Ecological Indicators 133 (2021) 108421

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Effects of grazing on macro-moth assemblages in two different biomes in Mongolia

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ARTICLE INFO

Keywords:
Lepidoptera
Livestock
Habitat disturbance
Diversity
Gradient
Specialist
Generalist
Functional trait
Beta diversity

ABSTRACT

Intensive land use, e.g. pastoralism, decreases biodiversity and leads to homogenization of habitats. However, the effect of land-use changes differs under varying climatic conditions. Thus, it is essential to study how land use affects biodiversity on a large scale. Moreover, species respond differently to environmental changes depending on whether they are specialists or generalists. We studied macro-moths in Mongolian pastures under two different grazing regimes (grazed and less grazed plots) in ten study sites that belong to two distinct biomes along a large-scale latitudinal gradient from desert to steppe. We explored 1) how livestock grazing affects macro moth diversity, species composition, and species richness, 2) how specialist and generalist moths respond to grazing in desert (Desert and xeric shrublands) and grassland (Temperate grasslands, savannas & shrublands). Moths are sensitive to environmental changes and suitable bioindicators. We also revealed a) indicators of grazing and b) indicators representative for certain sections of the latitudinal gradient. Totally, we recorded 80 species in the desert and 202 species in grassland in 2018 and 2019, which were DNA barcoded. In the desert, grazing did not affect macro-moth diversity, whereas grassland was negatively affected. However, not all moth families showed the same response to grazing. Species diversity, species richness, and abundance of Erebidae, Geometridae, and Noctuidae were significantly higher in the less grazed plots. Further, species dissimilarity between grazed and less grazed plots was mainly due to species replacement rather than species loss. In the desert, the species richness of both specialist and generalist moths did not differ between grazed and less grazed plots; in contrast, in grassland, the species richness of both groups was higher in less grazed plots. We found two indicator species of grazing in the desert: *Hyles chuvilini* in less grazed, and *Cucullia splendida* in grazed pasture. In grassland, we found ten indicator species exclusively for less grazed pastures: *Catarhoe cuculata*, *Euxoa ochrogaster*, *Lacanobia thalassina*, *Megalycinia strictaria*, *Mythimna comma*, *Polia bombycina*, *Rhyacia simulans*, *Sideridis kitti*, *Sideridis egena*, and *Smerinthus caecus*. These indicator species can be used as references for habitat quality and for moths' dispersal due to climate change in future studies. Among the environmental variables, plant species richness, altitude, and livestock number were the most important variables. Species composition of high altitudes in the desert was distinct, and higher species richness in this area indicated that high altitudes could serve as a refuge area during global warming and should receive conservation management.

1. Introduction

Desert and grassland biodiversity are vulnerable to synergetic effects of climate and land-use change (Wagner et al., 2021). Climate change affects species in multiple ways, such as by altering the geographical range of species, by changing phenology, and by disrupting the interaction between species, while land-use change leads to population declines and species losses (Wilson & Fox, 2021). One type of common land use is livestock grazing, which constitutes the main economic sector in some countries. For example, 10.7% of the gross domestic product in Mongolia is dependent on pastoralism, which is the primary type of land use in the country (Mongolian Statistical Information

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https://doi.org/10.1016/j.ecolind.2021.108421
Received 30 June 2021; Received in revised form 16 November 2021; Accepted 23 November 2021

Service, 2018). Therefore, sustainable land use is crucial for not only to the nation's economy, but also for maintaining healthy habitats for native biodiversity and wildlife. Although Mongolian animal husbandry is based on mobile pastoralism, the mobility of the herders is decreasing (Pfeiffer et al., 2018). They tend to concentrate near larger settlements, while at the same time the number of livestock has been steadily increasing since the privatization of livestock sector after socialism (Lkhagvadorj et al., 2013), the total number of livestock was 25 858 900 in 1990 and reached 67 068 486 in 2020 (Mongolian Statistical Information Service, 2021). Pasture degradation is intensifying as a result of overgrazing and climate change (Bat-Oyun et al., 2016; Na et al., 2018). Thomas et al. (2004) estimated that globally, 15–35 percent of all species are at risk of extinction due to interaction of habitat loss and climate change.

Livestock grazing usually negatively affects insect diversity by competing for food resources, feeding on them unintentionally, and reducing plant heterogeneity leading to the homogeneity of habitat structure and plant communities (Enkhtur et al., 2017; Klink et al., 2015). However, on the other hand, abandonment of grazing and traditional land use often leads to decreasing populations of many insect species in Europe (e.g., Schwarz and Fartmann, 2021). Habitat heterogeneity is an essential attribute for sustaining biodiversity (MacArthur and MacArthur, 1961). In a study of butterflies and day-active Geometridae, beta diversity decreased in landscapes with high agricultural intensity (Ekroos et al., 2010). However, intermediate livestock grazing is beneficial to some taxa, such as dung beetles (Klink et al., 2015). In recent years, researchers have become increasingly interested in the functional traits of species in the community (Boet et al., 2020). Depending on the functional traits, species respond differently to grazing. For example, generalist species benefit, while specialists are suffering (Warren et al., 2001), especially moths in grasslands and arid lands (Wagner et al., 2021). But the grazing itself is not good for the butterfly population if too intense, but if there is no grazing, habitats will be overgrown with bushes and trees within a shortperiod (Schwarz and Fartmann, 2021).

However, it is impossible to evaluate the abundance and diversity of every taxon continually. Fortunately, indicator species can reflect habitat quality and homogeneity. Moths can be suitable indicator species, they are dependent on plants at larval and adult stages, and they become food for others, thus connecting both lower and upper trophic levels (Enkhtur et al., 2017; Klink et al., 2015; Wagner et al., 2021). Climate change and habitat degradation are forcing moths and butterflies to disperse to higher latitudes (Warren et al., 2001), in Great Britain, ranges and populations of cold-adapted species have been shrinking, while in contrast, populations of warm-adapted species have increased in southern England (Fox et al., 2014). The annual average temperature in Mongolia increased by 2.2 °C from 1940 to 2008, indicating vulnerability to global warming (Batbold et al., 2014, Pfeiffer et al., 2018). In order to detect distributional changes, it is necessary to identify indicator species along the latitudinal gradient that could be used as references for later studies (Enkhtur et al., 2021).

However, under different climatic conditions, it is not clear how moths will respond to grazing. According to the dynamic equilibrium model, in arid areas (non-equilibrium), the effect of grazing on plant diversity is weaker compared to climate variables such as low precipitation. In contrast, in wetter areas (equilibrium), it is relatively stronger than climate variables (Ahlborn et al., 2020; Wang et al., 2017; Wesche et al., 2010). Since moth species are dependent on plants as food resources, they could show a similar response to grazing in arid and wetter biomes. Moreover, how moth species composition changes between intensively and lesser grazed plots is critical from a species conservation perspective. If the species composition of moths in grazed and less grazed pastures differs due to spatial turnover (i.e., species replacement), this indicates these pastures have distinct species compositions, and therefore, both pastures should be managed differently. If the difference is due to nestedness (i.e., species gain or loss), they can be considered and managed equivalent. In a study on moth diversity along the latitudinal gradient, community composition broke down into two distinct groups along biome boundaries: desert and grassland (Enkhtur et al., 2021). The present study aims to investigate the effect of livestock grazing on moth diversity with different feeding niche width in two contrasting biomes and to reveal indicator species for grazing pattern and along the latitudinal gradient.

We hypothesized:

Moth species richness and diversity are higher in less grazed plots than in grazed plots and their species compositions are different.

At grazed plots, generalized traits of moths will be dominant in the population over specialized traits.

In two different biomes, moths will show a different response to grazing. The moths should follow the dynamic equilibrium model showing less response to livestock grazing in desert compared to grassland.

Given high plant species richness, beta diversity of moths between grazed and less grazed plots is dominated by spatial turnover.

2. Material and methods

2.1. Study area

We conducted our study in the Mongolian pastures in two distinct biomes (1-Desert and Xeric Shrublands and 2-Temperate Grasslands, Savannas & Shrublands) along a large-scale latitudinal gradient (hereafter, 1- desert and 2- grassland) (Fig. 1 and Table S1). In the desert, we included study plots in the districts of Umnugobi Aimag, Dundgobi Aimag, and the southern part of Tuv Aimag (sites 1–5), while in grassland, we included the northern part of Tuv Aimag and Selenge Aimag (sites 6–10). Our study design is derived from the study design of former successful studies on plants (Ahlborn et al., 2020; Lang et al., 2020, 2019). They established a 600 km long transect along the latitudinal climatic gradient with 15 sites from Dalanzadgad (south) to Ulaanbaatar (north). At each site there were five plots (A, B, C, D, E) with different grazing intensities at fixed distances from the grazing hotspots (50 m, 150 m, 350 m, 750 m, and 1500 m): the most intensively grazed plots were chosen near a ger or a well (A) as already proven in other studies (Manthey and Peper, 2010; Stumpp et al., 2005). Pastures in Mongolia are not fenced, and direct measurement of grazing intensity is difficult as intensity varies as a result of open grazing conditions. In addition, precise data on the number of animals are not available (Wang et al., 2017). Thus, further standardization of grazing intensity was not feasible in this study. We slightly modified their study design, i.e., we included the seven existing sites and added three more northern sites (in Selenge Aimag), making the gradient 860 km long. Moreover, the used grazing distances were too close to each other to make a difference for moths; therefore, after discussing with Ahlborn and Lang and avoiding lights from the dwelling area, we used only the two extreme plots in each site (B, E).

In desert sites, annual mean precipitation ranges from 108 mm to 175 mm; altitude ranges from 1196 to 2241 m a.s.l., and the annual mean temperature ranges from 1.09° C to 3.68° C (Hijmans et al., 2005). The number of livestock in the study area (number represents livestock in the administrative unit of Bags, i.e., subdistricts, in the study areas 1–5) in the desert was 310.810 in 2018 and increased to 329.490 in 2019 (Mongolian Statistical Information Service, 2021). In grassland sites, the annual mean precipitation ranges from 212 to 318; altitude ranges from 619 to 1439 m a.sl. and the annual mean temperature ranges from −0.54 to −1.34 (Hijmans et al., 2005). The number of livestock in the study area in the grassland was 267.240 in 2018 and 291.050 in 2019 (see above, study areas 6–10) (Mongolian Statistical Information Service, 2021).

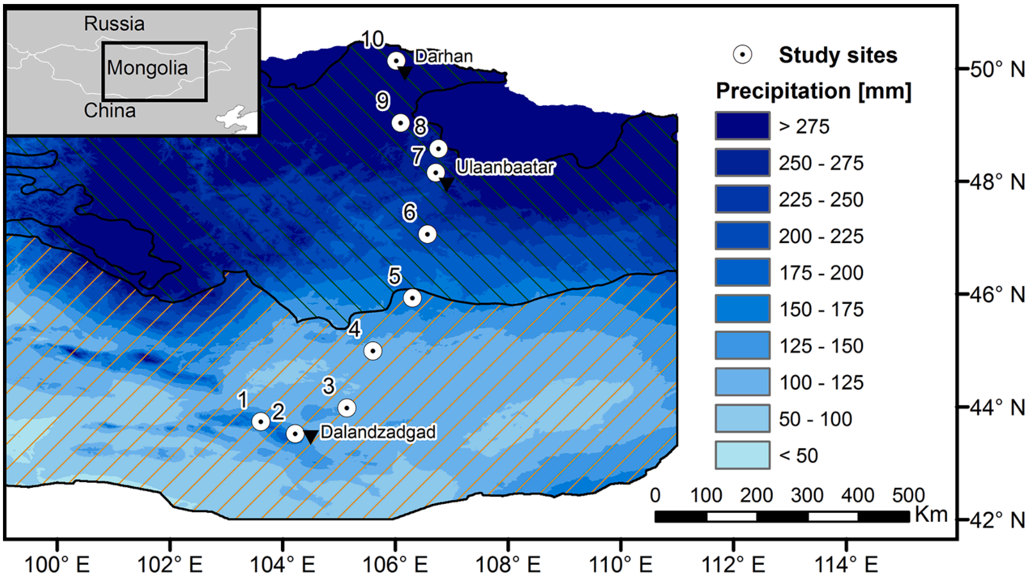

Fig. 1. Study area along the rainfall gradient in Mongolia (Lang et al., 2019; Ahlborn et al., 2020). The dark green hashed area represents Desert and xeric shrublands biome, and the orange hashed area represents Temperate grasslands, savannas & shrublands biome. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. *Moth sampling*

Moths were attracted by using recently developed LED lamps ("LepiLED", height ca. 88 mm, diameter ca. 62 mm, with four UV LEDs (365 nm), two blue (450 nm), one green (530 nm), and one cool white LED) powered by power bank batteries (EasyAcc 26 Ah), (Brehm, 2017), inside light "towers" (Bioform: Large R. Müller light trapping tower, mesh size 1 mm, 70 cm diameter, 180 cm high). Moths were manually sampled using collecting jars. In the field, we sorted and identified all individual moths at the morphospecies level, counted individuals of each morphospecies, and kept samples in glassine envelopes separately. We put light traps during the flight season of most night-active species (peak vegetation period) in Mongolia in two consecutive years in 2018 (June, July) and in 2019 (July, August). We took samples from 9 to 12 pm and skipped nights with intense moonlight (i.e., around full moon). At each site, three trapping nights were conducted, and we caught moths at the same time at grazed and less grazed plots of each site. Due to adverse weather conditions in some nights, only two trapping nights were successful in some plots. We brought all samples to Germany and mounted and identified specimens using identification keys and online identification sites (Knyazev, 2017; Rennwald and Rodeland, 2002; Steiner et al., 2014) at the University of Bayreuth and the collection of Phyletisches Museum, Friedrich Schiller University Jena. To verify the identification, we DNA barcoded at least two specimens per species (Enkhtur et al., 2021, in preparation).

2.3. *Environmental variables*

We included following variables as environmental variables:

1) sampling year (2018, 2019), 2) grazing regime (grazed and less grazed); 3) geography and altitude: latitude, longitude, altitude, solar radiation index; 4) local habitat characteristics: temperature during sampling time, vegetation cover, vegetation diversity, vegetation cover of functional groups, plant species richness; 5) weather variables: annual temperature, annual precipitation, mean diurnal range, wind speed.

Latitude, longitude and plant species data of 2014 (which were used to identify plant species of the field studies in 2018 and 2019) of sites 1–7 were taken from the studies of Ahlborn and Lang (2020; 2019).

2.4. *Ecological traits of moths*

We included feeding niche as an ecological trait of moths. For the classification of specialist and generalist species, we applied the method of Mangels et al. (2017) with a small modification. If a moth species feeds on one family of plants, it is regarded as a specialist; If a moth species feeds on plants of two or more families, it is considered a generalist. If it feeds on plants of more than five families, it is classified as a broad generalist. We obtained data on feeding niche from literature and expert elicitation.

2.5. *Statistical analysis*

All analyses were conducted using R version 3.6.3. For the estimation of species richness, we used the R-package *SpadeR* and applied iChao1 index, which is based on rare species. We checked for normal distribution of all factors with the Shapiro-Wilk normality test. To compare species richness, species diversity and abundance of grazed and less grazed sites, we used the paired *t*-test. We used *broom* (Robinson & Hayes, 2021), *tidyverse* (Wickham et al., 2021) and *purrr* (Henry and Wickham, 2020) packages for this analysis. To visualize the overlapping species between grazed and less grazed plots we used the *ggvenn* package (Linlin Yan, 2021).

To find indicator species, we calculated the indicator value index (IndVal) with the *indicspecies* package (Cáceres and Legendre, 2009). We used the species abundance matrix and the grazing intensity as classification vectors. We compared species richness and the abundance of specialist and generalist moths in grazed and less grazed plots in each biome with non-parametric Wilcoxon tests. To reveal the relationship between species richness of generalist and specialist moths and species richness of vegetation we applied Pearson correlations.

The analysis of moth community patterns and their environmental drivers was conducted with the R package *vegan*. First, we applied a Principal Component Analysis (PCA) to extract principal components from the distribution of a) vegetation guilds and b) numbers of different livestock species along the transect, thus reducing these matrices to one variable each, the first PCA axis. Then, we applied Redundancy Analysis (RDA) with Hellinger transformation of species data (Borcard et al.

2011) with a set of z-standardized environmental factors including latitude, longitude, altitude, wind speed, radiation, water vapor pressure, temperature, precipitation, Simpson's diversity of vegetation, vegetation cover, and the PCA scores of plant guilds and livestock abundances along the gradient. We searched with forward selection for the most significant environmental variables, but later optimized R^2 and AIC in parsimonious RDA by addition of further variables and computed the variance inflation factor (VIF) to exclude covariates with VIF > 3. We estimated the relationship of moth species richness and vegetation species richness with function gam of package *mgcv* (Wood, 2017) using the Poisson link function. In most analyses, we grouped all species into Noctuidae, Geometridae, Erebidae, and 'Other'. The latter category includes families only represented with a few (<10) species: Cossidae, Drepanidae, Notodontidae, Sphingidae, Lasiocampidae, Sesiidae, and Zygaenidae.

3. Results

3.1. Species assemblages

We collected a total of 11,117 individuals belonging to 236 macro-moth species. 7220 individuals of 80 species were found in desert, and 3897 individuals of 202 species were found in grassland Table 1). Species richness and abundance were higher in less grazed plots than in grazed plots in grassland, while species richness was similar in less grazed and grazed plots in desert (See Supplementary Table S2 for a full list of species).

Species richness was higher in the grassland, whereas the number of individuals was two times higher in the desert due to the presence of a single noctuid species (*Agrotis ripae*). Estimated species richness for the desert was 172 (iChao1, SE: 31.00, lower 95%: 128, upper 95%: 257). Thus, our observed species richness covers 50 % of estimated species richness, while estimated species richness for grassland was 289 (iChao1, SE: 14.92 lower 95%: 264, upper 95%: 324), here our sample covered 73 % of estimated species richness. In total, 48 species were shared between desert and grassland. The ten most abundant species were *Agrotis ripae, Anarta trifolii, Euxoa ochrogaster, Lithostege sp2, Isturgia arenacearia, Lygephila lubrica, Mythimna comma, Biston betularia, Hyles gallii*, and *Ipimorpha retusa*.

We compared species richness, species diversity and abundance of grazed and less grazed plots for each biome, namely desert and grassland (Table S3). In the desert, we could not find any significant difference for species richness ($t = -0.11267$, df = 9, p-value > 0.05), species diversity ($t = -1.6863$, df = 9, p-value > 0.05), and abundance ($t = 0.35862$, df = 9, p-value > 0.05). In contrast, grazed and less grazed plots in grassland showed significant differences in species richness: ($t = -3.2828$, df = 9, p-value < 0.05), species diversity: ($t = -2.8597$, df = 9, p-value < 0.05), and abundance: ($t = -2.9526$, df = 9, p-value < 0.01). Further, we compared moth families separately, in desert only species diversity of Geometridae differed significantly ($t = -3.0236$, df = 5, p-value < 0.01) between grazed and less grazed plots. In grassland, moth families responded differently to grazing regimes. Species diversity of geometrids and all metrics of noctuids and erebids were significantly higher in less grazed plots (Fig. 2 a-i). All metrics in the 'Other' group (remaining assemblage) did not differ significantly between grazed and less grazed plots (Fig. 2j-l).

Table 1
Species richness and abundance of macro-moths sampled in two biomes under different grazing regimes in the summer of two consecutive years.

Biome	Grazing	Year	Species richness	Abundance
Desert	Grazed	2018	33	304
Desert	Grazed	2019	38	3509
Desert	Less grazed	2018	28	311
Desert	Less grazed	2019	38	3096
Grassland	Grazed	2018	103	833
Grassland	Grazed	2019	98	750
Grassland	Less grazed	2018	117	1012
Grassland	Less grazed	2019	130	1302

3.2. Species composition

Venn diagrams show that the number of overlapping species between grazed and less grazed plots differed in the two biomes (Fig. 3 and Fig. 4). In the desert, the number of unique species was higher in grazed plots than in less grazed plots in noctuids and erebids, while the number of unique species of geometrids was the same in each grazing regime. Regarding the 'Other' group, there were not any unique species in each grazing regime. In contrast, in grassland, in all family groups the number of unique species was higher in less grazed plots than in grazed plots. The highest overlap of unique species between grazing regimes was found in erebids 62.5%, followed by noctuids, geometrids and 'Other'.

Further, we studied species dissimilarity between grazed and less grazed plots in each biome. The dissimilarity between grazed and less grazed plots was mainly due to species turnover (Fig. 5a). In both desert and grassland biomes, spatial nestedness (i.e., species loss or gain) was higher in grazed plots, indicating that some species disappeared in grazed plots (Fig. 5b). Lastly, we checked if vegetation species richness differs in grazed and less grazed plots in both biomes (Fig. 5c). In the desert, vegetation species richness was similar in grazed, and less grazed plots, while in grassland, vegetation species richness was higher in the less grazed plot.

For the intermediate level of vegetation species richness, species turnover was dominant, and at both extremes, nestedness was dominant (Fig. 6).

Species richness of specialist and generalist moths did not differ significantly between grazed and less grazed plots in the desert, while species richness of specialist ($t = -2.8777$, df = 9, p-value = 0.01825) and generalist moths ($t = -2.7255$, df = 9, p-value = 0.0234) was significantly higher in less grazed plots than grazed plots in grassland (Fig. 7).

The abundance of specialist moths ($t = 1.2742$, df = 7, p-value = 0.2433) and generalist moths ($t = 0.25853$, df = 9, p-value = 0.8018) was higher in the grazed plot in the desert though not significantly different. In contrast, the abundances of specialist and generalist moths were higher in less grazed plot than grazed plot in grassland, however, only the number of generalist individuals were significantly different ($t = -3.0192$, df = 9, p-value = 0.0145) (Fig. 8).

Against our expectation, species richness of generalists correlated stronger with species richness of vegetation than that of the specialists (Fig. 9). The highest correlation was found in Noctuidae (generalist: $r = 0.75$, $p < 0.001$, specialist: $r = 0.63$, $p < 0.001$), followed by Geometridae (generalist: $r = 0.58$, $p < 0.001$, specialist: $r = 0.50$, $p < 0.001$).

3.3. Indicator species analysis

Altogether, we revealed 12 indicator species in less grazed plots but only one species in grazed plots (Table 2). Two species were found in the desert, ten were found in grassland. Noctuidae (8 species) comprised the highest proportion of indicator species, followed by Geometridae and Sphingidae (each 2 species). No single species was associated with the less grazed plot in grassland. Five species were specialists, and six species were generalists, and for one species, the host plant information was not available.

The results of Indicator species analysis for the latitudinal gradient showed that 32 species were sampled in 2018 and 29 species were sampled in 2019 (Table 3). 11 indicator species were caught in both years. Totally seven indicator species of Noctuidae were associated with the desert. In contrast, 43 unique species (Noctuidae-16, Geometridae-11, Erebidae-11, Sphingidae-4, Lasiocampidae-1) were associated with the grassland biome. Some species expanded their observed range from 2018 to 2019: *Lacanobia thalassina* (generalist), *Polia bombycina*

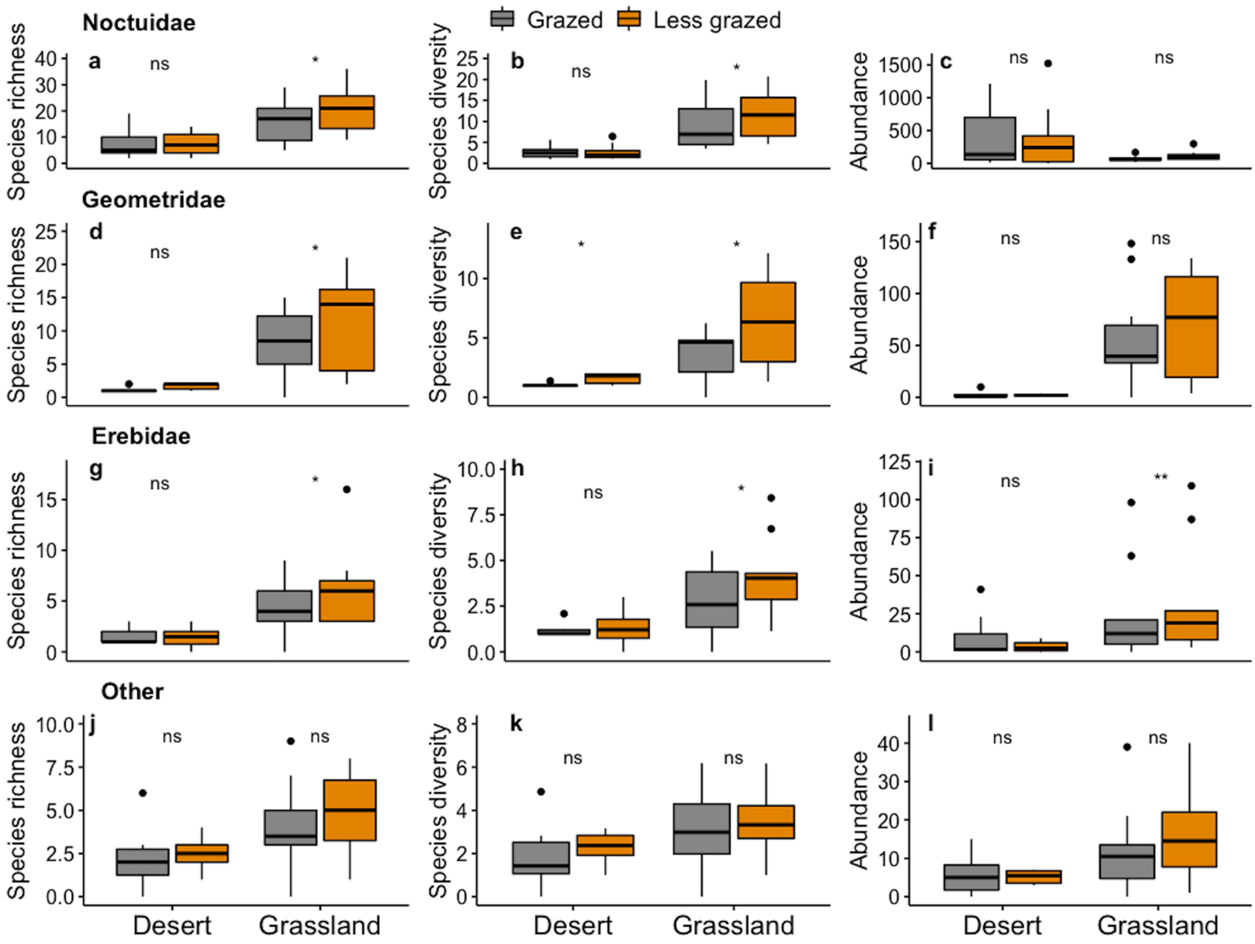

Fig. 2. Comparisons of species richness, species diversity, abundance (aggregated from 5 sites × 6 nightly samples in each biome) (a-c), Noctuidae (d-f), Geometridae (g-i), Erebidae (j-l), 'Other' for each biome under different grazing regimes. Significant differences are represented by stars: * $p < 0.05$, ** $p < 0.01$, ns = non-significant.

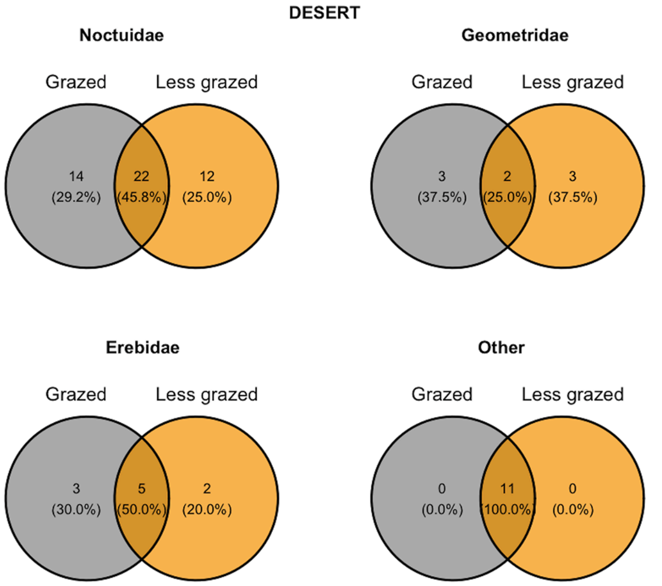

Fig. 3. Venn diagrams of desert biome demonstrate the overlapping of unique species between grazed and less grazed plots in the families of Noctuidae, Geometridae, Erebidae and group 'Other'. No unique species were found in both Grazed and Less grazed plots in the group 'Other'.

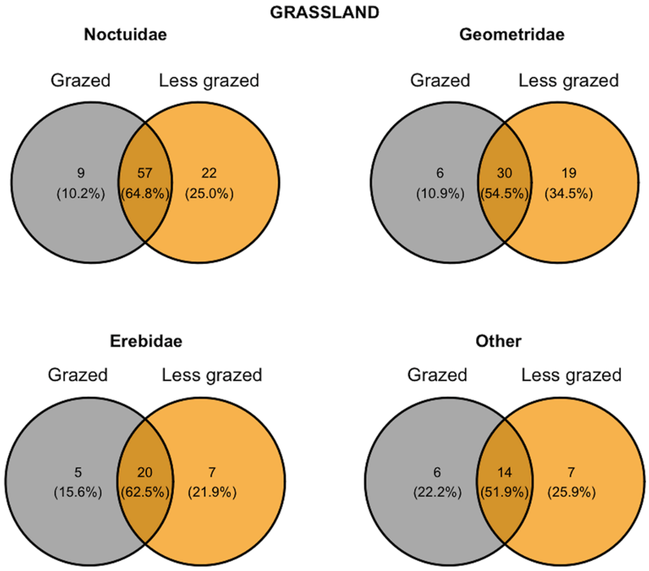

Fig. 4. Venn diagrams of grassland biome demonstrate the overlapping of unique species between grazed and less grazed plots in the families of Noctuidae, Geometridae, Erebidae and group 'Other'.

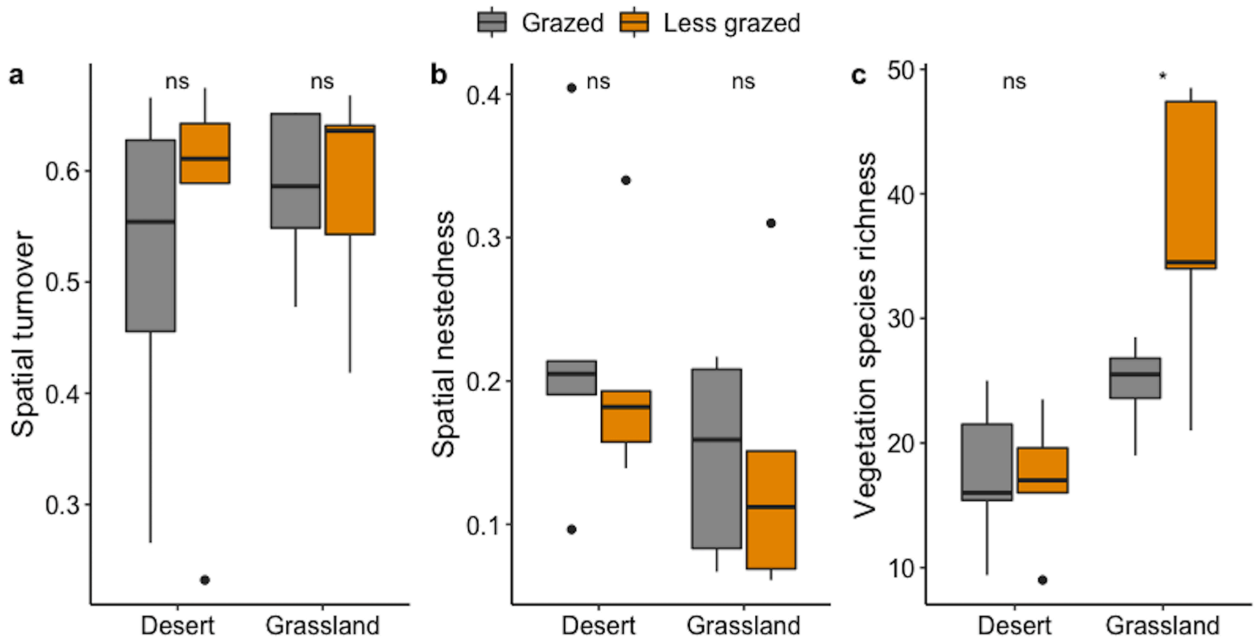

Fig. 5. a) Spatial turnover, b) spatial nestedness, and c) vegetation species richness under different grazing regimes in desert and grassland. Dots represent outliers, significant differences are represented by stars: * $p < 0.05$, ns = non-significant.

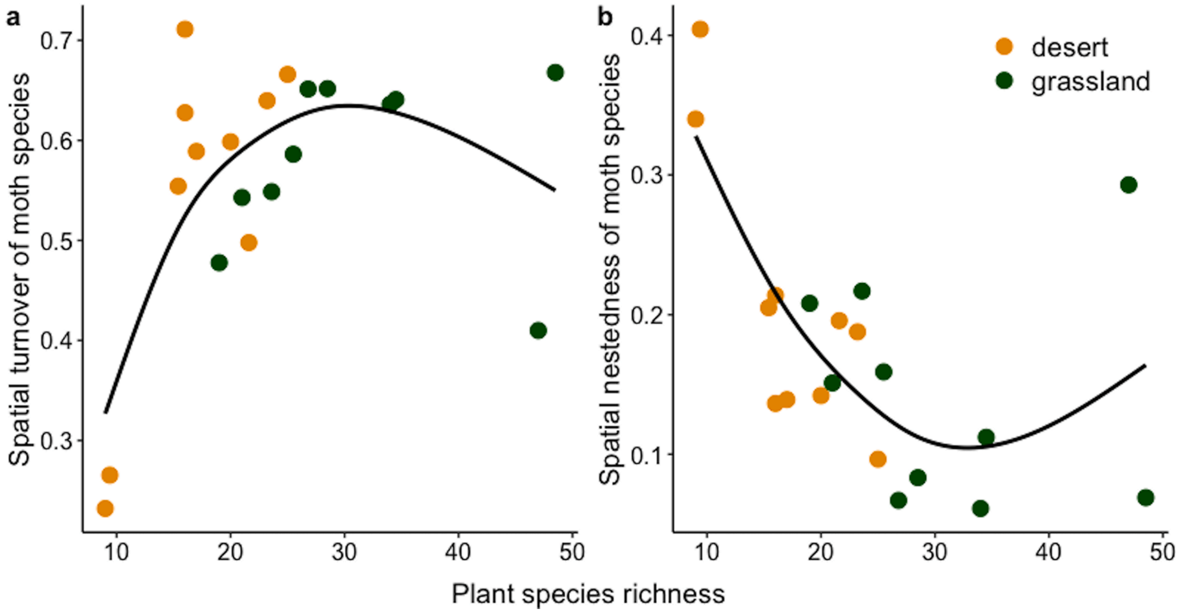

Fig. 6. Relationship between a) spatial turnover of moth species (between grazed and less grazed plots) and vegetation species richness, and b) along grazing nestedness and vegetation species richness. Orange circles indicate desert, green circles indicate grassland. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(generalist), *Scotopteryx chenopodiata* (generalist), and *Thetidia chlorophyllaria* (generalist). In contrast, two species reduced their observed range from 2018 to 2019: *Gastropacha quercifolia* (generalist) and *Lygephila lubrica* (specialist).

3.4. Effects of environmental variables

The climatic effect superimposed the grazing effect at the biome scale. The result of PERMANOVA showed that macro-moth species composition differed significantly between desert and grassland biomes. However, macro-moth species composition did not differ significantly between grazing regimes. We used an RDA ($F_{(1,4)} = 7.14$, $p < 0.01$) to investigate the impact of environmental parameters on moth community composition (Fig. 10). *Altitude*, *mean annual temperature*, *livestock composition*, *vegetation guild: grass*, *vegetation cover,* and *vegetation diversity* explained 59.5% of the variability in moth composition among sites and grazing regimes in two contrasting biomes. Environmental variables affected sites differently, e.g., Sites 1 and 2, situated in the mountains of Umnugobi, formed a group mainly impacted by *altitude*. Southern sites 3, 4, and 5 clustered together, and *livestock composition and temperature* were the critical environmental variables for this group. The northern sites were grouped, and *vegetation guild: grass, vegetation cover,* and *vegetation diversity* structured moth communities, especially the northernmost sites.

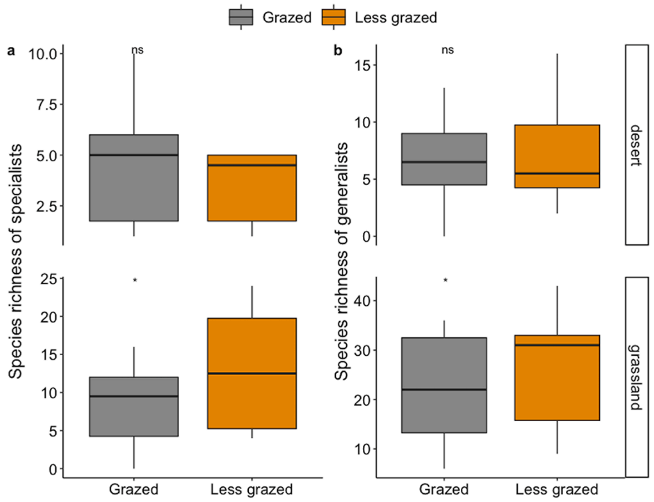

Fig. 7. Species richness of a) specialist and b) generalist moths in grazed and less grazed plots in two distinct biomes: desert and grassland as compared by T-test. Significant differences are represented by stars: * $p < 0.05$, ** $p < 0.01$, ns = non-significant.

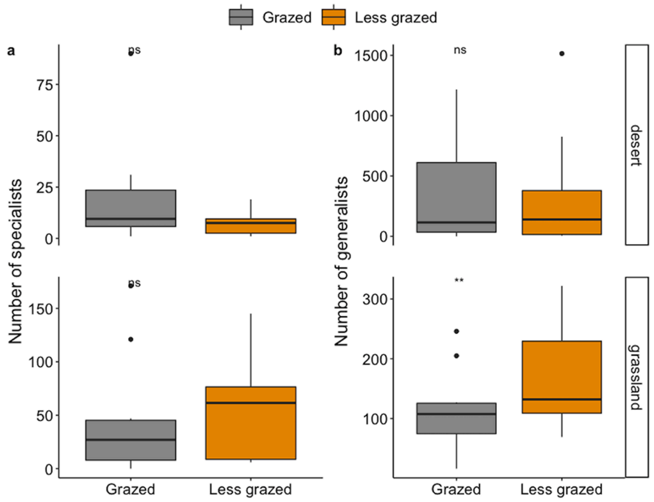

Fig. 8. Numbers of a) specialist and b) generalist moth individuals in grazed and less grazed plots in two distinct biomes: desert and grassland. Significant differences are represented by stars: * $p < 0.05$, ** $p < 0.01$, ns = non-significant.

Lastly, we aimed to study how vegetation species richness was responsible for the total species richness of all moths. Vegetation species richness significantly explained 69% of the variation in the communities (GAM: $R^2 = 0.69$, $p < 0.001$) (Figure S1).

4. Discussion

4.1. Species composition

Our study reveals that the moths responded differently to grazing in two contrasting biomes, and that moth families showed distinct responses. Moths followed a dynamic equilibrium model in which climatic variables overrode the effect of livestock grazing in the desert, while the livestock grazing effects on moth diversity were stronger in the grassland. To our knowledge, this is the first study that investigated indicator species of different grazing regimes in contrasting biomes in central Asia; and revealed indicator species for sections of the latitudinal gradient, which can be used as a reference for dispersal of moths due to climate change in later years. In this study, we also demonstrated how moth species richness and abundance differed in terms of feeding niche (i.e., generalist and specialist) between grazed and less grazed plots in contrasting biomes.

Strong wind and cold nights in the desert in 2018 probably lowered the sampling success. Thus, desert samples covered only 50% of available species richness. 2018 was an arid year throughout the sampling sites, and this situation could become the suitable precondition for potential pest species such as *Agrotis ripae*, *Anarta trifollii*, and *Euxoa ochrogaster* to appear in higher abundance in 2019. These species are generalist species and were found in most of the sites along the latitudinal gradient in Mongolia (Enkhtur et al., 2021). *A. trifolii* is regarded as an agricultural pest and widespread in dry and open areas (Wu et al., 2020). Some widespread species could even benefit from the warming climate and increase their abundance (Fox et al., 2014).

4.2. Effects of livestock grazing on moth diversity

Moths are more sensitive to disturbance than plants (Littlewood, 2008; Pöyry et al., 2006): Grassland plant communities were similar under different grazing intensities (Ahlborn et al., 2020). In contrast, our study corroborates the adverse effects of intense grazing on species diversity of moths in grassland (Ekroos et al., 2010; Littlewood, 2008; Rickert et al., 2012). However, the effect was not consistent across both studied biomes.

In the desert, climatic effects (i.e., drought) override the impact of livestock grazing; thus, species richness, species diversity, and abundance did not significantly differ between grazed and less grazed plots. This result was in line with the vegetation response to grazing in the desert (Ahlborn et al., 2020; Lang et al., 2020). In grassland, Geometridae, Noctuidae, and Erebidae were more sensitive to grazing. Day active geometrid moths were reported to be more sensitive than butterflies to increasing arable land cover (Ekroos et al., 2010).

In the desert, both grazed and less grazed plots had a similar number of unique species, and the number of overlapping species in both plots was high; however, the numbers of unique species of geometrids and noctuids in less grazed plots in grassland were almost double compared to those of the grazed plots indicating they were more sensitive to grazing.

Our study supports the results of Klink et al. (2015) who showed that at a moderate level of grazing, the diversity of arthropods is higher than at lower and upper levels. When the vegetation richness is intermediate, the dissimilarity between grazed and less grazed plots was due to moth species turnover, indicating habitat heterogeneity. At both extremes, the dissimilarities between grazed and less grazed plots were due to nestedness indicating original habitat homogeneity. In the most species-poor site 3, spatial nestedness was higher than spatial turnover, indicating that from less grazed plot to grazed plot, some moth species simply disappeared. This result was in line with the beta diversity pattern of vegetation. In the species-poor site 3, plant structures of grazed and less grazed plots differed due to spatial nestedness i.e., species loss (Table S4).

4.3. Indicator species

We found two indicator species in the desert: *Cucullia splendida* for grazed plots and *Hyles chuvilini* for less grazed sites. *C. splendida* is a specialist feeding on *Artemisia*. In grazed plots, such weeds are usually among the most abundant plants and they are tolerant to disturbance (Oyundelger et al., 2021). *H. chuvilini* feeds on *Euphorbia* species which are – despite their toxicity – probably sensitive against intensive grazing. In grassland, we revealed species indicators only for less grazed plots. *Polia bombycina* is an endangered species in parts of Europe, and it is dependent on shelter-providing structures such as hedgerow trees during the food search. Thus, *P. bombycina* not only could indicate less grazed pastures, but also could indicate surrounding forests or bushes

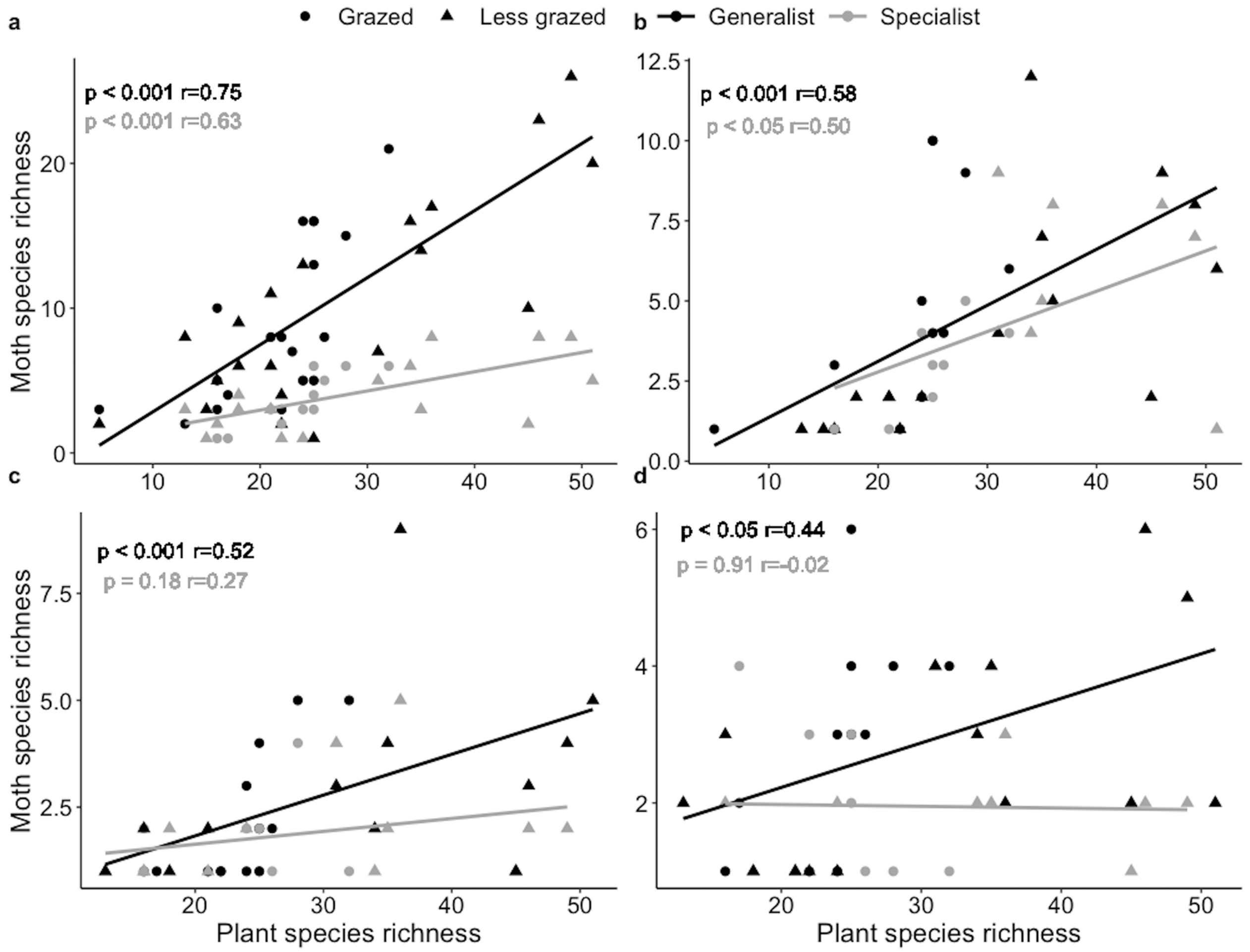

Fig. 9. Relationship between moth species richness and vegetation species richness for Generalists (black line) vs. Specialists (grey line). a) Noctuidae, b) Geometridae, c) Erebidae, d) 'Other'. Grazed and less grazed plots have been pooled for each of both groups.

Table 2
Indicator species of grazing intensities 1 = less grazed, 2 = grazed. Here we included species with indicator value above 0.7 and statistically significant. The shaded areas indicate the latitudinal ranges of each species. Columns 1 through 10 represent study sites.

Year	Grazing intensity	Family	Species	Feeding niche	Indicator value	*p* value	1	2	3	4	5	6	7	8	9	10
2019	1	Geometridae	*Catarhoe cuculata*	Specialist	0.894	0.0473									▨	▨
2019	2	Noctuidae	*Cucullia splendida*	Specialist	0.873	0.0418	▨	▨								
2019	1	Noctuidae	*Euxoa ochrogaster*	Generalist	0.882	0.0467						▨	▨			
2018, 2019	1	Sphingidae	*Hyles chuvilini*	Generalist	0.894	0.0455	▨									
2019	1	Noctuidae	*Lacanobia thalassina*	Generalist	0.777	0.0224							▨	▨	▨	▨
2019	1	Geometridae	*Megalycinia strictaria*	Not clear	0.787	0.0093							▨	▨	▨	▨
2018, 2019	1	Noctuidae	*Mythimna comma*	Generalist	0.814	0.0004						▨	▨	▨		
2019	1	Noctuidae	*Polia bombycina*	Generalist	0.776	0.0327							▨	▨	▨	▨
2018, 2019	1	Noctuidae	*Rhyacia simulans*	Generalist	0.913	0.0148							▨			
2019	1	Noctuidae	*Sideridis kitti*	Specialist	0.777	0.0338							▨	▨	▨	▨
2019	1	Noctuidae	*Sideridis egena*	Specialist	0.913	0.016							▨	▨		
2018, 2019	1	Sphingidae	*Smerinthus caecus*	Specialist	0.894	0.0465										▨

Table 3
Results of the Indicator Value (IndVal) analysis for 2018 and 2019 along the latitudinal gradient. We identified indicators for certain latitudes. Here we list species with an indicator value above 0.7 and statistical significance. Some species were indicators for more than one site, which is expressed by + sign.

Year	Site	Family	*Species*	A	B	INDVAL	*p* value
2018	8	Noctuidae	*Actebia fennica*	1	0.8333	0.913	0.0003
2018	6	Noctuidae	*Actebia poecila*	0.8537	0.6667	0.754	0.0013
2018	7 + 8	Noctuidae	*Agrotis clavis*	0.918	0.8182	0.867	1.00E-04
2018	4 + 5	Noctuidae	*Agrotis ripae*	0.941	1	0.97	0.0001
2018	4 + 5	Noctuidae	*Anarta stigmosa*	1	0.8182	0.905	0.0001
2018	10	Geometridae	*Arichanna sinca*	1	0.6667	0.816	0.0004
2018	9 + 10	Erebidae	*Calyptra thalictri*	1	0.5	0.707	0.0028
2018	10	Erebidae	*Catocala deuteronympha*	1	0.8333	0.913	0.0003
2018	10	Erebidae	*Catocala pacta*	1	0.8333	0.913	0.0003
2018	8	Erebidae	*Chelis dahurica*	0.8951	1	0.946	0.0001
2018	10	Noctuidae	*Cosmia puralina*	1	0.6667	0.816	0.0008
2018	10	Noctuidae	*Cucullia scopariae*	0.95	0.6667	0.796	0.0008
2018	10	Erebidae	*Euproctis similis*	1	0.5	0.707	0.0099
2018	8 + 9 + 10	Lasiocampidae	*Gastropacha quercifolia*	1	0.5	0.707	0.0033
2018	8	Noctuidae	*Hada plebeja*	1	0.5	0.707	0.0086
2018	10	Noctuidae	*Ipimorpha retusa*	1	0.6667	0.816	0.0002
2018	9 + 10	Geometridae	*Isturgia arenacearia*	0.9839	0.8333	0.905	0.0001
2018	8	Noctuidae	*Lacanobia thalassina*	1	0.6667	0.816	0.0002
2018	7 + 8	Noctuidae	*Lasionhada proxima*	0.9474	0.7273	0.83	4.00E-04
2018	10	Erebidae	*Leucoma candida*	0.88	0.8333	0.856	0.0003
2018	9 + 10	Erebidae	*Lygephila lubrica*	0.9176	0.8333	0.874	0.0001
2018	7	Erebidae	*Lygephila vicae*	0.7598	1	0.872	0.0003
2018	10	Erebidae	*Lymantria dispar*	1	0.6667	0.816	0.0006
2018	10	Noctuidae	*Mythimna conigera*	1	0.5	0.707	0.01
2018	9 + 10	Noctuidae	*Mythimna velutina*	1	0.5	0.707	0.0109
2018	10	Noctuidae	*Polia bombycina*	0.9643	0.6667	0.802	0.0003
2018	6 + 7	Noctuidae	*Rhyacia simulans*	0.9217	0.7273	0.819	9.00E-04
2018	10	Geometridae	*Scopula decorota przewalskii*	0.9444	0.8333	0.887	1.00E-04
2018	10	Geometridae	*Scopula rubiginata*	1	0.5	0.707	0.0089
2018	8	Geometridae	*Scotopteryx chenopodiata*	1	0.8333	0.913	0.0005
2018	10	Sphingidae	*Smerinthus caecus*	1	0.5	0.707	0.0087
2018	10	Geometridae	*Thetidia chlorophyllaria*	0.913	0.8333	0.872	0.0001
2019	7 + 8	Noctuidae	*Agrotis clavis*	0.925	0.5833	0.735	0.0085
2019	7 + 8 + 9	Noctuidae	*Agrotis exclamationis*	0.8889	0.6667	0.77	0.001
2019	8	Erebidae	*Autographa buraetica*	0.6364	0.8333	0.728	0.002
2019	7 + 10	Geometridae	*Biston betularia*	0.8958	0.9	0.898	1.00E-04
2019	10	Sphingidae	*Callambulyx tatarinovii*	0.7895	0.75	0.769	0.0012
2019	10	Erebidae	*Catocala bella*	1	0.5	0.707	0.0138
2019	10	Erebidae	*Catocala deuteronympha*	0.8824	0.75	0.813	0.0012
2019	1	Noctuidae	*Dichagyris vallesiaca*	0.8621	0.6667	0.758	0.0031
2019	1	Cossidae	*Eogystia hippophaecolus*	1	0.6667	0.816	0.0013
2019	1	Noctuidae	*Euxoa cursoria*	0.9489	0.8333	0.889	0.0006
2019	8 + 10	Lasiocampidae	*Gastropacha quercifolia*	0.8111	0.9	0.854	1.00E-04
2019	7	Noctuidae	*Heliothis ononis*	0.75	0.6667	0.707	0.0068
2019	2	Sphingidae	*Hyles chivulini*	0.7059	0.8	0.751	0.0007
2019	9 + 10	Geometridae	*Isturgia arenacearia*	0.9087	1	0.953	1.00E-04
2019	7 + 8 + 9	Noctuidae	*Lacanobia thalassina*	1	0.6111	0.782	0.0015
2019	7 + 8	Noctuidae	*Lasionhada proxima*	1	0.6667	0.816	0.0004
2019	9	Erebidae	*Lygephila lubrica*	0.8944	1	0.946	0.0002
2019	7	Erebidae	*Lygephila vicae*	0.9773	1	0.989	0.0001
2019	8	Noctuidae	*Malacosoma castrensis*	0.9091	0.8333	0.87	0.0001
2019	10	Sphingidae	*Marumba gaschkewitschii*	1	0.5	0.707	0.014
2019	8 + 10	Geometridae	*Megaspilates mundataria*	1	0.7	0.837	2.00E-04
2019	2	Noctuidae	*Panchrysia ornata*	1	0.6	0.775	0.0017
2019	9	Geometridae	*Pelurga comitata*	1	0.5	0.707	0.0063
2019	8 + 9	Geometridae	*Phibalapteryx virgata*	0.9077	0.75	0.825	0.0003
2019	8 + 9 + 10	Noctuidae	*Polia bombycina*	0.9672	0.625	0.778	0.0012
2019	9	Geometridae	*Scopula virgulata*	0.5882	0.8333	0.7	0.0098
2019	8 + 9	Geometridae	*Scotopteryx chenopodiata*	0.9167	0.5833	0.731	0.0019
2019	8	Sphingidae	*Sphinx ligustri*	1	0.6667	0.816	0.0017
2019	8 + 9 + 10	Geometridae	*Thetidia chlorophyllaria*	1	0.6875	0.829	0.0001

(Merckx et al., 2010). *Rhyacia simulans* is a vulnerable species in Ireland (Allen et al., 2016). *Sideridis kitti* is regarded as a nearly endangered species in Italy (Huemer, 2008) and too much grazing could have affected it negatively (Wagner, 2021). *Smerinthus caecus* feeds on *Salix* and *Populus*; thus, this species is not an indicator of pasture, but mirrors surrounding vegetation of bushes and trees.

In the case of indicator species for sections of the latitudinal gradient, from 2018 to 2019, some indicator species were apparently expanding their geographical range, whereas the range of some species was shrinking. *Gastropacha quercifolia* was an indicator species of less grazed pasture in a former study (Enkhtur et al., 2017), and this species is endangered in Europe due to the decline of the suitable habitat. In grazed plots, *Chenopodium* and *Atriplex* were abundant plants (Ahlborn et al., 2020) and *Lacanobia thalassina*, *Agrotis clavis, Actebia fennica* and *Agrotis ripae* feed (among others) on these annual plant species.

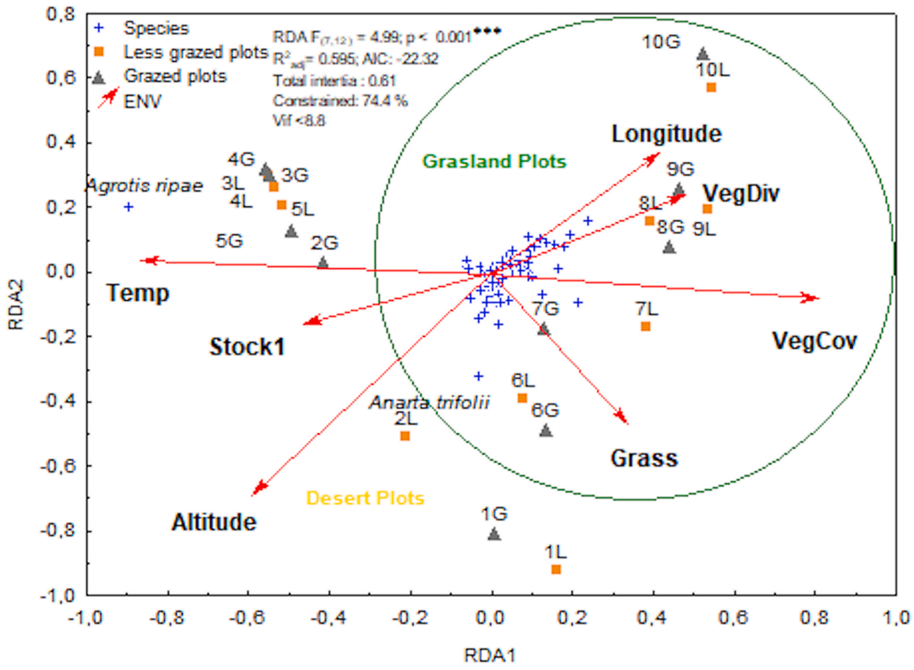

Fig. 10. Parsimonious redundancy analysis (RDA) based on the composition of macro-moth assemblages of grazed and less grazed plots at ten sites along our transect. Grassland plots within the green disk. Seven environmental factors explained 60 % of the model variation: mean annual temperature (Temp), 1st PCA axes of livestock composition (PC1.Stock), altitude, percentage of grass cover (Grass), percentage of vegetation cover (VegCov), Shannon diversity of vegetation (VegDiv) and eastern longitude. The species scores of the two most abundant species *Agrotis ripae* and *Anarta trifolii* are named. Orange squares show less grazed sites, gray triangles stand for grazed sites. Both axes of the RDA are highly significant ($p < 0.001$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.4. Relationships between traits and grazing

Against our expectation, the species richness of both specialist and generalist moths was significantly higher in less grazed plots in grassland. Polyphagous and grass-feeding insects are abundant in temperate ecosystems (Klink et al., 2015). However, not all moth families showed the same response to species rich vegetation. Only the generalists of Erebidae and 'Other' were more strongly correlated with the species richness of vegetation; since generalists are associated with many host plant species, they could be mirroring vegetation heterogeneity. In contrast, species richness of both generalists and specialists of Geometridae and Noctuidae were correlated with the vegetation species richness. This result is in line with Littlewood et al.'s (2008) result of higher occurrences of generalists in less grazed plots. In suitable habitat, generalists could also indicate habitat heterogeneity; in addition, many generalist species are grass feeders (Pöyry et al., 2006), thus in less grazed plots, species richness for both, generalists and specialists was higher than in grazed plots. In contrast, there was no clear pattern regarding the feeding niche of moths (i.e., generalist and specialist) in arid environments in the desert. Here, plant species richness did not differ significantly between grazed and less grazed plots, indicating habitat homogeneity.

4.5. Environmental effects on moth assemblages

Vegetation heterogeneity and density of the large herbivores are essential attributes for arthropod diversity (Klink et al., 2015). The grass was the most important functional group that structured moth species composition among all plant functional groups. Temperature and livestock density explained the variation of moth community composition in the desert, and species composition of grazed and less grazed plots was similar. We, therefore, conclude that the combined effect of climate and livestock grazing could cause all grazing types to become more homogenous and reduce environmental resilience. In contrast to desert, vegetation diversity and vegetation cover were important variables in grassland, and moth community composition not only differed between grazed and less grazed plots, but also differed among sites along the latitudinal gradient. Altitude defined species composition for site 1 in Bayandalai Soum and making it more distinct from other sites. We, therefore, assume an effect of altitude as found in other studies (Ashton et al., 2016; Brehm et al., 2007; Escobar et al., 2005). Species in higher altitudes are often endemic and sensitive to climate change (Ashton et al., 2016; Loope and Giambelluca, 1998), thus, species at higher altitudes could be in particular danger of extinction.

We studied how moths with different feeding niches differed in grazed and less grazed plots in two contrasting biomes. However, other important information, such as voltinism, hibernation, conservation status (Mangels et al., 2017) and other traits-related information was unavailable. From the conservation point of view, there is a need to explore the status of rare species and their potential need of conservation management. Currently, only one species in our samples, *Sphinx ligustri,* is on the Red List of Mongolia (Ministry of Environment and Green Development, 2013). However, reliable data on population sizes and conservation status of insect species are largely lacking. It is therefore vital to compile those missing data.

5. Conclusion

From the conservation point of view and sustainable management, it is crucial to disentangle the effects of livestock grazing for invertebrate herbivores (the "secret workers behind the curtain of ecosystems") under different climatic conditions. In the desert, we recommend conserving less grazed pasture only, while in the grassland, both grazed and less grazed pastures should receive attention. Both, the higher proportion of specialists and generalists in the less grazed plots in the grassland indicate that habitat change and climate change are synergistically affecting moth community composition. This is the first study to assess indicator species for different grazing regimes in contrasting biomes in Central Asia and to identify indicator species for sections of the latitudinal gradient that can serve as a reference for moth dispersal due to climate change in later years. In grasslands, Geometridae, Noctuidae, and Erebidae were more vulnerable to grazing than other moth families.

CRediT authorship contribution statement

Khishigdelger Enkhtur: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project

administration, Resources, Software, Validation, Visualization, Writing – original draft. **Gunnar Brehm:** Resources, Validation, Writing – review & editing. **Bazartseren Boldgiv:** Funding acquisition, Validation, Writing – review & editing. **Martin Pfeiffer:** Conceptualization, Formal analysis, Supervision, Validation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Christine Römermann, Julian Ahlborn, Birgit Lang, Munkhzul Oyunbileg for providing their study design and vegetation data. We thank Badamnyambuu Iderzorig, Uujin Togtokh, Enkhtur Dambiijantsan, Byambasuren Munkhjargal, Temuujin B., Davaadorj Enkhtur for their field assistance. We thank the local herders, especially the family of Byambaa for their hospitality. We also thank Badamnyambuu Iderzorig and Erdenetsetseg Batdelger, who helped with the transportation of moth samples to Germany. We are grateful to Tungalag Radnaakhand for confirming the plant species. A special thank goes to Enkhmandal Orsoo for mounting most specimens for identifications. We appreciate the help of Reinhold Stahlmann in creating the map of the study area. We are grateful to Christine Römermann for her comments on an early draft. We thank the anonymous reviewers for taking the time to review our manuscript and encouraged us to publish it. We sincerely appreciate their valuable comments and suggestions that helped improve our manuscript. This publication was funded by the University of Bayreuth Open Access Publishing Fund.

Funding

K.E. funded by DAAD (Research Grants Doctoral Programme in Germany, 2017/18 (57299294)). Field work was supported by Equal Opportunity Department, University of Bayreuth, and the Taylor Family-Asia Foundation Endowed Chair in Ecology and Conservation Biology, Mongolia.

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K.E.: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing-original draft. **G. B.:** Resources, Validation, Writing-review & editing. **B.B.:** Funding acquisition, Validation, Writing - review & editing and **M.P.L:** Conceptualization, Formal analysis, Supervision, Validation, Writing - review & editing.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.108421.

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