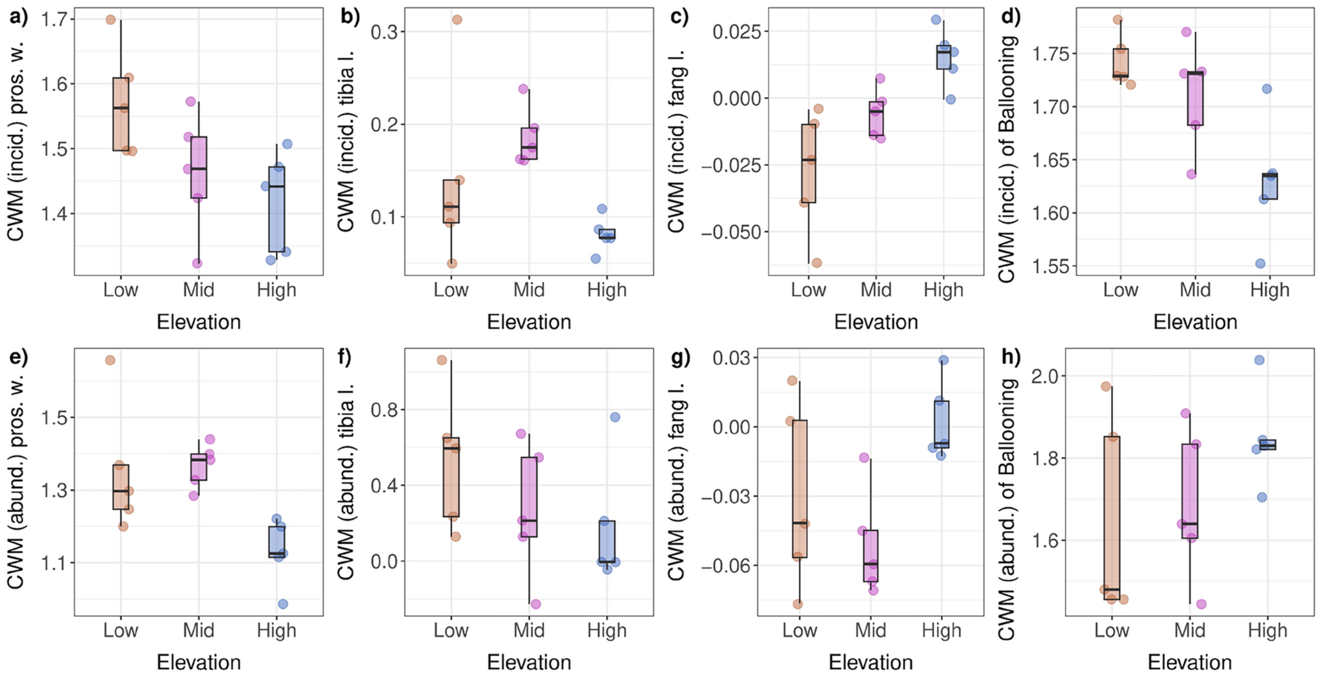

**FIGURE 5** | Community Weighted Means of prosoma width, relative length of tibia I, relative fang length, and ballooning frequency, incidence (a–d) and abundance-based (e–h).

just as $\beta_{\text{Tot}}$ did. The between-habitat taxonomic dominance of $\beta_{\text{Rep}}$ over $\beta_{\text{Ric}}$ is reflected by the similar number of species in each type of forest (305, 307 and 311 at low, mid and high elevation, respectively) and could be explained by two sets of processes acting over the spider assemblages. First, pervasive dispersal may lead to neutral processes of colonization and extinction dominating over environmental filtering and, as a result, the changes in environmental conditions within and across elevations may not constrain the numbers of species—low $\beta_{\text{Ric}}$ (Si et al. 2016). Second, although not constraining, the environmental and physical conditions, and available resources of each habitat (forest type) may vary enough to determine changes in species composition ($\beta_{\text{Rep}}$) via niche processes (Cole et al. 2010; Foord and Dippenaar-Schoeman 2016; Malumbres-Olarte et al. 2013; Nunes et al. 2016; Pitta et al. 2019).

Indeed, while taxonomic $\beta_{\text{Tot}}$ and $\beta_{\text{Rep}}$ are expected to increase with distance, $\beta_{\text{Ric}}$ and, to some extent, all measures of functional β should be more sensitive to local factors, as they have no real reason to change drastically within 100 km simply due to distance. The fact that functional $\beta_{\text{Tot}}$ and $\beta_{\text{Rep}}$ changed may reflect the changes in taxonomic diversity, and their positive relation with altitude may be caused by a greater variability in environmental conditions at higher altitudes driving higher β diversity, and not necessarily the distance itself (Weinstein et al. 2014).

### 4.4 | Functional Traits Behind Beta Diversity

Despite certain discrepancies between incidence and abundance-based CWM tests, it appears that body size (represented by prosoma width) is smaller in high elevation assemblages. Given the decrease in temperature with elevation, our findings are aligned with the idea that certain ectothermic organisms, such as spiders, on average may be smaller on average in colder environments, as their size may be limited by the (low) metabolic rates that they can reach (Entling et al. 2010; Monsimet et al. 2021).

The increase in proportional fang length with elevation is probably the first record of a spatio-climatic pattern in this morphologic trait. If fang length is an adaptation to prey speed (Gibb et al. 2014; Müller et al. 2022), our results might indicate that higher elevation forests host faster prey (as Diptera), perhaps because the local habitat conditions or structure favour their abundance (Müller et al. 2022). However, a simple alternative explanation is that smaller spiders have proportionally larger fangs, as the strength scales quadratically (based on the cross-sectional area of muscles) while our morphologic measures (prosoma width, leg length, fang length) scale linearly. Hence, smaller spiders may tend to be proportionally stronger than larger ones, which would also be reflected in the strength of chelicerae and, therefore, fangs.

Our finding of lower ballooning frequency in higher elevation assemblages may be similar to those found on oceanic islands (Carvalho and Cardoso 2014; Malumbres-Olarte et al. 2021). Mountain tops or high-elevation areas are sometimes termed 'sky islands', i.e., isolated habitat patches surrounded by a 'sea' of non-suitable habitats. Therefore, species inhabiting sky or oceanic islands may have evolved reduced dispersal capacity as a protection against venturing into non-suitable areas (Malumbres-Olarte et al. 2021).

## 5 | Conservation Management

Even at lower elevations of the Udzungwa Mountains, where human activities cause greater disturbances, the spider assemblages are diverse both locally (α) and regionally (β), taxonomically as well as functionally. Given the usual association between high β diversity and the presence of many small-range species (Jankowski et al. 2009), and the large number of rare (in abundance, with smaller population sizes) and unique species (to each locality) found, one might assume that many of them are endemic (Jankowski and Rabenold 2007). Therefore, protection levels and measures in the different conservation areas should remain strict. Furthermore, as shown by the uniqueness of our southernmost assemblages (in USNFR), a potential expansion of the Udzungwa Mountains National Park southwards that would expand habitats of all elevations would be highly recommended, and, if Nature Forest Reserves are included, they would potentially increase the conservation and educational capacities of the growing Tanzanian network (UNDP GEF 2020; Ract et al. 2024). Areas such as the Udzungwa Mountains with very high between- and within-habitat β diversities provide an excellent opportunity, through expansions of protected areas, to increase the chance of survival of innumerable small-range or habitat-restricted species in the face of climate change and human encroachment (Jankowski et al. 2009). If, ultimately, such expansions lead to larger and more connected protected areas, they will be particularly beneficial for the viability of rare species (which we found more abundant in low-elevation forests), whose populations often present distributions that are patchy and more vulnerable to climate and habitat changes.

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## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

The data that supports the findings of this study is available in Data S1, S2 and S3 of this article.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** aje70111-sup-0001-DataS1.csv. **Data S2:** aje70111-sup-0002-DataS2.csv. **Data S3:** aje70111-sup-0003-DataS3.docx.