Title: Trait distribution in Geometrid moth assemblages does not vary along a western Himalayan elevational gradient

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Abstract:

Elevation gradients pose challenges for flying insects due to shifts in temperature and air density, impacting their thermoregulation and flight abilities. Understanding how these challenges influence morphological traits across elevational gradients can provide insights into species distribution mechanisms. Geometrid moths, a model group for trait-based analysis among insects, show no significant variation in body size despite declining species diversity along a 1500m elevation span in the western Himalayas. Investigating 697 specimens of 120 Geometrid moth species, I assessed species diversity, turnover, and various traits related to body size and flight capabilities. Results indicate decreasing species diversity and increasing turnover with elevation. Although body length, wing loading, and maneuverability decrease with elevation, intraspecific variability remains insignificant, and trait overlap is high across elevations, suggesting no significant trait partitioning and niche differentiation among species. This supports the argument that species with similar ecological roles persist through turnover, maintaining consistency in trait values across assemblages. These findings align with previous inconsistencies in trait-environment relationships along elevational gradients in Geometrid moths, spanning neotropical and temperate regions. Additionally, the study reiterates the

importance of multivariate trait-based approaches in understanding species responses to environmental changes within diverse clades, overcoming taxonomic challenges.

Introduction:

The inhabitant fauna of mountainous regions, including flying insects, encounters varying physical parameters such as temperature and air density along elevation gradients (Dillon et al., 2006). This range of physical environments induces notable shifts in species demands, leading to observable variations in biological assemblages along the gradients.

At the nexus of trait-environment relationships are individual and species-level dynamics within communities, spanning various spatial scales. It reveals how organisms, with distinctive trait values, adapt to diverse environmental conditions (Gaston et al., 2009). The resultant trait distribution among coexisting species sheds light on the process of community assembly (Kearney et al., 2010; Lamanna et al., 2014). In low elevations, where warm temperatures and ample resources diminish environmental constraints, species diversify into different niches. Consequently, a lower overall trait overlap and narrower trait width facilitate the coexistence of diverse species. Whereas at higher elevations with higher environmental filters, species diversity decreases, and there is a higher overlap of trait space (Read et al., 2018).

Associated with the rules governing trait-based assemblages is the concept of species packing within niche space, encompassing trait overlap (Kearney et al., 2010; Lamanna et al., 2014). Whether trait overlap decreases or increases hinges on the interplay between niche packing and the displacement of functional trait values over evolutionary time (Macarthur & Levins, 1967; Ricklefs & O'Rourke, 1975). Nonetheless, the total niche occupied by an assemblage is anticipated to increase with growing species richness, aligning with MacArthur's model (MacArthur, 1965), where a 'niche' is defined as an n-dimensional hypervolume comprising biotic and abiotic factors (Blonder et al., 2014). In the tropical Himalayan Mountain system,

bat communities in the western Himalaya and bird communities in the eastern Himalaya exhibit higher niche overlap at lower elevations with greater species richness (Schumm et al., 2020; Chakravarty et al., 2023). However, the applicability of these patterns to insect taxa across elevational gradients and geographical regions remains unclear.

While Bergmann's rule established that species in colder regions should be larger for thermoregulation (Bergmann, 1848), there exists a lack of consensus on this rule among insects, exemplified by varied body size patterns across elevation and latitude gradients (Brehm & Fiedler, 2004; Shelomi, 2012). For arthropods, particularly insects, the decrease in mean temperature does not necessarily translate into analogous changes in body temperature (Stevenson, 1985). The regulation of body temperatures is contingent upon factors such as habitat, species shape, size, and behavior, all of which govern how species respond to temperature fluctuations (Porter & Gates, 1969; Bakken, 1976; Samejima & Tsubaki, 2010).

The aforementioned variability in body size among insects reflects the intricate interplay between ecological, physiological, and climatic factors. For instance, bees exhibit a decrease in body size with increasing elevation (Osorio-Canadas et al., 2022.), contrasting with an increase across latitudes (Gérard et al., 2018). Dragonflies and damselflies are generally larger in temperate regions than in the tropics (Svensson et al., 2023). Geometrid moths, a model group for many such studies, display diverse patterns, with some studies indicating a positive relationship between body size and elevation in tropical and temperate elevational gradients (Beck et al., 2016; Brehm et al., 2018), while others reveal no change in body size along an elevational gradient in the neotropics (Brehm & Fiedler, 2004). Further complicating matters, noctuid moths show larger body sizes at higher elevations in temperate regions (Heidrich et al., 2021).

Predominantly, studies of trait-environment relationships in insects have centered on body size, given its direct link to thermal sensitivity and other physiological and ecological traits (Chown & Gaston, 2010). However, the influence of body size allometry extends beyond thermal sensitivity, impacting flight-related morphology such as wing loading, and maneuverability which directly predicts power requirements during flight in insects (Grula et al., 2021). The morphological traits associated with flight in insects respond to the aerodynamic necessities dictated by their specific environments (Bartholomew & Casey, 1977).

Insects at higher elevations are predicted to exhibit reduced flight capabilities due to alterations in the aerodynamic forces generated by their wings (Dudley, 2002). To counteract the reduced air density at higher elevations, insects employ strategies such as longer wings relative to body size and greater wing area (Dudley, 2002; Dillon et al., 2006). Geometridae moths, the primary focus of this study, exemplify this phenomenon with their large wing areas compared to body mass (lower wing loading), facilitating energetically effective flight even at low temperatures (Heinrich, 1974; Casey & Joos, 1983).

The Geometridae family, known for its diversity, serves as a model for ecological studies (Beck et al., 2016; Brehm & Fiedler, 2004; Holm et al., 2019; Holm et al., 2019; Seifert et al., 2022) has received comparatively little attention in the context of testing macroecological patterns in the paleotropical montane systems. This study seeks to address this gap by examining Geometrid moth communities across an elevation gradient of 1500-3000 m in the western Himalaya, India. The study area, situated on the fringes of the Kedarnath Wildlife Sanctuary, typifies a western Himalayan gradient with stark habitat changes over a short spatial scale.

The overarching objective of this study is to investigate how individual traits, variability of traits among species, and niche overlap of Geometrid moth assemblages shift across an elevational gradient, considering changing species diversity. Given the inconsistent findings

regarding the impact of elevation on body size in prior studies (Brehm & Fiedler, 2004; Beck et al., 2016; Heidrich et al., 2021), the current research aims to ascertain whether these patterns extend to the broader trait-space for insects in the Himalayan gradient. The hypothesis posits that despite changes in species diversity, the body size and traits related to flight capabilities will not differ significantly across the elevation. Therefore, no significant alterations will occur in the overall trait-space at the assemblage level, and niche differentiation across the elevation

Materials and methods:

Study Area:

The study was done in 2018-2019 around the fringes of the Kedarnath Wildlife Sanctuary (KWLS) (30°25′–30°41′N, 78° 55′–79°22′E) located in the Chamoli-Rudraprayag district in the state of Uttarakhand. It is one of the most prominent protected areas in the western Himalaya (Map1), home to the endangered Himalayan Musk deer (*Moschus chrysogaster*). KWLS lies in the upper catchment area of the rivers Alakananda and Mandakini, which form the major tributaries of the river Ganga, covering an area of 975 sq. km. The elevation of the protected area ranges from 1160-7068 masl. Habitats range from mixed oak forests in the south to lush alpine meadows. The combination of human pressure, pristine forest areas, and a large altitudinal range make it an ideal site for biogeographic studies. The forest types are dominated by oak (*Quercus leucotrichophora, Quercus floribunda, Quercus glauca, and Quercus semecarpiflora*).

Field sampling:

The study area was stratified based on elevation & vegetation types to sample the moth diversity along the gradients. Sampling was done every 200m along the elevation from 1500m up to 3100m. I studied the changes across elevation, considering it as a factor in three catergories or classes. I categorized the sampling sites based on similar elevation and vegetation types as follows: Khalla, Mandal, Gondi (below 2000m: Low Elevation); Jatholi,

Ansuya, Kanchula Kharak (2000-2500m: Mid Elevation); Bulkhan and Shokharak (>2500m: High Elevation). At each site, 3-night sampling was done (details provided in the Table 1 of the Supplementary material) at different times of the night to maximize species capture in that area, as different species are active at different times of the night. The sampling sites are shown in Map 1. On each sampling date, two LepiLED (Brehm, 2017) light traps were operated for 3-4 hours after dusk, depending on the weather conditions. Logistic constraints do not permit all-night sampling. Sampling was done for a total ~140 hours from March to May in 2018. The minimum distance between the two light traps was 50 m, with lamps not in line of sight of neighbouring sites, so that cross-site sampling does not occur. The moths attracted to the trap were photographed and representative samples from each species were collected as vouchers. Collection was done with the aim of minimum three samples for each species, for morphological measurements. The specimens were collected only from March to May in 2018, as per the permit from the Forest Department. The specimens were then identified till species, as much as possible. The voucher specimens have been submitted to the Research Collections Facility at the National Centre for Biological Sciences, Bangalore, India.

Morphological trait measurement:

All voucher specimens were curated and photographed. We measured morphological traits on the scaled photographs of 697 specimens of 120 morphospecies for morphometry using the software Image J (Schneider et al., 2012). The measured traits were body length, wingspan, forewing length, hindwing length, forewing area, hindwing area. I also calculated wing loading [2*body length/ (forewing area + hindwing area)], and the ratio of hindwing area: to forewing area which is roughly termed maneuverability (Arrizabalaga-Escudero et al., 2019). These traits were measured because they are related to the body size and flight capability of moths, which might govern their occurrence and sustenance across elevational gradients.

Analyses:

Species diversity

To show sample completeness, I calculated the rarefied sample coverage at each of the elevation classes. I pooled the data collected from each light trapping night in each elevation class and calculated the rarefied species diversity extrapolated to the number of individuals, across the elevation classes. Both these analyses were done using the 'iNEXT' R package (Hsieh et al., 2016).

For beta diversity across the elevation, I calculated the overall beta-diversity (Sørensen pairwise dissimilarity), and species spatial turnover (Simpson's pairwise dissimilarity), all measured as average dissimilarity of the observed units to their group centroid (Anderson et al., 2006).

Variation in the individual trait value, intraspecific trait variability and niche overlap

For the subsequent analyses, the outliers in range of individual trait values were omitted, to arrive at more robust patterns**.** The outliers were few and not abundant species and hence would not affect the overall pattern. (details in Figure 4 and Table 2 of the Supplemenatary Material)

To look into intraspecific trait variation across the elevational gradient, I compared the homogeneity of dispersion (Anderson et al., 2006) for the assemblages in each elevation category. I used the *betadisper* function of the R package vegan (Oksanen et al., 2009) to calculate dispersion, which tests whether the variance or dispersion of two or more groups is significantly different or not based on Euclidean distance. This was followed by a permutest for the homogeneity of multivariate dispersion. An ANOVA was then performed to identify significance in the groups and a post hoc test to identify significant differences between specific elevation categories. These beta values refer to a species' position along a gradient or intraspecific trait variation defined by assemblage-level mean trait values (Ackerly & Cornwell, 2007).

I used two approaches to examine the response of community-trait values of Geometrid moths across the elevation classes. First, I investigated the response using community abundance-weighted mean trait value (CWM; Lavorel et al., 2008), a widely used method to calculate community trait values weighted by abundance of species in that community. Then I looked at the response of the mean trait values for each of the traits across the elevation. The change in both the community means with elevation was quantified using ordinary least squares regression. It is useful to look at both the approaches as the relationships between community-weighted mean (CWM) traits and elevation, is supposed to reflect selection towards locally optimal traits, but it is limited by the large amount of interspecific trait variation typically found within ecological communities (Muscarella & Uriarte, 2016).

To look at the niche overlap among species across the elevational gradient, body length, wing loading, and the ratio of hindwing area: forewing area (Maneuverability) were chosen as the least correlated variable. For this, I used O-statistic (Read et al., 2018) to generate a single community-level (pooling the assemblages across the elevation) overlap index across multiple traits by fitting non-parametric kernel density functions to the distribution of trait values within an elevation (Mouillot et al., 2005; Geange et al., 2011; Read et al., 2018). The median pairwise overlap was calculated by first determining the overlap of traits in each species pair, and then taking the median overlap of each species pair in a community. This median overlap value is called the O-statistic (O for overlap)

The R package *Ostats* (Read et al. 2022) was used to calculate O-statistic, the multivariate O-statistic estimation in this package relies on functions imported from the package *hypervolume* (Blonder et al., 2018). To test whether the degree of niche overlap among species in each elevation category is greater than or less than expected by chance, I evaluated the O-statistic against a null model, where the median of the pairwise hypervolume overlaps are weighted

against the abundances of the species pairs in each community or Standardized Effect Size (z-scores).

Results:

Species diversity

Species diversity showed lower diversity in the high elevation (Fig.1b). The Euclidean distance to centroid for Sørensen pairwise dissimilarity among the elevation categories were as follows: Low-Mid (0.314); Low-High (0.489) and Mid-High (0.34); similarly, the Simpson dissimilarity index (spatial turnover) was: Low-Mid (0.05); Low-High (0.14) and Mid-High (0.12) (Fig 1 c and d). This means, the species belonging to the low elevation were quite different (with higher spatial turnover) from the high elevation, than between Low and Mid, and Mid and High elevation classes.

Variation in the individual trait value, intraspecific trait variability and niche overlap

The average distance (Euclidean) to centroid which gives a measure of the dispersion of traits at the assemblage level, was higher in the lowest elevation (87.94) as compared to mid (78.63) and high (76.14) elevations. The distances are not significantly different from each other (ANOVA, $p>0.05$), which indicates that the intraspecific trait variation does not change across the elevation gradient (Fig.2)

The ordinary least squares regression did not show any significant effect of elevation on the Community-weighted means of traits across the elevation classes: Forewing Length ($p=0.57$), Hindwing Length ($p=0.534$), Body Length ($p=0.31$), Wingspan ($p=0.14$), Forewing Area ($p=0.41$), Hindwing Area ($p=0.32$), Wing loading ($p=0.14$), Maneuverabilty ($p=0.51$) (Fig.3). For the mean trait values, Forewing Length ($p=0.03$), Hindwing Length ($p=0.02$), and Hindwing area ($p=0.03$) showed a significant decline at high elevation. Body Length ($p=0.19$), Wingspan ($p=0.26$), Forewing Area ($p=0.23$), Wing Loading ($p=0.24$), Maneuverability

(p=0.19) did not show any significant change with elevation (Figure 2 in Supplementary Material). There is high variability and a weak pattern in the CWM across elevation, which makes it evident that the patterns are sensitive to the abundance of species. The species of same trait values are abundant across the elevation. The density plots of individual traits added in the Supplementary Material (Figure 3) would make it clearer.

There is a high level of niche overlap among the species of the Geometrid moth communities across the elevation, as shown by high (0.84) O-statistic index of the multivariate trait space (Fig. 4). This indicates that for each trait the observed niche overlap did not differ from that which would be expected due to chance.

Discussion:

The findings on Geometrid moth assemblages along a 1500m gradient in the western Himalaya provides valuable insights into the dynamics of individual traits, trait variability within the assemblages, and niche overlap across elevational gradients in response to changing species diversity. The results show a decrease in species diversity along the elevational gradient and that there is consistent species turnover from the low to the high elevations. However, elevation does not significantly impact morphological traits related to thermal sensitivity (body length) and flight capability (wing-loading and maneuverability) at the assemblage level in Geometrid moths.

Additionally, the study reveals the absence of significant intraspecific trait variation and significant niche differentiation among species across the elevation. This sheds light on the assemblage-level trait variability within Geometrid moth , revealing that ecological similarity remains high across elevational gradients. Supporting these findings, evidence from the Paleotropical region further underscores the lack of consistent trends in individual traits studied in Geometrid moths and other insect taxa across diverse elevation ranges in neotropic and

240 palearctic regions (Brehm & Fiedler, 2004b; Peters et al., 2016; Beck et al., 2016; Classen et
241 al., 2017).

242 *Species diversity across elevation*

243 Here, it is evident that trait-level patterns may not directly correlate with the occurrence,
244 diversity, and abundance of species. Geometrid moths across mountains either show a mid-
245 elevation peak or a decreasing trend with elevation, with temperature having minimal role in
246 their species richness patterns (Beck et al., 2017). It is noteworthy that other evolutionary
247 hypotheses of species diversity patterns, like phylogenetic history (McCain, 2009), climatic
248 variation (Colwell et al., 2008) or biotic interactions (Novotny et al., 2006) could be system -
249 specific.

250 In this study, species from the Ennominae family from the genera *Alcis, Arichanna*, *Abraxas,*
251 *Petelia* were quite abundant in the low and mid elevations, whereas *Dalima truncataria*,
252 *Blepharoctenucha virescens* were few. *Psyra crypta* was more abundant towards higher
253 elevations. There were singletons from the Geometrinae family like *Jodis, Tanaorhinus cf.*
254 *reciprocata.* The turnover of species from the low to high elevations seemed to be influenced
255 by higher abundance of species belonging to the Larentiinae subfamily, specifically from the
256 genera *Perizoma*, *Photoscotosia* known to specialize on herbaceous plants (Skou, 1986). These
257 findings are similar to the patterns of Geometrid moths in neotropical and palearctic mountain
258 gradients (Brehm & Fiedler, 2003; Brehm et al., 2013). Thus the results point towards effect
259 of microclimate variables (Hof et al., 2011) on the species diversity and turnover. Most likely,
260 host-plant availability is a strong factor in determining species distribution.

261 It is already known, that the flight morphology of Geometrid moths makes them 'poor' fliers,
262 such that their occurrence is tightly linked to their host-plant availability (Heidrich et al., 2021).
263 Further evidence of host-plant relationships and their long-term effect on species distributions,

could support this claim. However, the host-plant relationships for moths remain insufficiently understood in from this part of the globe.

Morphological trait variation across elevation

Elevation is adiabatically linked to temperature, and diverse moth families respond differently to the changing temperature due to their distinct thermal sensitivities (Bladon et al., 2020; Heidrich et al., 2021). Thermoregulation, a critical process controlled by the flight muscles in insects (Heinrich, 1974), is influenced by the flight characteristics unique to each taxon. Geometrid moths, characterized by larger wings relative to their body size, exhibit lower wing loading compared to other moth families, capable of flight over a wide range of temperatures (Casey & Joos, 1983). This trait allows them to engage in immediate flight without the need for warming up-characteristically referred to as 'cool moth' in Heinrich (2013). Consequently, it is not surprising that Geometrid moths demonstrate a lack of significant elevation-induced effects on flight-related traits.

Moreover, the overall morphological trait space (niche dimension) of Geometrid moths along the elevational gradient demonstrates little variation, likely due to the prevalence of species with similar traits at each elevation. However, it is crucial to acknowledge that the intraspecific variation of other physiological trade-offs, such as stress tolerance, resource use, and life history strategies along the biotic and abiotic axes, may unveil actual niche segregation among species (Mouillot et al., 2005; Wang et al., 2022). This interpretation exceeds the scope of this paper and requires further investigation. The consistent overall assemblage-level trait overlap in this study, further suggests that, despite decreasing species diversity, trait similarity and functional redundancy among species persist, contributing to a stable trait distribution pattern.

Species having similar 'function' not only emphasize enhanced temporal stability of communities (Pillar et al., 2013), but also provide a buffer against rapid species extinction on

the community's 'function' (Naeem, 1998). They are less likely to lose an entire functional group due to stochastic processes only (Biggs et al., 2020). Also, following community assembly rules, species of similar trait inhabit the same habitat, allowing them to 'function' under specific abiotic conditions (Díaz et al., 1998; Weiher et al., 1998). Notably, the only other research on trait-level patterns in moths across elevational gradients in the Himalaya, found significant trait variations and internal filters influencing community assembly of Hawkmoths (Mungee & Athreya, 2021). However, this study did not specifically focus on examining the mechanisms of community assembly concerning changing elevation and related abiotic factors.

Limitations and future possibilities

Heidrich et al. 2021 demonstrated a notable elevation-related increase in body size with elevation by incorporating sites from lower elevations into their analysis. Extending this approach to include additional sites from the species-rich lower elevations (<1500m) could substantially impact the observed patterns in our study. However, locating continuous gradients in deeper valleys from the foothills to over 3000m in this part of the Himalaya poses a significant challenge.

The sampling in this study was restricted to the spring-summer season due to logistic constraints. Reports from other western Himalayan elevational gradients, (Sanyal et al., 2017) and Dey (2019) indicate variations in species composition across seasons. Consequently, it would be worthwhile to investigate how the observed patterns hold across seasons. Additionally, examining how life history traits related to larval host plant use (i.e., diet breadth and host-plant growth form) and seasonal life cycle (i.e., overwintering stage and caterpillar phenology) are linked to adult body size and flight morphology in species-rich herbivore insect clades, Geometrids and alike, is crucial.

For species-rich taxa, trait- based conclusions are useful to overcome the taxonomic impediment (Wong et al., 2019). In the current context of increasing demand for monitoring insect populations, understanding traits that render species vulnerable to environmental alterations caused by human activities provides the foundation for predicting community-level response. Future studies should adopt a long-term perspective and a comprehensively examine potential shifts in the observed consistent trait-space. Such investigations may reveal range shifts in species due to changing thermal regimes, particularly in the fragile Himalayan ecosystem.

Conclusion

The findings of the study indicate a decline in species diversity and an increase in species turnover along elevational gradients. Notably, the elevation does not exert a significant influence on the body size and flight capability of Geometrid moths. Therefore, the results challenge prevailing notions about association between elevation and insect morphology. Additionally, the study supports the idea that species with similar ecological functions are sustained through the high turnover of species sharing similar trait values across assemblages.

In the case of Geometrid moths, the study underscores the insignificance of trait-environment relationships, as evidenced by previous research (Beck et al., 2016; Heidrich et al., 2018; Xing et al., 2018). Here, a clear need is identified to transition from a predominantly univariate approach, focused on single-trait responses along individual environmental gradients, to a multivariate approach that realistically considers the responses at species level across various environmental gradients typical of most human-dominated landscapes.

The study's implications for the vulnerable Himalayan Mountain system, particularly in the face of accelerated warming, emphasize the critical importance of comprehending species and trait distribution patterns for the formulation of effective conservation strategies.

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Data availability statement: The data that support the findings of this study are available from the corresponding author upon reasonable request. Upon the acceptance of the manuscript, the data will be made accessible in a designated data depository.

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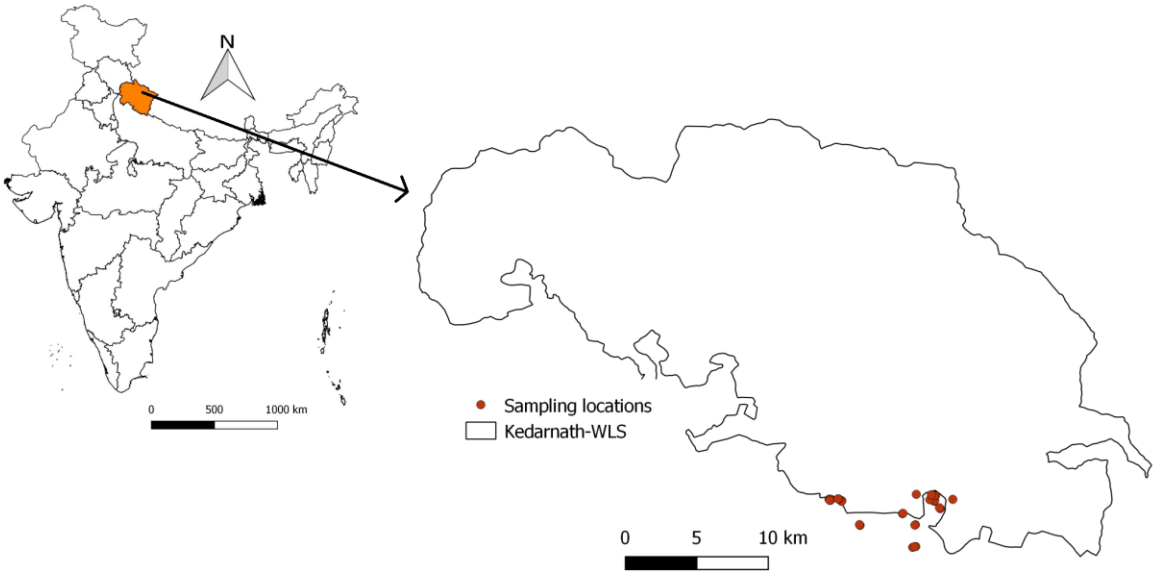

Map 1: Map showing the sampling locations in and around the buffer zone of Kedarnath Wildlife Sanctuary, which is located in northern side of the mountainous state of Uttarakhand (highlighted on the map of India on the left side)

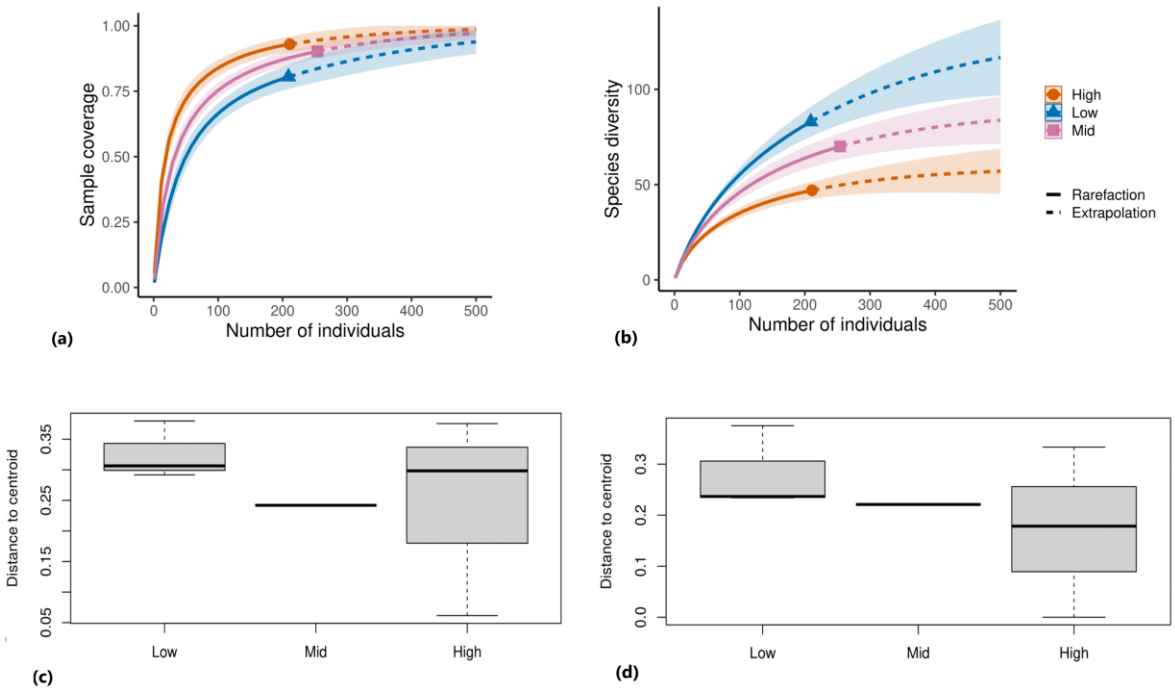

Figure 1: Rarefied curves for a) Sample coverage and b) Species diversity patterns extrapolated across the number of individuals; c) overall beta diversity measured as Sorensen

pairwise dissimilarity and d) the spatial turnover of the species measured as Simpson pairwise dissimilarity across the low, mid and high elevation assemblages

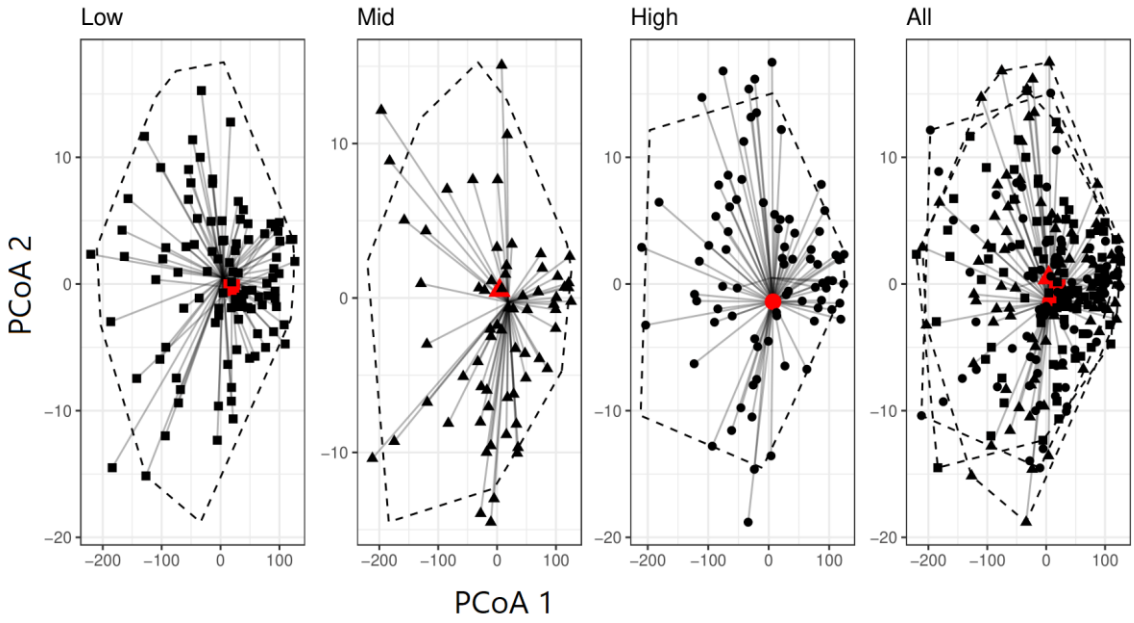

Figure 2: The figure shows the dispersion of traits as a measure of intraspecific trait variability in each of the assemblages along the elevation and all the elevations together (last panel). The beta-dispersions refer to a species' position along a gradient or intraspecific trait variation defined by community-level mean trait values (shown in red)

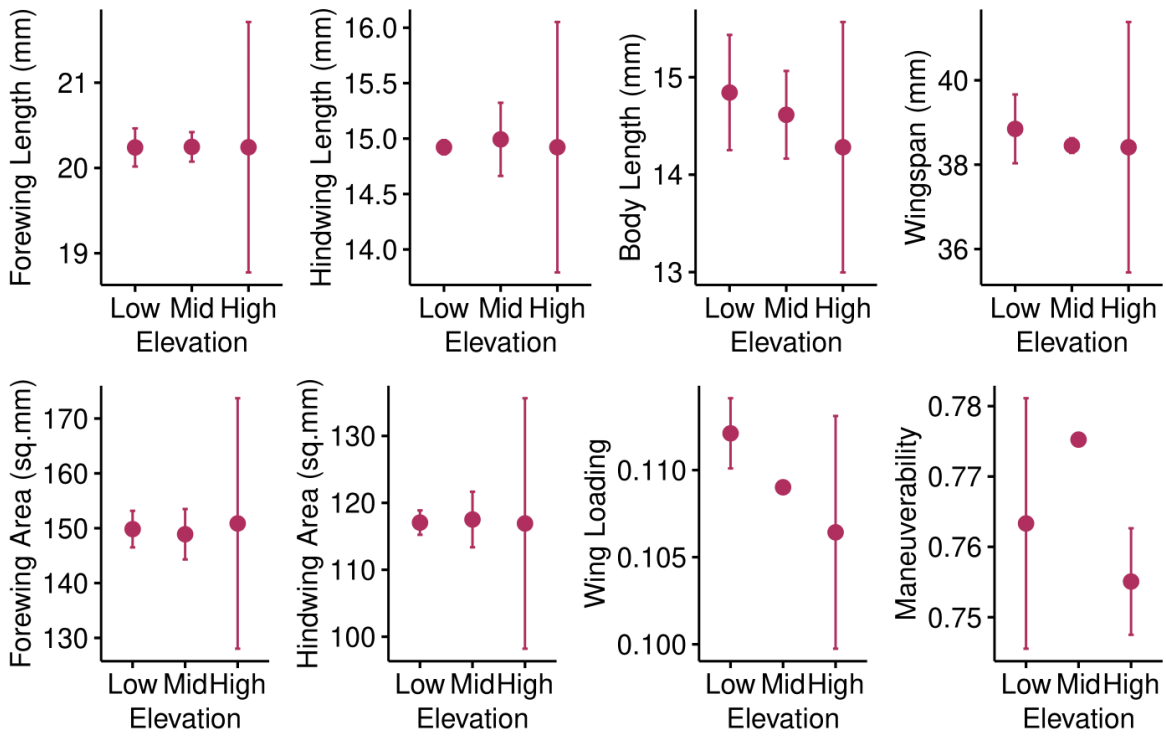

Figure 3: The figure shows the community weighted means (mean ± SE) of each of the traits across the low, mid and high-elevation assemblages.

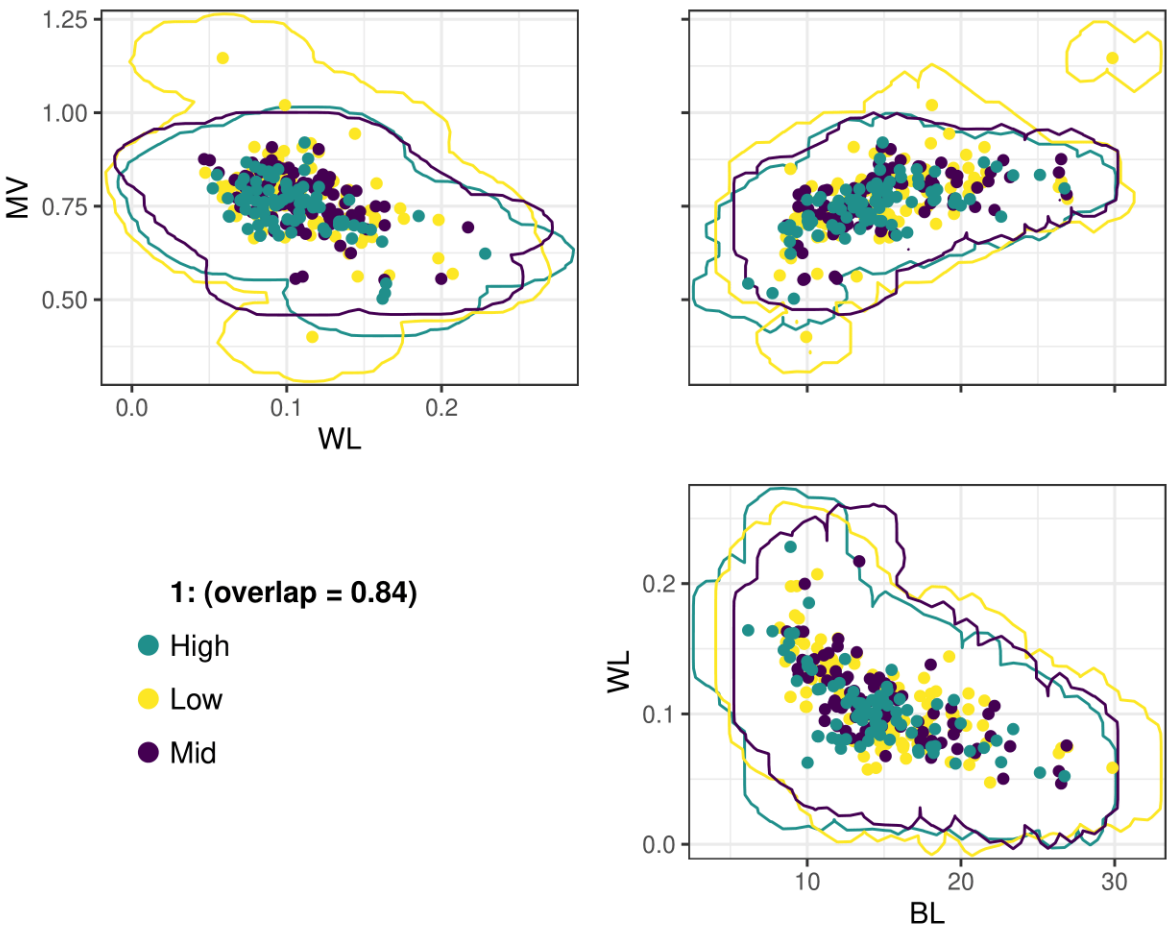

Figure 4: The figure shows the degree of overlap (O-statistic) of the multivariate trait-space, based on body length (BL), maneuverability (MV), and wing loading (WL) of the Geometrid moth assemblages in low, mid, and high elevations