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Morphospace disparity and species diversity in Sri Lankan phytophagous scarab beetles—A comparison by forest types, altitude and sites

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Abstract

1. Species diversity and morphological disparity are often linked, especially in lineages with evolutionary success. For invertebrates, their relation is poorly investigated, particularly under various ecochorological scales.
2. Here, we explore thirteen assemblages of phytophagous scarab beetles (Coleoptera: Scarabaeidae) in Sri Lanka and infer patterns of morphospace and species diversity along forest types, elevation zones and sampling sites. Disparity of body size and shape was analysed based on 20 linear measurements, considering separately three major lineages: the entire assemblage and their two sister subclades, Sericini and Pleurosticts excluding Sericini.
3. Diversity and disparity were investigated in three sets of landscape partitioning, from regional to local scale: forest type, elevation zone and locality.
4. Results showed divergent patterns of lineages at different geographical scales. Morphospace divergence and occupancy exhibited two distinct patterns. For the entire assemblage and Pleurosticts excluding Sericini, the morphospace volume expressed by median centroid size decreased with increasing altitude. In contrast, Sericini demonstrated a more confined morphospace across different forest types and elevation zones. However, similar patterns were not found for the Shannon diversity. Disparity of morphological shape was significantly correlated with species diversity in all three chorological categories only for the entire assemblage, while in Sericini this correlation was recovered only at locality-scale. Our results indicate that small changes in diversity are linked to small alterations in disparity, although significant shifts in diversity do not necessarily correspond to substantial disparity change.
5. Future research exploring the genealogical aspect of morphospace divergence should incorporate a phylogenetic framework, especially when comparing different systematic levels.

KEYWORDS
chafers, ecology, elevation, forest type, Sri Lanka

INTRODUCTION

Evolutionary success of lineages is often reflected in high species diversity and morphological disparity (Guillerme et al., 2020). However, the two phenomena are not necessarily connected (Hopkins, 2013; Ricklefs, 2012). Diverse taxa may display high or low morphological disparity (Minelli, 2016; Simões et al., 2016). The same applies for taxa with low diversity. The informative value of disparity on the evolution of organisms has been frequently investigated in palaeontology (Deline et al., 2018; Heard & Hauser, 1995; Romano, 2019; Romano et al., 2017). Discordance between taxonomic and morphological diversity is also apparent over evolutionary timescales (Roy et al., 2004). One major focus to investigate causalities of biodiversity is to explore factors that affect morphological evolution (Guillerme et al., 2020): Recognising morphological differentiation in response to adaptation or in relation to rates of molecular evolution helps to understand macroevolution of lineages, e.g., in respect of morphological key innovations (Eberle et al., 2014; Heard & Hauser, 1995; Hopkins & Gerber, 2017; Nel et al., 2018; Simões et al., 2016). It has been shown that phylogenetic sampling affects morphological disparity (Smith et al., 2021). Macroevolutionary patterns within species assemblies are known to be expressed differently at various geographical scales (Jønsson et al., 2015), particularly within species communities (Inward et al., 2011; Ribera et al., 2001), at which direct competition and ecological stress occur. At different chorological scales, patterns are not necessarily the same (Ricklefs, 2012). Due to 'environmental filtering', co-occurring species are likely to share traits that enable them to persist in a defined environment. Alternatively, disparity in key ecological traits between sympatric species that involve ecological divergence might allow them to coexist (Cardillo et al., 2008; García-Navas, 2019; see also neutral theory: Czekanski-Moir & Rundell, 2019).

Observed diversity across spatial scales is the result of speciation and interactions between species, primarily competition for shared resources (Ricklefs, 2012). Therefore, species richness is likely to be often linked with an increase of density of morphospace occupation (Jønsson et al., 2015; Triantis et al., 2016). Tropical regions harbour many more species than temperate regions. Diverse rainforests with high structural complexity possess a high number and variety of available niches allowing the extensive co-existence of taxa with divergent functional traits (García-Navas, 2019). Studies on vertebrates suggest a general tendency for the morphospace volume to increase with taxonomic diversity, while disparity within defined lineages tends not to vary with richness, even for tropical-temperate comparisons (Roy et al., 2004; Shepherd, 1998). Many studies focused on large-scale spatial patterns of taxonomic richness vs. morphological disparity, with only sparse reference to local phenomena (Ricklefs, 2012). Assessments of habitat filtering and competition at local scale are commonly addressed through the investigation of the distribution of community members across phylogenies (e.g., Cooper et al., 2008; Lanier et al., 2013). Extant terrestrial invertebrates have rarely been studied in this context, especially in tropical regions (Triantis et al., 2016) and in the context of disparity vs. diversity, and if so, often only body size rather than shape was investigated (Brehm et al., 2019; Salomão et al., 2021). This refers to both, studies representing descriptive baseline data about assemblages as well as investigation also the causalities of disparity and diversity. Since invertebrate species numbers are by several dimensions higher, they are particularly suitable to test findings that are so far mainly reported from vertebrates.

In this study, we therefore examined multiple assemblages of tropical phytophagous scarab beetles (Coleoptera: Scarabaeidae) in Sri Lanka and inferred their patterns of morphospace and species diversity across various spatial and ecological scales. Phytophagous scarabs are a monophyletic clade (Ahrens et al., 2014; Dietz et al., 2023; McKenna et al., 2019) which so far is referred to as 'pleurostict chafers' or Pleurosticts (Ahrens et al., 2014; Ritcher, 1958). Pleurosticts are a very diverse group of some 30,000 species, which rapidly diversified during the Late Cretaceous – Early Paleogene. Adults feed unspecifically on leaves of angiosperm plants (Ahrens et al., 2014), while larvae feed on humus and roots (Ritcher, 1958). The causes for their high diversity are yet poorly understood (Ahrens et al., 2014; Eberle et al., 2014).

Body size and shape variation (i.e., morphospace) are assumed to reflect differences in the species ecology and behaviour (Eberle et al., 2014; Inward et al., 2011; Wainwright & Reilly, 1994). At the global scale, morphospace reflects the general niche occupation of phytophagous scarab lineages (Pleurosticts) according to their different microhabitats and foraging behaviour (Eberle et al., 2014). However, since single lineages show only little divergence and previous studies' sampling was not yet considering local assemblages, it remained obscure whether direct competition between species occurred (Eberle et al., 2014). We addressed this by investigating morphospace disparity and species diversity in 13 different local assemblages along altitudinal and ecological gradients. We aimed to examine assembly patterns across three primary landscape partitions – regional to local scales – characterised by forest types, elevation zones, and collection sites. Increased morphological disparity may indicate the impact of direct interspecific competition. In scenarios, in which direct competition is absent, we anticipate a continuous Brownian motion-like increase of morphological disparity with diversity. Consequently, we expect to observe a positive correlation at both chorological and ecological levels.

MATERIALS AND METHODS

Specimens sampling

The studied species assemblage included all pleurostict chafers (Coleoptera: Scarabaeidae) that were sampled during four field campaigns in Sri Lanka. This tropical island is a highly suitable study area, with its topographic, climatic and vegetational diversity. Standardised sampling at 14 localities (L1–L14) covered almost all major biomes, altitudinal zones (0–2500 m) and different forest types (Figure 1, Table S1). One locality (L7) was excluded from final analysis, as it

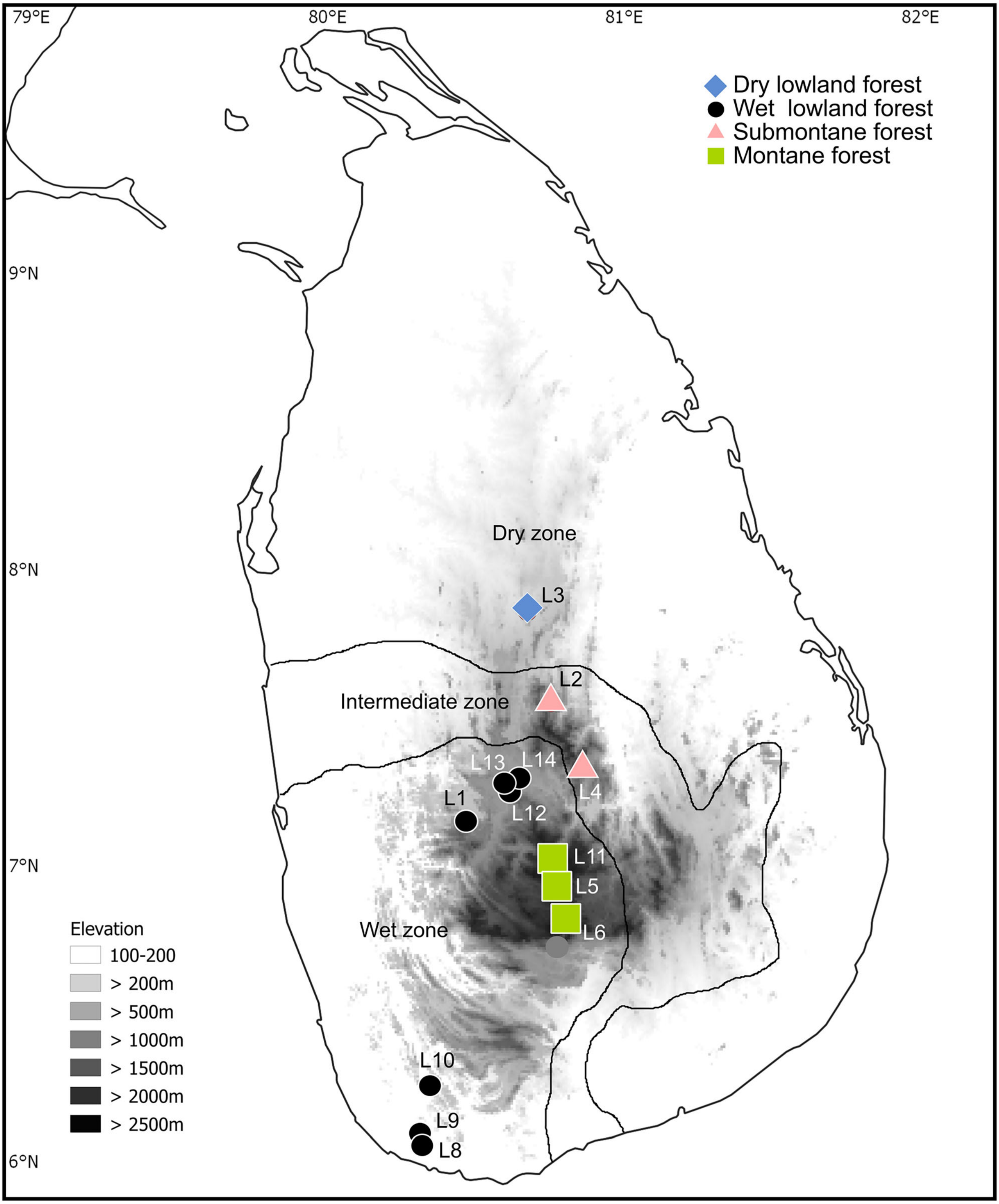

FIGURE 1 Map illustrating the location of sampling sites. L1: Aranayake; L2: Riverston; L3: NIFS Arboretum; L4: Deenston; L5: Nuwara Eliya; L6: Horton Plains; L8: Hiyare; L9: Kottawa; L10: Kanneliya; L11: Piduruthalagala; L12: Uda Peradeniya; L13: Gannoruwa; L14: Udawattakele. Coloured symbols represent the different forest types.

could not be sampled with the same frequency. We operated six UV-light traps per locality. In total, 60–72 sampling events were conducted in each location during both rainy and dry seasons. Species accumulation curves for individual localities showed species saturation and that about 80% of species at a locality have been captured in less than half of the total trapping events (before 34th trapping event)

(Ranasinghe et al., 2023). Specimens were sorted to morphospecies based on genital morphology using available taxonomic literature (Fabrizi & Ahrens, 2014; Ranasinghe et al., 2020, 2022).

Morphometric analysis and morphological disparity

Disparity may be assessed by qualitative characters or quantitative approaches (body shape/morphospace) (Guillerme et al., 2020; Nel et al., 2018). For comparability with former study with focus on evolutionary aspects of morphospace evolution in chafers (Eberle et al., 2014), we measured twenty linear distances (Figure S1) of 384 adult specimens from 105 species which were all individualised by a voucher number based on which every morphospecies/specimen can be retrieved for subsequent analysis or studies (Table S2). Measurements were taken directly from specimens using an ocular grid on a Wild M3Z stereomicroscope.

We analysed morphospace and morphological disparity. This was done separately for three different monophyletic lineages: (1) the entire assemblage (i.e., all Pleurosticts), (2) for Sericini only, and (3) for Pleurosticts excluding Sericini (i.e., other Pleurosticts). The latter two lineages are members of each of the two basal currently considered pleurostict sister clades (Ahrens et al., 2014; Dietz et al., 2023; McKenna et al., 2019). We treated them separately to explore the impact of lineage choice (Smith et al., 2021). Analyses were additionally partitioned for three major chorological landscape entities (from regional to local scale) based on (1) forest type, (2) elevation zone, and (3) sampling locality. Forest types included four entities: (a) evergreen wet lowland forests, (b) evergreen dry lowland forests, (c) submontane forests, and (d) montane forests. Elevation was partitioned in five units: EZ1: 0–500 m, EZ2: 501–1000 m, EZ3: 1001–1500 m, EZ4: 1501–2000 m, and EZ5: 2001–2500 m. At locality level, morphospace occupation referred to actually co-occurring species.

After a general examination of the raw data patterns, morphological disparity was calculated for all combinations of the three lineages, the three spatial partitions, and for shape and size. (1) Shape was defined as the original measurements that were transformed by a back projection method using the isometric size vector (Burnaby, 1966). The obtained variables were then subjected to a principal component analysis (PCA) using the covariance matrix, that is, without scaling. (2) An estimate of size was obtained by performing a PCA on the original measurements and retaining only the first principal component. Again, no scaling was applied. The first principal component reflects size because all distance variables are proportional to each other and thus reflect the vast majority of total variation in the data (Claude, 2008).

Observed disparity in subsets was calculated as the median centroid size using the dispRity-package (version 1.7.12) (Guillerme, 2018) in R (version 4.3.0) (R Core Team, 2023). Precisely, the centroid size based on distances between each individual in multidimensional morphospace and the centroid of the trait-matrix (or the size estimate) was calculated (Laliberté & Legendre, 2010). To test the robustness of our results and to account for the fact that different subsets had different numbers of individuals, each subset was fully bootstrapped 1000 times, allowing for duplicates. Disparity of each subset was calculated the same way as for the original data. Localities with less than three samples were discarded before analysing locality specific disparity. Furthermore, we assessed the percentual change of median centroid sizes from the 1000 bootstrap replicates.

Effects of forest type and taxon clade

Further data analysis was done in R 4.4.1, as follows: Morphometric data (Euclidean distance, Median Centroid size, body length) were analysed using generalised linear mixed-effects models using Template Model Builder (TMB) in *glmmTMB* (version 1.1.9, Brooks et al., 2017). We used this approach to address the imbalanced nature of our data. For each response variable, we tested a range of potential univariate parametric distributions before running glmmTMB models. Euclidean distance and body length were log-normally distributed, and corresponding glmmTMB models were fitted using Gaussian errors with a log link. Models had the following principal syntax:

$$\begin{aligned}&\text{glmmTMB}(\text{response} \sim \text{foresttype} * \text{taxon. clade} + \exp(\text{pos} + 0|\text{taxon}),\\&\quad \text{family} = \text{gaussian}(\text{link} = \text{“log”}))\end{aligned}$$

where response is the response variable, foresttype is the forest type (factor with three levels), taxon. clade indicates Sericini vs. other Pleurostics (factor with two levels), taxon is the name of the species considered (individual-level random effect) and pos indicates the Latitude/Longitude position. The star (*) operator indicates an interaction term. The exp.() part of the formula indicates a spatial exponential covariance structure, modelled as

$$\rho = \exp\left(-\exp(-\theta_2)d_{ij}\right)$$

where ρ is the spatial correlation, exp. is the exponential function, θ_2 is a correlation parameter, and d_{ij} is the spatial distance (Euklidean) between any pair of spatial coordinates.

For models on all taxa, taxon. clade was not included as an explanatory variable.

To analyse species richness data, we first calculated the Shannon index based on total abundance of each taxon per sample; Shannon index was then analysed using generalised least squares (GLS) models. Models were fitted with and without a range of variance and correlation functions to account for potential differences among localities (e.g. spherical spatial autocorrelation), but models without these functions generally had lower AICc values and were retained. GLS models had the same explanatory variables as the glmmTMB models.

Effects of elevation and lineage

Due to possible effects of spatial autocorrelation and imbalanced sampling, effects of elevation and taxon clade were analysed using generalised additive models implemented in the mgcv package in R (version 1.9–1, Wood, 2017). The principal syntax was

$$\begin{aligned}&\mathrm{gam}(\mathrm{response} \sim \mathrm{s}(\mathrm{Elevation,\ by = taxon.\ clade,\ bs = ``ts", k = 4)}\\&\quad + \mathrm{s}(\mathrm{Longitude,\ Latitude,\ bs = ``gp", k = 3}), \mathrm{select = T},\\&\quad \mathrm{family = gaussian(link = ``log"))}\end{aligned}$$

where s() defines the smooth (for Elevation, separately for each taxon clade), k sets the basis dimension of the smooth, ‘ts’ indicates thin-plate splines with a smoothing penalty, bs=‘gp’ indicates a Gaussian process smooth to account for a spatial covariance structure (a function of Latitude and Longitude), and the ‘select = T’ argument indicates that automatic selection of smoothness of the Elevation term.

Finally, we assessed the Pearson coefficient between mean disparity and species diversity for lineages and landscape partitions. The Pearson coefficient was calculated in R using the cor.test() function.

RESULTS

All assemblages investigated here included herbivorous Sericini as well as Rutelinae, Melolonthinae and Dynastinae (i.e., ‘other Pleurosticts’) (Table S2) but not floricolous diurnal species (e.g., Cetoniinae). Species diversity strongly varied among localities (Figure S2) but showed hump-shaped or linear patterns when looking at separate elevation zones or forest types (Figures 2, S2).

Morphospace analysis

Our morphospace analysis, based on linear measurements (Figure S1), revealed a large amount of variation explained simply by body size. For the entire dataset, the morphospace analysis revealed that a minimum of 95% of the cumulative variation was represented by principal component (PC) 1 (96.9%) for raw data and by PC 1 to 10 for size-corrected (i.e., shape) data (Table S3). The same was true for the dataset Pleurosticts without Sericini, while for Sericini 85% of variation was reflected in the raw data by PC 1 and 2, and for the shape data by PC 1 to 12. Plots of PC 1 and 2 for the raw data (Figure 3) confirmed a major morphospace divergence between principal pleurostict lineages while species of diverse groups (Sericini, Adoretini) overlapped. Among all traits, particularly body length and size of metacoxa contributed to divergence of morphospace (Figure S3).

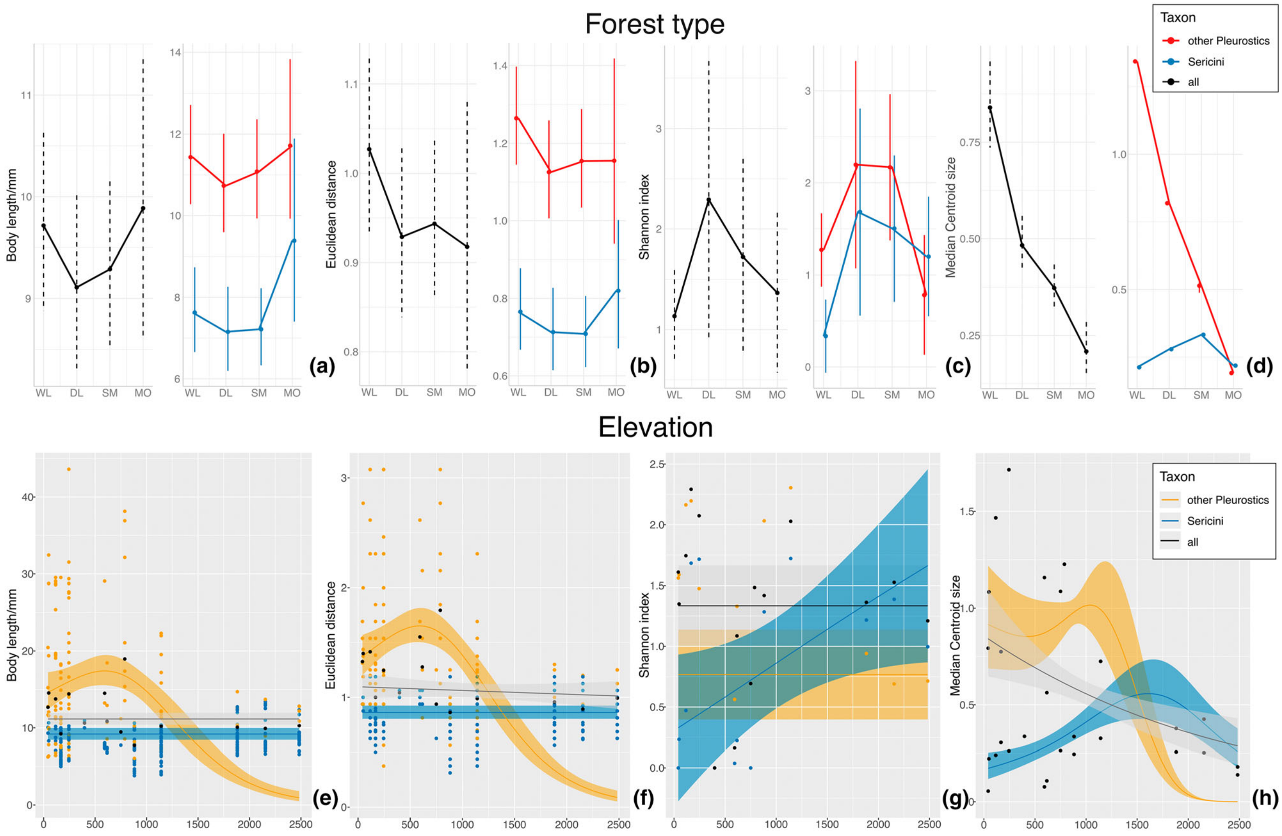

FIGURE 2 Effects of forest type (a–d), elevation (e–h) and lineage (a–h) on species diversity (expressed as Shannon index) and species’ disparity (expressed by the Euclidean distance and body length) and general morphospace volume (expressed by the median centroid size). The plots show predictions from generalised linear mixed-effects models (a–d) and generalised additive models (e–h). Error bars (a–d) and shading (e–h) show 95% confidence intervals.

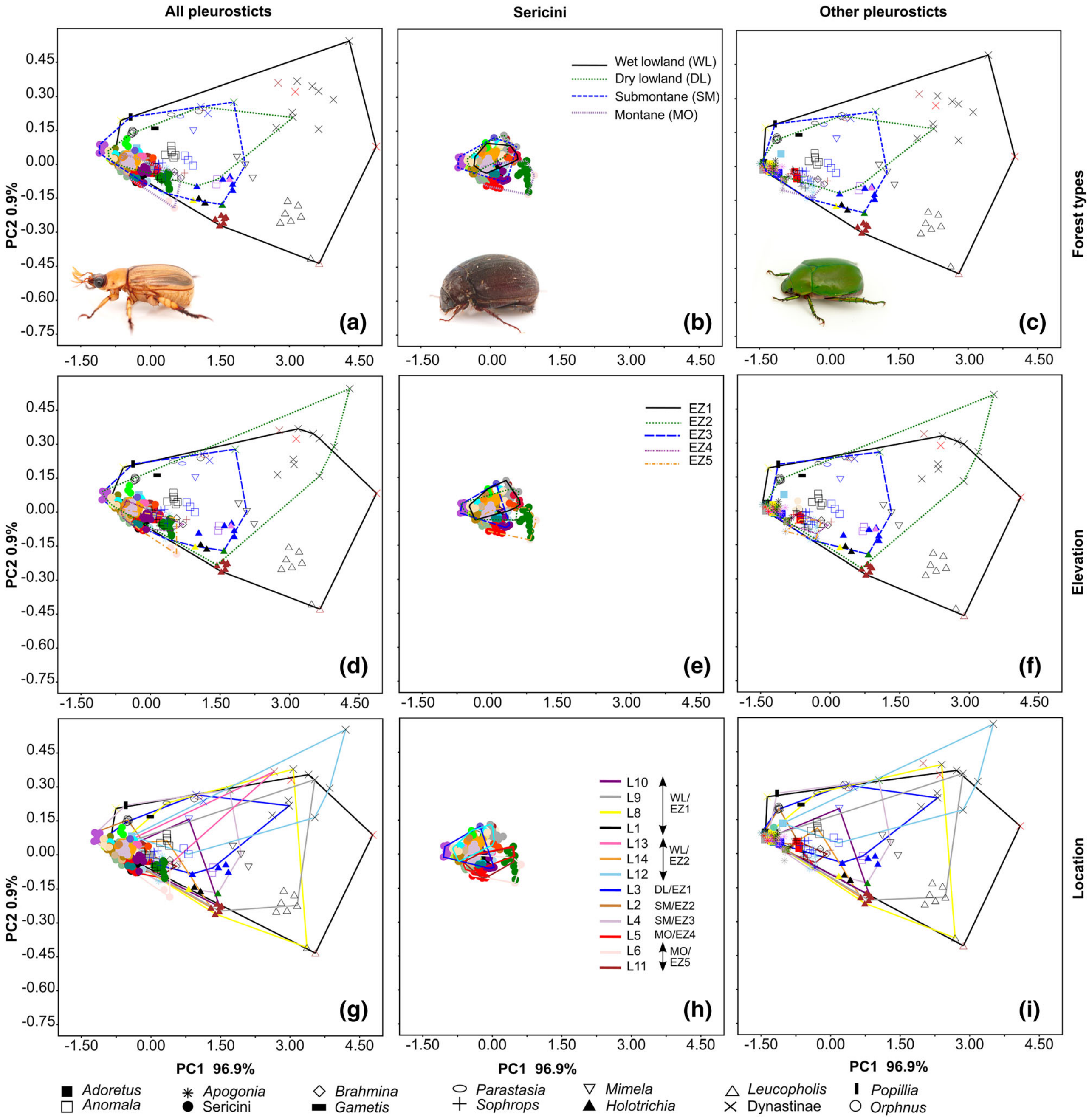

FIGURE 3 Patterns of morphospace disparity (plots of PC 1 and 2) derived from raw measurements of pleurostict chafer assemblages (all Pleurosticts (a, d, g), Sericini (b, e, h), other Pleurosticts (c, f, i)) partitioned for forest types (a–c), elevation (d–f) and localities (g–i). Symbols represent genus or other family-group level, colour of symbols single species, outlines group points according to unique forest types and elevation zones or localities.

Effects of forest type

When looking at the effects of forest type and elevation (see next section), there were considerable differences between patterns found in the raw data (Figures S2, S4-S8) and predictions derived from statistical models taking autocorrelations into account (Figure 2a–d).

When autocorrelation was taken into account, the entire assemblage followed the pattern of the Pleurosticts (excluding Sericini) (Figure 2a–c) for body length, Euclidean distance (Tables S4-S6), and Shannon diversity. Median centroid size (Figure 2d) showed very strong declines from wet lowland to montane forest for all groups except Sericini.

Body length variation considerably differed between localities, among generally smaller Sericini (4–13 mm) it was rather constant. In the raw data, it was higher in wet lowland forests than any other forest types (Figure S2) and slightly diminishing with increasing elevation, except for Sericini; yet, when proper generalised linear mixed-effects models were used (Figure 2a), there was a U-shaped pattern, going down from wet lowland to dry lowland forest, and then increasing again from submontane to montane forest (Figure 2a).

Species diversity for *all taxa* was not significantly related to forest type ($X^2 = 4.04$, DF = 3, $p = 0.26$). When the two major lineages were considered separately, species diversity differed strongly between forest types ($X^2 = 17.33$, DF = 3, $p < 0.001$; Figure 2c) and lineages ($X^2 = 8.01$, DF = 1, $p < 0.005$) and generally showed a hump-shaped relationship from wet lowland forest to montane forest, with highest species diversity in dry lowland forest (Figure 2c). Sericini had slightly lower species numbers than the other Pleurosticts.

Effects of elevation

Similar to the effects of forest types, also the effects of elevation differed between looking at the raw data only (Figures S2, S4–S8) and properly accounting for spatial autocorrelation (Figure 2e–h).

Morphospace divergence (body length, Euclidean distance; Figure 2e,f) and morphospace occupancy (median centroid size; Figure 2h) in the investigated chafer assemblages generally followed two distinctive patterns, one for the Pleurosticts excluding Sericini and one for Sericini (Figures 2, S2), which was valid also or the raw data (Figure S7) as well as for size-corrected data (Figure S8).

For species diversity, only the species diversity of Sericini showed a strong effect of elevation, increasing strongly and significantly from the lowest elevation zone to the highest (Figure 2g). This effect was essentially linear ($F_{3,24} = 1.680$, $p = 0.022$); additionally, there was a quadratic effect of longitude and latitude ($F_{3,24} = 2.483$, $p = 0.031$, not shown).

Morphospace occupancy (expressed as body size and Euclidean distance) showed constant responses to elevation in Sericini and all taxa, while there was a hump-shaped response for Pleurostics excluding Sericini with a maximum slightly above 1500 meters (Figure 2e,f).

Median centroid size (i.e., the overall morphospace occupancy size, Figure 2h) almost evenly decreased with increasing elevation, being dissimilar from the hump almost shaped curves of the two subclades with their maxima at different elevations. The amount of total variation in Pleurosticts excluding Sericini was inversed with increasing altitude, that is, for analyses accounting for spatial autocorrelation, general variation of median centroid size was almost constant (Figure 2h), while it was increasing for simple descriptive analysis (Figure S8).

Analysis of morphospace disparity

Divergence measured as morphospace disparity in terms of median centroid sizes of 1000 bootstrap replicates between species was generally reduced with size-corrected data (Figures S7, S8), while for Sericini little change was evident from the plots. The raw data morphospace volume of the assemblages decreased from wet lowland forests to dry lowland forest, submontane forest, and montane forest (Figure 3a); montane forest species occupied less than a quarter of the entire morphospace. The speciose Sericini contrasted these patterns for forest types and elevation zones. Their morphospace was more restricted and species of different forest types and elevation zones overlapped considerably (Figure 3b,e). Pleurosticts without Sericini showed similar patterns for forest types and elevation zones as all Pleurosticts (Figure 3c,f vs. a,d). No differences were observed between the highest elevation zones (EZ4, EZ5) representing montane forest. Individual localities (Figure S4) revealed for the entire assemblage a generally limited overlap in species' morphospace, while strong overlap occurred, also in Sericini (Figure S5), in some species-rich localities.

Correlations between disparity and species diversity

The correlation of disparity versus species diversity did not show the two distinctive patterns recognised above. A significant correlation for shape resulted only for the entire assemblage in all three chorological categories, that is, forest type, elevation, and location, and for Sericini as well for location (Table 1). Size data had a correlation of disparity versus species diversity only for elevation for the entire assemblage and Pleurosticts excluding Sericini as well in Sericini for location. This is also reflected by plots of morphospace disparity in terms of relative change of median centroid sizes from the mean based on bootstrap replicates derived from shape and size. They appear unrelated to the analogous diversity change of the same geo-entities. High diversity change is not necessarily showing high disparity change, although lowest diversity changes are often associated with low disparity (change), particularly in the more summarising geo-units, such as elevation zone or forest type. Sometimes, not always, particularly among localities, higher disparity changes were linked with higher diversity changes (Figure 4).

TABLE 1 Pearson correlation between the disparity (shape/size) and diversity for the entire assemblage (Pleurosticts all), Sericini and Pleurosticts excluding Sericini* (partitioned by forest types, elevation zones and localities). Significant correlation coefficients ($p < 0.05$) are printed in italics/bold.

	Shape		Size	
	r	*p*	*r*	*p*
Forest type				
Pleurosticts (All)	***0.964***	0.036	0.714	0.286
Sericini	0.601	0.398	0.553	0.447
Pleurosticts (part)*	0.434	0.566	0.922	0.078
Elevation zone				
Pleurosticts (All)	***0.887***	0.045	***0.980***	0.003
Sericini	0.028	0.964	0.753	0.141
Pleurosticts (part)*	0.370	0.539	***0.900***	0.037
Location				
Pleurosticts (All)	***0.600***	0.018	−0.018	0.949
Sericini	***0.848***	0.001	***0.867***	0.001
Pleurosticts (part)*	0.529	0.077	0.298	0.347

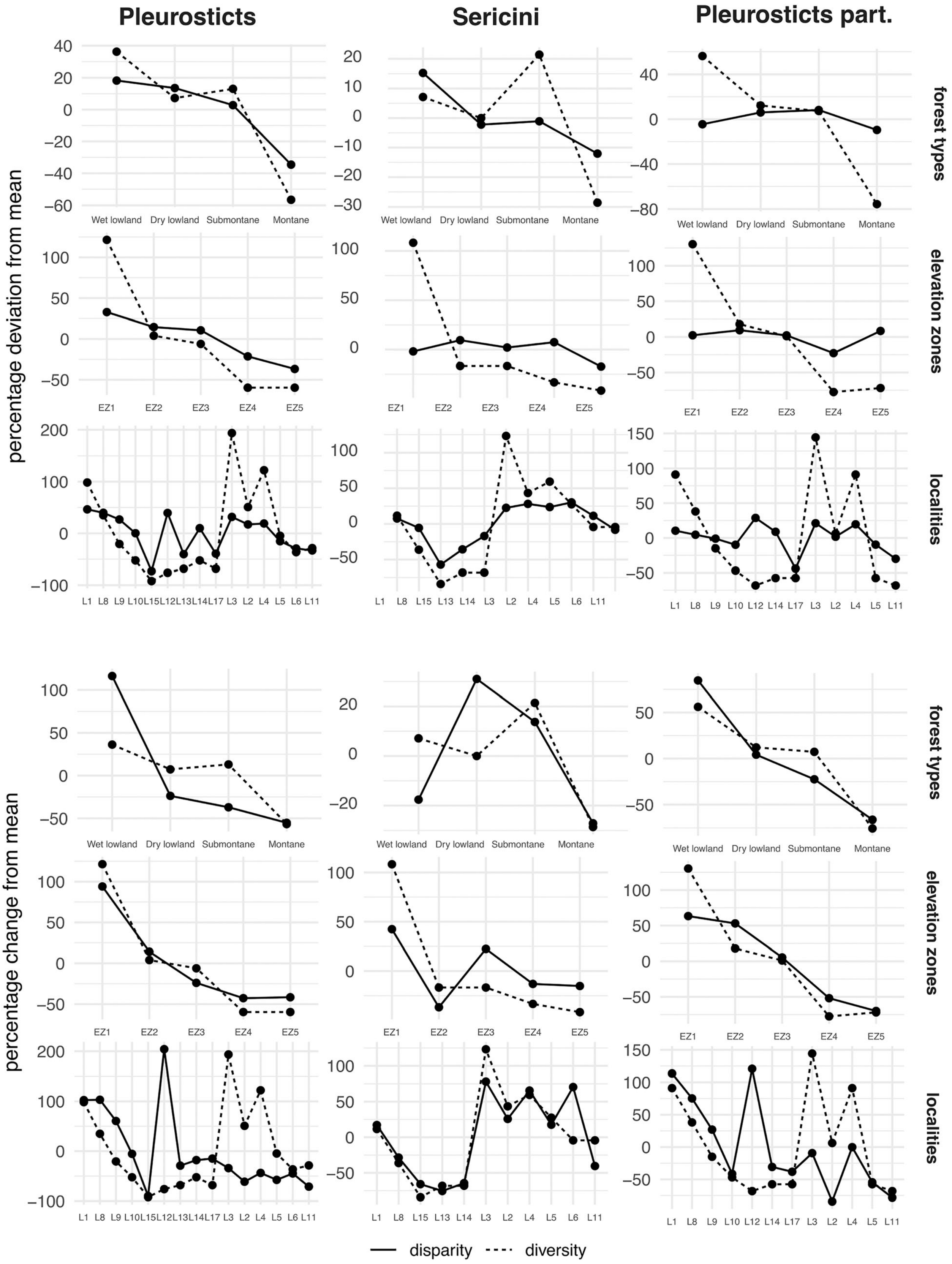

FIGURE 4 Comparison of morphological disparity in terms of shape (above) and size (below) and taxonomic diversity across three eco-spatial partitioning modes of the collected species. The columns represent the complete set of species and two taxonomic subsets. The y-axis displays percentage deviation from the mean per panel to accommodate both disparity and diversity measures on a unified scale. The line at $y = 0$ is the mean of all points in the respective panel.

DISCUSSION

Our study investigated for the first time the general link between morphological disparity and species diversity among phytophagous chafers at different ecochorological scales. Our results showed considerably divergent patterns for single chafer lineages at different geographical scale. This was particularly evident from the plots of morphospace occupation and its disparity (Figures 2–4) but also from correlation analysis between disparity and diversity (Table 1). Statistic support for the morphological differentiation of the chorological entities (i.e., different types of forest, elevation zone, or locality) and correlation with species diversity was likely influenced by the fact that some geographical entities were represented by fewer sampling sites than others (e.g., number of localities for certain elevation zones or forest types). This particularly affected the dataset of Pleurosticts excluding Sericini (Pleurosticts part), which was at higher altitude very poorly represented. Taking spatial autocorrelation into account by using generalised linear mixed-effects models (Figure 2a–d) and generalised additive models (Figure 2e–h), refined the picture of the differences including the patterns of their variation between the two principal assemble lineages and as well for the entire assemblage.

The volume of morphospace that is occupied by the lineages is supposed to mirror the heterogeneity of the species' ecological niches and may thus indicate resource partitioning and competition avoidance (Inward et al., 2011; Wainwright & Reilly, 1994). At larger geographical scales, the relationship between species diversity and disparity is shaped by the evolution of species or lineages (Hao et al., 2020). However, at a local scale, the assembled species are in competition for space and resources. If competition or in consequence competition avoidance occurs, we may expect different patterns on regional and local scales which is what we observed here with the phytophagous chafer assemblages.

We interpret the generally decreasing variation of morphospace and body size with increasing elevation along associated forest types as reduced ecological niche space in which generally less species cooccur (Figure 2). This effect was even stronger for size than for shape. In contrast to the other Pleurosticts, which largely varied in body size (Figure 2), Sericini showed an almost constant size of morphospace clusters (i.e., the summed two-dimensional extension of plots; per entity and cumulated) across all three landscape partitions, as well as almost constant disparity and less pronounced altitude-related decrease of diversity (Figures 2 and 3). Sericini together with their Afrotropical sister lineage Ablaberini (+ their Australasian/Neotropical sister lineage Sericoidinae; see Dietz et al., 2023) form the sister clade to all other Pleurosticts (Ahrens et al., 2014; Dietz et al., 2023; Eberle et al., 2017; McKenna et al., 2019), therefore, the lineage incongruity in morphospace disparity cannot be easily explained by different group ages. However, it should be taken into consideration that several Sericini in this study may have a common ancestor younger than the common ancestor of all here locally occurring non-Sericini species. A test of such a hypothesis would require a comprehensive global phylogeny incorporating all the Sri Lankan species which is far from being available.

High species numbers of Sericini, especially at higher elevations, might reflect their evolutionary success (Ahrens, 2004a) in contrast to most other phytophagous Pleurosticts. This success might be linked to the adaptation to lower temperatures, for example by reduced size or optimised digging mechanics and behaviour, which is reflected also in morphospace (Eberle et al., 2014). Also, body size appears to be relevant in this context, which is why we explore in this study the two components of the morphospace, size (PC1 of raw data) and shape (i.e., size corrected data). Body size contrasts of lineages along the elevational gradients which extends Horne et al.'s (2018) hypothesis that temperature–body size trends of insect across altitudes are not stringent but sometimes present. Increased size in scarab chafers is generally linked with significantly longer larval development: smaller species may have bivoltine cycles (Ahrens et al., 2009), whereas larger species may have a 2- or 3-year life cycle (Ritcher, 1958). Deviation from successful adaptations to faster, energetically less expensive development is likely to result in reduced fitness of the species. In consequence, body shape and size of species may tend to be conserved (i.e. towards smaller body size), resulting in a narrow and more constant morphospace occupation (Figure S4) with simultaneously occurring higher species numbers. Finally, evolutionary key innovations in Sericini such as the metacoxal enlargement or the modification of the elytral base shared by all their species (Eberle et al., 2014; Pacheco et al., 2022) might have catalysed evolutionary change in other traits such as weight reduction in Sericini (Ahrens, 2006; Eberle et al., 2014), so that directed selection and competition would be triggered in multiple dimensions along a complex evolutionary pathway.

Polyphagous herbivory and virtually unlimited food resources in a tropical forest are supposed to exclude interspecific competition and to facilitate a similar ecology of many species, particularly in Sericini (Eberle et al., 2014). Thus, competition for food seems unsuited to explain divergence in morphospace of Pleurosticts as discussed here or earlier (Eberle et al., 2014). However, the striking morphospace divergence between pairs of sister lineages of Pleurosticts with divergent feeding habits revealed that strong directed selection on morphospace might be linked with resource partitioning although being catalysed by other factors such as feeding-related locomotion behaviour (Eberle et al., 2014). This is also confirmed by divergent patterns among different functional morphological traits in different habitats, such as forest or crop cultivations (García-Atencia et al., 2024). Divergent patterns in which feeding habits are related to locomotion behaviour, and thus the morphospace, are also known from dung beetles for which resource competition and partitioning is very well documented (Inward et al., 2011). In this context, parental care and reported parallelisms are a major indicator for selection pressure (Emlen & Philips, 2006). A clear change of disparity patterns of assemblages between local and regional scales, based on which we might deduct resource competition and partitioning also for Sericini, however, was not evident from the current analyses (see also Figure S5). To test this further in detail, it would be necessary to explore divergence patterns and disparity of species being part of the different chorological geo-units. However, this was here not feasible due to the limited number of specimens in many localities/species.

The studied assemblages showed higher species richness and disparity in wet lowland forests and at low elevations. This confirms that landscapes with high productivity and diverse ecological niches support lineages with different ecological attributes. Since species' ecological properties are reflected in their morphology, more ecological niches result in greater morphological differentiation (Wainwright & Reilly, 1994).

However, morphological disparity can also be triggered when biotic selective constraints are weak and abiotic interaction and/or niche partitioning are more important (Chartier et al., 2021). Physical environmental conditions can be highly linked with biogeographic and physiological patterns among lineages (Mani, 1968). Areas with harsh environments like high altitudes with less resources and little habitat structure, allow only certain well-adapted species to survive (García-Navas, 2019). Therefore, higher elevations typically harbour the least species (McCoy, 1990), although the complexity of climatic conditions, biogeographical history, focal taxon, as well as the elevational and geographical extend of the mountains (Mani, 1968) are important influencing factors which might result inverse or alternative diversity patterns for selected lineages due to their biogeographic origin (Ahrens, 2004b). Yet, many studies report a significant decline of diversity with increased elevation (García-Lopez et al., 2012; Salomão et al., 2021), as reported here. Decreasing disparity in our chafer assemblages was caused by the absence of many species, which are unrelated to each other, at higher elevations that were present in lower altitudes. Factors that might explain reduced species richness in chafers in higher altitudes are lower temperatures and in result the reduced vegetation height. The first would not favour larger species with long larval development. The latter reduces ecological niches and increases interspecific competition. Non-overlapping clusters of montane Sericini species in morphospace (Figure S4) supported this theory by suggesting interspecific competition avoidance. However, lowland species' clusters were also generally distinct (Figures 2 and 3), but overlap between a few species occurred, particularly in species rich assemblages. Thus, competition avoidance might exist also in less harsh environments. Finally, one should also consider the possibility of the 'artefact' of disparity, which might not be stringently due to more ecological vacancies or competition avoidance. It is well known that most closely related (and morphologically most similar) species in Sericini (and likely also most other organismal groups) tend to not co-occur with each other (Ahrens, 2004a, 2004b; Fabrizi & Ahrens, 2014) since diversification of Sericini in Asian mountains seems to be particularly driven by geography (Ahrens, 2007; Eberle et al., 2017).

However, in contrast to adults that may occupy the immense, three-dimensional angiosperm food space, very little is known about larval coexistence in the two-dimensional soil layers, which might be more restrictive for coexistence of species (Ahrens et al., 2009). Therefore, studies are needed that investigate larvae in combination with adults in the framework of molecular phylogenies. We need to explore community composition more rigorously at different landscape scales to disentangle the driving forces of diversity vs. disparity in the context of assemblage evolution among pleurostict chafers. Furthermore, future studies might consider phylogenetic correction in disparity analysis (Brusatte et al., 2011) to investigate in more detail the genealogic component of morphospace divergence, particularly when comparing different systematic levels (see also Eberle et al., 2014).

AUTHOR CONTRIBUTIONS

U. G. Sasanka L. Ranasinghe: Conceptualization; investigation; writing – original draft; visualization; writing – review and editing; formal analysis; data curation. **Jonas Eberle:** Conceptualization; investigation; methodology; visualization; writing – review and editing; writing – original draft; formal analysis; supervision. **Suresh P. Benjamin:** Writing – review and editing; resources; supervision. **Christoph Scherber:** Methodology; writing – review and editing; visualization; formal analysis; validation. **Dirk Ahrens:** Conceptualization; investigation; funding acquisition; writing – original draft; methodology; validation; writing – review and editing; project administration; data curation; supervision; resources.

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CONFLICT OF INTEREST STATEMENT

We have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at https://zenodo.org, reference number https://doi.org/10.5281/zenodo.11277426.

ETHICS STATEMENT

The study was done with following research and collection permits of the Department of Wildlife Conservation, the Department of Forest Conservation, the Divisional Forest Office Kandy and Galle (Permit no: WL/3/2/61/18, R&E/RES/NFSRCM/2019-01, R&E/RES/NFSRCM/EXTENSION/2020, K/G/01/06/03, M/0/03/2019.).

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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: Supplementary Figure.

Data S2: Supplementary Tables.

Suppl. Table 2. Morphometric measurements and metadata of all studied specimens. Metadata include species identification, higher classification, voucher number, occurrence data regarding sampling location in Sri Lanka, elevation zone (EZ) and forest type (F). Units of measurements are mm. WL: evergreen wet lowland forests, LD: evergreen dry lowland forests, SM: sub-montane forests, MO: montane forests; EZ1: 0-500 m, EZ2: 501-1000 m, EZ3: 1001-1500 m, EZ4: 1501-2000 m, EZ5; 2001-2500 m; L1: Aranayake; L2: Riverston; L3: NIFS Arboretum; L4: Deenston; L5: Nuwara Eliya; L6: Horton Plains; L8: Hiyare; L9: Kottawa; L10: Kanneliya; L11: Piduruthalagala; L12: Uda Peradeniya; L13: Gannoruwa; L14: Udawattakele.

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