

Diversity and distribution of macro-moths in Mongolia

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This thesis is dedicated to all creatures who lost their lives for the sake of science.



"Be kind to all creatures; this is the true religion" Buddha

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Summary

Globally, ~8.7 million species are estimated to exist on Earth, and one million species are facing extinction due to human intervention. Biodiversity improves the environment's resilience to disturbances, plays a vital role in sustaining ecosystem functions, and provides ecosystem services to humanity. The significant drivers of biodiversity loss are habitat loss, human population and consumption growth, and climate change. Climate warming will cause cold-adapted species to migrate to higher elevations or latitudes, searching for suitable habitats. Another factor that affects species richness and community composition is an ecological disturbance. However, it is still unclear how species will respond and how many species will disappear in the near future.

Species richness (alpha diversity) is used to measure biodiversity since it is practical and widely applicable; however, even for similar environments, the number of species differs; therefore, it is crucial to determine the underlying causes. Beta diversity considers the changes in species composition among areas and can be partitioned into two parts, according to the origin of differences: turnover and nestedness. Turnover reflects the process of environmental filtering, while nestedness reflects colonization, such as the effects of a lack of available resources. For observing potential environmental and climate change, indicator species are used to monitor the environmental condition and assess the ecological integrity. However, how species respond to environmental change depends on their functional traits. Environmental disturbances such as overgrazing eliminate specialist species, while generalists benefit, resulting in a more homogeneous, less resilient environment.

It is predicted that there will be massive biodiversity losses if current human population growth continues and if people do not change the way they interact with nature. However, globally, the availability of biodiversity data is not equal: differences may occur spatially (most databases are covering Europe and North America), taxonomically (focus on large animals such as mammals and birds and charismatic organisms such as butterflies), historically (long-term data is missing), and analytically (general pattern is missing). Therefore, we do not know exactly which species are disappearing in many places of the world and where conservation management should focus. So, it is necessary to learn how many species exist, how disturbance affects their distribution, how they respond to disturbance depending on their ecological niches, etc. in order to conserve biodiversity.

In this thesis, I integrated and analyzed published data on geometrid moths and interpreted their diversity pattern; moreover, I studied the diversity and distribution of macro moths in the field and further investigated the effects of livestock grazing on moth assemblages under different climatic conditions. The central part of the thesis was

conducted at ten sites located along the latitudinal gradient in Mongolia, totaling a transect length of 860 km from the Gobi Desert into the steppe.

I found a breakpoint at 46° N for both the beta diversity pattern of moth communities and precipitation and temperature. In the desert, beta diversity was due to species loss/gain, and in grassland, it was caused by species replacement. The low number of species and the relatedness of beta diversity to species loss in the desert reflect the lower productivity of this ecosystem. Based on the overlapping breakpoints of environment and community structure, I expect the grassland sites to become more similar to desert sites if global temperatures continue to rise, leading to a more nested pattern of moth diversity. The contrasting patterns of beta diversity in deserts and grasslands mean that different conservation approaches are necessary.

My thesis demonstrates that moths in the two contrasting biomes responded differently to grazing and that moth families showed different responses. In the desert, climate variables overrode the effects of grazing, whereas, in the grassland, the effects of grazing were more pronounced. For the first time, I assessed indicator species for distinct grazing regimes in contrasting biomes in Mongolia and identified indicator species for sections of the latitudinal gradient. The results of the literature review and up-to-date field studies serve as baseline data for future research that will be useful in identifying changes. In addition, areas at the highest elevations in desert habitat that may serve as refuges for biodiversity, as reflected by moths, should be studied in more detail and over the long term.

Future studies should aim to 1) Compile and integrate records for other moth families and create a species checklist. 2) Investigate and compile trait-related information. 3) Evaluate the population size of rare species of moths and update the conservation status. 4) Study the phylogenetic diversity of moths in Mongolia. 5) Predict the potential and projected distribution of moths in the Palearctic region.

Zusammenfassung

Weltweit gibt es schätzungsweise 8,7 Millionen Arten auf der Erde, und ein Million Arten sind vom Aussterben bedroht, weil der Mensch eingreift. Die biologische Vielfalt verbessert die Widerstandsfähigkeit der Umwelt gegenüber Störungen, spielt eine wichtige Rolle bei der Aufrechterhaltung der Ökosystemfunktionen und erbringt Ökosystemleistungen für die Menschheit. Die wichtigsten Ursachen für den Verlust der biologischen Vielfalt sind der Verlust von Lebensräumen, das Wachstum der menschlichen Bevölkerung und ihres Konsums, sowie der Klimawandel. Die Klimaerwärmung wird dazu führen, dass kälteangepasste Arten auf der Suche nach geeigneten Lebensräumen in höhere Lagen oder Breitengrade abwandern. Ein weiterer Faktor, der den Artenreichtum und die Zusammensetzung der Lebensgemeinschaften beeinflusst, sind ökologische Störungen. Es ist jedoch noch unklar, wie die Arten darauf reagieren und wie viele Arten in naher Zukunft verschwinden werden.

Der Artenreichtum (Alpha-Diversität) wird zur Messung der biologischen Vielfalt verwendet, da er praktisch und weithin anwendbar ist; allerdings ist die Anzahl der Arten selbst in ähnlichen Umgebungen unterschiedlich; daher ist es von entscheidender Bedeutung, die dem zugrunde liegenden Ursachen zu ermitteln. Die Beta-Diversität berücksichtigt die Veränderungen in der Artenzusammensetzung zwischen verschiedenen Gebieten und kann je nach dem Ursprung der Unterschiede in zwei Teile unterteilt werden: Arten-Turnover und *Nestedness* (Verschachtelung). Der *Turnover* spiegelt den Prozess der Umweltfilterung wider, während die *Nestedness* die Besiedlungsgeschichte widerspiegelt, beispielsweise die Auswirkungen eines Mangels an verfügbaren Ressourcen. Zur Beobachtung potenzieller Umwelt- und Klimaveränderungen werden Indikatorarten verwendet, um den Umweltzustand zu überwachen und die ökologische Integrität eines Habitats zu bewerten. Wie die Arten auf Umweltveränderungen reagieren, hängt jedoch von ihren funktionellen Merkmalen ab. Umweltstörungen wie Überweidung eliminieren spezialisierte Arten, während Generalisten davon profitieren, was dann zu einer homogeneren, weniger widerstandsfähigen Umwelt führt.

Wenn das derzeitige Bevölkerungswachstum anhält und die Menschen ihren Umgang mit der Natur nicht ändern wird ein massiver Verlust an biologischer Vielfalt prognostiziert. Die Verfügbarkeit von Daten zur biologischen Vielfalt ist jedoch weltweit uneinheitlich, daher ergeben sich auf den verschiedenen Ebenen große Unterschiede: räumlich (die meisten Datenbanken decken Europa und Nordamerika ab), taxonomisch (Schwerpunkt auf großen Tieren wie Säugetieren und Vögeln und charismatischen Organismen wie Schmetterlingen), historisch (es fehlen langfristige Daten), analytisch (es fehlen allgemeine Muster). Daher wissen wir an vielen Orten der Welt nicht genau, welche Arten verschwinden und worauf sich das Erhaltungsmanagement konzentrieren sollte.

Um die biologische Vielfalt zu erhalten, muss man also wissen, wie viele Arten es gibt, wie sich Störungen auf ihre Verbreitung auswirken, wie sie je nach ihrer ökologischen Nische auf Störungen reagieren usw.

In dieser Arbeit habe ich die veröffentlichte Daten über Nachtfalter der Geometridae in der Mongolei zusammengefasst und analysiert und ihre Diversitätsmuster interpretiert. Darüber hinaus habe ich die Diversität und Verteilung von Makrofalterarten im Feld untersucht und die Auswirkungen der Beweidung durch Vieh auf die Nachtfaltergemeinschaften unter verschiedenen klimatischen Bedingungen untersucht. Der Hauptteil der Arbeit wurde an zehn Standorten entlang des Breitengradgradienten in der Mongolei durchgeführt, die insgesamt eine Transektlänge von 860 km von der Wüste Gobi bis in die Steppe aufweisen.

Ich fand einen Bruchpunkt bei 46° N sowohl für das Beta-Diversitätsmuster der Mottengemeinschaften als auch für Niederschlag und Temperatur. In der Wüste war die Beta-Diversität auf den Verlust bzw. die Zunahme von Arten zurückzuführen, während sie im Grasland durch den Austausch von Arten verursacht wurde. Die geringe Artenzahl und der Zusammenhang zwischen der Beta-Diversität und dem Artenverlust in der Wüste spiegeln die geringere Produktivität dieses Ökosystems wider. Aufgrund der sich überschneidenden Bruchpunkte von Gemeinschaftsstruktur und Umweltgradienten erwarte ich, dass sich die Graslandstandorte den Wüstenstandorten annähern werden, wenn die globalen Temperaturen weiter steigen, was zu einem stärker verschachtelten Muster der Diversität der Nachtfalter führen wird. Die gegensätzlichen Muster der Beta-Diversität in Wüsten und Grasland bedeuten, dass unterschiedliche Ansätze zum Schutz der Arten erforderlich sind.

Meine Doktorarbeit zeigt, dass die Nachtfalter in den beiden kontrastierenden Biomen unterschiedlich auf die Beweidung reagieren und dass die Mottenfamilien unterschiedliche Reaktionen zeigen. In der Wüste überlagerten die Klimavariablen die Auswirkungen der Beweidung, während im Grasland die Auswirkungen der Beweidung stärker ausgeprägt waren. Zum ersten Mal habe ich Indikatorarten für unterschiedliche Beweidungsregime in kontrastierenden Biomen in der Mongolei bestimmt und Indikatorarten für Abschnitte des Breitengradienten ermittelt. Sowohl die Ergebnisse der Literaturrecherche, als auch die aktuellen Feldstudien dienen als Basisdaten für künftige Forschungen, die bei der Detektion von Veränderungen hilfreich sein werden. Darüber hinaus sollten die höchstgelegenen Gebiete in Wüstenhabitaten eingehender und langfristig untersucht werden, weil sie als Refugien für die Artenvielfalt dienen können, wie es sich am Beispiel der Nachtfalter gezeigt hat, eingehender und langfristig untersucht werden.

Künftige Studien sollten folgende Ziele fokussieren: 1) Zusammenstellung und Integration von Datensätzen für andere Nachtfalterfamilien und Erstellung einer Arten-Checkliste. 2) Untersuchung und Zusammenstellung von Informationen zu funktionalen Merkmalen verschiedener Arten. 3) Bewertung der Populationsgröße seltener Nachtfalterarten und Aktualisierung ihres Schutzstatus. 4) Untersuchung der phylogenetischen Vielfalt der Nachtfalter in der Mongolei. 5) Vorhersage der potenziellen und voraussichtlichen Verbreitung von Nachtfaltern in der paläarktischen Region.

1. Introduction

1.1 Diversity, distribution, decline

Biodiversity, i.e., the variety of life forms, can be studied and understood in multiple ways. Generally, it can be studied at three main levels: 1) genetic diversity, 2) organismal diversity, and 3) ecological diversity (Gaston and Spicer, 2013). The object of diversity varies in these levels; however, in many cases, species richness (number of species) is used to measure biodiversity since it is practical, widely applicable, and comparable with already existing data. In contrast, species diversity can be expressed as the number of species and relative abundance of each species. However, even for similar environments, the number of species differs; therefore, it is crucial to find out the underlying causes (Qian et al., 2005). Is the change due to the number of species, or is it due to species replacement? Several methods measure the similarity and dissimilarity between study sites (Jaccard, Sorensen). Beta diversity considers the changes in species composition among areas and can be partitioned into two parts, according to the origin of differences (Baselga, 2010): turnover and nestedness. Turnover reflects the process of environmental filtering, while nestedness reflects colonization, such as the effects of a lack of available resources (Fontana et al., 2020). However, under-sampling could also lead to high species turnover (Tuomisto, 2010).

Biodiversity can be referred to as the “workers behind the curtain of the ecosystem”, without them, the ecosystem will malfunction (Tilman et al., 2014). Diversity improves the resilience of the environment to disturbance (Schindler et al., 2015), and according to the portfolio effect, a species-rich community is more stable than a species-poor community to environmental changes by averaging fluctuations of each species (Schindler et al., 2010). For example, agricultural intensification reduces plant diversity, which will lead to homogenization and less stability (Régnière et al., 2012). As a result, this will, in turn, decrease the community's stability and abundance (Haddad et al., 2011).

Biodiversity provides ecosystem services for humankind, which can be classified into four types: provisioning, regulating, cultural, and supporting (Wallace, 2007). But services of some species are not direct, their function contributes to other services. For example, insects play an essential role in the food web, recycling nutrients and pollinating those more than 80 percent of flowering plants that rely only on insects (Wagner, 2020). However, other animals and creatures also have the right to live, not only to provide the need for humankind.

Worldwide ~8,7 million species are predicted to exist on the earth, and ~1.2 million species are named (Mora et al., 2011). However, biodiversity is not distributed evenly

across the world, and depending on the type of taxa, species richness differs. There exists an overall trend of latitudinal and altitudinal gradients of species richness, though it varies among regions and taxonomic groups (Hillebrand, 2004; Willig et al., 2003). Many studies have documented that energy is a limiting factor; thus, species richness decreases under cold conditions in high latitude and altitude (Eggleton, 2020; Von Humboldt and Bonpland, 1807) and also depends on the geographical scale (range of latitude). The warming climate makes cold-adapted species migrate to higher altitudes or latitudes, searching for suitable environments (Hickling et al., 2006). Especially species that live in extreme conditions, such as in higher altitudes or latitudes, have less room to escape (Pimm, 2008). They will undergo upslope shifts and finally face mountain top extinction (Condamine and Sperling, 2018). Another example comes from a long-term study of mountain butterflies. If species are dependent on specific host plants and are less mobile, spatial mismatch between species and their host plants could happen since the velocity of range shifts differ among species (Rödger et al., 2021).

A further factor that affects species richness and community composition is a disturbance. According to the intermediate disturbance hypothesis, the diversity is highest at the intermediate disturbance. At both extremes, diversity reduces either due to competitive exclusion of dominant species or local extinction caused by severe disturbances. And according to the dynamic equilibrium model, disturbance itself depends on the ecosystem's productivity (Huston, 1979; Svensson et al., 2012). For example, for the species richness of plants, unimodal responses to grazing intensity have been observed (Wang and Wesche, 2016).

Therefore, it is necessary to gain knowledge on how many species exist, how disturbances affect their distribution, how they respond to disturbance depending on their ecological niches, etc. in order to conserve biodiversity. It is predicted that there will be massive biodiversity losses if current human population growth continues and if people do not change their way they interact with nature (Tilman et al., 2017).

1.2 The importance of compiling and combining baseline data for biodiversity

Globally, the availability of biodiversity data is not equal. First, spatially, it is heavily skewed towards Europe and North America, especially in terms of systematically collected long-term data. Some "global" studies of biodiversity decline should be interpreted with caution since such results, based on specific sites, are not representative for the global scale (Cardoso and Leather, 2019; Simmons et al., 2019; Theng et al., 2020; Thomas et al., 2019; Wagner, 2020). Robust diversity data representing all major world biomes are required (Thomas et al., 2019). Tropical regions are poorly studied. The same is true for most parts of central and eastern Asia.

Second, taxonomically, another problem is that some taxa are understudied, especially for the organisms regarded as not charismatic or too small to be noticed compared to big animals like mammals or birds, and if they are active at night and hide during day time. Current discussion of biodiversity loss tends to focus on vertebrates, and studies of arthropods fall by the wayside (Ceballos et al., 2015; Seibold et al., 2019). However, insects contribute about 90 percent of biodiversity in the world (Briggs, 2017), and they have been referred to as the “little things that run the world” (Wilson, 1987). Therefore, to understand, mitigate and proact the mass extinction, it is necessary to assess their diversity, distribution, and abundance (Régnier et al., 2015). Moreover, studies on insect biodiversity are not evenly distributed across the world. Usually, they are limited to specific regions, taxa, and dates. As a result, there are large gaps in biodiversity research.

Third, historically, many taxa lack baseline data (Theng et al., 2020), which are essential for determining future changes, such as identifying biodiversity loss, migration, and invasion. Although there are many historical records of biodiversity and researchers are constantly studying, collecting, and publishing them, they are scattered in the literature. Fortunately, there are several databases on biodiversity, like gbif.org, which collect and combine records of species. However, some data, such as very old records or those published in native languages (not in English), and some museum data could have been missing. Fourth, analytically, to see the whole picture, it is essential to fit the missing pieces together; therefore, it is crucial to compile and combine all available knowledge and reveal the hidden pattern.

1.3 Climate change and habitat loss

"There is enough on Earth for everybody's need, but not enough for everybody's greed" Gandhi

It has been reported that 1 million species are threatened with extinction due to human activities (Tollefson, 2019). The major drivers of biodiversity loss are habitat loss, human population and consumption growth, and climate change (Lacher and Roach, 2018). Climate change affects all levels of biodiversity, from individuals to biomes and their phenology, geographical range, and physiology (Bellard et al., 2012). However, it is still unclear how species will respond and how many species will disappear in the near future (Sinervo et al., 2010). Global average sea level increased until now by 0.20 m, global climate zones have shifted, Arctic sea ice area decreased, and global temperature increased by 1.07°C between 2010-2019 (IPCC, 2021). Extreme events like hot temperature, drought, and heavy precipitation will intensify if the current global warming continues (IPCC, 2021). Even species with a wide climatic envelope would decrease their range under moderate climate scenarios (Beaumont and Hughes, 2002).

1. Introduction

More and more land is being transformed into cropland, and even more and more animals are being grazed to feed the increasing human population. In the world, 40 percent of the terrestrial area is used by large herbivores as a pasture (White et al., 2000). By 2050, it is expected that damage to the environment caused by overgrazing could rise to 70% worldwide (Zhang et al., 2021). We are destroying ours and snatching away other creatures' homes to fulfill our greed; even four earth globes are not enough to reach the consumption demand of humankind (Wilson, 2002). In Mongolia, the synergistic effects of climate change and intensive land use make the grassland more vulnerable, and due to extreme drought, plant species are reduced (Kowal et al., 2021; Nandintsetseg et al., 2021). As a result, it further leads to intense sandstorm events and makes it not only a national but also an international issue (Han et al., 2021). The situation could even be worsened when the temperature increases by 6°C as predicted for the mid of 21st century (Kowal et al., 2021).

1.4 Land degradation in Mongolia

Mongolia has one of the most extensive grasslands globally (Miao et al., 2017) and covers an estimated 1.2 million km² with arid rangelands (Pfeiffer et al., 2018). The grassland is very vulnerable and has high ecological value, regionally and globally. However, due to climate change and intense land uses, such as livestock grazing and mining, many parts of the country are facing degradation and desertification (Han et al., 2021). The primary land use is agricultural land (Figure 1), and it consists mainly of pastoralism, which makes up 10 % of the gross domestic product (Mongolian Statistical Information Service, 2018).

1. Introduction

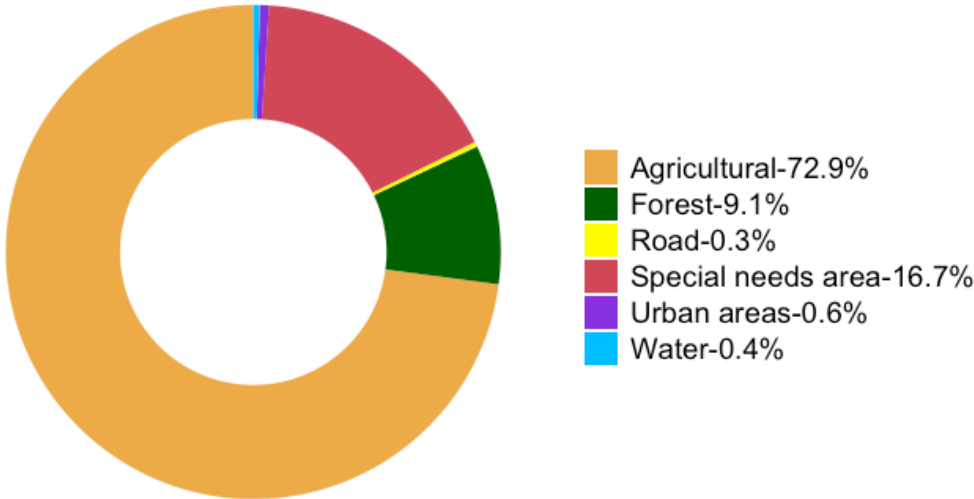


Figure 1 Land use types in Mongolia (National Statistical Office, 2020)

After socialism, the livestock industry transferred to private ownership in the 1990s, the number of animals increased rapidly, especially the number of goats due to the worldwide need for cashmere (Liu et al., 2013). In 2020, total livestock reached 67,068,486, and 27,720,250 of them constitute goats (Figure 2) (Mongolian Statistical Information Service, 2021).

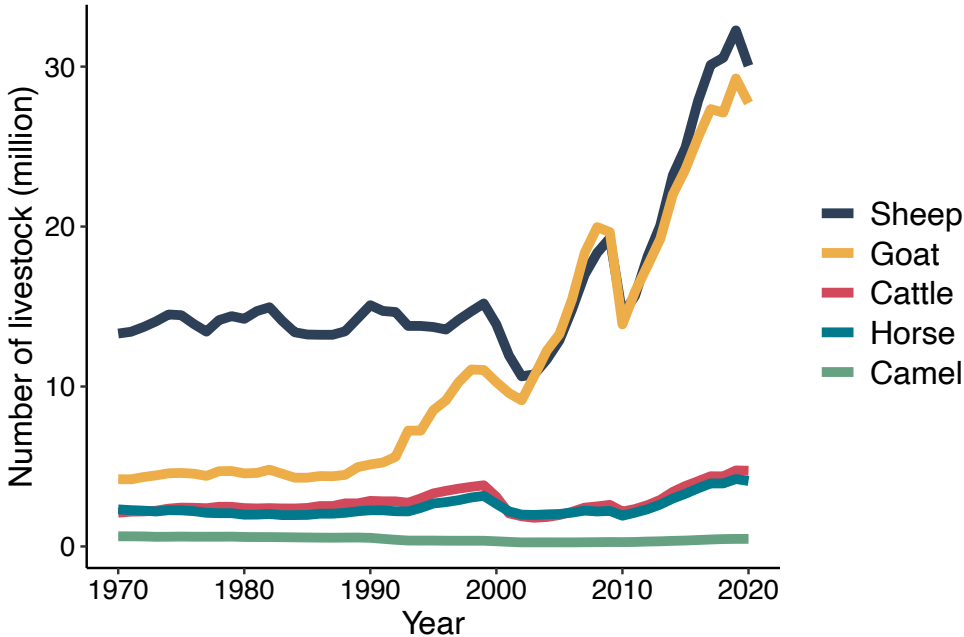


Figure 2 Number of livestock (in million) in Mongolia (National Statistical Office, 2020).

Hence, sustainable land use is crucial for supporting the nation's economy and maintaining healthy environments for local biodiversity and wildlife. However, despite the traditional Mongolian nomadic pastoralist lifestyle, herders tend to move less and concentrate near larger settlements (Pfeiffer et al., 2018). Thus, multiple effects like increasing temperature, drought, overgrazing, less mobility, and depleting utilization of natural resources worsen the situation, which brought the decrease of vegetation cover and land degradation of more than 75 percent of the country (Bat-Oyun et al., 2016; Han et al., 2021; Na et al., 2018; Wang et al., 2019). Globally, the synergistic effect of habitat loss and climate change could bring 15–35 percent of all species at risk of extinction (Thomas et al., 2004). In Mongolia, it has been reported that overgrazing affects negatively the diversity of flies, moths, plants, and crane flies (Clement et al., 2018; Enkhtur et al., 2017; Fernández-Giménez et al., 2017; Yadamsuren et al., 2015).

To reduce the biodiversity loss due to human impact, policies on agriculture practice and land use should be changed (Balmford et al., 2005; Christensen et al., 2004). It is necessary to understand their effects on biodiversity on large scale. According to the dynamic equilibrium model, the effect of grazing on plants differs depending on the climate condition (Ahlborn et al., 2020; Wang and Wesche, 2016).

1.5 Biodiversity research along a latitudinal gradient in Mongolia

From the conservation perspective, by gaining an insight into the diversity and distribution pattern of species and revealing the underlying factors, such as a latitudinal gradient, we can design efficient and effective conservation management and mitigate the sixth mass extinction (Willig and Presley, 2018).

For example, intense land use, known as the leading cause of the arthropod decline, affects diversity at a landscape scale (Seibold et al., 2019). Therefore, conservation management should be performed at this scale. The overall picture should be investigated at a large scale for appropriate conservation management and how species composition changes across the whole gradient.

The latitudinal gradient in Mongolia spans between the latitudes of 41°35' N and 52° 09' N over 1,259 km. A study on ant community structure along the north-south gradient was one of the first studies conducted along that latitudinal gradient in Mongolia (Pfeiffer et al., 2003). Low temperature played an important role in structuring the community pattern of ants. There also exists a soil pattern in which soil becomes dryer in the south than north (Nandintsetseg and Shinoda, 2011). Paknia et al. (2013) investigated Mongolian tenebrionid communities and reported that the species richness of the darkling beetles decreased with latitude. Along the wide latitudinal gradient from Germany and

Mongolia to Africa and further Antarctica, local and large-scale drivers were responsible for freshwater bacteria's diversity and distribution pattern (Ferrera et al., 2017). In a plant functional trait study along the aridity gradients from Siberia to Mongolia, C3- and C4-plants responded to aridity differently and contrasting trends were observed in changes of leaf traits (Ivanova et al., 2019). Ahlborn et al. (2020) and Lang et al. (2019) studied the vegetation community along the gradient in Mongolia and revealed that the effect of grazing on plant diversity in moist areas was more pronounced than in dry areas (Ahlborn et al., 2020), while plant traits did not show a clear pattern not only along the gradient, but also to the effect of grazing (Lang et al., 2020, 2019).

But despite these efforts, there remain still research gaps on many other taxa along the Mongolian latitudinal gradient. Although it is essential to evaluate much more taxa, it requires experts for each taxon, and it is very time-consuming and costly for conservation management and decision-makers. Moreover, due to conflicting results of scientists, it isn't effortless to decide for policymakers on conservation management (Eitel, 2021). Eitel (2021) pointed out that researchers' results on the effects of grazing on grassland are contradictory: for instance, some studies state that livestock leads to deterioration (Fernández-Giménez et al., 2017; Hilker et al., 2014), while another says that intermediate grazing promotes vegetation development (Eckert et al., 2015). Therefore, the mechanisms still need to be understood, and systematic knowledge has to be developed to address biodiversity loss proactively.

1.6 Moths as Indicator species

For observing potential environmental and climate change, indicator species are used to monitor the environmental condition and assess the ecological integrity. An indicator species is a species whose occurrence, disappearance, or abundance reflects a particular environmental condition and may indicate a potential ecological change in a specific ecosystem (Lindenmayer et al., 2000).

How species respond to environmental change depends on their functional traits, such as feeding niche: specialist or generalist, voltinism: univoltine or multivoltine, body size: big or small, and color variation among individuals of given species: variable or not so variable and so on (Betzholtz et al., 2017; Coulthard et al., 2019; Kotiaho et al., 2005; Mattila et al., 2009, 2006). Rare species are vulnerable to environmental changes and likely to go extinct and if the ecological function of rare species cannot be replaced by common species, the functioning of the respective ecosystem will fail (Mouillot et al., 2013).

Moths are sensitive to environmental changes, reflect habitat quality, and can represent the biodiversity changes of other insects (Bachand et al., 2014; Choi, 2008; Enkhtur et al., 2017; Kitching et al., 2000; Ricketts et al., 2001; Summerville et al., 2004; Wagner et al., 2021). Moths are attracted to light traps in about 25m radius; thus, they can reveal habitat differences even at small spatial scales (Wirooks, 2006). They are closely reliant on various plants (e.g., trees, shrubs, grass, algae, lichen, forb and fungi, fiber, and even other insects) (James et al., 2018). They act as pollinators, and at both adult and larval stages, they become food sources for other animals. Thus, they can indicate the diversity of both lower and upper trophic levels and the efficiency of land management (Bachand et al., 2014; Choi, 2008; Merckx et al., 2013). Hence, the decline of moth diversity and biomass creates a cascading effect in both, the upper and lower direction of food web (Wagner et al., 2021). Especially if the moths and host plants, or moths and higher trophic level animals have a strong relationship, i.e., are specialists, the effect can be substantial (Harrower and Gilbert, 2018).

Despite their ecological importance, long-term studies show that moths are declining, and shifting their range poleward and contracting their ranges (Breed et al., 2013; Forsman et al., 2016; Fox, 2013; Franzén and Johannesson, 2007; Groenendijk and Ellis, 2011; Martay et al., 2017; Mason et al., 2015; Valtonen et al., 2017). Moths with a small geographical range and ecological niche width are dependent on particular plant species, i.e., specialists and univoltine species are more vulnerable to environmental changes (Wagner et al., 2021). The main drivers of the decline are climate change and anthropogenic land-use change, such as habitat degradation, agricultural intensification and urbanization (Dennis et al., 2019; Forister et al., 2010; Wagner et al., 2021). Several studies (Fox, 2013; Mattila et al., 2006; Seibold et al., 2019) reported that moths are decreasing in many regions across the world. However, the results of these studies should not be generalized across a large scale (Salcido et al., 2020; Wagner et al., 2021). Therefore, Wagner et al. (2021) emphasized that compiling the historical data in less studied areas and studying the potential factors for the declination of moths is essential.

In contrast, the changing habitat is beneficial for some moth species, especially for the generalists and for good flyers (Valtonen et al., 2017). In disturbed habitats like intensively used agricultural areas, polyphagous moths are more abundant, and they usually feed on weeds (Choi, 2008; Ekroos et al., 2010). However, not all moth families are equally sensitive to the environmental changes. Among the moth families, moths of the family of Geometridae are known as good indicators of ecological gradients (Ashton, 2013; Beck et al., 2002, p. 2; Holloway, 1985; Holloway et al., 1992; Intachat et al., 1997), while Noctuidae are known as good indicators of disturbance (Kitching et al., 2000).

Thus, by studying moth assemblages, revealing indicator species at a particular area and gaining knowledge on their functional traits, it is possible to monitor, protect,

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and restore the environment, implement appropriate conservation management, predict potential extinction, and proact.

For my master thesis, I studied how livestock grazing affected moths and determined the indicator species for heavily grazed and slightly grazed plots. The study found that heavily grazing negatively affects the diversity of moths and demonstrated that moths are accurate bioindicators.

For my doctoral study, I aimed to expand my previous research (Enkhtur et al., 2017) by 1) sampling baseline data for geometrid moths, 2) revealing indicator species both, for overgrazing in two distinct biomes and latitudinal gradients in Mongolia, and 3) studying how moths with different functional traits respond to livestock grazing in two distinct biomes.

1.7 Research objectives

This study aims to raise awareness on compiling and integrating historical records and establishing the taxa's baseline data within a country, which is crucial to detect any later changes due to climate change and other environmental disturbances. I focused to gather records of geometrids in this thesis, as they are considered the most susceptible to environmental changes and may represent other families. Another reason is that, during my master's study, geometrid moths were the most interesting to me. That study (Enkhtur, 2017) took place in my home country, Mongolia, and it already showed that in this area many aspects of the biogeography of moths were still unknown. Therefore, I chose geometrid moths as a starting point to establish baseline data for moths in Mongolia. In order to gain further insight into the ecological niche of individual species my objective was to study the current diversity and distribution pattern of macro-moth communities along an ecological (latitudinal) gradient in Mongolia. Further, I aimed to study how livestock grazing affects macro-moth communities in two distinct biomes and which moth families and the functional trait are more responsive to grazing.

This thesis consists of three manuscripts:

Manuscript I In the first study, I provided a species checklist of geometrid moths and analyzed diversity and distribution patterns and potential environmental drivers.

Manuscript II In the second study, I studied macro-moths in Mongolia along an 860 km latitudinal climatic gradient to gain knowledge on community composition, alpha, beta, and gamma diversity as well as underlying factors of the recorded distribution: These data can be used as baseline information for further studies related to climate change. In addition, I investigated how macro-moth community changes, whether the change is due to species replacement or species loss and if there exists a latitudinal breakpoint in the beta diversity pattern.

Manuscript III In the third study, I examined the effects of livestock grazing on moth communities in Mongolian rangelands under two different grazing regimes (grazed and less grazed plots) along a large-scale latitudinal gradient from desert to steppe in two distinct biomes, desert (Desert and xeric shrublands) and grassland (Temperate grasslands, savannas & shrublands). I also investigated how livestock grazing affects macro-moth families differently and how specialist and generalist moths respond to grazing. Further, I also revealed a) bio-indicators of grazing and b) bio-indicators representative for certain sections of the latitudinal gradient.

1.8 Material and Methods

1.8.1 Study area

Located in the center of the Asia, Mongolia stretches along a steep climatic gradient at the interface between the Siberian taiga in the north and the Gobi Desert in the south. Yearly average temperatures increase from 1.1°C in Ulaanbaatar to 4.3°C in southern Dalanzadgad, while precipitation is higher in the northern part of Mongolia (200–350 mm per year) and decreases in southern direction (100–200 and even below 100 mm in Gobi desert) (Pfeiffer et al., 2020). These latitudinal gradients of precipitation and temperature form a sequence of vegetation belts running from north to south, with forest steppe, steppe, semi-desert, and desert replacing each other (Lavrenko and Karamysheva, 1993). The fieldwork for the thesis (for **Manuscript II** and **III**) was conducted at sites located along latitudinal gradient in Mongolia (Figure 3).

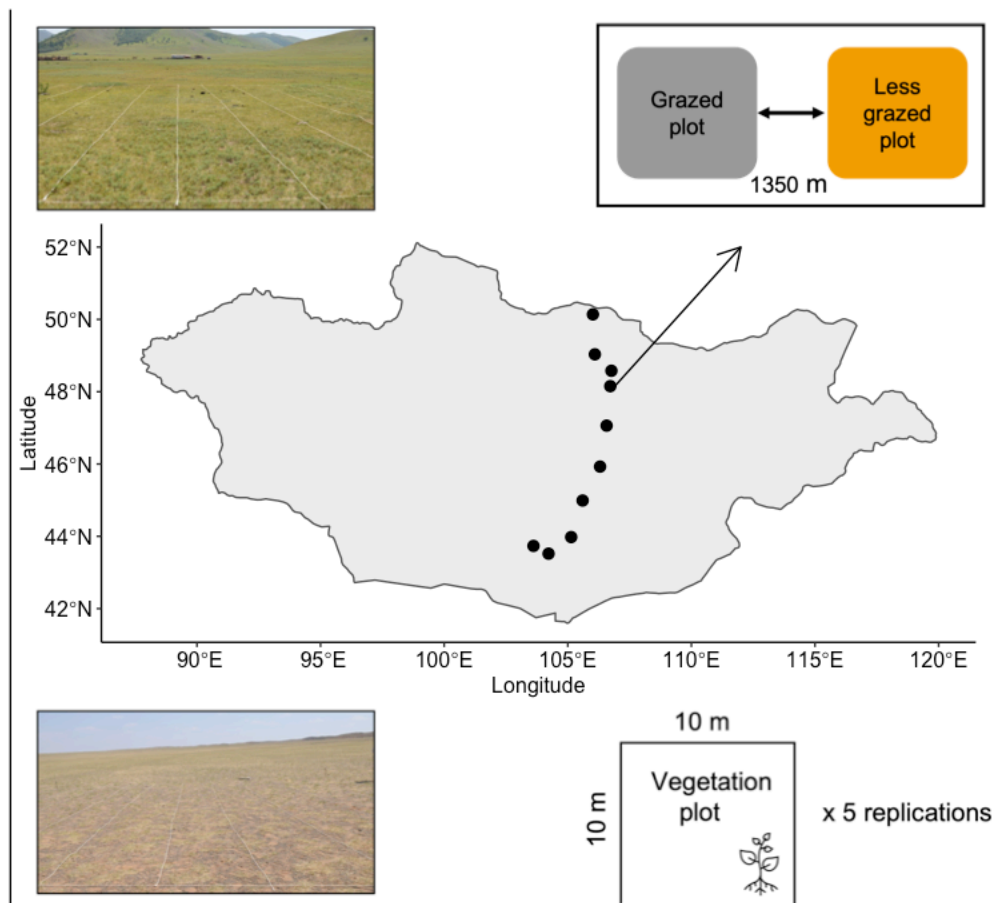


Figure 3 Study area. Above the graph shows typical grassland, below graph shows typical desert. In each site, distance between grazed and less grazed plot were 1350 m.

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We followed the study design of Lang et al. (2019) and Ahlborn et al. (2020) and sampled seven of their original 15 study sites that were spread at a south–north gradient of 600 km. We added three further sites to this transect in northern direction, totaling in a transect length of 860 km.

1.8.2 Data collection

1.8.2.1 Compiling historical data on geometrid moths

I compiled geometrid moth records from published scientific articles, our previous research (Enkhtur et al., 2020) from the collections of Siberian Zoological Museum, the Global Biodiversity Information Facility (GBIF) (GBIF.org, 2019), and the Barcode of Life Data System (Bold System) (Ratnasingham and Hebert, 2007) (Figure 4). I used Google Scholar to search the literature.

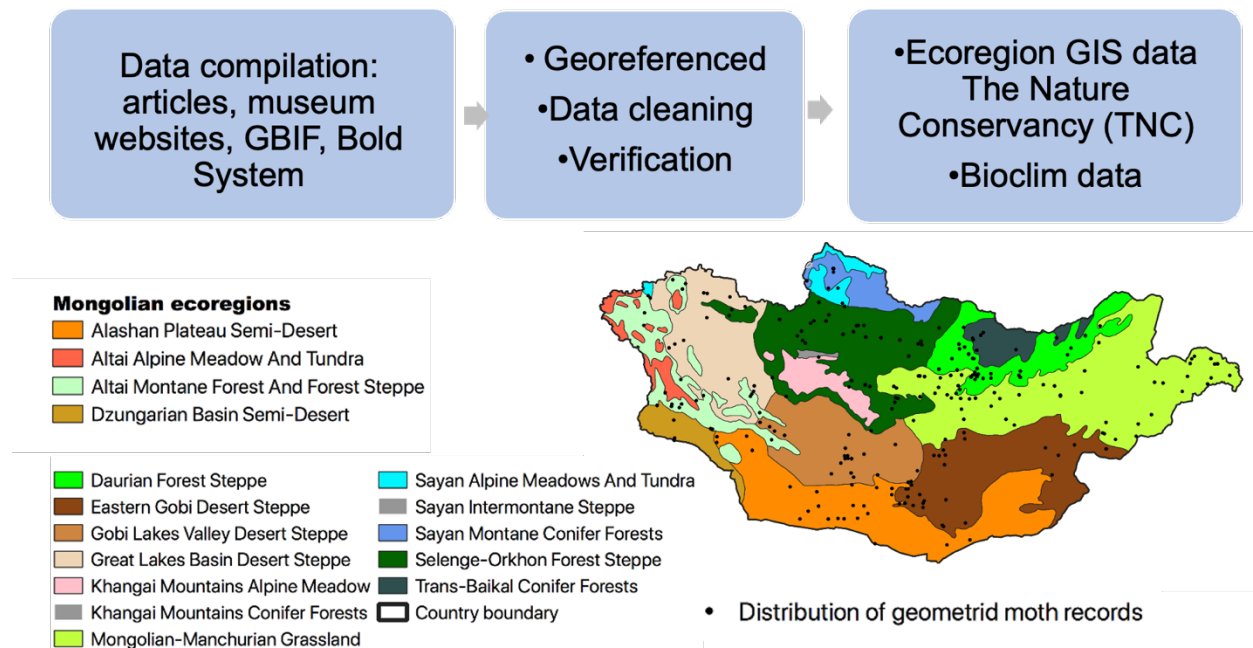


Figure 4 Data compilation of geometrid moth records within Mongolian ecoregions

1.8.2.2 Field Sampling of macro-moths along a latitudinal gradient

We caught moths manually using special 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) (Brehm, 2017) together with the Bioform light “tower”. EasyAcc 26 Ah power banks were used as batteries (Figure 5).



Figure 5 Led lamp (Brehm, 2017) used to catch moths.

Moths were collected in killing jars and then sorted to morphospecies and after that separated into glassine envelopes according to morphospecies. We took samples between 9.00 and 12.00 pm at nights without full moon in two consecutive years (2018 and 2019).

This period covers the flight season of most nocturnal moth species in Mongolia (Enkhtur et al., 2017). At each site and in each year, we sampled with three replicates (ten sites x two years x three nights = 60 sampling nights). The southern five sites are located in desert and xeric shrublands biome (desert), and the northern five sites are located in temperate grasslands, savannas & shrublands biome (grassland).

Due to adverse weather conditions only five catching nights were successful at some sites (Sites 1, 5, and 10). For analyses, all night samples of each site were aggregated. I brought all samples to Germany and mounted and identified specimens using identification keys (Steiner, 2014) and online identification web sites for moths and butterflies (Rennwald et al., 2002; Knyazev, 2017). Afterwards, I submitted one or two specimens of each morphospecies for DNA barcoding to Canadian Centre for DNA

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Barcoding (CCDB) to corroborate our identification of morphospecies. The results on the creation of a DNA barcode library for the collected species will be published in a separate paper (in preparation).

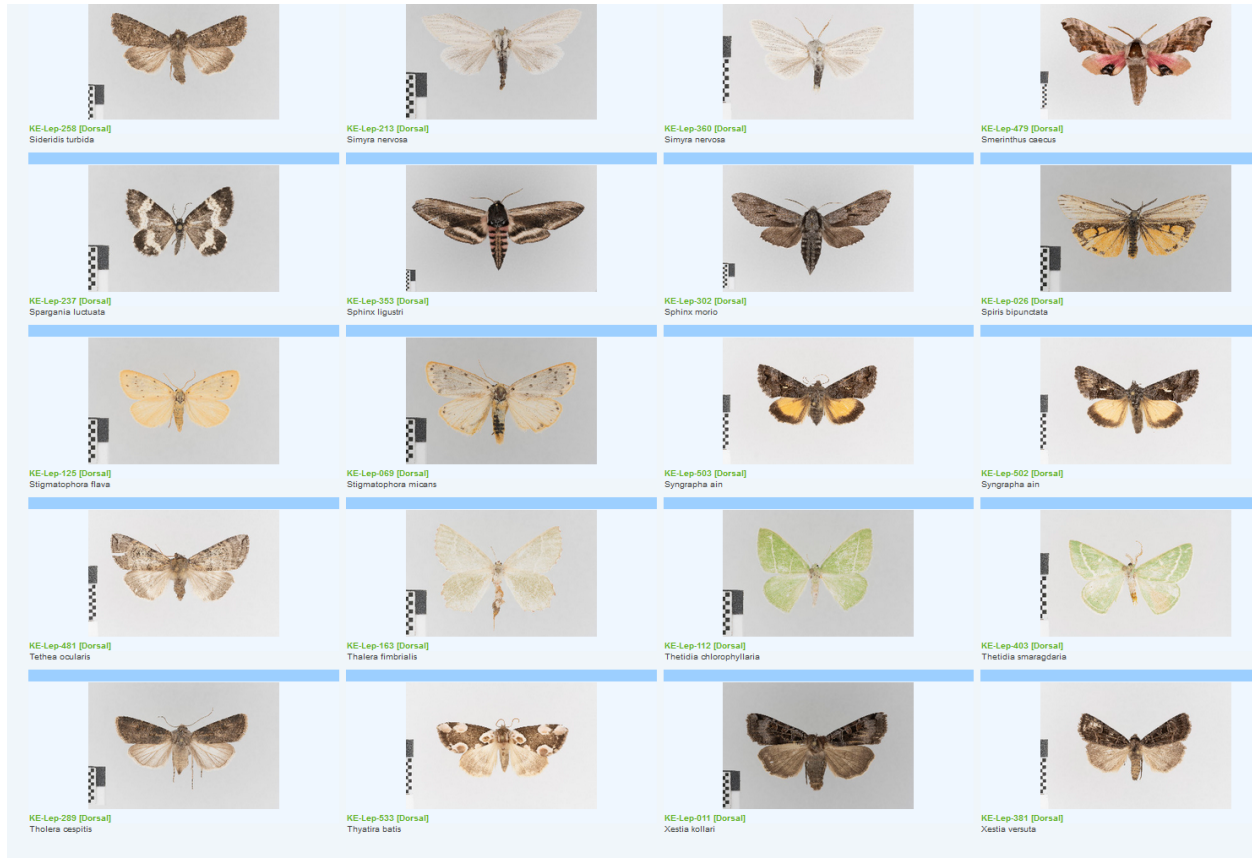


Figure 6 Moth images on Bold system. All images taken by Gunnar Brehm.

Superfamilies of Mimallonoidea, Drepanoidea, Lasiocampoidea, Bombycoidea, Geometroidea, and Noctuiodea are included in the clade of Macroheterocera. In this study we also included Sesiidae, Zygaenidae and Cossidae because of their traditional assignment to the (non-monophyletic) macro-moths.

1.8.2.3 Field Sampling of plants along a latitudinal gradient

To study vegetation structure, I measured *vegetation cover* and plant species richness in a 10m x 10m area with five replications per site (Figure 3). Livestock droppings were counted in the plots to assess grazing pressure. We received vegetation data from Julian Ahlborn (Leibniz Centre for Agricultural Landscape Research) and Christine Römermann (University of Jena) for comparison and easier identification of our samples in the field.

1.8.3 Environmental data

We used Bioclim data with 30 arc seconds resolution as climatic variables (Fick and Hijmans, 2017). For **Manuscript I**, Ecoregion GIS data for Mongolia were downloaded from The Nature Conservancy (TNC). Livestock data for each site was extracted from Mongolian statistical information service.

1.8.4 Statistics

All analyses were performed using R version 3.6.3 (R Core Team, 2020). Prior to analyses, we checked for normal distribution of all factors with Shapiro-Wilk normality test analyses, and also by using QQ plot. Depending on these results we chose the appropriate statistical tests or applied log-transformation to normalize data for calculation. In most analysis, we grouped all species into Noctuidae, Geometridae, Erebidiae, and 'Other'. The latter category includes families only represented with a few (<10) species: Cossidae, Drepanidae, Notodontidae, Sphingidae, Lasiocampidae, Sesiidae, and Zygaenidae.

We applied Good Turing Theory, iChao1 index and rarefaction curve to estimate species richness. For comparison of unique species, species richness, species diversity, abundances and beta diversity of macro-moths of each site and biome we used the non-parametric Wilcoxon test and non-parametric Kruskal-Wallis test, and paired *t*-test depending on the normality. Non-Metric Multidimensional Scaling Analysis (NMDS) correspondence analysis and permanova were used to study the dissimilarity of species and family composition between study sites. We determined niche structure of moth communities along the climatic gradient by analyzing coenoclines of the ten most abundant species by applying generalized additive models (GAM) according to the method of Hoffmann et al (2019).

To check for strong linear dependencies among explanatory variables we computed the variance inflation factor (VIF) for each variable. To study the relationship between variables and distance matrices of communities a linear regression (LM), general linear model (GLM), generalized additive models, Pearson correlation and Procrustes analysis were applied. For choosing the best model between models for each predictor variable, we used Akaike's Information Criterion (AIC) and also compared R^2 of each model. K-means clustering was applied to ten sites to cluster them into groups based on their similarity. To visualize species overlap between biomes and grazing regimes we drew Venn diagrams (Linlin Yan, 2019). We applied Baselga's approach to calculate the pairwise beta diversity among sites and also species composition differences along the latitudinal gradient (Baselga, 2010). Piecewise regressions were

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used to reveal a breakpoint of beta diversity between macro-moth communities along the latitudinal gradient by examining breakpoints between 43° and 50° with a 1° interval and chose a breakpoint with the lowest residual standard error (Crawley, 2012). To find indicator species I calculated the indicator value index (IndVal) (Cáceres and Legendre, 2009).

2 Synopsis

2.1 Results and Discussion

In this thesis, I integrated and analyzed available data on geometrid moths and interpreted their diversity pattern in Mongolia; moreover, I studied the diversity and distribution of macro moths in the field and further investigated the effects of livestock grazing on moth assemblages under different climatic conditions. Both, the results of the literature review and up-to-date field studies, serve as baseline data for future research that will be useful in identifying changes and pointing out where conservation measures are needed.

In **Manuscript I**, I compiled a checklist of the geometrid moths of Mongolia based on a comprehensive literature review. In addition, I analyzed the spatial patterns, species richness, and diversity of moths in 14 ecoregions of Mongolia and evaluated environmental variables with respect to their distribution. In **Manuscript II**, I studied macro-moths in Mongolia, examined how macro-moth community composition changes along a latitudinal gradient and estimated alpha, beta, and gamma diversity. I found differing beta-diversity patterns along the gradient and identified the factors responsible for these distinct patterns. In **Manuscript III**, I examined how livestock grazing affects the diversity, species assemblage, and species richness of macro-moth species and how specialized and generalist moths respond to grazing in deserts (desert and xeric scrub) and grasslands (temperate grasslands, savannas, and scrub). I also identified (a) indicators of grazing and (b) indicators that are representative of specific sections of the latitudinal gradient.

Estimated species richness almost doubles the observed species richness

In total, I compiled 1973 records of 388 species of moth during my studies (**Manuscript I**). However, I expect to find more species with more extensive sampling, especially in the remote parts of southern, eastern and western Mongolia. Moreover, detailed research in museums would have undoubtedly brought more records and species. Additionally, I expect to find Orthostixinae and Alsophilinae from Mongolia since the species of these subfamilies were recorded in adjacent areas, such as in Kazakhstan and China (Viidalepp, 1996), but not in our study. However, although our compiled data are incomplete, they reveal the knowledge gaps and under-sampled areas and provided a first estimate of the approximate species number throughout Mongolia ($S_{Est} = 663$).

Further, I visualized the distribution and diversity pattern of geometrid moths and evaluated the main environmental factors that shape the communities. Since annual precipitation and maximum temperature of the warmest months define the geometrid assemblages in Mongolia, they are vulnerable to global warming. This result was in line with other studies (Beck et al., 2011; Beck and Vun Khen, 2007; Brehm et al., 2003). Rising temperatures and changing precipitation affect all aspects of biodiversity by changing the geographical range and phenology of species (Parmesan, 2006). The species list I present here can be a tool helping to monitor these changes. For example, according to our literature survey, *Rhodostrophia jacularia* was the most frequently recorded species in the past (Enkhtur et al., 2020); however, during our fieldwork in 2018 and 2019, this species was caught only a few times. Since *R. jacularia* lives in desert and steppe habitats, increasing temperature may already exceed its survival threshold, and the species may adapt to the increasing temperature or it may lead to extinction of the species or shifting of its niche (Román-Palacios and Wiens, 2020). However, the reasons for this shift in abundance are still unclear and require further detailed monitoring.

As a result of this study, I found out that long-term data on species distribution were unavailable in Mongolia, and there was a need of an up-to-date study which systematically collects data and aims to show how moth species assemblages change along the latitudinal gradient. That led to the next study question: Are species along the gradient replaced with others or do some of the species simply disappear?

Beta diversity has a breakpoint along the latitudinal gradient

In **Manuscript II**, I found a breakpoint at 46° N for both, beta diversity pattern of moth communities and also in precipitation and temperature. In desert beta diversity was due to species loss or gain, while in grassland beta diversity was caused by species replacement. Similar contrasting patterns have been observed in other studies (Baselga et al., 2012; Soininen et al., 2018).

The low number of species and the relatedness of beta diversity to species loss in the desert reflect the lower productivity of this ecosystem. Based on the overlapping breakpoints, I expect that the grassland sites will become more similar to desert sites if global temperatures continue to rise, leading to a more nested pattern of moth diversity. The contrasting patterns of beta diversity in deserts and grasslands mean that different conservation approaches are necessary. Therefore, I suggest conserving the entire grassland gradient, while in the desert conserving only the most species-rich area. The most species-rich site in the desert was the highest elevated site, which differed in species composition from all others, suggesting that high elevation sites in hot arid habitats may function as a refuge for biodiversity. Species in higher altitudes are often endemic and

sensitive to climate change (Ashton et al., 2016; Loope and Giambelluca, 1998), thus, species at higher altitude could be in particular danger of extinction.

The transitional zone along the gradient was the most species-poor site, which was in line with the study of Ahlborn et al. (2020), who studied plant communities; the local reduction of alpha diversity of this site may reduce gamma diversity on a regional level. Therefore, I recommend abandoning the transitional zone from grazing for better recovery.

Higher species richness and lower abundance in the grassland could be explained by the theory of competitive exclusion. Greater plant heterogeneity in the grassland could ultimately reduce competitive exclusion in the moth population and facilitate the co-occurrence of more species at an even ratio. In contrast, lower species richness and higher abundance of certain tolerant species (Noctuidae: *Agrotis ripae* and *Anarta trifolii*) adapted to the few plant species growing there prevail in the desert (Sánchez-Bayo and Wyckhuys, 2019). The high abundances of *A. ripae* and *A. trifolii* may signal that the process of desertification has already accelerated, and some specialists may have been even extirpated at these sites prior to our study. Are those species indicators of disturbance? Are there any latitude level indicator species which could be used as reference species to study the migration of moths due to climate change? How does the co-effect of climate variables and livestock grazing affect moth communities at desert and grassland biomes? These questions that arose from the results of **Manuscript II** are leading to **Manuscript III**.

Effects of grazing on macro-moths depend on the climatic condition

In **Manuscript III**, I investigate the effects of livestock grazing on moth communities under different climatic conditions. In addition, I identify indicator species for both, latitude and livestock grazing. In **Manuscripts I** and **II**, moth community composition was subdivided by biome boundaries; therefore, in **Manuscript III**, I chose to study communities at the biome level.

My study demonstrates that moths in two contrasting biomes responded differently to grazing, and that moth families showed different responses. In the desert, climate variables overrode the effects of grazing, whereas in the grassland, the effects of grazing were more pronounced. These results corroborate the study of Ahlborn et al. (2020), who reported similar effects for the vegetation. In grasslands, Geometridae, Noctuidae, and Erebidae were more susceptible to grazing. For the first time, I assessed indicator species for distinct grazing regimes in contrasting biomes in Central Asia and also identified indicator species for sections of the latitudinal gradient. These indicator species provide

a baseline for a further study of moth distribution in later years as a result of climate change.

Several studies have found that environmental disturbances such as overgrazing eliminate specialist species, while generalists benefit, resulting in a more homogeneous, less resilient environment (Mangels et al., 2017; Wagner et al., 2021). Since species respond differently to grazing depending on their functional traits, I hypothesized generalist species would be dominant in the grazed plot; in contrast, specialist species would be prevalent in the less grazed plot. However, contrary to my hypothesis, in grassland species richness of both, specialist and generalist moths, was significantly higher in the less grazed plots, indicating that the broader feeding niche of generalists, couldn't balance the impact of grazing and that generalists can also be indicators of habitat heterogeneity. In contrast, specialist and generalist moths did not show significantly different responses to the grazing in the desert, probably because vegetation homogeneity did not differ between grazed and less grazed plots.

At intermediate vegetation richness, the dissimilarities in moth communities between grazed and less grazed plots were due to species turnover, indicating habitat heterogeneity. At both extremes, however, the beta diversity was due to nestedness indicating habitat homogeneity. Combined effect of climate and livestock grazing could cause all grazing types to become more homogenous and reduce environmental resilience. In the desert, I recommend conserving less grazed pasture only, while in the grassland, both grazed and less grazed pastures should receive attention.

As a consequence of climate change and the increasing number of goats, the desert in the south is extending more and more to the northern part of Mongolia (Liu et al., 2013). Although goat cashmere is one of the most important export products in Mongolia, the government should stop supporting this non-sustainable agricultural practice. In this way, the future consequences of climate change could at least be slowed down.

2.2 Future direction of research

Integrating the current knowledge on biodiversity is crucial, and we can compare it to a puzzle game. It isn't easy to see the whole picture without fitting the pieces together. However, after fitting the pieces together, the puzzle picture would be again only a puzzle piece of a much larger puzzle. Similar to this, biodiversity is not limited to the country's border. Therefore, researchers globally should integrate the compiled local knowledge and study the pattern at a worldwide scale.

2 Synopsis

My literature review study on geometrid moths was just the starting point and other families of macro (e.g., Noctuidae and Erebidae, and Sphingidae) and micro moths also lack a species checklist in Mongolia. Thus, there is a further need for research on the less abundant families of moths in the region.

In my thesis, I learned that species richness (i.e., alpha diversity) of moths decreased from north to south in Mongolia. In wetter grassland, species richness is high; in harsh drought desert, species richness is lower, and drought acts as an environmental filter for moth assemblages. Even though we now understand the current diversity and distribution patterns of moths and the associated environmental factors, important questions are left to be answered about conservation management and the future distribution of moth communities.

For example, could the pattern of alpha diversity represent phylogenetic diversity (i.e., evolutionary measure of diversity) in a harsh environment? Are the desert species adapted to the harsh climate and evolutionarily distinct from the species in the grassland? From the conservation point of view, we have to protect areas with high species richness and areas with evolutionarily distinct species. An assessment of phylogenetic diversity would help us to answer the latter question and implement a more effective conservation management. Moreover, if the temperature keeps rising, how will biodiversity react to it? Since the species richness of moths in central Asia was negatively correlated with temperature, it is a crucial question to answer.

I studied how moths with different feeding niches differed in grazed and less grazed plots in two contrasting biomes. However, other important biological information on species was not available, e.g. on voltinism, hibernation, conservation status (Mangels et al., 2017), and additional traits-related information. From the conservation point of view, there is a need to explore the status of rare species and their potential need for conservation management. Currently, only one species in our samples, *Sphinx ligustri*, is on the Red List of Mongolia (*Red Data Book of Mongolia*, 2013). Therefore, it is vital to compile those missing data because reliable data on population sizes and conservation status of moths are lacking in Mongolia.

Future studies should aim to

- compile and integrate records for other moth families and create a species checklist,
- investigate and compile trait related information,
- evaluate the population size of rare species of moths and update their conservation status,
- study the phylogenetic diversity of moths in Mongolia,
- predict the potential and projected distribution of moths in the Palearctic region.

By answering those questions, we will approach one step closer to understanding the impact of climate change on biodiversity and implementing a more effective conservation management.

2.3 Conclusion

Although it was challenging to compile historical data on geometrid moths, visualize, and analyze the distribution and diversity pattern under environmental drivers in full detail, our study could reveal the knowledge gaps and under-sampled areas and provide a first estimate of the approximate species number throughout Mongolia. Next, our second study demonstrates how moth diversity in Central Asia changes from south to north throughout a long latitude, and assesses the environmental variables that drive these changes. The different patterns of spatial turnover and nestedness in desert and grassland habitats suggest that contrasting conservation approaches are needed. Therefore, we propose to conserve the entire gradient of grassland, as opposed to conserving the most species-rich habitats in the desert. However, local diversity patterns could extend to the regional scale; therefore, species-poor habitats should also be restored by abandoning grazing. In addition, areas at the highest elevations in desert habitat that may serve as refuges for biodiversity, as reflected by moths, should be studied in more detail and over the long term. The high occurrences of *A. ripae* and *A. trifolii* indicate that the process of desertification and homogenization has already intensified and we need to take action to stop it before the situation deteriorates even further. From a conservation and sustainable management perspective, it is critical to study the effects of livestock grazing on invertebrate herbivores under different climatic conditions, as vegetation heterogeneity and densities of large herbivores are essential characteristics for arthropod diversity. Reducing the goat population may improve the overall grazing situation. Identifying moth community composition, niche patterns, and indicator species helps to conserve moths and biodiversity in general in terms of their sensitivity to environmental change. The results of my studies are the most recent and systematically collected baseline data for future research.

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4 Manuscripts


4 Manuscripts

4.1 Manuscript I



Article

Diversity and Distribution Patterns of Geometrid Moths (Geometridae, Lepidoptera) in Mongolia

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Abstract: Geometrids are a species-rich group of moths that serve as reliable indicators for environmental changes. Little is known about the Mongolian moth fauna, and there is no comprehensive review of species richness, diversity, and distribution patterns of geometrid moths in the country. Our study aims to review the existing knowledge on geometrid moths in Mongolia. We compiled geometrid moth records from published scientific papers, our own research, and from the Global Biodiversity Information Facility (GBIF) to produce a checklist of geometrid moths of Mongolia. Additionally, we analyzed spatial patterns, species richness, and diversity of geometrid moths within 14 ecoregions of Mongolia and evaluated environmental variables for their distribution. In total, we compiled 1973-point records of 388 geometrid species. The most species-rich ecoregion in Mongolia was Daurian Forest Steppe with 142 species. Annual precipitation and maximum temperature of the warmest month were the most important environmental variables that correlated with NMDS axes in an analysis of geometrid assemblages of different ecoregions in Mongolia.

Keywords: beta diversity; ecoregions; environmental variables; location; NMDS; species checklist

1. Introduction

Regarded as disturbing pests or less charismatic than butterflies, moths are nevertheless creatures with an important role in the ecosystem and the potential to serve as environmental indicators [1–4]. Moths are globally distributed and it is estimated that more than 130,000 described species exist [5], far more than the more conspicuous and mostly diurnal butterflies with ca. 20,000 species. Many moths are pollinators, but due to their nocturnal activity they are not well studied [6]. In a recent review from the current literature, Hahn and Brühl reported that in Europe and North America there are 227 moth–plant interactions with 129 moth species involved [6]. Geometrid moths (Geometridae), constituting one of the biggest families of Lepidoptera, are a species-rich and easily recognizable family that have served as indicators for environmental changes in many previous studies [7–10]. These groups also appear to be effective at colonizing habitats after natural or anthropogenic disturbances [11]. There are approximately 24,000 described species of Geometridae worldwide [12]. Although Mongolia is one of the largest countries (rank 19th in size) on Earth, little is known about its moth fauna, and there is no comprehensive review of species richness, diversity, and distribution patterns of geometrid moths in the country. A few researchers attempted to summarize information to mainly confirm this lack of information [13].

Mongolia is a country that encompasses landscapes with a high variety of climatic and geographic features with forest in the north, high mountains in the west, desert in the south, and steppes in the

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Abstract

Geometrids are a species-rich group of moths that serve as reliable indicators for environmental changes. Little is known about the Mongolian moth fauna, and there is no comprehensive review of species richness, diversity, and distribution patterns of geometrid moths in the country. Our study aims to review the existing knowledge on geometrid moths in Mongolia. We compiled geometrid moth records from published scientific papers, our own research, and from the Global Biodiversity Information Facility (GBIF) to produce a checklist of geometrid moths of Mongolia. Additionally, we analyzed spatial patterns, species richness, and diversity of geometrid moths within 14 ecoregions of Mongolia and evaluated environmental variables for their distribution. In total, we compiled 1973-point records of 388 geometrid species. The most species-rich ecoregion in Mongolia was Daurian Forest Steppe with 142 species. Annual precipitation and maximum temperature of the warmest month were the most important environmental variables that correlated with NMDS axes in an analysis of geometrid assemblages of different ecoregions in Mongolia.

Keywords: beta diversity; ecoregions; environmental variables; location; NMDS; species checklist

1. Introduction

Regarded as disturbing pests or less charismatic than butterflies, moths are nevertheless creatures with an important role in the ecosystem and the potential to serve as environmental indicators [1–4]. Moths are globally distributed and it is estimated that more than 130,000 described species exist [5], far more than the more conspicuous and mostly diurnal butterflies with ca. 20,000 species. Many moths are pollinators, but due to their nocturnal activity they are not well studied [6]. In a recent review from the current literature, Hahn and Brühl reported that in Europe and North America there are 227 moth–plant interactions with 129 moth species involved [6]. Geometrid moths (Geometridae), constituting one of the biggest families of Lepidoptera, are a species-rich and easily recognizable family that have served as indicators for environmental changes in many previous studies [7–10]. These groups also appear to be effective at colonizing habitats after natural or anthropogenic disturbances [11]. There are approximately 24,000 described species of Geometridae worldwide [12]. Although Mongolia is one of the largest countries (rank 19th in size) on Earth, little is known about its moth fauna, and there is no comprehensive review of species richness, diversity, and distribution patterns of geometrid moths in the country. A few researchers attempted to summarize information to mainly confirm this lack of information [13].

Mongolia is a country that encompasses landscapes with a high variety of climatic and geographic features with forest in the north, high mountains in the west, desert in the south, and steppes in the eastern and central parts of Mongolia [14,15]. Altogether, it comprises 16 ecoregions [16] (Figure 1). Ecosystems change along a latitudinal gradient from forest in the north, over steppe and semi-desert to desert in the south [17]. In most areas of the country, livestock herding is a dominant land-use practice, and due to overgrazing, some pasture lands have recently been degraded [18]. With recent discoveries of various mineral resources, mining has become not only the main economic sector, but also the major reason for environmental disturbance in Mongolia. Together with climate change, it is the major driver for habitat loss and environmental changes [14,19]. As a result of these anthropogenic changes, many species are disappearing, but there is little information about which species are at greatest risk of becoming extinct, especially for the less studied taxa.

In order to monitor diversity loss and gain, and to further study the influence of environmental disturbance and climate change on geometrid moths in Mongolia, we need an up-to-date dataset that mirrors the current state of knowledge and that includes all species already recorded. Given this knowledge gap, this study aims to review, summarize, and evaluate the existing knowledge on geometrid moths in Mongolia. It will provide a baseline for further studies, as well as define research priorities in the field. In this study, we aim to: (1) provide a checklist of geometrid moths of Mongolia, setting a

baseline for future studies, (2) analyze distribution patterns and species richness and diversity of geometrid moths within ecoregions of Mongolia, and (3) analyze which environmental variables are most important in determining their distribution. We are aware that all results can only give a provisional status due to the data situation, especially the results for Objectives 2 and 3 can only be given with caution; however, our detailed review of the current data will help to define the needs for further research more efficiently.

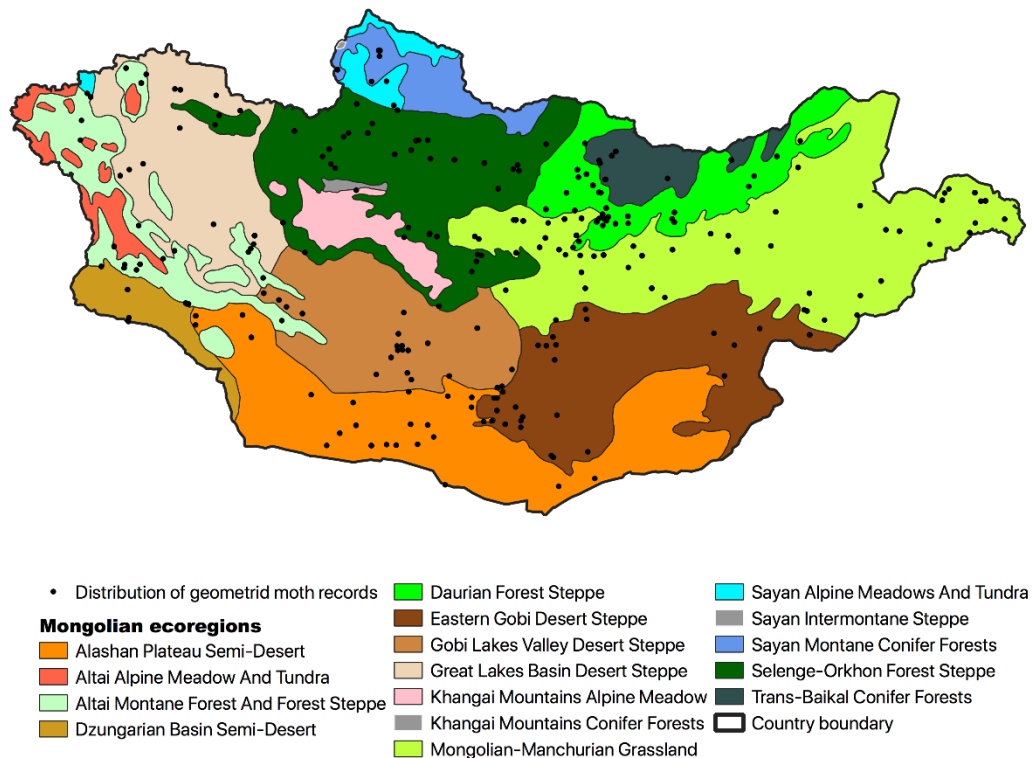


Figure 1. Mongolian 14 ecoregions with distribution of 1557 geometrid moth records (211 of 1973 records are missing exact locations, 205 records were sampled at the same location, but at different time period). For two small ecoregions (marked in gray), there is no scientific knowledge of geometrid moths.

1.1. Study Review

Information on the species composition of Macrolepidoptera of Mongolia began to accumulate from the end of the nineteenth century, as a result of the works of collectors such as Fritz Dörries, Hauberhauer and Leder, and others. Otto Staudinger [20] published the first paper on the collection of Fritz Dörries, who made a trip in 1879 to Khentii Mountains to collect Lepidoptera. This resulted in data on the location of 75 species of geometrids in central and western parts of Mongolia [20]. Later, Staudinger published several papers and books on the fauna of Palaearctic Lepidoptera which included some geometrid species from Mongolia [21–23]. In 1964, a Mongolian–German expedition conducted a biological survey, as a result of the expedition 214 Lepidopteran exemplars were sampled. Burchard Alberti later published the results on Lepidoptera and nine geometrid species were listed in the paper [24]. Likewise, Joseph Moucha listed four geometrid species from a Mongolian–Czech entomological–botanical expedition, which was conducted around 1960 [25]. Grigory Grum-Grshimailo found three geometrid species from Selenge Aimag in the collection of M.I. Molleson [26]. Alexander Mikhailovich Djakonov [27,28] recorded a new occurrence of *Horisme scosiata* and described one new species *Scotopteryx transbaicalica* from the family of Geometridae based on old material of Staudinger. Other researchers such as Karl Dietze [29], Eugen Wehrli [30], and Fritz Heydemann [31] also described new species. In the fourth volume and its supplementary of “Die Gross-Schmetterlinge der Erde. Die Spanner des Palaearktischen Faunengebietes“ series edited by Adalbert Seitz, 34 geometrid species were listed for Mongolia [32,33].

The most important contribution to the collection and study of Mongolian geometrid moths were made by Russian and Soviet expeditions led by Pyotr Kuzmich Kozlov and later by Soviet–Mongolian expeditions [34–36]. During the survey of Soviet–Mongolian expeditions, Jaan Viidalepp recorded a total of 201 geometrid species. Viidalepp later in 1999 compiled a checklist of geometrid moths of the former U.S.S.R and in this monograph 210 species were included for Mongolia [37]. Particularly rich and diverse material on Lepidoptera (41,000 specimens) were collected by the Hungarian expeditions conducted by Zoltán Kaszab, who made six entomological collecting trips along latitudinal and longitudinal gradients in Mongolia, between 1963 and 1968. András Vojnits published several papers based on the Kaszab’s collections dedicated to subfamilies of Geometridae in the period between 1974 and 1979. He recorded 177 species from the whole collection, described 39 species new to the fauna of Mongolia and four species new to science [38–44]. Malcolm J. Scoble [45] presented 66 taxa from Mongolia.

Other researchers also contributed to the study of Mongolian geometrid moths. For instance, Gantigmaa Ch. and coworkers recorded 90 species in the West Khentii of Northern Mongolia [46]. In the book “Biodiversity of Sokhondinsky Reserve”, 29 geometrid

species from Mongolia have been included [47]. Beljaev and Vasilenko [48] noted 29 species of geometrid moths in Mongolia. Vasilenko and colleagues [49–51] recorded eight species and described one new species *Rhodostrophia ustyuzhanini* in Western Mongolia. In 2012 and 2013, we collected 70 geometrid species from central and northern parts of Mongolia [4]. Mironov and Glasworthy [52] reported 57 species with two species (*Eupithecia ankini*, *Eupithecia munguata*) new to science and 12 species new to the fauna of Mongolia. Erlacher et al. studied six geometrid species from Mongolia and described one new species *Charissa beljaevi* [53–55]. In 2019, Makhov and Beljaev [56] studied the geometrid moths of the Baikal Region and recorded 14 species from Mongolia. In six volumes of “The Geometrid Moths of Europe”, 117 moth species are listed from Mongolia. We validated our species checklist with these volumes [57–62].

2. Materials and Methods

We compiled geometrid moth records from published scientific papers, from our work [63] (all sample identifications were double checked by curator T. Enkhbayar, Department of Biology, National University of Mongolia), from the collections of the Siberian Zoological Museum (curator - S.V.Vasilenko) [64], and also from the Global Biodiversity Information Facility (GBIF) [65]. Lastly, we checked the “Revised, annotated systematic checklist of the Geometridae of Europe and adjacent areas, Vols 1–6” [62]. From the Museum collections we could only get country-level information, not the exact location. From GBIF data, we included 380 records into our species list [65]. Fourteen specimens of six species were found in the public data of The Barcode of Life Data System (Bold System) [66].

We used Google Scholar to search the literature with following search strings:

With all of the words: Mongol (in English Mongolia, in German Mongolei, thus it was better to use only Mongol);

With at least one of the words: Geometrid OR Larentiinae OR Desmobathrinae OR Ennominae OR Archiearinae OR Geometrinae OR Oenochrominae OR Orthostixinae OR Sterrhinae;

As a result of the search, 184 literatures appeared, though many of them were about geometrid moths of Inner Mongolia. These we excluded from our list.

Without the words: Inner Mongolia.

After excluding Inner Mongolia, 96 results remained and of these, 73 were relevant to our study.

Totally, we compiled 1973-point records of 388 geometrid species (Table S1). Of these records, 87 species were missing information on exact locations, these 87 species are used to estimate species richness and listed in the species checklist but are excluded from other analysis. We georeferenced species locations from literature and generated coordinates of each location with Google Earth [67]. After that we cross-checked each species name in “The Global Lepidoptera Names Index” [68]. Moreover, experts on geometrid moths such as Axel Hausmann, Jaan Viidalepp, Gunnar Brehm, Sven Erlacher, and Pasi Sihvonen validated most species of our checklist and provided further literatures.

In the next step we used the sampled data in order to estimate true species richness, to evaluate the distribution of species within Mongolia, and to identify regions that have been undersampled so far by species rarefaction. For these reasons, we transformed all species locations into $2^{\circ} \times 2^{\circ}$ grid cells, resulting in 51 grid cells inhabited by 301 species. Of 301 species, 121 were unique species occurring only once within 51 grids. To estimate species richness we applied Good Turing Theory, which uses unique species for estimation [69]. We used the application SuperDuplicates (<https://chao.shinyapps.io/SuperDuplicates/>) for the estimation with the following setting: Data type: incidence data; Number of observed species (SOBs): 388; Number of uniques (Q1): 208 (we combined the 121 unique species with the former mentioned 87 species without locations).

Further we calculated rarefaction curves for single ecoregions to assess collection quality in different areas of Mongolia. Four ecoregions (Altai Alpine Meadow and Tundra, Dzungarian Basin Semi-Desert, Khangai Mountains Alpine Meadow and Sayan Alpine Meadows, and Tundra) were strongly under sampled, having species richness below 15, thus we excluded them from the analysis to avoid misleading interpretation.

To estimate the rarefaction curve across grid cells and ecoregions, we calculated interpolation and extrapolation of species richness using the ‘iNEXT’ package: Interpolation and extrapolation for species richness in R [70,71] with 0.95 confidence interval and prepared the rarefaction plots with ‘devtools’ package [72] and ggiNEXT function of ‘ggplot2’ package [73].

We performed Non-Metric Multidimensional Scaling Analysis (NMDS) to check the dissimilarity of geometrid species composition between ecoregions based on the zero-adjusted Bray–Curtis dissimilarity measure using ‘phytomosaic/ecole’ and ‘vegan’ package [74–76]. For estimation of pairwise similarities between ecoregions, we calculated the estimated abundance based Soerensen Index by abundance data using online program SpadeR [77]. We preferred Soerensen Index over Jaccard Index, while the result was a little bit higher than Jaccard. This estimated abundance based index can

detect unseen shared species and is appropriate to evaluate beta diversity of samples under sampling bias [78].

We used 19 Bioclim data with 30 arc seconds resolution as climatic variables for the region [79]. We extracted these variables for the fourteen ecoregions. Ecoregion GIS data for Mongolia were downloaded from The Nature Conservancy (TNC) [80]. In two ecoregions no geometrid moths were found, namely, Khangai Mountains Conifer Forests and Sayan Intermontane Steppe (Figure 1). We thus excluded these ecoregions from the further analysis. To check for strong linear dependencies among explanatory variables we computed the variance inflation factor (VIF) for each variable in R package 'vegan'. We excluded variables with VIF values higher than 10 [81] (Table 1). We chose the most significant environmental variables with forward selection method by using vegan's 'ordistep' function [81]. Variables selected by forward selection method were fitted into the ordination plot using vegan's 'entfit' function.

All analysis were performed in R [82] and most graphs were made with package 'ggplot2' [73].

Table 1. List of the environmental [79] variables* for the fourteen ecoregions used in this study. All variables have been entered into forward selection method for selecting most important variables. The selected variables were later fitted in the Non-Metric Multidimensional Scaling Analysis (NMDS). Colors refer to the map in Figure 1.

Ecoregions	Bio1	Bio2	Bio5	Bio6	Bio7	Bio10	Bio11	Bio12	Biome [83]
Alashan Plateau Semi-Desert	5.1	14.1	28.6	-20.3	49	20.6	-11.7	85	Deserts and Xeric Shrublands
Altai Alpine Meadow and Tundra	-4.5	12.3	17.1	-28.1	45.2	10.3	-20.3	199	Montane Grasslands and Shrublands
Altai Montane Forest and Forest Steppe	-1.8	13.1	20.5	-26.8	47.3	13.4	-18.5	148	Temperate Conifer Forests
Dzungarian Basin Semi-Desert	3.9	14	27.4	-23	50.4	19.6	-13.9	91	Deserts and Xeric Shrublands
Daurian Forest Steppe	-1.5	13.9	23.7	-29.1	52.9	16	-21	306	Temperate Grasslands, Savannas and Shrublands
Eastern Gobi Desert Steppe	3.3	13.4	27.6	-22.5	50.1	19.8	-14.7	130	Deserts and Xeric Shrublands
Gobi Lakes Valley Desert Steppe	0.7	14.6	23.8	-24.3	48.1	15.9	-15.5	141	Deserts and Xeric Shrublands
Great Lakes Basin Desert Steppe	-1.6	13.5	24.2	-31.7	55.9	16.6	-23.1	147	Deserts and Xeric Shrublands
Khangai Mountains Alpine Meadow	-5.6	14.3	17.3	-30.5	47.8	9.7	-22.1	261	Montane Grasslands and Shrublands
Mongolian-Manchurian Grassland	0.3	13.6	25.4	-26.4	51.8	17.6	-18.7	224	Temperate Grasslands, Savannas and Shrublands
Sayan Alpine Meadows and Tundra	-8.4	13.6	16.3	-34.9	51.2	8.5	-27.3	355	Montane Grasslands and Shrublands
Sayan Montane Coniferous Forests	-5.1	13.7	19.2	-31.3	50.4	11.4	-23.5	381	Temperate Conifer Forests
Selenge-Orkhon Forest Steppe	-3.2	14.3	20.6	-29.7	50.3	12.9	-21.4	277	Temperate Grasslands, Savannas and Shrublands
Trans-Baikal Coniferous Forests	-3.3	13.4	22.1	-31.1	53.2	14.6	-23.3	366	Boreal Forests/ Taiga

*Environmental variables with VIF under 10. Bio1 - Annual Mean Temperature [C°]; Bio2 - Mean Diurnal Range [C°]; Bio5 - Max Temperature [C°]; Bio6 - Min Temperature [C°]; Bio7 - Temperature Annual Range [C°]; Bio10 - Mean Temperature of Warmest Quarter [C°]; Bio11 - Mean Temperature of Coldest Quarter [C°]; Bio12 - Annual precipitation [mm].

3. Results

Altogether, we recorded 388 geometrid species of six subfamilies: Archiearinae, Desmobathrinae, Ennominae, Geometrinae, Larentiinae, and Sterrhinae (Appendix Table 1). The most species-rich subfamily was Larentiinae with 203 species, while we recorded only one species in the subfamily Desmobathrinae. For 301 species with exact location data (Table S1), we recorded species richness within $2^\circ \times 2^\circ$ grid cells in whole Mongolia (Figure 2).

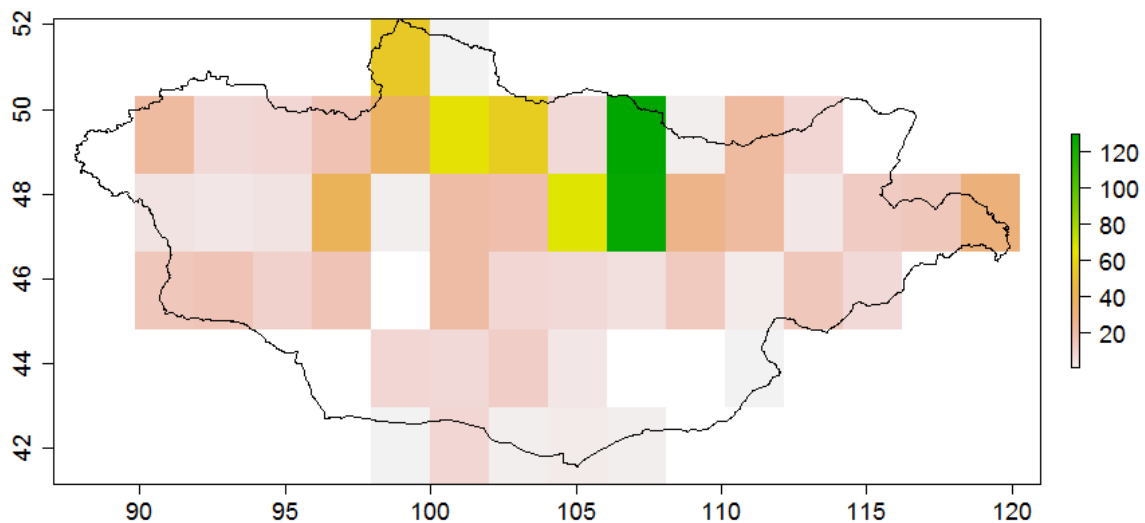


Figure 2. A map of study region (Mongolia) with distribution of $2^\circ \times 2^\circ$ grid cell records. Colors represent the species richness ($n = 301$) within grid cells.

Species richness was highest in the northern central part of the country, with 133 species recorded near Darkhan-Uul Aimag and the capital Ulaanbaatar. Four most frequently recorded species were *Rhodostrophia jacularia* (in $n = 32$ grids), *Scopula beckeraria* ($n = 18$), *Scopula albiceraria* ($n = 17$), and *Horisme aquata* ($n = 17$).

As a result of the Good–Turing theory, estimated species richness for whole Mongolia was 663.19 with 0.95 confidence interval (606.80–734.12), which is nearly double the observed species richness (Q2.est = 78.51; se = 32.31; Undetected # species = 275.19; Undetected percentage (%) = 41.49). Also, we constructed a sample-based interpolation and extrapolation curve of 301 species with exact reported location within 51 grids. The

interpolated and extrapolated estimators of species richness show similar results (Figure 3), the curve was not asymptotic, indicating under-sampling of the communities.

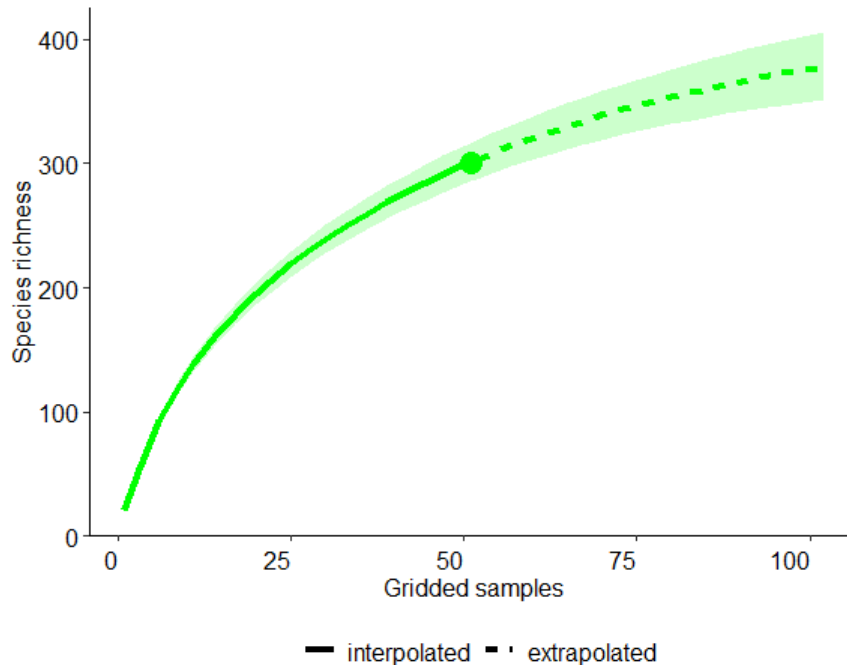


Figure 3. A sample-based interpolation and extrapolation curve of geometrid moths collected from Mongolia with 0.95 confidence interval. 51 grids were sampled with altogether 301 species. Axes X and Y represent the number of gridded samples and species richness, respectively.

In the next step we used the fourteen Mongolian ecoregions (Figure 1) to investigate the distribution of the sampled geometrid species in more detail. The most species-rich ecoregion was Daurian Forest Steppe with 142 species, while Khangai Mountains Alpine Meadow was the lowest in species richness with only three species of geometrid moths (Figure 4). One species (*Rhodostrophia jacularia*) occurred in 10 ecoregions, there were five further generalist species (*Euphyia unangulata*, *Eupithecia nephelata*, *Scopula albiceraria*, *Scopula beckeraria*) that occurred in eight to nine ecoregions. In contrast, 126 species were recorded only in one ecoregion. Four ecoregions were clearly under-sampled (Altai Alpine Meadow and Tundra, Dzungarian Basin Semi-Desert, Khangai Mountains Alpine Meadow, Sayan Alpine Meadows and Tundra) thus to avoid misleading interpretation, we excluded those ecoregions from further analysis.

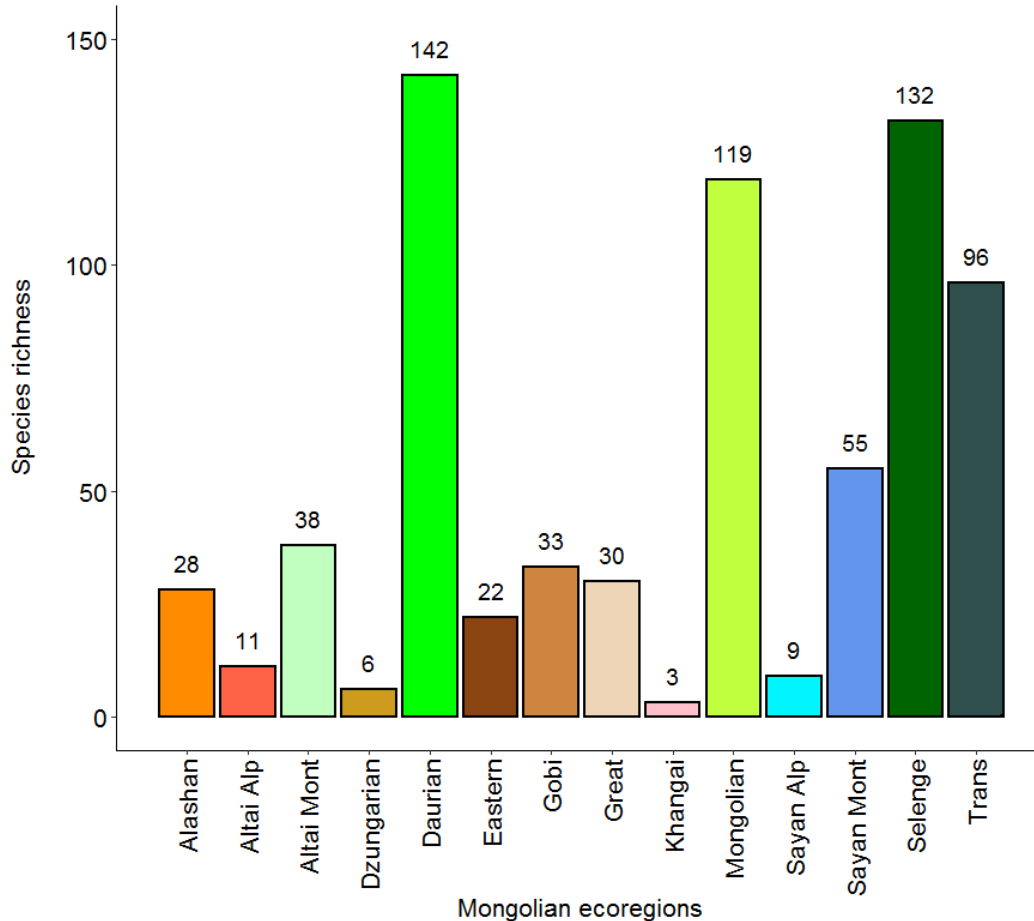


Figure 4. Geometrid moth species richness of 14 ecoregions of Mongolia. Under-sampled ecoregions are Altai Alp, Dzungarian, Khangai, and Sayan Alp. Colors refer to the map in Figure. 1. Ecoregion abbreviations: Alashan: Alashan Plateau Semi-Desert, Altai Alp: Altai Alpine Meadow and Tundra, Altai Mont: Altai Montane Forest and Forest Steppe, Dzungarian: Dzungarian Basin Semi-Desert, Daurian: Daurian Forest Steppe, Eastern: Eastern Gobi Desert Steppe, Gobi: Gobi Lakes Valley Desert Steppe, Great: Great Lakes Basin Desert Steppe, Khangai: Khangai Mountains Alpine Meadow, Mongolian: Mongolian-Manchurian Grassland, Sayan Alp: Sayan Alpine Meadows and Tundra, Sayan Mont: Sayan Montane Coniferous Forests, Selenge: Selenge-Orkhon Forest Steppe, Trans: Trans-Baikal Coniferous Forests.

Interpolation and extrapolation curves of particular ecoregions differ in their shapes, thus indicating different “sample quality”. Curves of Alashan Plateau Semi-Desert, Altai Montane Forest and Forest Steppe, Eastern Gobi Desert Steppe, Gobi Lakes Valley Desert Steppe, and Great Lakes Basin Desert Steppe are not asymptotic, only half of the estimated maximum species richness is sampled; while curves of Daurian Forest Steppe, Mongolian-Manchurian Grassland, Selenge-Orkhon Forest Steppe and Trans-Baikal Coniferous Forests are half asymptotic, thus tending to increase, while the curve of Sayan Montane Coniferous Forests is flattening, thus pointing to complete sampling of the moth community (Figure 5).

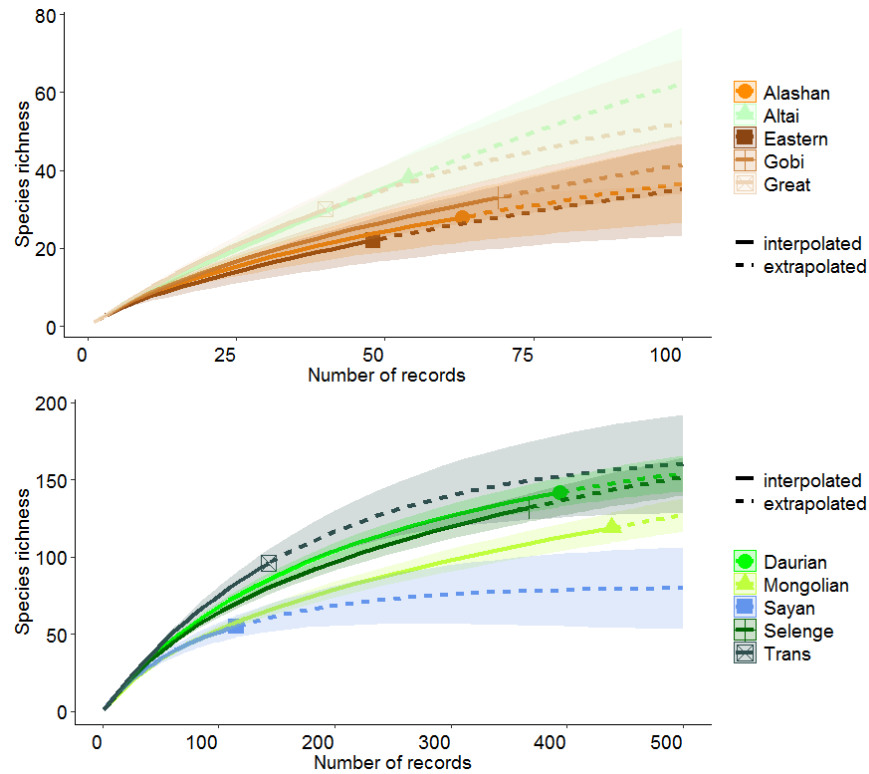


Figure 5. Sampling unit-based interpolation and extrapolation curves of ecoregions with 0.95 confidence interval. Axes X and Y axes represent the number of records and species richness, respectively. Ecoregions are jointly drawn on plots according to their grouping in the NMDS graph (Figure 6). Colors refer to the map in Figure 1. Ecoregion abbreviations as in Figure 4.

For assessment of beta-diversity, we calculated estimates of the abundance-based Sorensen Index between ecoregions (Table 2). We excluded ecoregions with fewer than 20 species to avoid sampling bias in similarity analysis. The highest pairwise estimated Sorensen Similarity Index was between Eastern Gobi Desert Steppe and Gobi Lakes Valley Desert Steppe ($\beta_s = 0.942$), while the lowest were between Trans-Baikal Coniferous Forests and both of Gobi Lakes Valley Desert Steppe, Great Lakes Basin Desert Steppe ($\beta_s = 0.076$).

Table 2. Pairwise estimates of similarity between ecoregions with online tool Spade [69]. Shown is the estimated abundance-based Sorensen Index. Colors refer to the map in Figure 1. Ecoregion abbreviations as in Figure 4. Highest and lowest values in bold.

C _{12(i,j)}	Alashan	Altai	Daurian	Eastern	Gobi	Great	Mongolian	Sayan	Selenge	Trans
Alashan	1	0.504	0.184	0.595	0.716	0.446	0.433	0.097	0.206	0.244
Altai		1	0.451	0.64	0.742	0.702	0.523	0.311	0.594	0.445
Daurian			1	0.188	0.324	0.267	0.669	0.499	0.769	0.685
Eastern				1	0.942	0.644	0.533	0.127	0.424	0.141
Gobi					1	0.8	0.679	0.14	0.371	0.076
Great						1	0.497	0.301	0.544	0.139
Mongolian							1	0.417	0.719	0.522
Sayan								1	0.631	0.447
Selenge									1	0.606
Trans										1

An NMDS ordination biplot (stress = 0.05) shows two separate groups of geometrid species communities within ecoregions (Figure 6). Altai Montane Forest and Forest Steppe, Alashan Plateau Semi-Desert, Eastern Gobi Desert Steppe, Gobi Lakes Valley Desert Steppe, and Great Lakes Basin Desert Steppe are clustered in the first group, Sayan Montane Coniferous Forests, Mongolian-Manchurian Grassland, Daurian Forest Steppe, Selenge-Orkhon Forest Steppe, and Trans-Baikal Coniferous Forests are grouped in the second group. Precipitation was positively correlated with NMDS1, while temperature was positively correlated with NMDS2, both correlations were highly significant ($p < 0.01$). Number of records was positively correlated with both axes but was not significant (Table 3).

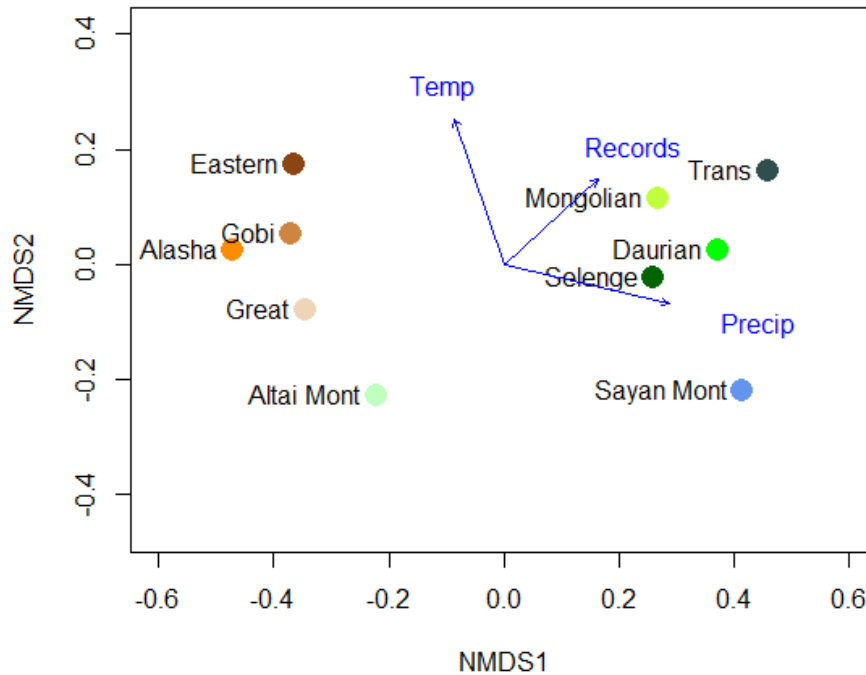


Figure 6. Non-metric multidimensional scaling (NMDS) ordination of 10 ecoregions of Mongolia according to their dissimilarity in geometrid moth species assemblage (zero-adjusted Bray-Curtis dissimilarity index for presence-absence data; stress 0.05). Significant variables are drawn in blue arrows. Temp: Maximum temperature of warmest month, Precip: Precipitation, Records: Number of records of geometrid moths. Colors refer to the map in Figure 1. Ecoregion abbreviations as in Figure 4.

Table 3. NMDS vector fitted values. Temp: Max temperature of warmest month, Precipitation: Annual precipitation, Records: Number of records of geometrid moths.

Variable	NMDS1	NMDS2	r ²	Pr (> 0)
Temperature	-0.32277	0.94648	0.7473	0.009
Precipitation	0.97252	-0.23281	0.9183	0.001
Records	0.73924	0.67344	0.5096	0.095

4. Discussion

In this study, we compiled a geometrid species checklist for Mongolia, examined species richness and diversity of geometrid communities among ecoregions. In addition, we investigated which environmental variables impact the distribution of geometrid moths. Compiling a species checklist on geometrid moths from a variety of sources published since 1892 was quite challenging, as names of species and locations were changing over the years, while sample efforts in different studies and areas differed considerably.

Despite all our efforts we may not have included all species recorded in Mongolia in our list.

In total, we found 1973 records of 388 geometrid species of six subfamilies, but these records were not evenly sampled. The sample-based interpolation and extrapolation curve of gridded sample was not asymptotic, indicating that our records do not represent the whole potential geometrid fauna in Mongolia (Figure 3). Species richness for whole Mongolia was estimated as 663.19 species with Good–Turing theory and this estimated species richness was nearly double the observed species richness. These results confirm the rarefaction analysis and show that our inventory of geometrid moths in Mongolia is still incomplete, with less than 60% of the estimated species being recorded. The fact that countrywide diversity was highest in the grid cell of the capital draws further attention towards an obvious sampling bias with undersampling for the rest of the country. Moreover, we expect to find species of two other subfamilies, Orthostixinae and Alsophilinae in Mongolia. Species of these subfamilies were recorded in adjacent areas, such as in Kazakhstan and in China [37]. However, according to Müller et al. Alsophilinae is transferred to Ennominae, while the subfamily status of Orthostixinae is still not clear [62].

Given the huge size of Mongolia the estimated richness of 663 geometrid species for the whole country seems to be not high. But we wanted to compare the species richness of Mongolia with species richness of other countries similar in size. Norway + Sweden + Finland (1,173,940 km²) together are similar in size to Mongolia (1,564,000 km²). Altogether, for these countries, 341 geometrid species are recorded [84]. If we compare observed species richness (388) of Mongolia with the richness of those countries, it is almost similar; if we compare estimated species richness (663), it is almost double.

However, Scandinavia is an area at high latitudes, with harsh climate, not really suited for an ectotherm group like moths. Further south, Iberian Peninsula and Balearic Islands together, have 589 geometrid species (According to a personal information of Javier Gastón, one of the authors of the paper, due to scientific efforts the total number of Geometridae recorded on Iberian Peninsula and the Balearic Islands is now 605 species.) [85] and their areas (596,740 km² + 4564 km²) are almost three times smaller than the landlocked area of Mongolia, which is situated at higher latitude. Comparisons between distant countries are always somewhat lacking, but no figures on geometrid species richness are available for the countries in Inner Asia (e.g., Kazakhstan).

The most frequently recorded species, which occurred in 10 ecoregions of Mongolia, was *Rhodostrophia jacularia*, an inhabitant of steppe and semi-desert [34,86]. Sihvonen and Nupponen [87] studied female wing shape of this species, but we could not find other studies related to the biology of this species.

Most records were found in Daurian Forest Steppe, Selenge-Orkhon Forest Steppe, and Mongolian-Manchurian Grassland. For many ecoregions, rarefaction curves were not asymptotic, thus revealing that sampling there was incomplete. Two ecoregions have no geometrid moth records at all and were thus excluded from analysis, namely Khangai Mountains Conifer Forests and Sayan Intermontane Steppe. The less studied areas comprise higher altitude areas from central Mongolia, as well as border regions. Sampling in these ecoregions, many of them with high habitat heterogeneity, will certainly expand our checklist.

To assess beta diversity among these unevenly sampled groups we used an estimator for Soerenson similarity that includes unseen species in the calculation [70]. The results, on the one hand, reflect the high habitat heterogeneity of Mongolia, with its steep ecological north-south gradient and the diverse biomes of the country that promote high beta diversity (Table 1). On the other hand, it proved that ecoregions that include similar biomes had higher similarity of moth communities, a result corroborated by NMDS. The most similar ecoregions were Eastern Gobi Desert Steppe and Gobi Lakes Valley Desert Steppe that adjoin each other ($\beta_s = 0.942$).

In NMDS, ecoregions were grouped in two big groups. The first group included Alashan Plateau Semi-Desert, Eastern Gobi Desert Steppe, Gobi Lakes Valley Desert Steppe, Great Lakes Basin Desert Steppe and Altai Montane Forest and Forest Steppe, while in the second group there were Daurian Forest Steppe, Mongolian-Manchurian Grassland, Sayan Montane Coniferous Forests, Selenge-Orkhon Forest Steppe, and Trans-Baikal Coniferous Forests. The geographically nearest ecoregions were grouped together, and also the ecoregions included in the same group belonged to mostly same biome type (Table 1). The first group comprised mostly Deserts and Xeric Shrublands except Altai Montane Forest and Forest Steppe, while three ecoregions of the second group belonged to Temperate Grasslands, Savannas and Shrublands.

Environmental variables that shaped species distribution were nominated by forward selection in NMDS and included annual precipitation and maximum temperature of warmest quarter. Number of records was also selected as variable, but only temperature and precipitation were significant in NMDS, thus corroborating the general robustness of our analysis, which was less influenced by sample effort. The aforementioned groups of ecoregions in NMDS differ along the precipitation gradient and

within groups in temperature, e.g., the montane forests regions of both groups have lower values of NMDS2.

In a study on Borneo, geometrid moths showed a similar relationship with precipitation and temperature [88]. Temperature has also been a major impact on geometrid species distribution in the Andes [89]. Moreover, habitat disturbance played a big role in shaping the geometrid moth ensemble in northern Borneo [90]. Similarly, grazing proved to be a factor influencing community pattern in Mongolian moths [4]. Temperature, rainfall and habitat disturbance are impacted by climate change and anthropogenic influence, so we expect future changes within the Mongolian geometrid communities. The species list we present here can be a tool helping to monitor these changes.

Finally, we have to admit that our study has a few weaknesses. We compiled records only from literature (we apologize if we missed any) due to limited time and funding. A total of 87 of the 388 species in our checklist are still missing an exact location. This information may be available in the museum collections pinned to the respective specimens. A detailed research in museums would have certainly brought more records and species. In addition, all our records were not systematically collected, which might affect the statistical analysis. The mere fact that data were sampled over a long period of time in different research projects, with different ways of sampling certainly impacts the value of a statistical analysis. For example, in our field study [4], we used UV light, but in other studies normal light bulbs were used, sometimes even moths have even been collected during day time. Together with the general problem of undersampling, these points hamper a more detailed analysis of the Mongolian geometrid communities at the present time.

Nevertheless, due to our study, future directions of research on Mongolian Geometridae have become more clear: geometrid moths are really under-studied in Mongolia. We found two unsampled and four extremely under-sampled ecoregions and for all ecoregions expected species numbers were higher than recorded ones. So, we expect to find many more amazing moth species in future collections in the respective regions.

5. Conclusions

In total, 1973 records of 388 species were recorded, but we also expect that many more species will be recorded in the future in more elaborated sampling designs, especially from locations of southern, eastern and western Mongolia. Despite the fact that our compiled data is not good enough to analyze the distribution and diversity pattern in full detail, our study could reveal the knowledge gaps and undersampled areas, provide a first estimate of the approximate species number in whole Mongolia ($n = 663$), visualize the currently recorded distribution and diversity pattern of geometrid moths of Mongolia and evaluate the main environmental factors that shape the communities.

Supplementary Materials: The following are available online at www.mdpi.com/xxx/s1, Table S1: Occurrence data of geometrid moths compiled from Mongolia.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix

Table 1: Checklist of geometrid moths in Mongolia. Note that we conducted all analysis at species level. Here subspecies are listed to show compiled data in more detail. The listed references include in most cases articles with location information.

Subfamily	Species	Author	Year	Reference
Archiearinae	<i>Archiearis notha</i>	Hübner	1802	[34]
Archiearinae	<i>Archiearis parthenias</i>	Linnaeus	1761	[34]
Archiearinae	<i>Archiearis parthenias sajana</i>	Prout	1912	[46]
Archiearinae	<i>Leucobrephephos middendorffii</i>	Ménétriés	1858	[41]
Desmobathrinae	<i>Gypsochroa renitidata</i>	Hübner	1817	[57]
Ennominae	<i>Abraxas grossulariata</i>	Linnaeus	1758	[21,34,46,63,65]
Ennominae	<i>Abraxas grossulariata dsungarica</i>	Wehrli	1939	[38]
Ennominae	<i>Alcis deversata</i>	Staudinger	1892	[34,39,46,63,65]
Ennominae	<i>Alcis extinctaria</i>	Eversmann	1851	[23,34,36,39,65,91]
Ennominae	<i>Alcis jubata</i>	Thunberg	1788	[37]
Ennominae	<i>Alcis repandata</i>	Linnaeus	1758	[65]
Ennominae	<i>Alloharpina conjungens</i>	Alphéraky	1892	[33]
Ennominae	<i>Amraica superans</i>	Butler	1878	[33]
Ennominae	<i>Angerona prunaria</i>	Linnaeus	1758	[24,34,46,63,65]
Ennominae	<i>Angerona prunaria kentearia</i>	Staudinger	1892	[39]
Ennominae	<i>Angerona prunaria mongoligena</i>	Bryk	1949	[62]
Ennominae	<i>Apeira syringaria</i>	Linnaeus	1758	[63]
Ennominae	<i>Apocheima hispidaria</i>	Denis & Schiffermüller	1775	[34]
Ennominae	<i>Apocolotois almatensis</i>	Djakonov	1952	[39]
Ennominae	<i>Apocolotois smirnovi</i>	Romanoff	1885	[39]
Ennominae	<i>Arichanna barteli</i>	Prout	1915	[32,45]
Ennominae	<i>Arichanna melanaria</i>	Linnaeus	1758	[34,46,65,91]
Ennominae	<i>Arichanna melanaria decolorata</i>	Staudinger	1892	[45]
Ennominae	<i>Arichanna melanaria praeolivina</i>	Wehrli	1933	[39]
Ennominae	<i>Aspitates conspersaria</i>	Staudinger	1901	[23,45]
Ennominae	<i>Aspitates curvaria</i>	Eversmann	1852	[1,8,14]
Ennominae	<i>Aspitates forbesi</i>	Munroe	1963	[65]
Ennominae	<i>Aspitates gilvaria</i>	Denis & Schiffermüller	1775	[23,24,34,36,63,91]
Ennominae	<i>Aspitates gilvaria minimus</i>	Vojnits	1975	[39]
Ennominae	<i>Aspitates insignis</i>	Alphéraky	1883	[36,39]
Ennominae	<i>Aspitates kozhantchikovi</i>	Munroe	1963	[36,65]
Ennominae	<i>Aspitates mongolicus</i>	Vojnits	1975	[39,65]
Ennominae	<i>Aspitates mundataria</i>	Stoll	1782	[34,46,63,65]
Ennominae	<i>Aspitates mundataria uncinataria</i>	Vojnits	1975	[39]
Ennominae	<i>Aspitates obscurata</i>	Wehrli	1953	[33,34,39]
Ennominae	<i>Aspitates staudingeri</i>	Vojnits	1975	[39]
Ennominae	<i>Aspitates taylorae sibirica</i>	Djakonov	1955	[36,65]
Ennominae	<i>Aspitates tristrigaria</i>	Bremer & Grey	1853	[34,37]
Ennominae	<i>Astegania honesta</i>	Prout	1908	[34]
Ennominae	<i>Biston betularia</i>	Linnaeus	1758	[34,46,63,91]
Ennominae	<i>Biston betularia sibiricus</i>	Fuchs	1899	[37]
Ennominae	<i>Cabera exanthemata</i>	Scopoli	1763	[23,34,46,65]
Ennominae	<i>Cabera exanthemata hamica</i>	Wehrli	1939	[39]
Ennominae	<i>Cabera pusaria</i>	Linnaeus	1758	[34,39,63]
Ennominae	<i>Calcaritis pallida</i>	Hedemann	1881	[47]
Ennominae	<i>Chariaspilates formosaria</i>	Eversmann	1837	[37]
Ennominae	<i>Charissa agnataria</i>	Staudinger	1897	[55]
Ennominae	<i>Charissa ambiguata</i>	Duponchel	1830	[34,36,46,65]
Ennominae	<i>Charissa ambiguata ophthalmicata</i>	Lederer	1853	[39]
Ennominae	<i>Charissa beljaevi</i>	Erlacher et al., 2017	2017	[55]
Ennominae	<i>Charissa bidentatus</i>	Shchetkin & Viidalepp	1980	[46]

Ennominae	<i>Charissa creperaria</i>	Erschoff	1877	[34,55,65]
Ennominae	<i>Charissa difficilis</i>	Alphéraky	1883	[21,24,34,39,65]
Ennominae	<i>Charissa gozmanyi</i>	Vojnits	1975	[14]
Ennominae	<i>Charissa macguffini</i>	Smiles	1979	[65]
Ennominae	<i>Charissa ochrofasciata</i>	Staudinger	1895	[21,30,34,36,39,55,65]
Ennominae	<i>Charissa remmi</i>	Viidalepp	1988	[56,63]
Ennominae	<i>Charissa sibirata</i>	Guenée	1858	[21,24,30,34,36]
Ennominae	<i>Charissa subsplenditaria</i>	Wehrli	1922	[63,92]
Ennominae	<i>Charissa turfosaria</i>	Wehrli	1922	[30,34,39,45,62]
Ennominae	<i>Charissa vastaria</i>	Staudinger	1892	[30,34]
Ennominae	<i>Chiasmia aestimaria</i>	Hübner	1809	[65]
Ennominae	<i>Chiasmia aestimaria kuldshana</i>	Wehrli	1940	[39]
Ennominae	<i>Chiasmia clathrata</i>	Linnaeus	1758	[23,24,26,34,36,46,63,65,91]
Ennominae	<i>Chiasmia clathrata djakonovi</i>	Kardakoff	1928	[38,39]
Ennominae	<i>Chiasmia saburraria</i>	Eversmann	1851	[21,34,65]
Ennominae	<i>Chiasmia saburraria kenteata</i>	Staudinger	1892	[38]
Ennominae	<i>Cleora cinctaria</i>	Denis & Schiffermüller	1775	[34,46,63]
Ennominae	<i>Colotois pennaria</i>	Linnaeus	1760	[46]
Ennominae	<i>Deileptenia ribeata</i>	Clerck	1759	[63]
Ennominae	<i>Digrammia rippertaria</i>	Duponchel	1830	[34]
Ennominae	<i>Ectropis crepuscularia</i>	Denis & Schiffermüller	1775	[34,46]
Ennominae	<i>Eilicrinia orias</i>	Wehrli	1933	[45]
Ennominae	<i>Elophos banghaasi</i>	Wehrli	1922	[30,34,45]
Ennominae	<i>Ematurga atomaria</i>	Linnaeus	1758	[23,24,34,36,46,65]
Ennominae	<i>Ematurga atomaria krassnojarscensis</i>	Fuchs	1899	[39]
Ennominae	<i>Ennomos autumnaria</i>	Werneburg	1859	[46]
Ennominae	<i>Epione repandaria</i>	Hufnagel	1767	[34]
Ennominae	<i>Epione vespertaria</i>	Linnaeus	1767	[34,39]
Ennominae	<i>Epirranthis diversata</i>	Denis & Schiffermüller	1775	[63]
Ennominae	<i>Erannis jacobsoni</i>	Djakonov	1926	[34,46,65]
Ennominae	<i>Gnophopsodos ravistriolaria</i>	Wehrli	1922	[36]
Ennominae	<i>Gnophopsodos ravistriolaria ravistriolaria</i>	Wehrli	1922	[55]
Ennominae	<i>Gnophopsodos stemmataria</i>	Eversmann	1848	[39]
Ennominae	<i>Gnophopsodos tholeraria</i>	Püngeler	1901	[50]
Ennominae	<i>Gnophos bipartitus</i>	Vojnits	1975	[39]
Ennominae	<i>Gnophos rubefactaria</i>	Püngeler	1902	[37]
Ennominae	<i>Heliomata glarearia</i>	Denis & Schiffermüller	1775	[46]
Ennominae	<i>Hypomecis punctinalis</i>	Scopoli	1763	[46]
Ennominae	<i>Hypomecis roboraria</i>	Denis & Schiffermüller	1775	[23,34,39,63]
Ennominae	<i>Hypoxystis pluviaria</i>	Fabricius	1787	[34,46,63]
Ennominae	<i>Isturgia altaica</i>	Vojnits	1978	[43]
Ennominae	<i>Isturgia arenacearia</i>	Denis & Schiffermüller	1775	[63,91]
Ennominae	<i>Isturgia arenacearia mongolica</i>	Vojnits	1974	[38]
Ennominae	<i>Isturgia falsaria</i>	Alphéraky	1892	[34]
Ennominae	<i>Isturgia halituaria</i>	Guenée	1858	[48]
Ennominae	<i>Isturgia kaszabi</i>	Vojnits	1974	[38]
Ennominae	<i>Isturgia murinaria</i>	Denis & Schiffermüller	1775	[34,36]
Ennominae	<i>Isturgia murinaria uralica</i>	Wehrli	1937	[63]
Ennominae	<i>Jankowskia bituminaria</i>	Lederer	1853	[65]
Ennominae	<i>Jankowskia bituminaria raddensis</i>	Wehrli	1941	[93]
Ennominae	<i>Lomasipilis marginata</i>	Linnaeus	1758	[23,34,46,65]
Ennominae	<i>Lomasipilis opis amurensis</i>	Hedemann	1881	[38]
Ennominae	<i>Lomographa buraetica</i>	Staudinger	1892	[34]
Ennominae	<i>Lomographa temerata</i>	Denis & Schiffermüller	1775	[46]
Ennominae	<i>Lycia hirtaria</i>	Clerck	1759	[63]
Ennominae	<i>Lycia lapponaria</i>	Boisduval	1840	[37]
Ennominae	<i>Macaria alternata</i>	Denis & Schiffermüller	1775	[34,46,91]
Ennominae	<i>Macaria artesiaria</i>	Denis & Schiffermüller	1775	[34,38]
Ennominae	<i>Macaria brunneata</i>	Thunberg	1784	[36,38,91]
Ennominae	<i>Macaria circumflexaria</i>	Eversmann	1848	[38,46,63,91]

Ennominae	<i>Macaria costimaculata</i>	Graeser	1888	[34]
Ennominae	<i>Macaria latefasciata</i>	Staudinger	1896	[21,34]
Ennominae	<i>Macaria liturata</i>	Clerck	1759	[65]
Ennominae	<i>Macaria liturata pressaria</i>	Christoph	1893	[37]
Ennominae	<i>Macaria loritaria</i>	Eversmann	1837	[36]
Ennominae	<i>Macaria notata</i>	Linnaeus	1758	[34,63]
Ennominae	<i>Macaria notata kirina</i>	Wehrli	1940	[38]
Ennominae	<i>Macaria serenaria</i>	Staudinger	1896	[21,34]
Ennominae	<i>Macaria signaria</i>	Hübner	1809	[38,46]
Ennominae	<i>Macaria wauaria</i>	Linnaeus	1758	[34,36]
Ennominae	<i>Megalycinia strictaria</i>	Lederer	1853	[21,34,39,46,63]
Ennominae	<i>Megametopon piperatum</i>	Alphéraky	1892	[34,39,65]
Ennominae	<i>Narraga fasciolaria</i>	Hufnagel	1767	[34,63]
Ennominae	<i>Odontopera bidentata</i>	Clerck	1759	[21,35,40,47,66]
Ennominae	<i>Odontopera bidentata exsul</i>	Tchetrerikov	1905	[36,39]
Ennominae	<i>Odontopera bidentata rava</i>	Vojnits	1975	[39,65]
Ennominae	<i>Ourapteryx persica</i>	Ménétriés	1832	[34]
Ennominae	<i>Ourapteryx sambucaria</i>	Linnaeus	1758	[63,65]
Ennominae	<i>Perconia strigillaria</i>	Hübner	1787	[46,63]
Ennominae	<i>Petrophora kaszabi</i>	Vojnits	1978	[43]
Ennominae	<i>Phaselia narynaria</i>	Oberthür	1913	[49]
Ennominae	<i>Phaselia serrularia</i>	Eversmann	1847	[65]
Ennominae	<i>Phthonandria emaria</i>	Bremer	1864	[39]
Ennominae	<i>Plagodis dolabraria</i>	Linnaeus	1767	[34]
Ennominae	<i>Plagodis pulveraria</i>	Linnaeus	1758	[21,34,65]
Ennominae	<i>Plagodis pulveraria singularis</i>	Vojnits	1975	[39]
Ennominae	<i>Pleogynopteryx bituminaria</i>	Lederer	1853	[21,34,39]
Ennominae	<i>Pseudopanthera macularia</i>	Linnaeus	1758	[34]
Ennominae	<i>Pseudopanthera macularia cryptica</i>	Beljaev	1997	[94]
Ennominae	<i>Selenia dentaria</i>	Fabricius	1775	[39]
Ennominae	<i>Selenia dentaria alpestris</i>	Wehrli	1940	[37]
Ennominae	<i>Selenia ononica</i>	Kostjuk	1991	[37]
Ennominae	<i>Selenia sordidaria</i>	Leech	1897	[39]
Ennominae	<i>Selenia tetralunaria</i>	Hufnagel	1767	[34,36,46,63]
Ennominae	<i>Siona lineata</i>	Scopoli	1763	[23,26,34,36,39,46,63,65]
Ennominae	<i>Spartopteryx kindermannaria</i>	Staudinger	1871	[36,39,46]
Ennominae	<i>Xandrames dholaria</i>	Moore	1868	[33]
Ennominae	<i>Yezognophos vittaria</i>	Thunberg	1792	[65]
Geometrinae	<i>Chlorissa viridata</i>	Linnaeus	1758	[34]
Geometrinae	<i>Dyschloopsis impararia</i>	Guenée	1858	[21,24,34,40,41,65]
Geometrinae	<i>Geometra papilionaria</i>	Linnaeus	1758	[40,46,63]
Geometrinae	<i>Geometra papilionaria herbacearia</i>	Ménétriés	1859	[41,65]
Geometrinae	<i>Hemistola chrysoprasaria</i>	Esper	1794	[46,63]
Geometrinae	<i>Hemistola chrysoprasaria lissas</i>	Prout	1912	[40]
Geometrinae	<i>Hemistola zimmermanni</i>	Hedemann	1879	[34,40,41]
Geometrinae	<i>Hemitheia aestivaria</i>	Hübner	1799	[46]
Geometrinae	<i>Jodis lactearia</i>	Linnaeus	1758	[37]
Geometrinae	<i>Microloxia herbaria</i>	Hübner	1813	[34,65]
Geometrinae	<i>Microloxia herbaria advolata</i>	Eversmann	1837	[41]
Geometrinae	<i>Thalera chlorosaria</i>	Graeser	1890	[34,40,41,91]
Geometrinae	<i>Thalera fimbrialis</i>	Scopoli	1763	[63]
Geometrinae	<i>Thetidia atyche</i>	Prout	1935	[40,41]
Geometrinae	<i>Thetidia chlorophyllaria</i>	Hedemann	1879	[37]
Geometrinae	<i>Thetidia correspondens</i>	Alpheraky	1883	[49]
Geometrinae	<i>Thetidia volgaria</i>	Guenée	1858	[21,34,40,46,65]
Geometrinae	<i>Thetidia volgaria mongolica</i>	Staudinger	1897	[41]
Larentiinae	<i>Acasis appensata</i>	Eversmann	1842	[46,65]
Larentiinae	<i>Anticlea badiata</i>	Denis & Schiffmüller	1775	[34,63]
Larentiinae	<i>Anticlea derivata</i>	Denis & Schiffmüller	1775	[24,34,46,63]
Larentiinae	<i>Aplocera plagiata roddi</i>	Vasilenko	1995	[59]
Larentiinae	<i>Baptria tibiale</i>	Esper	1804	[34,42]
Larentiinae	<i>Campptogramma bilineata</i>	Linnaeus	1758	[46]
Larentiinae	<i>Carsia sororiata</i>	Hübner	1813	[23,34,36]

Larentiinae	<i>Catarhoe cuculata</i>	Hufnagel	1767	[37,46,59,63]
Larentiinae	<i>Catarhoe rubidata</i>	Denis & Schiffermüller	1775	[46]
Larentiinae	<i>Chloroclysta miata</i>	Linnaeus	1758	[36]
Larentiinae	<i>Cidaria distinctata</i>	Staudinger	1892	[37]
Larentiinae	<i>Cidaria fulvata</i>	Forster	1771	[34,44,63,65]
Larentiinae	<i>Coenocalpe lapidata</i>	Hübner	1809	[21,23,34,36,46,65]
Larentiinae	<i>Coenotephria korschunovi</i>	Viidalepp	1976	[34]
Larentiinae	<i>Colostygia aptata</i>	Hübner	1813	[34,65]
Larentiinae	<i>Cosmorhoe ocellata</i>	Linnaeus	1758	[37]
Larentiinae	<i>Dysstroma citrata</i>	Linnaeus	1761	[34,46,63,65]
Larentiinae	<i>Dysstroma citrata septentrionalis</i>	Heydemann	1929	[36]
Larentiinae	<i>Dysstroma citratum kamtshadalarium</i>	Beljaev & Vasilenko	2002	[48]
Larentiinae	<i>Dysstroma infuscata</i>	Tengström	1869	[65]
Larentiinae	<i>Dysstroma latefasciata</i>	Blöcker	1908	[34,44,65]
Larentiinae	<i>Dysstroma pseudimmanata</i>	Heydemann	1929	[31,34,44]
Larentiinae	<i>Dysstroma truncata</i>	Hufnagel	1767	[23,31,34,44,65,91]
Larentiinae	<i>Dysstroma truncata transbaicalensis</i>	Heydemann	1929	[36]
Larentiinae	<i>Ecliptopera capitata</i>	Herrich-Schäffer	1839	[63]
Larentiinae	<i>Ecliptopera dimita</i>	Prout	1938	[37]
Larentiinae	<i>Ecliptopera umbrosaria</i>	Motschulsky	1861	[34]
Larentiinae	<i>Ecliptopera oblongata</i>	Guenée	1858	[44]
Larentiinae	<i>Electrophaes chimakaleparia</i>	Oberthür	1893	[44]
Larentiinae	<i>Electrophaes corylata</i>	Thunberg	1792	[46,65]
Larentiinae	<i>Entephria caesiata</i>	Denis & Schiffermüller	1775	[34,36,44]
Larentiinae	<i>Entephria kuznetzovi</i>	Viidalepp	1976	[34,45]
Larentiinae	<i>Entephria tzygankovi</i>	Wehrli	1929	[36]
Larentiinae	<i>Epirrhoe alternata</i>	Müller	1764	[23,34,36]
Larentiinae	<i>Epirrhoe hastulata</i>	Hübner	1790	[34,36,44,46]
Larentiinae	<i>Epirrhoe hastulata reducta</i>	Djakonov	1929	[48]
Larentiinae	<i>Epirrhoe pupillata</i>	Thunberg	1788	[23,34,36,44,46,63,65,91]
Larentiinae	<i>Epirrhoe tristata</i>	Linnaeus	1758	[23,34,46]
Larentiinae	<i>Epirrita autumnata</i>	Borkhausen	1794	[21,34]
Larentiinae	<i>Epirrita autumnata smetanini</i>	Beljaev & Vasilenko	2002	[48]
Larentiinae	<i>Epirrita autumnata tunkunata</i>	Bang-Haas	1910	[36]
Larentiinae	<i>Esakiopteryx volitans</i>	Butler	1878	[44]
Larentiinae	<i>Eulithis mellinata</i>	Fabricius	1787	[34]
Larentiinae	<i>Eulithis populata</i>	Linnaeus	1758	[36,44,63,91]
Larentiinae	<i>Eulithis prunata</i>	Linnaeus	1758	[34,44,46]
Larentiinae	<i>Eulithis pyraliata</i>	Denis & Schiffermüller	1775	[23,34,44,46,63,65]
Larentiinae	<i>Eulithis pyropata</i>	Hübner	1809	[91]
Larentiinae	<i>Eulithis testata</i>	Linnaeus	1761	[23,34,44,46,63]
Larentiinae	<i>Euphyia coangulata</i>	Prout	1914	[21,23,24,34,36,44,65]
Larentiinae	<i>Euphyia intersecta</i>	Staudinger	1882	[21,23,34]
Larentiinae	<i>Euphyia unangulata</i>	Haworth	1809	[34,46,63,65]
Larentiinae	<i>Eupithecia selinata</i>	Herrich-Schäffer	1861	[34]
Larentiinae	<i>Eupithecia absinthiata</i>	Clerck	1759	[95]
Larentiinae	<i>Eupithecia actaeata</i>	Walderdorff	1869	[52]
Larentiinae	<i>Eupithecia addictata</i>	Dietze	1908	[37]
Larentiinae	<i>Eupithecia aggregata</i>	Guenée	1858	[37]
Larentiinae	<i>Eupithecia amplexata</i>	Christoph	1881	[34,65]
Larentiinae	<i>Eupithecia anikini</i>	Mironov & Galsworthy	2014	[52]
Larentiinae	<i>Eupithecia aporia</i>	Vojnits	1975	[41,45]
Larentiinae	<i>Eupithecia assimilata</i>	Doubleday	1856	[52]
Larentiinae	<i>Eupithecia bastelbergeri</i>	Dietze	1910	[52]
Larentiinae	<i>Eupithecia biornata</i>	Christoph	1867	[34,65]
Larentiinae	<i>Eupithecia bohatschi</i>	Staudinger	1897	[25,34,65]
Larentiinae	<i>Eupithecia carpophilata</i>	Staudinger	1897	[34,65]
Larentiinae	<i>Eupithecia catharinae</i>	Vojnits	1969	[65]
Larentiinae	<i>Eupithecia centaureata</i>	Denis & Schiffermüller	1775	[34,63,65]
Larentiinae	<i>Eupithecia chingana</i>	Wehrli	1926	[45]
Larentiinae	<i>Eupithecia corroborata</i>	Dietze	1908	[36]
Larentiinae	<i>Eupithecia denotata</i>	Hübner	1813	[34]
Larentiinae	<i>Eupithecia despectaria</i>	Lederer	1853	[34,37]

Larentiinae	<i>Eupithecia dissertata</i>	Püngeler	1905	[34,36,65]
Larentiinae	<i>Eupithecia djakonovi</i>	Shchetkin	1956	[37]
Larentiinae	<i>Eupithecia dolosa</i>	Vojnits	1977	[45]
Larentiinae	<i>Eupithecia ericeata</i>	Rambur	1833	[52,65]
Larentiinae	<i>Eupithecia extensaria</i>	Freyer	1844	[36,65]
Larentiinae	<i>Eupithecia fennoscandica</i>	Knaben	1949	[36,96]
Larentiinae	<i>Eupithecia fuscicostata</i>	Christoph	1887	[65]
Larentiinae	<i>Eupithecia graciliata</i>	Dietze	1906	[34]
Larentiinae	<i>Eupithecia hannemanni</i>	Vojnits & De Laever	1973	[65]
Larentiinae	<i>Eupithecia holti</i>	Viidalepp	1973	[34,65,97]
Larentiinae	<i>Eupithecia illaborata</i>	Dietze	1904	[52]
Larentiinae	<i>Eupithecia impolita</i>	Vojnits	1980	[52]
Larentiinae	<i>Eupithecia inculta</i>	Vojnits	1975	[65]
Larentiinae	<i>Eupithecia indigata</i>	Hübner	1813	[63]
Larentiinae	<i>Eupithecia innotata</i>	Hufnagel	1767	[21,34,65]
Larentiinae	<i>Eupithecia intricata</i>	Zetterstedt	1839	[34]
Larentiinae	<i>Eupithecia inveterata</i>	Vojnits	1987	[65]
Larentiinae	<i>Eupithecia irriguata</i>	Hübner	1813	[65]
Larentiinae	<i>Eupithecia kozlovi</i>	Viidalepp	1973	[34,97]
Larentiinae	<i>Eupithecia kuldschaensis</i>	Staudinger	1892	[34,65]
Larentiinae	<i>Eupithecia laboriosa</i>	Vojnits	1977	[65]
Larentiinae	<i>Eupithecia lariciata</i>	Freyer	1841	[34,36,65]
Larentiinae	<i>Eupithecia leptogrammata</i>	Staudinger	1882	[65]
Larentiinae	<i>Eupithecia linariata</i>	Denis & Schiffermüller	1775	[65]
Larentiinae	<i>Eupithecia mima</i>	Mironov	1989	[65]
Larentiinae	<i>Eupithecia minusculata</i>	Alphéraky	1883	[34,65]
Larentiinae	<i>Eupithecia mongolica</i>	Vojnits	1974	[65]
Larentiinae	<i>Eupithecia morosa</i>	Vojnits	1976	[65]
Larentiinae	<i>Eupithecia munguata</i>	Mironov & Galsworthy	2014	[52]
Larentiinae	<i>Eupithecia necessaria</i>	Vojnits	1977	[41,45]
Larentiinae	<i>Eupithecia nephelata</i>	Staudinger	1897	[21,23,34,65]
Larentiinae	<i>Eupithecia nobilitata</i>	Staudinger	1882	[36,65]
Larentiinae	<i>Eupithecia olgae</i>	Mironov	1986	[52]
Larentiinae	<i>Eupithecia opisthographata</i>	Dietze	1906	[34]
Larentiinae	<i>Eupithecia perfuscata</i>	Vojnits	1975	[65]
Larentiinae	<i>Eupithecia pernotata</i>	Guenée	1858	[48]
Larentiinae	<i>Eupithecia pimpinellata</i>	Hübner	1813	[34,65]
Larentiinae	<i>Eupithecia propria</i>	Vojnits	1977	[65]
Larentiinae	<i>Eupithecia pusillata</i>	Denis & Schiffermüller	1775	[52]
Larentiinae	<i>Eupithecia pygmaeata</i>	Hübner	1799	[65]
Larentiinae	<i>Eupithecia recens</i>	Dietze	1904	[34,36]
Larentiinae	<i>Eupithecia relaxata</i>	Dietze	1904	[65]
Larentiinae	<i>Eupithecia repentina</i>	Vojnits & De Laever	1978	[52]
Larentiinae	<i>Eupithecia rubellata</i>	Dietze	1904	[41,45]
Larentiinae	<i>Eupithecia saisanaria</i>	Staudinger	1882	[52]
Larentiinae	<i>Eupithecia satyrata</i>	Hübner	1813	[36]
Larentiinae	<i>Eupithecia selinata</i>	Herrich-Schäffer	1861	[95]
Larentiinae	<i>Eupithecia simpliciata</i>	Haworth	1809	[52]
Larentiinae	<i>Eupithecia sinuosaria</i>	Eversmann	1848	[23,34,36]
Larentiinae	<i>Eupithecia subbrunneata</i>	Dietze	1904	[52]
Larentiinae	<i>Eupithecia subexiguata</i>	Vojnits	1974	[65]
Larentiinae	<i>Eupithecia subfuscata</i>	Haworth	1809	[34]
Larentiinae	<i>Eupithecia suboxydata</i>	Staudinger	1897	[65,98]
Larentiinae	<i>Eupithecia subtacincta</i>	Hampson	1895	[37]
Larentiinae	<i>Eupithecia subumbrata</i>	Denis & Schiffermüller	1775	[23,34,65]
Larentiinae	<i>Eupithecia succenturiata</i>	Linnaeus	1758	[95]
Larentiinae	<i>Eupithecia sutiliata</i>	Christoph	1877	[65]
Larentiinae	<i>Eupithecia thalictrata</i>	Püngeler	1902	[52]
Larentiinae	<i>Eupithecia undata</i>	Freyer	1840	[65]
Larentiinae	<i>Eupithecia veratraria</i>	Herrich-Schäffer	1848	[95]
Larentiinae	<i>Eupithecia vicina</i>	Mironov	1989	[65]
Larentiinae	<i>Eupithecia virgaureata</i>	Doubleday	1861	[21,23,34,65]
Larentiinae	<i>Eupithecia vulgata</i>	Haworth	1809	[21,23,34]
Larentiinae	<i>Eupithecia vulgata lepsaria</i>	Staudinger	1882	[37]
Larentiinae	<i>Eupithecis unedonata</i>	Mabille	1868	[33]

Larentiinae	<i>Eustroma reticulatum obsolata</i>	Djakonov	1929	[48]
Larentiinae	<i>Gagitodes sagittata</i>	Fabricius	1787	[44,46,63]
Larentiinae	<i>Gagitodes sagittata albiflua</i>	Prout	1939	[48]
Larentiinae	<i>Horisme aemulata</i>	Hübner	1813	[23,34,46,65]
Larentiinae	<i>Horisme aquata</i>	Hübner	1813	[23,34,36,46,65,91]
Larentiinae	<i>Horisme falcata</i>	Bang-Haas	1907	[25,27,34,36,63,65]
Larentiinae	<i>Horisme incurvaria</i>	Erschoff	1877	[34,36,65]
Larentiinae	<i>Horisme lucillata</i>	Guenée	1858	[23,34]
Larentiinae	<i>Horisme parcata</i>	Püngeler	1909	[65]
Larentiinae	<i>Horisme scotosiata</i>	Guenée	1858	[21,23,34,63,65]
Larentiinae	<i>Horisme tersata</i>	Denis & Schiffermüller	1775	[34,65]
Larentiinae	<i>Horisme tersata tetricata</i>	Guenée	1858	[37]
Larentiinae	<i>Horisme vitalbata</i>	Denis & Schiffermüller	1775	[21,23,34,36,46,65]
Larentiinae	<i>Hydrelia flammeolaria</i>	Hufnagel	1767	[44,46]
Larentiinae	<i>Hydria cervicalis</i>	Scopoli	1763	[34]
Larentiinae	<i>Hydria undulata</i>	Linnaeus	1758	[34,65]
Larentiinae	<i>Hydriomena furcata</i>	Thunberg	1784	[21,23,34,36,44]
Larentiinae	<i>Hydriomena impluviata</i>	Denis & Schiffermüller	1775	[21,34,36]
Larentiinae	<i>Hydriomena impluviata djakonovi</i>	Beljaev & Vasilenko	2002	[48]
Larentiinae	<i>Hydriomena ruberata</i>	Freyer	1831	[65]
Larentiinae	<i>Juxtephria consentaria</i>	Freyer	1846	[36,44,65]
Larentiinae	<i>Kyrtolitha obstinata</i>	Staudinger	1892	[34]
Larentiinae	<i>Laciniodes denigrata abiens</i>	Prout	1938	[33]
Larentiinae	<i>Lampropteryx albigirata</i>	Kollar	1848	[65]
Larentiinae	<i>Lampropteryx jameza</i>	Butler	1898	[37]
Larentiinae	<i>Lampropteryx minna</i>	Butler	1881	[44,45,65]
Larentiinae	<i>Lampropteryx suffumata</i>	Denis & Schiffermüller	1775	[63]
Larentiinae	<i>Leptostegna tenerata</i>	Christoph	1881	[99]
Larentiinae	<i>Lithostege coassata mongolica</i>	Vojnits	1978	[42]
Larentiinae	<i>Lithostege coassata ochraceata</i>	Staudinger	1897	[42,65]
Larentiinae	<i>Lithostege mesoleucata</i>	Püngeler	1899	[34,42]
Larentiinae	<i>Lithostege pallescens</i>	Staudinger	1897	[21,34]
Larentiinae	<i>Lobophora halterata</i>	Hufnagel	1767	[44,46]
Larentiinae	<i>Martania taeniata</i>	Stephens	1831	[44]
Larentiinae	<i>Mesoleuca albicillata</i>	Linnaeus	1758	[34,37,44,46]
Larentiinae	<i>Mesotype verberata</i>	Scopoli	1763	[44]
Larentiinae	<i>Nebula lamata</i>	Staudinger	1897	[21,34]
Larentiinae	<i>Nebula mongoliata</i>	Staudinger	1897	[21,34,44,65]
Larentiinae	<i>Odezia atrata</i>	Linnaeus	1758	[23,34]
Larentiinae	<i>Orthonama obstipata</i>	Fabricius	1794	[34]
Larentiinae	<i>Pelurga comitata</i>	Linnaeus	1758	[34,44,63,65]
Larentiinae	<i>Pelurga taczanowskiaria</i>	Oberthür	1880	[63,91]
Larentiinae	<i>Perizoma alchemillata</i>	Linnaeus	1758	[34,36,44]
Larentiinae	<i>Perizoma bifaciata</i>	Haworth	1809	[65]
Larentiinae	<i>Perizoma blandiata</i>	Denis & Schiffermüller	1775	[23,34]
Larentiinae	<i>Perizoma hydrata</i>	Treitschke	1829	[36,44,65]
Larentiinae	<i>Perizoma minorata</i>	Treitschke	1828	[46]
Larentiinae	<i>Phibalapteryx virgata</i>	Hufnagel	1767	[34,36,42,91]
Larentiinae	<i>Photoscotosia palaeartica</i>	Staudinger	1882	[23,34]
Larentiinae	<i>Plemyria rubiginata</i>	Denis & Schiffermüller	1775	[34,44,65]
Larentiinae	<i>Plesioscotosia pulchrata</i>	Alphéraky	1883	[23,34]
Larentiinae	<i>Povilasias kashghara</i>	Moore	1878	[51]
Larentiinae	<i>Pseudentephria remmi</i>	Viidalepp	1976	[35]
Larentiinae	<i>Pseudobaptria corydalaria</i>	Graeser	1889	[34]
Larentiinae	<i>Rheumaptera hastata</i>	Linnaeus	1758	[34,36,44,46,65]
Larentiinae	<i>Rheumaptera subhastata</i>	Nolcken	1870	[36]
Larentiinae	<i>Rheumaptera subhastata commixta</i>	Matsumura	1925	[48]
Larentiinae	<i>Schistostege nubilaria</i>	Hübner	1799	[23,34,36,42,65]
Larentiinae	<i>Scotopteryx chenopodiata</i>	Linnaeus	1758	[23,34,46,63,65]
Larentiinae	<i>Scotopteryx chenopodiata sibirica</i>	Bang-Haas	1907	[42]

Larentiinae	<i>Scotopteryx golovushkini</i>	Kostjuk	1991	[65]
Larentiinae	<i>Scotopteryx sinensis</i>	Alphéraky	1883	[23,34]
Larentiinae	<i>Scotopteryx transbaicalica</i>	Djakonov	1955	[28,34,36]
Larentiinae	<i>Spargania luctuata</i>	Denis & Schiffermüller	1775	[23,34,44,63,65]
Larentiinae	<i>Stamnodes danilovi</i>	Erschoff	1877	[21,23,34,36,42,65]
Larentiinae	<i>Stamnodes danilovi djakonovi</i>	Alphéraky	1916	[33]
Larentiinae	<i>Stamnodes pauperaria</i>	Eversmann	1848	[65]
Larentiinae	<i>Thera obeliscata</i>	Hübner	1787	[34,91]
Larentiinae	<i>Thera variata</i>	Denis & Schiffermüller	1775	[23,34]
Larentiinae	<i>Trichopterigia consobrinaria</i>	Leech	1891	[44]
Larentiinae	<i>Trichopteryx carpinata</i>	Borkhausen	1794	[65]
Larentiinae	<i>Xanthorhoe abrasaria</i>	Herrich-Schäffer	1855	[36,44,65]
Larentiinae	<i>Xanthorhoe deflorata</i>	Erschoff	1877	[23,34,44,65]
Larentiinae	<i>Xanthorhoe montanata</i>	Denis & Schiffermüller	1775	[34,36,46]
Larentiinae	<i>Xanthorhoe quadrifasiata tannuensis</i>	Prout	1924	[45,63]
Larentiinae	<i>Xanthorhoe sajanaria</i>	Prout	1914	[36,44]
Larentiinae	<i>Xanthorhoe sajanaria djakonovi</i>	Vasilenko	1995	[100]
Larentiinae	<i>Xanthorhoe spadicearia</i>	Denis & Schiffermüller	1775	[44,46]
Larentiinae	<i>Xanthorhoe stupida aridela</i>	Prout	1937	[37]
Larentiinae	<i>Zola terranea</i>	Butler	1879	[34]
Sterrhinae	<i>Cleta jacutica</i> (Axel Hausmann: probably only one <i>Cleta</i> species occurring in Mongolia)	Viidalepp	1976	[36]
Sterrhinae	<i>Cleta perpusillaria</i>	Eversmann	1847	[65]
Sterrhinae	<i>Cyclophora albipunctata</i>	Hufnagel	1767	[46]
Sterrhinae	<i>Cyclophora pendularia</i>	Clerck	1759	[46]
Sterrhinae	<i>Glossotrophia rufotinctata</i>	Prout	1913	[49]
Sterrhinae	<i>Holarctias rufinaria</i>	Staudinger	1861	[58]
Sterrhinae	<i>Idaea aureolaria</i>	Denis & Schiffermüller	1775	[23,34,46]
Sterrhinae	<i>Idaea biselata extincta</i>	Staudinger	1897	[101]
Sterrhinae	<i>Idaea muricata</i>	Hufnagel	1967	[34]
Sterrhinae	<i>Idaea muricata minor</i>	Sterneck	1727	[40]
Sterrhinae	<i>Idaea nitidata</i>	Herrich-Schäffer	1861	[37]
Sterrhinae	<i>Idaea nudaria</i>	Christoph	1881	[37]
Sterrhinae	<i>Idaea pallidata</i>	Denis & Schiffermüller	1775	[34,40]
Sterrhinae	<i>Idaea rufaria</i>	Hübner	1799	[65]
Sterrhinae	<i>Idaea rusticata</i>	Denis & Schiffermüller	1775	[40,63]
Sterrhinae	<i>Idaea serpentata</i>	Hufnagel	1767	[23,34,36,41,63]
Sterrhinae	<i>Idaea straminata</i>	Borkhausen	1794	[34,91]
Sterrhinae	<i>Idaea straminata sibirica</i>	Djakonov	1926	[40]
Sterrhinae	<i>Ochodontia adustaria</i>	Fischer de Waldheim	1840	[23,34,65]
Sterrhinae	<i>Rhodometra sacraria</i>	Linnaeus	1767	[34]
Sterrhinae	<i>Rhodostrophia jacularia</i>	Hübner	1813	[21,23,34,36,40,41,63,65]
Sterrhinae	<i>Rhodostrophia tyugui</i>	Vasilenko	1998	[64]
Sterrhinae	<i>Rhodostrophia ustyuzhanini</i>	Vasilenko	2006	[49]
Sterrhinae	<i>Rhodostrophia vibicaria</i>	Clerck	1759	[34,46,63]
Sterrhinae	<i>Scopula aequifasciata</i>	Christoph	1881	[47]
Sterrhinae	<i>Scopula albiceraria</i>	Herrich-Schäffer	1847	[21,25,34,65]
Sterrhinae	<i>Scopula albiceraria vitellinaria</i>	Eversmann	1851	[40,41]
Sterrhinae	<i>Scopula beckeraria</i>	Lederer	1853	[34,40,41,63,65]
Sterrhinae	<i>Scopula beckeraria amataria</i>	Wehrli	1927	[36,40,65]
Sterrhinae	<i>Scopula cajanderi</i>	Herz	1903	[41,46]
Sterrhinae	<i>Scopula caricaria</i>	Reutti	1853	[46]
Sterrhinae	<i>Scopula contramutata</i>	Prout	1920	[34]
Sterrhinae	<i>Scopula cumulata</i>	Alphéraky	1883	[65]
Sterrhinae	<i>Scopula decorata</i>	Denis & Schiffermüller	1775	[21,23,34,41,63,65]
Sterrhinae	<i>Scopula decorata przewalskii</i>	Viidalepp	1975	[36,40,65]
Sterrhinae	<i>Scopula dignata</i>	Guenée	1858	[34]
Sterrhinae	<i>Scopula floslactata</i>	Haworth	1809	[37]
Sterrhinae	<i>Scopula frigidaria</i>	Möschler	1860	[47]
Sterrhinae	<i>Scopula immorata</i>	Linnaeus	1758	[23,34,36,40,46,63,65]

Sterrhinae	<i>Scopula immutata contramutata</i>	Prout	1913	[58]
Sterrhinae	<i>Scopula impersonata</i>	Walker	1861	[34]
Sterrhinae	<i>Scopula impersonata macescens</i>	Butler	1879	[40,41]
Sterrhinae	<i>Scopula incanata</i>	Linnaeus	1758	[34,41,65]
Sterrhinae	<i>Scopula latelineata</i>	Graeser	1892	[49]
Sterrhinae	<i>Scopula marginepunctata</i>	Goeze	1781	[23,34,63]
Sterrhinae	<i>Scopula nigropunctata</i>	Hufnagel	1767	[34]
Sterrhinae	<i>Scopula nigropunctata subcandidata</i>	Walker	1863	[37]
Sterrhinae	<i>Scopula ornata</i>	Scopoli	1763	[34,41,46]
Sterrhinae	<i>Scopula permutata</i>	Staudinger	1897	[34,39,65]
Sterrhinae	<i>Scopula rubiginata</i>	Hufnagel	1767	[34,40,41,63,65,91]
Sterrhinae	<i>Scopula ternata</i>	Schrank	1802	[25,34,36,46]
Sterrhinae	<i>Scopula tessellaria</i>	Boisduval	1840	[65]
Sterrhinae	<i>Scopula umbelaria</i>	Hübner	1813	[34,46,63]
Sterrhinae	<i>Scopula umbelaria graeseri</i>	Prout	1935	[41,65]
Sterrhinae	<i>Scopula virgulata</i>	Denis & Schiffermüller	1775	[23,34,40,41,46,63,65,91]
Sterrhinae	<i>Scopula virgulata substrigaria</i>	Staudinger	1900	[36]
Sterrhinae	<i>Timandra griseata</i>	Petersen	1902	[46]
Sterrhinae	<i>Timandra paralias</i>	Prout	1935	[34,40]
Sterrhinae	<i>Timandra reompta</i>	Prout	1930	[40,63]

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4.2 Manuscript II

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Alpha and beta diversity patterns of macro-moths reveal a breakpoint along a latitudinal gradient in Mongolia

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Little is known about the diversity and distribution patterns of moths along latitudinal gradients. We studied macro-moths in Mongolia along an 860 km latitudinal climatic gradient to gain knowledge on community composition, alpha, beta, and gamma diversity as well as underlying factors, which can be used as baseline information for further studies related to climate change. We identified 236 species of moths of ten families. Our study shows that the diversity of moths increased with the latitude, i.e., low species richness in the south and higher richness in the north. Moth community composition changed along the gradient, and we revealed a breakpoint of beta diversity that divided grassland and desert communities. In the desert, beta diversity was driven by species loss (i.e., nestedness), and few tolerant species existed with high abundance. In contrast, in the grassland, beta diversity was driven by species replacement with more unique species, (i.e., species which occurred only in one site). We found the lowest species diversity in the transitional zones dominated by few generalist species such as *Agrotis ripae* and *Anarta trifolii*. Low precipitation and an increasing number of grazing goats are drivers of species loss. We suggest different conservation strategies regarding the contrasting patterns of beta diversity in desert and grassland.

Biodiversity loss has become a pressing global issue in the last decades¹. Since biodiversity is crucial to maintain ecosystem functions, it is important to study the distribution of organisms and their response to climate change and human disturbance. Recently, a preponderance of studies reported strong declines in insect diversity^{2–5}. For example, in Germany's protected areas flying insect biomass declined by more than 75% within only 27 years, however, the cause is still unclear⁶.

As Simmons et al.³ stated, some “global” studies on insect decline should be cautiously interpreted because results based on particular locations do not represent a global scale. Robust insect diversity data representing all major biomes of the world are required⁷. However, data availability is strongly biased across the world towards Europe and North America, especially regarding systematically collected long-term data. Tropical regions are poorly studied. The same is true for the most parts of central and eastern Asia, especially in regard to the diversity and distribution patterns of moths in eastern Russia, northern China and Mongolia. During a previous literature review of studies on geometrid moths, we found that long-term data were unavailable from these regions⁸. This study is an important “puzzle piece” in filling this gap for future research.

There are approximately 1550 species of Lepidoptera reported in Mongolia⁹; however, there is no complete checklist available. In geometrid moths, a recent checklist reported 388 observed species, but species richness was estimated to be 663 ± 56^8 . Recently, 21 new species have been recorded from western and central Mongolia¹⁰ and the family Alucitidae was first time reported for Mongolian fauna in 2015 in the Mongolian Altai Mountains¹¹. Moreover, several species new for the fauna of Mongolia were reported in Sphingidae, Noctuidae, Cossidae, and Ypsolophidae^{12–16}. In the Global Biodiversity Information Facility (GBIF), 919 species of 30 families of Lepidoptera are recorded for Mongolia¹⁷. This is certainly an underestimate, and not all occurrence data in the literature have been uploaded in GBIF. To summarize, data have been collected incompletely, non-continuously

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Title : Alpha and beta diversity patterns of macro-moths reveal a breakpoint along a latitudinal gradient in Mongolia

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Abstract

Little is known about the diversity and distribution patterns of moths along latitudinal gradients. We studied macro-moths in Mongolia along an 860 km latitudinal climatic gradient to gain knowledge on community composition, alpha, beta, and gamma diversity as well as underlying factors, which can be used as baseline information for further studies related to climate change. We identified 236 species of moths of ten families. Our study shows that the diversity of moths increased with the latitude, i.e., low species richness in the south and higher richness in the north. Moth community composition changed along the gradient, and we revealed a breakpoint of beta diversity that divided grassland and desert communities. In the desert, beta diversity was driven by species loss (i.e., nestedness), and few tolerant species existed with high abundance. In contrast, in the grassland, beta diversity was driven by species replacement with more unique species, (i.e., species which occurred only in one site). We found the lowest species diversity in the transitional zones dominated by few generalist species such as *Agrotis ripae* and *Anarta trifolii*. Low precipitation and an increasing number of grazing goats are

drivers of species loss. We suggest different conservation strategies regarding the contrasting patterns of beta diversity in desert and grassland.

Introduction

Biodiversity loss has become a pressing global issue in the last decades ¹. Since biodiversity is crucial to maintain ecosystem functions, it is important to study the distribution of organisms and their response to climate change and human disturbance. Recently, a preponderance of studies reported strong declines in insect diversity ²⁻⁵. For example, in Germany's protected areas flying insect biomass declined by more than 75 percent within only 27 years, however, the cause is still unclear ⁶.

As Simmons et al. ³ stated, some "global" studies on insect decline should be cautiously interpreted because results based on particular locations do not represent a global scale. Robust insect diversity data representing all major biomes of the world are required ⁷. However, data availability is strongly biased across the world towards Europe and North America, especially regarding systematically collected long-term data. Tropical regions are poorly studied. The same is true for the most parts of central and eastern Asia, especially in regard to the diversity and distribution patterns of moths in eastern Russia, northern China and Mongolia. During a previous literature review of studies on geometrid moths, we found that long-term data were unavailable from these regions ⁸. This study is an important "puzzle piece" in filling this gap for future research.

There are approximately 1550 species of Lepidoptera reported in Mongolia ⁹; however, there is no complete checklist available. In geometrid moths, a recent checklist reported 388 observed species, but species richness was estimated to be 663 ± 56 ⁸. Recently, 21 new species have been recorded from western and central Mongolia ¹⁰ and the family Alucitidae was first time reported for Mongolian fauna in 2015 in the Mongolian Altai Mountains ¹¹. Moreover, several species new for the fauna of Mongolia were reported in Sphingidae, Noctuidae, Cossidae, and Ypsolophidae ¹²⁻¹⁶. In the Global Biodiversity Information Facility (GBIF), 919 species of 30 families of Lepidoptera are recorded for Mongolia (¹⁷). This is certainly an underestimate, and not all occurrence data in the literature have been uploaded in GBIF. To summarize, data have been collected incompletely, non-continuously with different efforts, at specific locations, published, and scattered in the literature, thus rendering it impossible to investigate the changes of moth diversity at temporal and spatial scales.

In response to this need, our study focuses on moth diversity and species composition across a latitudinal gradient. Biodiversity across latitudinal gradients is especially important to study as they are the largest and strongest climatic gradients globally. Alpha diversity is the diversity of local communities, while beta diversity is the spatial change in composition between local communities¹⁸. Beta diversity links alpha and gamma diversity, i.e., large-scale diversity. To measure alpha diversity, we used Hill numbers: species richness, Shannon diversity and Simpson diversity. Hill numbers are a linear measure of diversity, which traditional indices are not, they have the same units and are comfortable to compare sites^{19,20}. They account for different levels of diversity and mirror species richness and evenness.

Measuring alpha diversity is vital for conservation purposes since it quantifies the biodiversity of a particular habitat through the baseline measure of species presence and abundance within a local community. Species richness (number of species present) of moths can reflect habitat quality and be an indicator of species sensitivity to environmental changes^{21,22}. Pronounced declines of species richness along the latitudinal gradient from the equator to the poles have been demonstrated for almost all taxa in different regions of the world^{23–25,26}. This general trend of declining diversity and richness across latitudes is accompanied by environmental factors such as temperature along altitudinal gradients, land use, and precipitation²⁷. As precipitation increases with latitude in most parts of Central Asia^{27,28}, this could regionally superimpose patterns of moth richness and diversity patterns.

One crucial question is how species composition changes along latitudinal gradients, i.e., whether the change is due to species replacement or species loss/gain. Different types of measures for beta diversity are available^{29–32}. We applied the widely used method by Baselga et al.³³, which partitions beta diversity into turnover and nestedness. Doing so enables us identifying the leading causes for the differentiation and is further useful for implementing better conservation strategies. Turnover reflects the process of environmental filtering, while nestedness reflects colonization, such as the effects of a lack of available resources³⁴.

In Mongolia, on the one hand, a latitudinal or climatic gradient can be one type of environmental filtering. Mongolia is located between 41°35' and 52°06' N. This climatic gradient is characterized by higher rainfall and lower temperature in the north and lower precipitation and higher temperature in the south³⁵.

On the other hand, grazing patterns represent another type of environmental filtering. In Mongolia, the dominant land use type in the country is free-ranging livestock grazing, thus overgrazing can be the cause of colonization or extinction from one habitat to another³⁶. Recently, the number of livestock is increasing, and nowadays, herders

tend to be more sedentary than former herders, which causes local to regional pasture degradation. Moreover, the effects of climate change and overgrazing are accelerating each other in a positive feedback loop ³⁶.

We tested the hypothesis that species diversity and species richness declines with latitude in Mongolia. Moreover, we hypothesized that precipitation positively influences diversity and richness, and that (over-) grazing negatively influences diversity and richness. These (and possibly other environmental variables) could regionally superimpose the expected large-scale latitudinal patterns, resulting in inverse latitudinal gradient patterns and / or breakpoints.

In addition, we investigated (without an a priori hypothesis), how moth species composition or beta diversity differed between sites, and if beta diversity was mainly influenced by spatial turnover (species replacement) or nestedness (species loss or gain). Moreover, our study provides new data on the regional species pool of Mongolia, i.e., how many and which moth species are present, and explores the gamma diversity of moths in Mongolia.

This is the first comprehensive study on macro-moths over large geographic scales in Mongolia and it forms the baseline for future studies. It is necessary to gain knowledge of moth diversity and distribution patterns at local and large-scale level (i.e., alpha and gamma diversity) and how local diversities are organized and vary at large-scale (beta diversity) ^{37,38} to develop an effective conservation strategy for the Mongolian moth species and their habitats. Different conservation strategies are required depending on the beta diversity patterns (nestedness or turnover). For the areas with species loss, it is recommended to protect certain species-rich sites; in contrast, for the areas with species replacement, several large different types of sites are needed to be protected³³. Species-poor sites usually hold only a subset of species-rich sites (³⁹). In a study of birds and snails, habitat homogeneity was responsible for the nestedness of the animal communities ^{40,41}. However, it must be noted that habitat simplification can reduce local species richness, and the whole community would be similar, leading to homogenization ^{42,43}. Thus, it is vital to see both, the smaller more detailed picture as well as the bigger picture in order to consider the fragmentation between the sites and successfully implement conservation plans, both locally and regionally. If the temperature keeps rising and livestock numbers keep increasing, even species-rich sites would be transformed into species-poor sites, making the whole community unable to sustain itself. Some species will disappear due to the loss of suitable habitat, and only species which have tolerance to the disturbance will be left ^{39,44}. Moreover, in the face of climate change northern sites have the potential of becoming more similar to current day ecological conditions in southern sites. This could lead to homogenization, resulting in a less diverse assemblage. By tracking moth biodiversity along a latitudinal gradient, this study is using

a space-for-time substitution (e.g., southern sites could predict future results for northern sites). Thus, our results not only provide necessary baseline reference data, but also essential insights on the future of biodiversity change in a warming world.

Results

Alpha diversity. In total, we caught 11,115 macro-moth individuals of 236 species of ten families: 7 Cossidae, 3 Drepanidae, 35 Erebididae, 58 Geometrididae, 6 Lasiocampidae, 108 Noctuididae, 7 Notodontidae, 1 Sesiidae, 10 Sphingidae, and 1 Zygaenidae (see the full species list in Table S2 in the supplementary material). Estimated species richness was 461 (iChao1, SE: 22.96, lower 95%: 392, upper 95%: 581), therefore, our samples cover 51% of the estimated species richness. The three most species-rich families were Noctuididae (45.8% of species), Geometrididae (24.6%) and Erebididae (14.8%) (Fig. 1). The other families together constituted 14.8% of all species and we combined them into one group (“Other”).

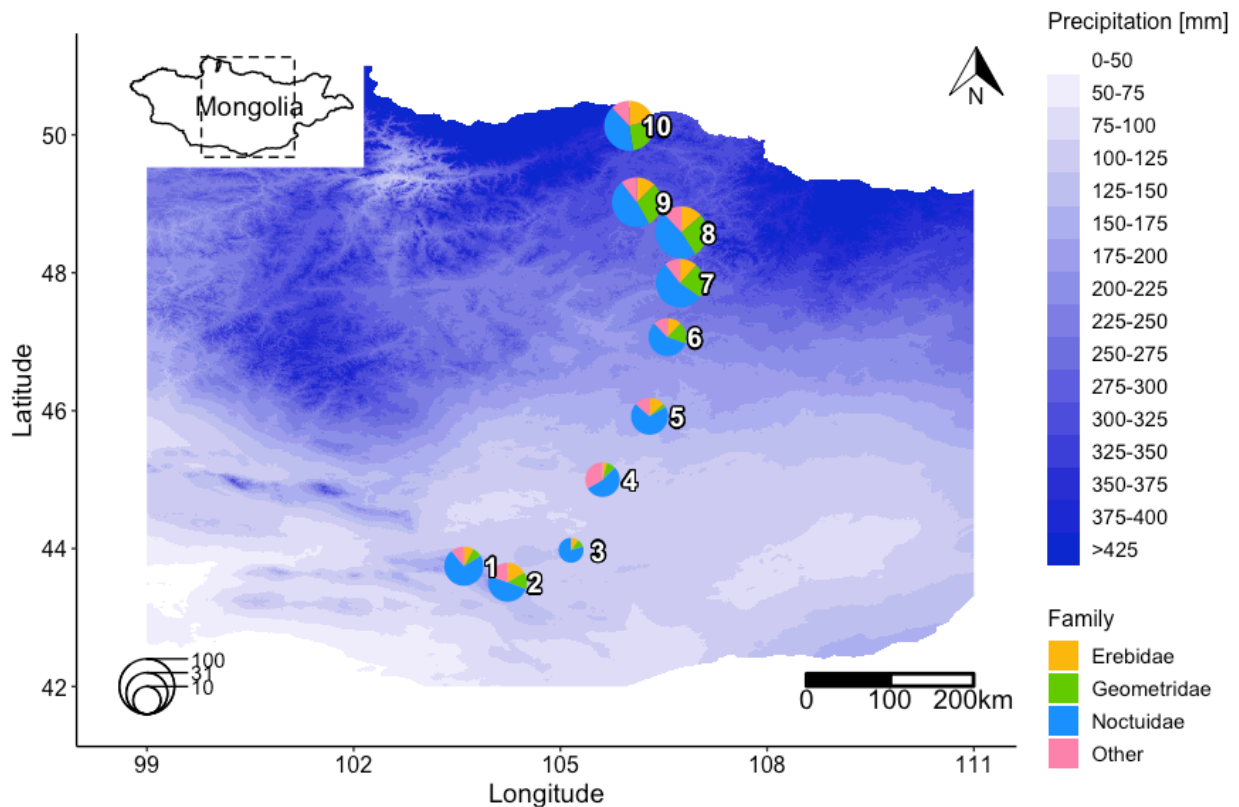


Figure 1 Study area with pie charts showing the percentage species composition of the main moth families: Erebididae, Geometrididae, Noctuididae and all other families along the precipitation gradient. In group *Other*: These families are combined: Cossidae, Drepanidae, Lasiocampidae, Notodontidae, Sesiidae, Sphingidae, and Zygaenidae. Pie sizes correspond to species richness of the site (legend on the lower left side) See

species richness and diversity of each site in Table S3 in supplementary material. Figure was produced using R software (version 3.6.3, R Core Team, <https://www.r-project.org/>).

Noctuidae had the highest abundance represented with 8839 specimens, with the commonest species *Agrotis ripae* Hübner, with 5986 individuals collected at nine out of ten sites, especially dominating the sites in the desert. Moth family composition patterns changed along the latitudinal gradient. In the grassland sites, Erebidae, Geometridae, and Noctuidae (and “Other”) shared similar proportions whereas Noctuidae heavily dominated in all desert sites (Fig. 2). K-means clustering separated all sites into two groups of southern “desert” (1–5) and northern “grassland” (6–10) sites (see scree plot in Fig. S1 in supplementary material).

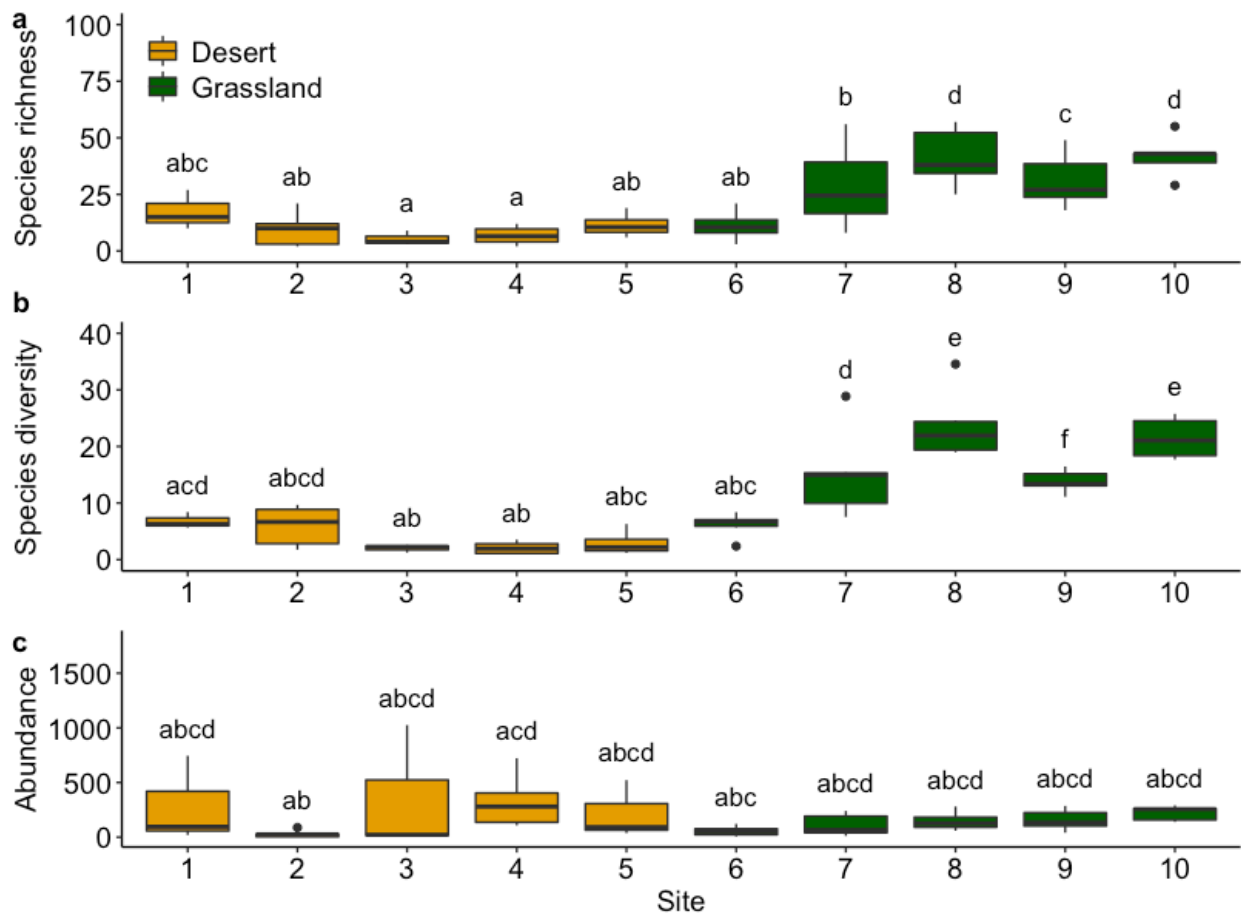


Figure 2 Species richness, Shannon diversity and abundance of ten sites along the latitudinal gradient. Diversity metrics were compared with Wilcoxon test based on the sampling nights of each site. Different letters show significant differences between sites. See the further comparison of species richness, species diversity and abundance at the family level in Fig. S2, Table S4, Table S5 and Table S6 of supplementary material.

Overall, moth species richness (Fig. 2a) , species diversity (Fig. 2b), and abundance (Fig. 2c), of the grassland sites (6–10) were significantly higher ($p < 0.005$) than those of the desert sites (1–5). Among the desert sites, species diversity at Site 2 was higher than in all other sites. The most species-rich site was site 8 (grassland), and the most species poor-site was Site 3 (desert). We investigated which functional group of vegetation was responsible for high species richness of moths. As a result of GLM, *forb* impacted the species richness of moths (LM: $R^2=0.55$, $p = 0.012$). Hill numbers were positively correlated with precipitation and forb cover, and negatively correlated with temperature, wind and number of goats (Table 1).

Table 1 Pearson correlation coefficients of Hill numbers with environmental variables

Hill numbers	Precipitation	Temperature	Forb cover	Goat number	Wind
Species richness	0.92***	-0.76***	0.99***	-0.75***	-0.91***
Shannon diversity	0.89***	-0.73***	0.96***	-0.80***	-0.87***
Simpson diversity	0.92***	-0.76***	0.92***	-0.75***	-0.88***

Species abundance and richness pattern. The ten most abundant species responded differently to annual temperature and annual precipitation. *Agrotis ripae* and *Anarta trifolii* showed a decelerating exponential response to increasing annual temperature (Fig. S3 in the appendix), whereas the abundance of *Lithostege* sp. 2 was increasing with increasing annual precipitation. *Hyles gallii*, *Lygephila lubrica* and *Isturga arenacaria* were mainly present at the more humid northern sites. At low temperature and high precipitation all ten species coexisted, whereas at high temperature and low precipitation, only two species (*Agrotis ripae*, *Anarta trifolii*) formed the community alone (Fig. 3a, b). A linear regression model shows that species richness of moths was decreasing with increasing annual temperature ($R^2 = 0.36$, $p < 0.001$) and increasing with rising annual precipitation ($R^2 = 0.57$, $p < 0.001$). In the grassland sites, species richness was higher than in the desert sites (Kruskal-Wallis Test: $p < 0.001$) (Fig. 3c, d).

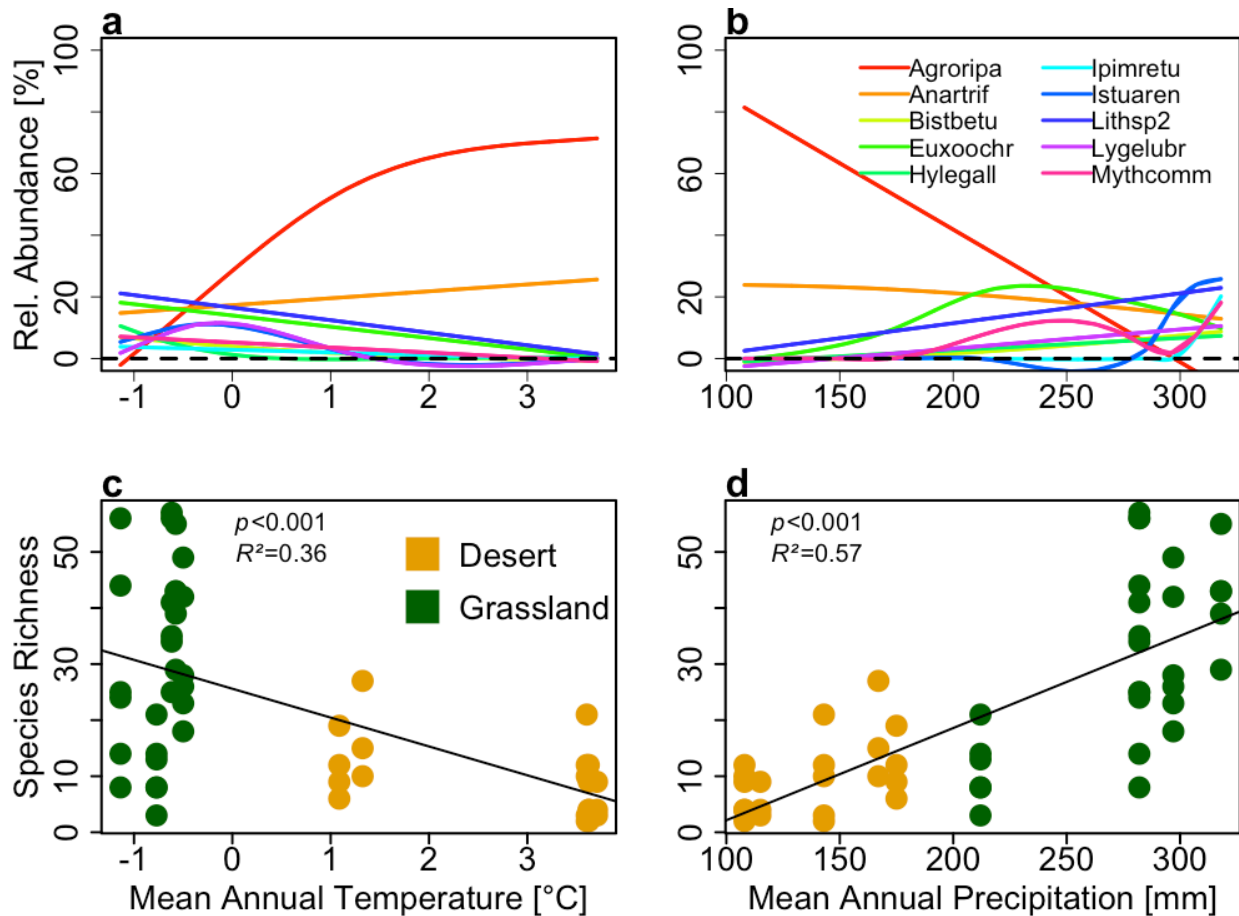


Figure 3 Species relative abundance and species richness impacted by environmental variables. X axes titles are printed only for the lower graphs. GAM shows a) the relative abundance vs. mean annual temperature and b) the relative abundance vs. mean annual precipitation. The general linear regression model demonstrates that both species richness is impacted by c) mean annual temperature and d) mean annual precipitation. Species abbreviations: *Agrotis ripae* (Agroripa), *Anarta trifolii* (Anartrif), *Biston betularia* (Bistbetu), *Euxoa ochrogaster* (Euxoochr), *Hyles gallii* (Hylegall), *Ipimorpha retusa* (Ipimretu), *Isturgia arenacearia* (Istuaren), *Lithosteges sp2* (Lithsp2), *Lygephila lubrica* (Lygelubr), *Mythimna comma* (Mythcomm).

We found 96 unique species in total, i.e., species which occurred only in one site. Overall, the unique species numbers of the grassland sites ($n = 70$) were higher than those of the desert sites ($n = 26$, Kruskal-Wallis Test: $p < 0.005$). Site 3 had only one unique species, whereas Site 10 had 27 unique species (See Fig. S4 in supplementary material).

Beta diversity According to K-means clustering we classified the ten sites into two groups and performed a correspondence analysis based on the family matrix, which indicated clear distinction in the composition of major families in two groups (Fig. 4). Noctuidae and Cossidae were more abundant in the desert sites, while other families were remarkably abundant in the grassland sites. Distinction between these groups was significant (Permanova: $R^2= 0.37$, $p<0.006$).

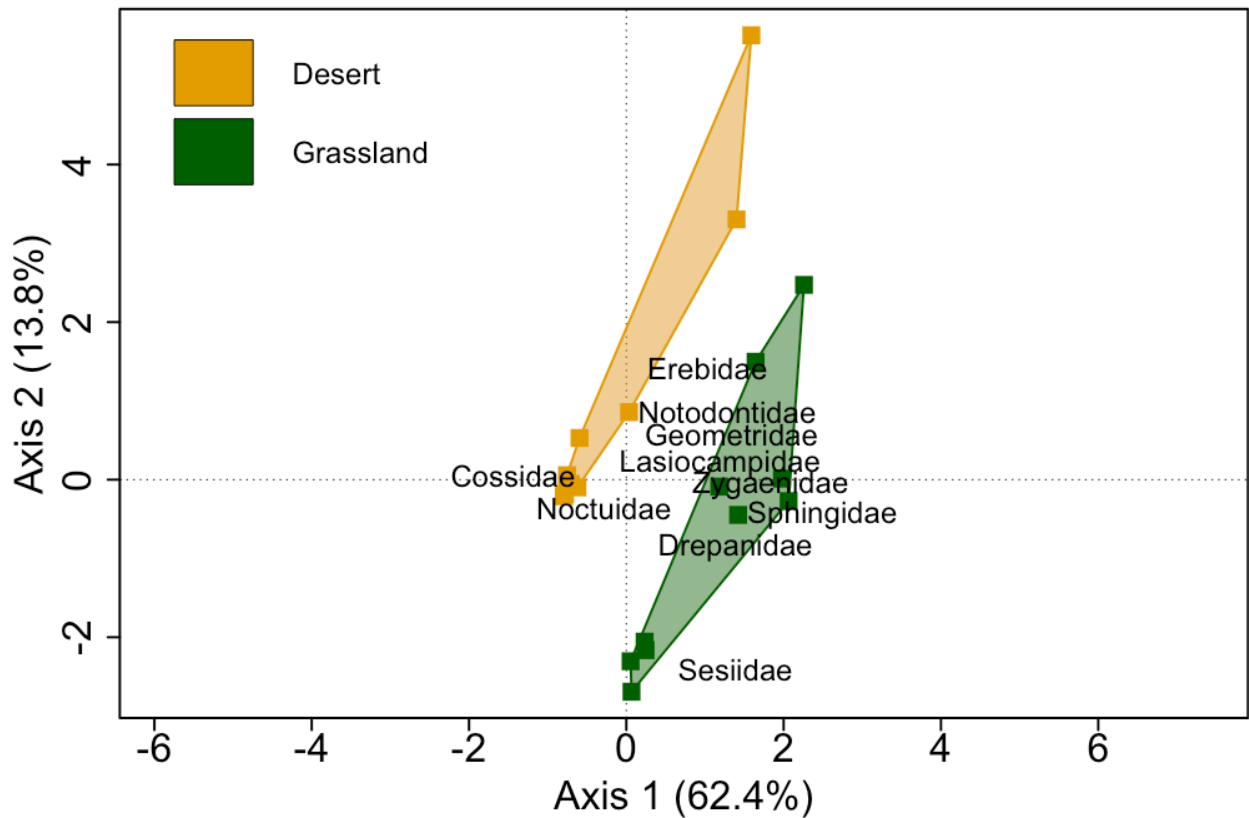


Figure 4 Correspondence analysis of the major families sampled from all sites separated markedly desert (yellow polygon) and grassland (green polygon) sites. Noctuidae and Cossidae were more associated with desert sites, whereas other families were associated with grassland sites. First two axes of the graph together explain 76.2 % of the variation.

Venn diagrams show the species overlap between the moth composition of the desert and the grassland sites in four family groups. The highest overlap was in Noctuids, followed by Erebids and others, the lowest overlap was in Geometrids (See Fig. S5 in supplementary material).

Mean beta diversity of macro-moth species among the sites as calculated with Jaccard's index was intermediate; $\beta_j = 0.82$ (range = 0.78 – 0.86). The outer sites of the gradient with the more extreme environmental conditions had the highest average beta diversity, while sites in the middle had the lowest average beta diversity (Fig. 5a). A linear regression model indicated that with increasing distance Jaccard's similarity decreases ($R^2 = 0.52$ $p < 0.001$) (see Fig. S6 in supplementary material).

We checked the contributions of spatial turnover and nestedness to the result of mean beta diversity. Taken together, the contribution of spatial turnover (mean $\beta_t = 0.69$; range = 0.60 – 0.77) was much higher than that of nestedness (mean $\beta_n = 0.13$; range = 0.08 – 0.27), which means that species replacement was higher than species loss or gain.

Regarding pair-wise beta diversity, Sites 2 and 10 were significantly higher than other sites in terms of turnover (Fig. 5b). Only Site 3 was significantly higher in terms of nestedness (Fig. 5c), all other sites, except Site 8 were not significantly different. The sites with the highest and lowest average species replacement were the same as those with the highest and lowest beta diversity (Fig. 5a).

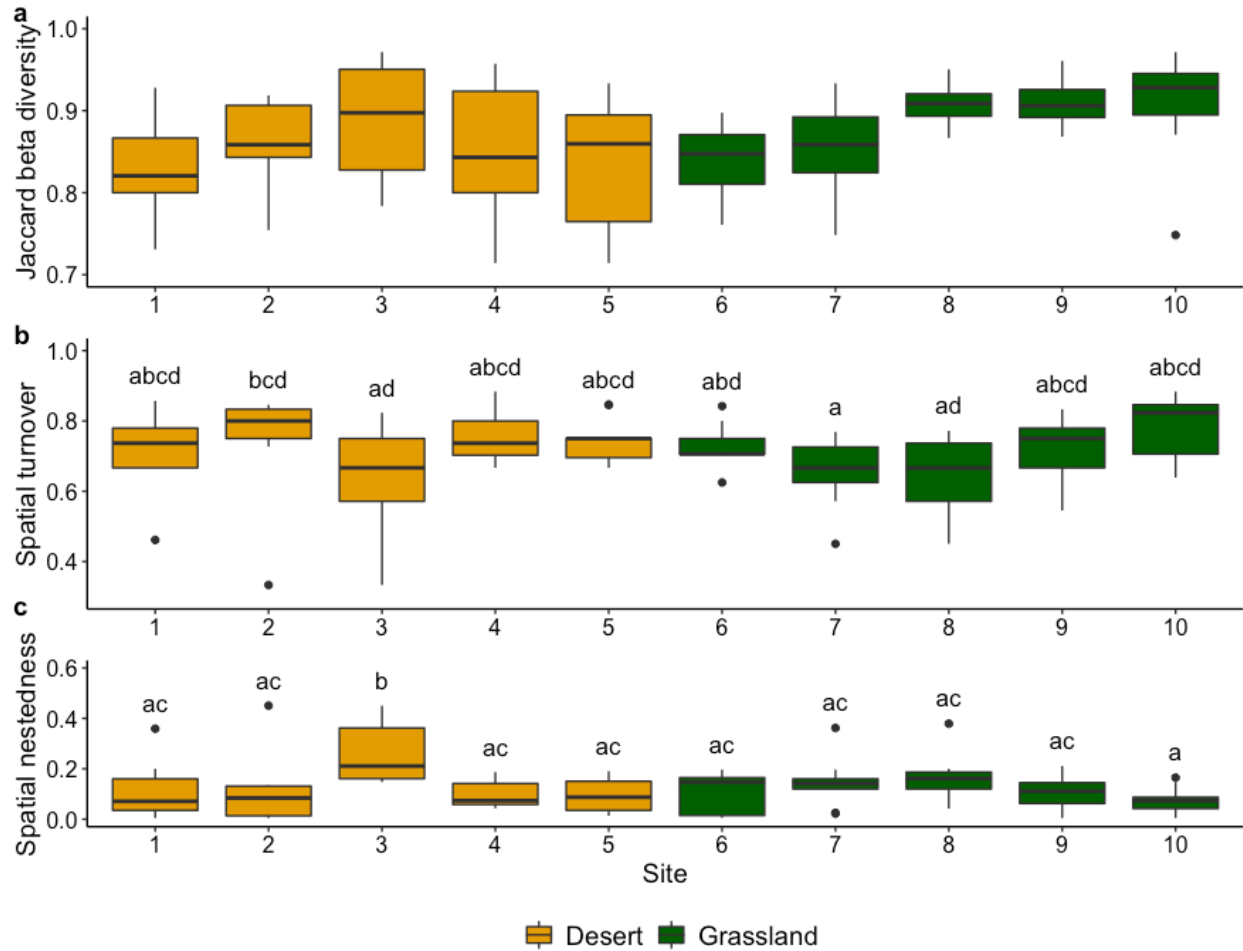


Figure 5 Mean pair-wise a) Jaccard beta diversity b) spatial turnover c) spatial nestedness of the ten study sites. Diversity metrics were compared with Wilcoxon test based on the average diversity measures of each site. Different letters show significant differences between sites.

We found a breakpoint at 46 °N as a result of the piecewise regression of Jaccard's beta diversity, spatial turnover, and spatial nestedness versus latitude (Figure 6). The fit of the piecewise regression models was significantly higher than the simple linear regression models for all components: R^2 increased from 0.02 to 0.16 (Anova: $F_{2, 52} = 5.26$, $p < 0.001$) for Jaccard beta diversity, from 0.01 to 0.19 (Anova: $F_{2, 52} = 7.36$, $p < 0.001$) for spatial turnover, and from 0.05 to 0.26 (Anova: $F_{2, 52} = 8.50$, $p < 0.001$) for spatial nestedness.

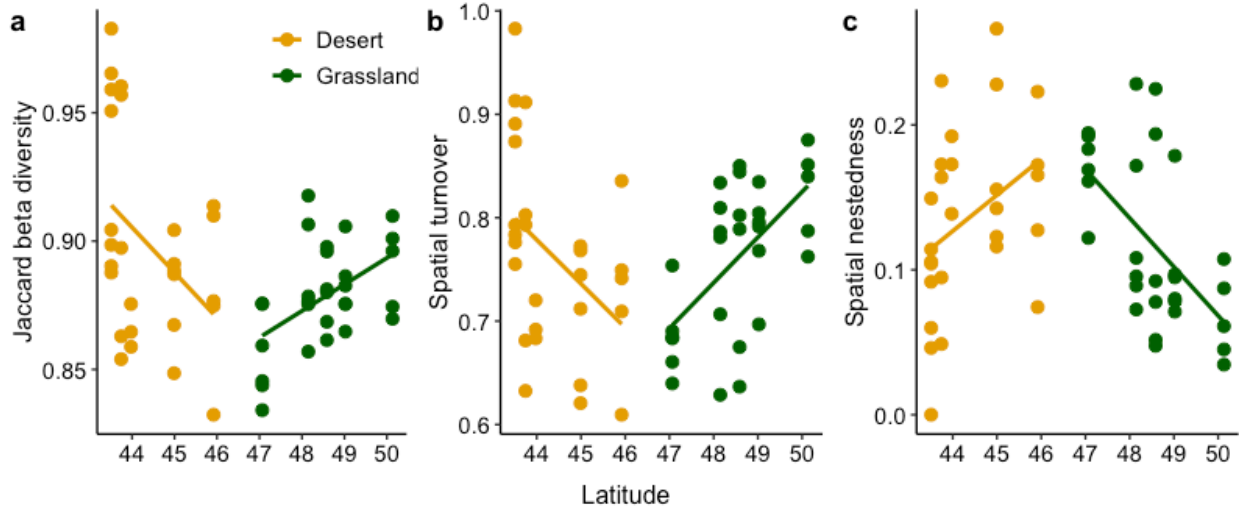


Figure 6 Beta diversity measures along the latitudinal gradient: a) Jaccard's beta diversity along latitude b) spatial turnover along latitudinal gradient and c) spatial nestedness along latitude. Desert sites (1-5), grassland sites (6-10)

Jaccard's beta diversity indices significantly differed above (slope=0.004) and below 46°N (slope=-0.09) and showed an opposing trend ($R^2= 0.16$ $p < 0.001$). Moreover, spatial turnover and nestedness responded in opposite directions with latitude and were significantly different in the desert and the grassland biomes. In the desert, species turnover showed a decreasing trend (slope= -0.54) ($R^2= 0.19$, $p < 0.001$); in contrast, nestedness showed an increasing trend (slope=0.45) ($R^2= 0.26$, $p < 0.001$). In the grassland, species turnover (slope=0.03) and nestedness (slope=-0.02) showed contrasting trends. In the desert sites, moth communities' species loss or gain was dominant, while for the grassland sites, species replacement played the dominant role. The breakpoint of beta diversity pattern was matched by an RDA analysis of plant communities (See Fig. S7 in supplementary material). We found also a breakpoint at 46° N as a result of the piecewise regression of precipitation ($R^2= 0.96$, $p < 0.001$) and temperature ($R^2= 0.89$, $p < 0.001$).

The next step was to test the correlation between environmental variables and beta diversity components, and environmental variables were affecting spatial turnover and spatial nestedness differently. *Precipitation* and *vegetation cover* were positively correlated with turnover, whereas negatively correlated with nestedness. In contrast, *temperature*, *livestock number*, and *wind* were negatively correlated with turnover, while positively correlated with nestedness (Table 2). In the desert, none of the environmental variables was significant for nestedness.

Table 2 Pearson correlation coefficients between environmental variables and beta diversity measurements for total (along whole latitudinal gradient), above ($>46^\circ$) and below ($<46^\circ$) the 46° of latitude. Significant variables are shown in bold with stars indicating the level of significance.

		Turnover	Nestedness
Precipitation	Total	0.22	-0.34**
	$>46^\circ$	0.60***	-0.56**
	$<46^\circ$	0.18	-0.19
Temperature	Total	-0.006	0.14
	$>46^\circ$	0.22	-0.27
	$<46^\circ$	0.09	-0.06
Vegetation cover	Total	0.41**	-0.45***
	$>46^\circ$	0.55**	-0.49**
	$<46^\circ$	0.36*	-0.34
Livestock number	Total	-0.40**	0.41**
	$>46^\circ$	-0.54**	0.50**
	$<46^\circ$	-0.23	0.22
Wind	Total	-0.11	0.25
	$>46^\circ$	-0.56**	0.52**
	$<46^\circ$	0.40*	-0.37
Altitude	Total	-0.05	0.18
	$>46^\circ$	-0.57**	0.57**
	$<46^\circ$	0.37	-0.36

Using procrustes analysis we compared the distance matrix of moth species with distance matrices of *vegetation* and *livestock*. The matrix of moth species was highly significantly correlated with both matrices of *vegetation* ($r=0.74$, $P=0.001$) and *livestock number* ($r=0.80$, $P=0.002$), thus corroborating their strong influence on moth community patterns.

In addition, we analyzed if there existed an interaction between environmental variables and biome types and the species richness and diversity of macro-moths (see the results of the negative binomial generalized regression and linear regression in Table S8 in the supplementary material). Interaction effects were only found for the *livestock*, *wind*, and *elevation*. Depending on the biome type species richness of macro-moths responded to *livestock*, *wind*, and *elevation* differently. In the grassland these factors affected the species richness of moths negatively, whereas in the desert there was no effect (Fig. S8).

Discussion

We studied alpha and beta diversity of macro-moths and associated environmental variables along a large-scale latitudinal gradient in Mongolia for the first time. Against our expectation, we detected two distinct moth communities along the latitudinal gradient, which significantly changed between Site 5 (Dundgobi Aimag) and Site 6 (Tuv Aimag) at 46° N. We assume that this distinction is driven by the pronounced climatic gradient, namely *precipitation* and *temperature*. In piecewise regression of diversity on the *precipitation* and *temperature* we demonstrated this split at 46° N. As we hypothesized, we observed higher moth species richness and species diversity in the grassland sites than in the desert sites. In contrast, moth abundance was lower at grassland sites than in the desert sites. This contradicts with a study on darkling beetles in Mongolia in which species richness declined gradually with latitude. This contrast between moths and beetles could be explained by a higher temperature and desiccation tolerance observed in beetles' ⁴⁵. Our study results were in line with the study of Ahlborn et al. ²⁷, who studied plant communities. In both studies, species richness was low in Site 3 (Tsogtovoo Soum, Khetsuu khoshuu) indicating the need for extra conservation for these transitional sites. In terms of the moth population, our observation of higher species richness and lower abundance in the grassland could be explained by the theory of competitive exclusion. There is higher plant heterogeneity in the grassland, which could ultimately reduce competitive exclusion in the moth population, allowing for the maintenance of several species (high richness) at a similar proportion (similar abundance across species/ high evenness). In contrast, lower species richness and higher abundance of certain tolerant species adapted to the few plant species growing in desert prevail ².

The differentiating species richness and species diversity of moths between the desert and the grassland sites could be explained by the biotic (*plant species richness* and *livestock number*) and abiotic (*precipitation* and *wind*) variables, which were significantly correlated with the diversity of moths as measured by Hill numbers. Since herbivorous insects rely on plants, both in larval and adult stages, as their food and habitat, it is logical to expect a higher moth species richness in areas with a higher plant species richness⁴⁶. Indeed, variable *Forb* was highly positively correlated with the Hill numbers. In contrast, variable *Goat* was the significant factor among all livestock types and negatively correlated with moth species richness. Herders raise high numbers of goats for income from cashmere, especially in Gobi desert, as one of the common export products of Mongolia³⁵. Water and energy (i.e. temperature) availability are the important factors determining overall species richness along the latitudinal gradient. *Precipitation* is the limiting factor for species diversity in the south, while *temperature* is the limiting factor in the north in several taxa^{24,25}. In our study, only *precipitation* was a significant variable, positively correlated with the Hill numbers.

While variable *Wind* was negatively correlated with the Hill numbers and similar patterns were observed in other studies related to wind on moth catches⁴⁷. In the first year of the sampling period, strong wind negatively affected the southern sites' catch successes.

In a study of moths in Finland⁴⁸ the authors observed a contrasting pattern with species that were expanding their ranges poleward due to global warming and were increasing in species richness and decreasing in abundance over time in higher latitudes. The higher abundances in the desert sites in our case were, however, due to only the two heavily dominant Noctuidae species, namely *Agrotis ripae* and *Anarta trifolii*.

At almost all sites, *Agrotis ripae* and *Anarta trifolii* occurred; they were the most abundant species. *A. ripae*, which is called “sand dart moth”, lives mainly in sand dune areas; the caterpillars rest in the sand during the daytime and come out to feed at night⁴⁹. Habitats are characterized by bare ground with sparse vegetation. The study of Spalding et al.⁵⁰ showed that bare ground is an essential factor for the sand dune moth species, such as *Luperina nickerlii*; disturbance could be helpful to create bare ground. Due to desertification and livestock trampling, the soil becomes more sandy and loose; this will create more suitable living conditions for *A. ripae*. Both *A. ripae* and *A. trifolii* can be regarded as generalists and highly migrant species. Their mobility increases with temperature⁵¹. Thus, both species appear to be suitable indicators of global warming and desertification.

In the grassland sites, the number of unique species was higher than in the desert sites, which implies that in suitable habitats, like grassland sites, more specialists occurred that were adapted to specific habitats. In contrast, in harsher, more arid habitats like desert sites, more generalists occurred. Rabl et al.⁴⁶ found only a small number of unique species in a relatively species-poor rainforest area (i.e., in a creek habitat). Similarly, Beitzholtz and Franzen⁵¹ reported that specialists prefer suitable habitats; they are prone to stick to their habitats and vulnerable to extinction. Species, such as generalists, are even benefiting disturbance, while specialists are declining^{1,4}. Moreover, the number of generalists and specialists are related to beta diversity. Beta diversity increases as the number of specialists increase^{52,53}.

Moth species' host plant preferences could explain differences in major family composition in the desert and the grassland sites. In the desert sites, the moth assemblage composition mainly consists of Noctuids and Cossids, while proportions of Geometrids, Erebid, and others were low. In contrast, family ratios were almost the same in all grassland sites. Many Noctuids are not restricted to specific habitats and are generalists (or even cosmopolitans) in comparison to members of other families. For

example, *A. ripae* is polyphagous⁵⁴ and usually, polyphagous species can better survive in disturbed areas.

Most adults of Sphingidae, Geometridae, and Arctiinae usually feed on flower nectar, while most caterpillars of Notodontidae, Drepanidae, and Lasiocampidae mostly feed on the leaves of trees and shrubs⁴⁹. Several species whose larvae feed on trees and undergrowth were found in Sphingidae, Geometridae, and Arctiinae in the grassland sites; thus, we suggest that surrounding forest and shrubs were also responsible for the higher species richness of these families in the grassland sites. In addition, the species richness of Arctiinae is high in areas with complex vegetation types⁵⁵. This can explain the high richness of Erebidae in the grassland sites. Venn diagrams (Fig. S5) also showed that species overlap between the desert and the grassland sites of Noctuids, Erebids, and others were similar in percentage (20–27%); in contrast, the species overlap of Geometrids was very low with only four species in common (7.4%). Geometrid moths are sensitive to the environmental changes; thus, the low overlap of Geometrids could indicate better habitat quality in the grassland sites compared to the desert sites.

Beta diversity was mainly driven by species replacement rather than species nestedness. Average pair-wise beta diversity and spatial turnover were high in the external sites and gradually decreased towards the middle of the gradient; in contrast, average nestedness was high in the middle and low in the outer parts. The macro-moth assemblages at northern and southern sites were shaped by forest-steppe and desert, habitats that are distinct from each other. Habitat differences gradually decrease to the middle part, where the steppe runs in gently undulating terrain and becomes a transition zone between these habitats resulting in less difference among moth assemblages. The higher beta-diversity in the outer parts results from high species turnover, while nestedness or difference in species numbers played a less critical role. A similar diversity pattern was reported by Paknia et al.⁴⁵ in Mongolian tenebrionid beetle communities. Generally, turnover is due to abiotic factors, while nested patterns may be attributed to species loss caused by high *livestock numbers* and low *precipitation*.

Intensive land use transforms habitats, making them more similar. The more similar habitats become, the less diverse species they can support. Relative to the larger pool of species found across more distinct habitats, this more homogeneous subset of species becomes capable of dispersing further in more homogeneous habitats. In addition to enhanced dispersal capabilities, more homogenous habitats can support more generalist species that have broad niches. Overall, such traits can decrease beta diversity. However, there is a nuanced caveat. Due to the homogeneity of the habitat, a few tolerant species may persist, leading to species loss which can result in higher beta diversity due to nestedness³⁷. In comparison, we observed species replacement

happened in areas with high precipitation and high vegetation cover which increases the beta diversity.

Average beta diversity along the latitudinal gradient had a breakpoint, which was revealed at 46° N, indicating a change in moth communities between desert and grassland sites. In arid areas south of 46° N, turnover decreased, and nestedness increased. In contrast, in wet areas north of 46° N, turnover increased, and nestedness decreased. In arid areas species richness decreased, and beta diversity was due to species loss, indicating lower productivity within a harsh environment. The decreasing turnover in the southern sites thus mirrors the physical limiting factor (i.e., lower precipitation). This contrasting patterns of turnover and nestedness have been documented in several studies ^{23,52}.

A breakpoint in both precipitation (mean annual precipitation: 193 mm) and temperature (mean annual temperature: 0.15 °C) was also found at 46° N. Since the breakpoints are overlapping, we predict that as global temperatures continue to rise, the grassland sites will become more similar to desert sites. In turn, we predict that this trend towards habitat homogenization will lead to a more nested pattern of moth diversity.

Temperature had no significant effect on beta diversity patterns of moths along the latitudinal gradient, both above and below 46°N. Higher precipitation rate, and higher vegetation cover and diversity were responsible for the higher beta diversity in northern sites. *Precipitation* was also a significant variable for species richness.

The results of Procrustes analysis showed that vegetation structure and livestock composition determined the moth assemblage pattern. Along the whole gradient, the effects of *precipitation*, *vegetation cover*, and *vegetation richness* on the species richness and diversity of macro-moths did not change regardless of biome type. However, *livestock*, *altitude* and *wind* affected the species richness and diversity of moths differently, depending on the biome type. In the desert, the vegetation is scarce even without livestock grazing, and the climatic effect is stronger than the effect of livestock grazing. The dynamic equilibrium model could explain the insensitivity of macro-moths of the desert to the number of livestock. In the arid environment, the impact of precipitation overrides the influence of disturbance (in our case, livestock grazing) ⁵⁶. In the desert, decreasing species richness and diversity of moths with increasing *altitude* and *wind speed* can be attributed to their low ranges of thermal tolerance compared to the moths in the grassland. ⁵⁷. Thus, moths living in higher altitude arid environments are in more danger of becoming extinct due to global warming.

Our study shows how moth diversity changes in Central Asia from south to north over a long latitudinal transect and assesses the environmental factors responsible for

those changes. Identifying the community composition pattern is useful for the conservation of not only moths, but also biodiversity in general. Our species list represents 51 percent of all estimated moth species along the latitudinal gradient in Mongolia; this result is the most up to date and systematically collected baseline data for future research.

Moths of the desert Site 3 were more vulnerable to a decrease in species diversity because of low precipitation and high livestock numbers. The local reduction of alpha diversity may result in reduced gamma diversity on regional level. Since 1940, the temperature in the area has increased by 2 °C, while *precipitation* has decreased by 7%. At the same time the number of *goats* increased from four million to 20 million, and large-scale fires occurred repeatedly. As a result, the desert in the south is expanding more and more to the northern part of Mongolia⁵⁸. The most negative effect of livestock is due to the high number of goats. Although cashmere from goats is one of the main export products of Mongolia, the government should stop its support of this unsustainable agricultural practice. Doing so could at least slow down the future consequences of climate change.³⁷

Moths are effective bioindicators²². Their contrasting patterns of spatial turnover and nestedness in desert and grassland habitats imply that different conservation approaches are needed. Therefore, we suggest that the whole gradient of the grassland has conservation value. Decreasing the number of goats can improve the situation of pasture overall. However, local diversity patterns could scale up to regional; therefore, we recommend abandoning this transitional zone from grazing for recovery. In addition, Site 1 that exists at the highest elevation can function as a refuge area for biodiversity as mirrored by moths should deserve conservation management by excluding livestock grazing.

In contrast, the species richness of the desert sites is similar except for Site 3 (species poor site) and one (species rich site). Thus, there is no exceptional management required for desert Sites 2, 4, and 5.

The high abundances of *A. ripae* and *A. trifolii* indicate that the process of desertification has already intensified and even at those sites some specialists could have already been extirpated before our study. In the future, we aim to study the co-effect of climatic variables and livestock grazing on moth communities at different latitudes. Specifically, we will aim to investigate whether *A. ripae* and *A. trifolii* are indicators of grazing. In addition, we aim to reveal latitude level indicator species, which could be used as reference species to study the migration of moths due to climate change.

Methods

Study area. Our study was conducted in the provinces of Umnugobi Aimag, Dundgobi Aimag, Tuv Aimag and Selenge Aimag in Mongolia, at ten study sites located along the latitudinal gradient from the Gobi Desert in the south to the Siberian forests in the north, covering various climatic zones³⁶. The southernmost site (43° N, 104° E) is located in semidesert (annual precipitation 146 mm, mean annual temperature -3.45 °C), while the northernmost site (50° N, 105° E) is located in forest steppe (annual precipitation 318 mm, mean annual temperature -0.56 °C) (

Figure). Livestock herding is one of the major economic sectors in Mongolia, with > 65 million animals³⁶. Detailed information on the study sites is given in supplementary material Table S1. We followed the study design of Lang et al.⁵⁹ and Ahlborn et al.²⁷ and sampled seven of their original 15 study sites that were spread at a south–north gradient of 600 km. We added three further sites to this transect in northern direction, totaling in a transect length of 860 km.

Moth Sampling. Moths were attracted with 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)⁶⁰ in combination with Bioform light “towers” (large R. Müller light trapping tower, mesh size 1mm, 70cm diameter, 180cm high) and EasyAcc 26 Ah power bank batteries. For moth collection, killing jars filled with CN were used. All samples were sorted to morphospecies level in the field and kept in glassine envelopes. Moths were sampled manually because the method usually better covers small species than automatic traps⁶¹. Sampling took place from 9.00–12.00 pm. To avoid temporal effects, specimens were collected in two consecutive years in 2018 (June–July) and in 2019 (July–August) at the peak of vegetation season leaving out nights dominated by full moon. This period covers the flight season of most nocturnal moth species in Mongolia²². At each site and in each year, we sampled with three replicates (ten sites x two years x three nights = 60 sampling nights). The southern five sites are located in desert and xeric shrublands biome (desert), and the northern five sites are located in temperate grasslands, savannas & shrublands biome (grassland).

Due to adverse weather conditions five catching nights were successful at some sites (Sites 1, 5, and 10). For analyses, all night samples of each site were aggregated. We brought all samples to Germany and mounted and identified specimens using identification keys⁴⁹ and online identification web sites for moths and butterflies^{62,63}. Afterwards, we submitted one or two specimens of each morphospecies for DNA barcoding to Canadian Centre for DNA Barcoding (CCDB) to corroborate our identification of morphospecies. The results on the creation of a DNA barcode library for

the collected species will be published in a separate paper (in preparation). Superfamilies of Mimallonoidea, Drepanoidea, Lasiocampoidea, Bombycoidea, Geometroidea, and Noctuoidea are included in the clade of macroheterocera⁶⁴. In this study we also included Sesiidae, Zygaenidae and Cossidae because of their traditional assignment to the (non-monophyletic) macro-moths.

Environmental data. We included *precipitation, temperature, wind, altitude, plant cover, plant species composition* and the *number of livestock* as environmental variables. We obtained climatic variables from WorldClim dataset⁶⁵. To study vegetation structure, we measured *vegetation cover* and plant species richness in a 10m x 10m area with five replications per site. Livestock droppings were counted in the plots to assess grazing pressure. We received vegetation data from Julian Ahlborn (Leibniz Centre for Agricultural Landscape Research) and Christine Römermann (University of Jena) for comparison and easier identification of our samples in the field. Botanist Tungalag Radnaakhand (National University of Mongolia) verified the identification of plant species from dried specimens of our herbarium. We obtained livestock abundance data for each site from the National Statistical Office of Mongolia⁶⁶ (Table S6). We measured coordinates and elevation of the sites with a Garmin Oregon 700 GPS.

Data analysis. Prior to analyses, we checked all variables for normal distribution by using QQ plot. Depending on these results we chose the appropriate statistical tests or applied log-transformation to normalize data for calculation.

Alpha diversity. We quantified moth alpha diversity (Hill numbers) of each site, i.e., species richness ($q=0$), Shannon diversity, the exponential of Shannon entropy ($q=1$), and the reciprocal Simpson's diversity ($q=2$) using the R-package 'vegan'⁶⁷. We estimated species richness with iChao1 index using R-package *SpadeR*. This index is an improved version of Chao1. To estimate species richness, it uses rare species or the number of singletons. To compare species richness, species diversity, and abundances of all macro-moths of each site along the latitudinal gradient and explore the community pattern at the species and family levels, we used the non-parametric Wilcoxon tests based on data from sampling nights. For comparison the number of unique species of desert and grassland, we used the non-parametric Kruskal-Wallis Test. To study how species richness changes along the climatic gradient, we applied two widely used climatic variables from WorldClim dataset⁶⁵: mean annual temperature (Bio1) and mean annual precipitation (Bio12). We determined niche structure of moth communities along the climatic gradient by analyzing coenoclines of the ten most abundant species. We applied generalized additive models (GAM) with Gaussian distribution and link function to produce the coenoclines. For coenoclines, we used the method of Hoffmann et al³². A general linear model (GLM) was used to calculate the relationship between species

richness and climatic variables. Pearson correlation was applied to correlate the Hill numbers of each site with environmental variables.

Beta diversity. To investigate the major family composition of communities we performed correspondence analysis using the R-package 'vegan'²⁸. K-means clustering of unsupervised learning algorithm was applied to ten sites to cluster them into groups based on their similarity. Clustering was conducted on major family matrices with Hellinger transformation. To study species composition differences between macro-moth communities, we applied permanova on species composition matrix (log+1 transformation with Bray-Curtis similarity) using *adonis* function of the R-package 'vegan'. To visualize species overlap between desert and grassland sites, we draw Venn diagrams by using the 'ggvenn' package⁶⁸. Southern sites in desert biome are shown in yellow, northern sites in grassland biome are shown in green.

For calculating the pairwise beta diversity among sites and also species composition differences along the latitudinal gradient, we applied the Baselga's³³ approach with Jaccard's dissimilarity index, which partitions beta diversity into two components: spatial turnover and nestedness^{34,52}. Partitioning beta diversity measurements are essential to understand the differences between communities; even if two sites have the same beta diversity, the difference can be due to species replacement or species loss or gain²³.

Spatial turnover is the replacement of some species by other species from one site to the next. Nestedness implies that the species assemblage of a species-poor site is the subset of a different species-rich site. We used the R package 'betapart'⁶⁹ to calculate beta diversity and its respective partitions. Sampling nights with only one species were excluded from the analysis. We used non-parametric Wilcoxon tests to compare Jaccard's beta diversity, spatial turnover and nestedness among sites based on data from sampling nights. Piecewise regressions were used to reveal a breakpoint of beta diversity between macro-moth communities along the latitudinal gradient. We examined breakpoints between 43° and 50° with a 1° interval and chose a breakpoint with the lowest residual standard error⁷⁰. We performed this procedure for the beta diversity components separately. We compared piecewise regression models with corresponding simple linear regression models with ANOVA to estimate the improvement of the model fit. To check the model fit, we also compared the R² of piecewise regression models with the R² of the simple linear regression models.

We used Procrustes analysis in R package 'vegan' to compare the distance matrix of the moth community with distance matrices of the vegetation guild and livestock abundances at the sites. A significant result demonstrates the similarity of a matrix with a target matrix suggesting an interaction of the observed patterns. To study how the

interaction between biome type and environmental variables affect the species richness and the diversity of macro-moths across the whole gradient, we applied generalized linear regression model with negative binomial family and linear regression, respectively. Negative binomial distribution is applied to avoid overdispersion. To fit the negative binomial generalized model, we used `glm.nb` function of 'MASS' package and to fit the linear regression `lm` function of 'stats' package were used. Precipitation, vegetation cover, vegetation richness, livestock, wind, and altitude were included in the model as a predictor variable, while species richness, Shannon diversity, Simpson diversity were response variables. For additive and interaction models, biome was used as a categorical variable. For each predictor variable we built three models: 1) using only a predictor variable without biome, 2) additive model: predictor variable + biome, 3) interaction effect: predictor variable x biome. For choosing the best model between these three models for each predictor variable, we used Akaike's Information Criterion (AIC).

All analyses were performed using R version 3.6.3⁷¹.

Data availability

Species list of all sites and other supporting information can be found in the Supplementary Material of this article.

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Author contributions

K.E., G.B., B.B. and M.P. designed research. K.E. performed research, analyzed data and wrote the paper with inputs from M.P., G.B. and B.B. All authors have read and agreed to the published version of the manuscript.

Competing interests

The authors declare no competing interests.

Supplementary material

Table S1 Detailed description of study sites.

Site	Group	Site names	Coordinates	Altitude	Sampling period
1	Desert	Umhubobi Aimag, Bayandalai Soum, Khuv, Khaalganii khuudas	43.74442 103.59985	2163	June 2018, August 2019
2	Desert	Umnugobi Aimag, Dalanzadgad, Shatiin am	43.51139 104.23272	1916	June 2018, August 2019
3	Desert	Umnugobi Aimag, Tsogtovoo Soum, Khetsuu khoshuu	43.97555 105.1534	1542	June 2018, August 2019
4	Desert	Dundgobi Aimag, Khuld Soum, Dov Dev	44.99908 105.61159	1218	June 2018, August 2019
5	Desert	Dundgobi Aimag, Saintsagaan Soum, Khargim	45.91909 106.29333	1471	June 2018, July 2019
6	Grassland	Tuv Aimag, Bayan-Unjuul Soum, Khalzan Ukhaa	47.06541 106.55341	1439	June 2018, July 2019
7	Grassland	Tuv Aimag, Ulaanbaatar city, Songinokhairkhan district, 21st khoroo, Partizan, Tsagaan chuluutiin am	48.14886 106.73609	1283	June 2018, July 2019
8	Grassland	Selenge Aimag, Tunkhel village, Khailaast	48.5862 106.75533	1070	June 2018, July 2019
9	Grassland	Selenge aimag, Baruun kharaa soum, Bayangol	49.02225 106.10812	834	June 2018, July 2019
10	Grassland	Selenge Aimag, Zuunburen Soum, Gangiin tokhoi	50.13164 105.99805	619	June 2018, July 2019

Table S2 Number of captured individuals and species richness in each sampling site based on the collection of 2018 and 2019.

#	Family	Species	1	2	3	4	5	6	7	8	9	10
1	Cossidae	<i>Acossus sp</i>	0	0	0	1	1	0	0	0	0	0
2	Cossidae	<i>Catopta sp</i>	3	0	0	0	0	0	0	0	0	0
3	Cossidae	<i>Cossidae sp1</i>	0	0	0	0	1	0	0	0	0	0
4	Cossidae	<i>Cossidae sp2</i>	0	0	0	0	1	0	0	0	0	0
5	Cossidae	<i>Cossidae sp5</i>	0	0	0	0	0	1	0	0	0	0
6	Cossidae	<i>Eogystia hippophaecolus</i>	15	0	0	6	4	0	0	0	0	0
7	Cossidae	<i>Eogystia sibirica</i>	0	0	0	1	0	3	0	0	0	0
8	Drepanidae	<i>Drepana falcataria</i>	0	0	0	0	0	0	1	0	0	0
9	Drepanidae	<i>Tethea ocularis</i>	0	0	0	0	0	0	0	1	0	1
10	Drepanidae	<i>Thyatira batis</i>	0	0	0	0	0	0	0	0	0	1
11	Erebidae	<i>Arctia flavia</i>	0	0	0	0	0	0	1	2	0	1
12	Erebidae	<i>Arctia matronula</i>	0	0	0	0	0	0	0	3	0	0
13	Erebidae	<i>Atolmis rubricollis</i>	0	0	0	0	0	0	1	1	0	1
14	Erebidae	<i>Callistege fortalitium</i>	0	0	0	0	0	0	0	0	1	0
15	Erebidae	<i>Calyptra thalictri</i>	0	1	0	0	0	0	0	0	4	4
16	Erebidae	<i>Catocala bella</i>	0	0	0	0	0	0	0	0	0	5
17	Erebidae	<i>Catocala deuteronympha</i>	0	0	0	0	0	0	0	1	0	83
18	Erebidae	<i>Catocala fulminea</i>	0	0	0	0	0	0	0	0	0	1
19	Erebidae	<i>Catocala nupta japonica</i>	0	0	0	0	0	0	0	0	0	31
20	Erebidae	<i>Catocala pacta</i>	0	0	0	0	0	0	0	0	0	16
21	Erebidae	<i>Chelis daturica</i>	0	0	0	0	0	0	4	44	4	0
22	Erebidae	<i>Chelis mongolica</i>	0	0	0	0	2	1	0	0	1	1
23	Erebidae	<i>Chrysothrum flavomaculata</i>	0	0	0	0	0	1	2	6	0	0
24	Erebidae	<i>Diacrisia purpurata</i>	0	0	0	0	0	0	0	1	0	1
25	Erebidae	<i>Diacrisia sannio</i>	0	0	0	0	0	0	0	0	0	2
26	Erebidae	<i>Dicallomera angelus</i>	0	0	0	2	0	0	0	0	2	0
27	Erebidae	<i>Drasteria chinensis</i>	43	11	2	0	30	0	3	3	0	0
28	Erebidae	<i>Drasteria rada</i>	2	0	0	0	1	0	0	0	1	0
29	Erebidae	<i>Eilema flavociliata</i>	0	0	0	0	0	0	0	0	0	1
30	Erebidae	<i>Emmelia trabealis</i>	0	0	0	0	0	0	2	0	0	1
31	Erebidae	<i>Epatolmis caesarea</i>	0	3	0	0	0	0	0	0	0	0
32	Erebidae	<i>Eublemma rosea</i>	3	0	0	0	1	1	2	0	0	0

33	Erebidae	<i>Eublemma sp</i>	0	1	0	0	0	0	0	0	0	0
34	Erebidae	<i>Euproctis similis</i>	0	0	0	0	0	0	0	1	0	5
35	Erebidae	<i>Hypena obesalis</i>	0	2	0	0	0	0	0	0	0	0
36	Erebidae	<i>Ivela ochropoda</i>	0	0	0	0	0	0	0	0	1	3
37	Erebidae	<i>Leucoma candida</i>	0	0	0	0	0	0	1	2	1	22
38	Erebidae	<i>Lygephila ludicra</i>	0	0	0	0	0	0	2	4	171	32
39	Erebidae	<i>Lymantria dispar</i>	0	1	0	0	0	0	0	0	0	17
40	Erebidae	<i>Polypogon tentacularia</i>	0	0	0	0	0	0	0	1	0	0
41	Erebidae	<i>Setina irrorella</i>	0	0	0	0	0	1	0	1	1	0
42	Erebidae	<i>Spiris bipunctata</i>	0	0	0	0	0	0	0	1	0	1
43	Erebidae	<i>Spiris striata</i>	0	0	0	0	0	0	0	1	0	0
44	Erebidae	<i>Stigmatophora flava</i>	0	0	0	0	0	0	0	0	2	1
45	Erebidae	<i>Stigmatophora micans</i>	0	0	0	0	0	0	2	2	1	1
46	Geometridae	<i>Abraxas grossulariata</i>	0	0	0	0	0	0	0	0	0	2
47	Geometridae	<i>Alcis sp1</i>	0	0	0	0	0	0	0	1	0	0
48	Geometridae	<i>Arichanna melanaria</i>	0	0	0	0	0	0	0	0	0	8
49	Geometridae	<i>Aspitates curvaria</i>	0	1	0	0	0	0	0	0	0	0
50	Geometridae	<i>Biston betularia</i>	0	0	0	0	0	0	40	2	23	57
51	Geometridae	<i>Cabera leptographa</i>	0	0	0	0	0	0	0	0	0	1
52	Geometridae	<i>Catarhoe cuculata</i>	0	0	0	0	0	0	9	6	11	1
53	Geometridae	<i>Chiasmia clathrata</i>	0	0	0	0	0	0	1	3	4	1
54	Geometridae	<i>Deileptenia sp</i>	0	0	0	0	0	1	0	0	0	0
55	Geometridae	<i>Digrammia rippertaria</i>	0	0	0	0	0	0	1	0	0	0
56	Geometridae	<i>Epirrhoe pupillata</i>	0	0	0	0	0	0	2	0	0	0
57	Geometridae	<i>Epirrhoe supergressa</i>	0	0	0	0	0	0	2	0	0	2
58	Geometridae	<i>Euphyia unangulata</i>	0	0	0	0	0	0	1	0	2	0
59	Geometridae	<i>Eupithecia centaureata</i>	0	0	0	0	0	0	0	1	0	0
60	Geometridae	<i>Eupithecia intricata</i>	0	1	0	0	0	0	0	0	0	0
61	Geometridae	<i>Eupithecia laricata</i>	0	0	0	0	0	1	0	0	0	0
62	Geometridae	<i>Eupithecia subumbrata</i>	0	0	0	0	0	0	0	3	0	0
63	Geometridae	<i>Gagitodes sagittata</i>	0	0	0	0	0	0	0	0	1	0
64	Geometridae	<i>Geometra rana</i>	0	0	0	0	0	0	0	5	3	3
65	Geometridae	<i>Hemistola veneta</i>	0	0	0	0	0	0	0	17	6	45
66	Geometridae	<i>Hylaea fasciaria</i>	0	0	0	0	0	0	0	0	0	1
67	Geometridae	<i>Hypomecis punctinalis</i>	0	0	0	0	0	0	0	0	1	0
68	Geometridae	<i>Hypomecis roboraria</i>	0	0	0	0	0	0	1	2	0	0

69	Geometridae	<i>Idaea serpentata</i>	0	0	0	0	0	0	0	0	0	1
70	Geometridae	<i>Idaea straminata</i>	0	0	0	0	0	0	0	0	2	0
71	Geometridae	<i>Isturgia arenacearia</i>	0	0	0	0	0	0	11	3	95	125
72	Geometridae	<i>Isturgia kaszabi</i>	0	0	0	0	0	0	0	1	2	0
73	Geometridae	<i>Jankowskia athleta</i>	0	0	0	0	0	0	0	18	1	0
74	Geometridae	<i>Juxtephria consentaria</i>	0	0	0	0	0	0	0	3	5	3
75	Geometridae	<i>Lampropteryx sp1</i>	0	0	0	0	0	0	0	1	0	0
76	Geometridae	<i>Lithostege sp2</i>	0	9	0	3	0	58	11	163	69	22
77	Geometridae	<i>Macaria AH01Mg</i>	0	0	0	0	0	0	0	1	1	0
78	Geometridae	<i>Macaria alternata</i>	0	0	0	0	0	0	0	0	0	1
79	Geometridae	<i>Macaria artesiaria</i>	0	0	0	0	0	0	0	0	0	1
80	Geometridae	<i>Macaria sp 2</i>	0	0	0	0	0	0	0	0	1	0
81	Geometridae	<i>Macaria sp 3</i>	0	0	0	0	0	0	0	0	1	0
82	Geometridae	<i>Macaria wauaria</i>	0	0	0	0	0	0	0	3	14	6
83	Geometridae	<i>Megalycinia strictaria</i>	1	0	0	0	0	0	7	6	26	0
84	Geometridae	<i>Megaspilates mundataria</i>	0	0	0	0	0	0	0	10	0	17
85	Geometridae	<i>Odontopera bidentata</i>	0	0	0	0	0	0	3	1	0	0
86	Geometridae	<i>Pelurga comitata</i>	0	0	0	0	0	0	0	0	5	1
87	Geometridae	<i>Phibalapteryx virgata</i>	0	0	0	0	1	0	0	39	34	19
88	Geometridae	<i>Rheumaptera hastata</i>	0	0	0	0	0	1	0	0	0	0
89	Geometridae	<i>Rhodostrophia jacularia</i>	1	4	5	2	0	2	0	3	0	0
90	Geometridae	<i>Rhodostrophia vibicaria</i>	0	0	0	0	0	0	1	8	0	0
91	Geometridae	<i>Schistostege nubilaria</i>	0	0	0	0	0	0	3	3	2	0
92	Geometridae	<i>Scopula albiceraria</i>	0	0	0	0	0	0	0	1	3	0
93	Geometridae	<i>Scopula decorota przewalskii</i>	0	0	0	0	0	1	1	1	0	17
94	Geometridae	<i>Scopula immorata</i>	0	0	0	0	0	0	0	1	0	0
95	Geometridae	<i>Scopula rubiginata</i>	0	0	0	0	0	0	0	0	0	31
96	Geometridae	<i>Scopula subpunctaria</i>	1	0	0	0	0	0	1	1	9	1
97	Geometridae	<i>Scopula virgulata</i>	0	0	0	0	0	0	6	10	25	2
98	Geometridae	<i>Scotopteryx chenopodiata</i>	0	0	0	0	0	0	1	36	3	0
99	Geometridae	<i>Spargania luctuata</i>	0	0	0	0	0	0	1	0	0	0
100	Geometridae	<i>Stamnodes danilovi</i>	0	1	0	0	0	0	0	0	0	0
101	Geometridae	<i>Thalera chlorosaria</i>	0	0	0	0	0	0	0	0	0	1
102	Geometridae	<i>Thetidia chlorophyllaria</i>	0	0	0	0	0	0	0	1	2	6

103	Geometridae	<i>Thetidia smaragdaria</i>	0	0	0	0	0	0	3	6	1	3
104	Lasiocampidae	<i>Dendrolimus superans</i>	0	0	0	0	0	0	3	0	13	0
105	Lasiocampidae	<i>Gastropacha populifolia</i>	0	0	0	0	0	0	0	1	0	0
106	Lasiocampidae	<i>Gastropacha quercifolia</i>	0	4	0	0	0	0	2	33	5	9
107	Lasiocampidae	<i>Malacosoma castrensis</i>	0	1	0	1	0	0	0	11	1	0
108	Lasiocampidae	<i>Malacosoma neustria transmongolicum</i>	0	0	0	1	0	0	0	0	0	0
109	Lasiocampidae	<i>Phyllodesma ilicifolia</i>	0	1	0	0	0	0	0	0	0	0
110	Noctuidae	<i>Abrostola tripartita</i>	0	0	0	0	0	0	1	1	0	0
111	Noctuidae	<i>Actebia fennica</i>	1	0	0	0	0	0	1	12	0	0
112	Noctuidae	<i>Actebia poecila</i>	3	1	0	0	4	7	2	0	0	0
113	Noctuidae	<i>Actebia praecox</i>	0	0	0	0	0	0	0	0	0	2
114	Noctuidae	<i>Actebia squalida</i>	0	0	0	1	6	1	0	0	0	0
115	Noctuidae	<i>Agrotis clavis</i>	0	0	0	0	0	0	13	45	3	2
116	Noctuidae	<i>Agrotis exclamationis</i>	0	0	0	0	0	2	11	19	4	4
117	Noctuidae	<i>Agrotis ipsilon</i>	0	0	0	1	2	1	0	0	0	0
118	Noctuidae	<i>Agrotis ripae</i>	356	6	1445	1714	2413	20	21	10	1	0
119	Noctuidae	<i>Agrotis segetum</i>	0	0	0	0	5	0	0	0	0	0
120	Noctuidae	<i>Amphipoea fucosa</i>	0	0	0	0	0	0	0	0	0	4
121	Noctuidae	<i>Anaplectoides prasina</i>	0	0	0	0	0	0	0	1	0	0
122	Noctuidae	<i>Anarta colletti</i>	1	0	0	0	0	0	0	0	0	0
123	Noctuidae	<i>Anarta stigmosa</i>	1	0	0	34	4	0	0	0	0	0
124	Noctuidae	<i>Anarta trifolii</i>	191	48	34	125	169	53	110	8	55	8
125	Noctuidae	<i>Apamea lateritia</i>	28	0	0	0	0	0	2	4	3	5
126	Noctuidae	<i>Apamea maillardi</i>	0	0	0	0	0	0	0	0	2	0
127	Noctuidae	<i>Autographa buraetica</i>	2	0	0	0	0	0	1	8	2	0
128	Noctuidae	<i>Bryophila orthogramma</i>	0	0	0	0	0	0	0	0	0	1
129	Noctuidae	<i>Calamia decipiens</i>	1	0	0	0	0	0	0	0	0	0
130	Noctuidae	<i>Caradrina montana</i>	21	8	8	0	1	0	0	4	0	0
131	Noctuidae	<i>Caradrina sp2</i>	4	0	15	4	0	0	0	0	0	0
132	Noctuidae	<i>Cardepia sociabilis</i>	0	0	0	1	0	0	0	0	0	0
133	Noctuidae	<i>Chersotis ocellina</i>	0	0	0	0	0	0	1	0	1	0
134	Noctuidae	<i>Chilodes repeteki</i>	0	0	0	1	0	0	0	0	0	0
135	Noctuidae	<i>Coenobia rufa</i>	1	3	0	0	0	0	0	0	0	0
136	Noctuidae	<i>Conisania arida</i>	0	0	0	0	0	0	2	4	0	0
137	Noctuidae	<i>Cosmia pyralina</i>	0	0	0	0	0	0	0	0	0	13

138	Noctuidae	<i>Cryptocala chardinyi</i>	0	0	0	0	0	0	0	1	1	0
139	Noctuidae	<i>Cucullia absinthii</i>	0	0	0	0	1	0	0	0	0	0
140	Noctuidae	<i>Cucullia argentea</i>	0	0	0	0	0	0	0	1	2	6
141	Noctuidae	<i>Cucullia artemisiae</i>	0	0	0	0	0	0	0	1	1	0
142	Noctuidae	<i>Cucullia biradiata</i>	1	0	0	0	0	0	0	2	0	0
143	Noctuidae	<i>Cucullia cineracea</i>	0	0	0	0	0	1	0	0	2	2
144	Noctuidae	<i>Cucullia dracunculi</i>	0	0	0	0	0	0	0	1	3	1
145	Noctuidae	<i>Cucullia fraudatrix</i>	0	0	0	0	1	0	0	0	1	0
146	Noctuidae	<i>Cucullia scopariae</i>	0	1	1	0	0	0	1	0	2	21
147	Noctuidae	<i>Cucullia sp2</i>	0	0	0	0	0	0	0	0	1	0
148	Noctuidae	<i>Cucullia splendida</i>	4	7	0	1	8	4	1	0	4	13
149	Noctuidae	<i>Cucullia umbratica</i>	0	0	0	0	0	0	3	2	2	0
150	Noctuidae	<i>Diachrysis stenochrysis</i>	0	0	0	0	0	0	0	1	0	0
151	Noctuidae	<i>Dichagyris kaszabi</i>	0	3	0	0	0	0	0	0	0	0
152	Noctuidae	<i>Dichagyris musiva</i>	0	0	0	0	0	0	0	0	0	1
153	Noctuidae	<i>Dichagyris sp</i>	0	0	1	0	0	0	0	0	0	0
154	Noctuidae	<i>Dichagyris vallesiaca</i>	15	2	0	0	0	0	0	0	0	0
155	Noctuidae	<i>Enargia paleacea</i>	0	0	0	0	0	0	0	0	2	5
156	Noctuidae	<i>Eremohadena sp</i>	0	0	0	0	1	0	0	0	0	0
157	Noctuidae	<i>Euchalcia mongolica</i>	0	0	0	0	0	0	1	2	1	1
158	Noctuidae	<i>Euchalcia renardi</i>	0	0	0	0	0	0	0	2	0	0
159	Noctuidae	<i>Eurois occulta</i>	0	0	0	0	0	0	0	0	1	0
160	Noctuidae	<i>Euxoa basigramma</i>	1	0	0	0	0	0	0	0	0	0
161	Noctuidae	<i>Euxoa cursoria</i>	91	2	0	0	1	0	1	0	0	0
162	Noctuidae	<i>Euxoa decorans</i>	5	1	0	0	0	0	0	0	0	0
163	Noctuidae	<i>Conisania sp</i>	1	0	0	0	5	2	6	8	19	25
164	Noctuidae	<i>Euxoa ochrogaster</i>	56	3	4	11	56	64	55	21	129	33
165	Noctuidae	<i>Euxoa oranaria</i>	1	0	0	0	0	0	0	0	0	0
166	Noctuidae	<i>Euxoa sp</i>	1	0	0	0	0	0	0	0	0	0
167	Noctuidae	<i>Euxoa tritici</i>	0	0	0	0	0	2	0	2	1	13
168	Noctuidae	<i>Feltia nigrita</i>	0	0	0	0	0	0	0	1	0	0
169	Noctuidae	<i>Hada plebeja</i>	0	0	0	0	0	0	0	7	0	0
170	Noctuidae	<i>Hadena aberrans</i>	0	0	0	0	0	0	0	2	1	0
171	Noctuidae	<i>Hadena corrupta</i>	0	0	0	0	0	0	1	1	0	0
172	Noctuidae	<i>Hadena variolata</i>	1	1	0	0	0	1	0	2	0	2
173	Noctuidae	<i>Heliothis adauca</i>	0	0	0	0	0	0	0	0	2	0

174	Noctuidae	<i>Heliothis ononis</i>	0	0	0	0	0	0	9	2	3	0
175	Noctuidae	<i>Hoplodrina octogenaria</i>	0	0	0	0	0	0	0	0	1	3
176	Noctuidae	<i>Hyssia cavernosa</i>	0	0	0	0	0	0	1	1	0	2
177	Noctuidae	<i>Ipimorpha retusa</i>	0	0	0	0	0	0	0	0	0	98
178	Noctuidae	<i>Lacanobia aliena</i>	0	0	0	0	0	8	1	8	0	0
179	Noctuidae	<i>Lacanobia contigua</i>	0	0	0	0	0	0	9	1	6	0
180	Noctuidae	<i>Lacanobia thalassina</i>	0	0	0	0	0	0	23	20	8	0
181	Noctuidae	<i>Lasionycta imbecilla</i>	0	0	0	0	0	0	0	4	0	0
182	Noctuidae	<i>Lasionycta proxima</i>	0	0	0	0	0	0	15	30	1	0
183	Noctuidae	<i>Lygephila pastinum</i>	0	0	0	0	0	0	0	0	1	0
184	Noctuidae	<i>Lygephila viciae</i>	0	0	0	0	0	0	72	11	1	0
185	Noctuidae	<i>Mamestra brassicae</i>	0	0	0	4	15	0	0	1	0	0
186	Noctuidae	<i>Mythimna albiradiosa</i>	0	0	0	1	3	0	1	0	0	0
187	Noctuidae	<i>Mythimna comma</i>	1	0	0	0	0	16	10	12	11	88
188	Noctuidae	<i>Mythimna conigera</i>	0	0	0	0	0	0	0	0	2	6
189	Noctuidae	<i>Mythimna opaca</i>	0	0	0	0	0	0	0	4	1	0
190	Noctuidae	<i>Mythimna oxygala</i>	0	0	0	0	0	0	5	1	0	1
191	Noctuidae	<i>Mythimna pallens</i>	0	0	0	0	0	0	8	1	0	1
192	Noctuidae	<i>Mythimna separata</i>	0	1	0	0	0	0	0	0	0	0
193	Noctuidae	<i>Mythimna velutina</i>	0	0	0	0	0	0	0	7	33	24
194	Noctuidae	<i>Naenia contaminata</i>	0	0	0	0	0	0	0	0	0	1
195	Noctuidae	<i>Ochropleura plecta</i>	0	0	0	0	0	0	1	0	0	0
196	Noctuidae	<i>Panchrysia dives</i>	0	0	0	0	0	0	0	1	0	1
197	Noctuidae	<i>Panchrysia ornata</i>	0	6	0	0	0	0	0	0	0	0
198	Noctuidae	<i>Plusia putnami</i>	0	0	0	0	0	0	0	0	0	1
199	Noctuidae	<i>Polia altaica</i>	0	0	0	0	1	0	6	1	0	0
200	Noctuidae	<i>Polia bombycina</i>	0	0	0	0	0	0	1	15	11	30
201	Noctuidae	<i>Polia nebulosa</i>	0	0	0	0	0	0	0	3	3	0
202	Noctuidae	<i>Prognorisma albifurca</i>	0	0	0	0	0	0	2	0	0	0
203	Noctuidae	<i>Protoschinia scutosa</i>	0	1	1	0	0	0	1	0	0	0
204	Noctuidae	<i>Pyrrhia umbra</i>	0	0	0	0	0	0	0	1	0	0
205	Noctuidae	<i>red_noc</i>	0	0	0	0	0	0	0	0	1	0
206	Noctuidae	<i>Resapamea mammothus</i>	0	0	0	0	0	0	2	3	1	0
207	Noctuidae	<i>Resapamea vulpecula</i>	0	7	0	0	0	0	3	1	0	0
208	Noctuidae	<i>Rhyacia ledereri</i>	0	0	0	0	0	2	7	0	0	0
209	Noctuidae	<i>Rhyacia lucifera</i>	1	0	0	0	0	0	0	0	0	0

210	Noctuidae	<i>Rhyacia simulans</i>	3	0	0	0	2	54	16	6	1	0
211	Noctuidae	<i>Sideridis egena</i>	1	0	0	5	13	13	27	7	6	1
212	Noctuidae	<i>Sideridis kitti</i>	0	0	0	0	0	0	6	11	0	3
213	Noctuidae	<i>Sideridis turbida</i>	0	0	0	0	0	1	2	0	0	0
214	Noctuidae	<i>Simyra nervosa</i>	0	1	0	0	0	0	1	19	0	0
215	Noctuidae	<i>Syngrapha ain</i>	0	0	0	0	0	0	1	0	0	6
216	Noctuidae	<i>Xestia kollari</i>	0	0	0	0	0	1	0	0	1	1
217	Noctuidae	<i>Xestia versuta</i>	0	0	0	0	1	0	0	1	0	0
218	Notodontidae	<i>Clostera albosigma</i>	0	0	0	0	0	0	0	0	2	9
219	Notodontidae	<i>Clostera anachoreta</i>	0	0	0	0	0	0	0	0	0	1
220	Notodontidae	<i>Furcula furcula</i>	0	0	0	0	0	0	0	0	0	1
221	Notodontidae	<i>Nerice davidi</i>	0	0	0	0	0	0	0	1	0	1
222	Notodontidae	<i>Notodontidae</i> sp1	0	0	0	1	0	2	0	0	0	0
223	Notodontidae	<i>Phalera bucephala</i>	0	0	0	0	0	0	0	0	1	0
224	Notodontidae	<i>Ptilodon kuwayamae</i>	0	0	0	0	0	0	0	1	0	0
225	Sessidae	<i>Sessidae</i> sp1	0	0	0	0	0	0	2	0	0	0
226	Sphingidae	<i>Callambulyx tatarinovii</i> <i>eversmanni</i>	0	0	0	0	0	0	0	2	0	5
227	Sphingidae	<i>Deiliphila</i> sp	0	0	0	0	0	0	1	1	0	0
228	Sphingidae	<i>Hyles chivilini</i>	5	14	0	3	0	0	1	1	0	0
229	Sphingidae	<i>Hyles gallii</i>	0	0	0	0	0	2	41	18	17	22
230	Sphingidae	<i>Hyles hippophaes</i>	0	1	0	0	0	0	0	0	0	0
231	Sphingidae	<i>Laothoe amurensis</i>	0	0	0	0	0	0	5	11	17	8
232	Sphingidae	<i>Marumba gaschkewitschii</i>	0	0	0	0	0	0	0	0	0	2
233	Sphingidae	<i>Smerinthus caecus</i>	0	0	0	0	0	0	0	1	1	8
234	Sphingidae	<i>Sphinx ligustri</i>	0	0	0	0	0	0	0	13	1	0
235	Sphingidae	<i>Sphinx morio</i>	0	0	0	1	0	0	2	1	0	0
236	Zygaenidae	<i>Jordanita</i> sp1.	0	0	0	0	0	0	0	0	2	0

Table S3 Species diversity (Hill numbers) and abundance along the transect from south (#1) to north (#10). The high individual numbers of sites 3, 4 and 5 are due to the high abundance of *Agrotis ripae*.

Site	Species richness	Shannon diversity	Simpson diversity	Abundance
1	38	7.54	4.	866
2	35	16.28	278.30	157
3	12	1.31	1.10	1516
4	27	1.71	1.25	1925
5	32	1.89	1.30	2752
6	35	14.12	9.63	328
7	87	31.90	16.58	646
8	118	45.50	21.00	866
9	96	28.94	14.73	937
10	100	37.76	22.14	1105

Table S4 The results of GLMs comparing the species richness of four main families or family groups (Noctuidae, Geometridae, Erebidae and Others) among ten study sites along the latitudinal gradients.

Family	Site	Estimate	Standard error	z- value	p value	p adjusted
Noctuidae	Site1	1.856	0.177	10.501	9E-26	8.56E-25
Noctuidae	Site2	0.916	0.228	4.015	6E-05	0.0003
Noctuidae	Site3	-0.122	0.300	-0.405	0.685	0.685
Noctuidae	Site4	0.378	0.259	1.458	0.145	0.290
Noctuidae	Site5	0.683	0.240	2.845	0.004	0.013
Noctuidae	Site6	0.806	0.233	3.454	0.001	0.002
Noctuidae	Site7	1.545	0.206	7.506	6.09E-14	4.87E-13
Noctuidae	Site8	1.68	0.202	8.300	1.04E-16	9.35E-16
Noctuidae	Site9	1.349	0.212	6.377	1.81E-10	1.09E-09
Noctuidae	Site10	1.362	0.211	6.453	1.10E-10	7.67E-10
Erebidae	Site1	1.163	0.250	4.653	3.28E-06	2.95E-05
Erebidae	Site2	-0.064	0.479	-0.135	0.893	1
Erebidae	Site3	-0.47	0.750	-0.627	0.531	1
Erebidae	Site4	-0.47	0.750	-0.627	0.531	1
Erebidae	Site5	0.223	0.433	0.515	0.606	1
Erebidae	Site6	-0.316	0.453	-0.697	0.486	1
Erebidae	Site7	0.683	0.339	2.012	0.044	0.265
Erebidae	Site8	0.916	0.323	2.839	0.005	0.036
Erebidae	Site9	0.733	0.335	2.188	0.029	0.201
Erebidae	Site10	1.499	0.293	5.120	3.05E-07	0.000003
Geometridae	Site1	1.099	0.333	3.296	0.001	0.006
Geometridae	Site2	-1.86E-14	0.667	-3E-14	1	1
Geometridae	Site3	-0.405	0.601	-0.675	0.500	1
Geometridae	Site4	-0.405	0.601	-0.675	0.500	1
Geometridae	Site5	-0.405	0.782	-0.519	0.604	1
Geometridae	Site6	0.288	0.441	0.652	0.514	1
Geometridae	Site7	1.299	0.376	3.455	0.001	0.004
Geometridae	Site8	1.863	0.358	5.201	1.99E-07	1.99E-06
Geometridae	Site9	1.828	0.359	5.091	3.57E-07	3.21E-06
Geometridae	Site10	1.714	0.362	4.736	2.18E-06	1.75E-05
Other	Site1	1.023	0.267	3.852	0.000	0.001
Other	Site2	0.174	0.414	0.421	0.674	1
Other	Site4	0.357	0.393	0.907	0.365	1
Other	Site5	0.223	0.463	0.482	0.630	1
Other	Site6	0.474	0.427	1.111	0.267	1
Other	Site7	0.762	0.356	2.139	0.032	0.162
Other	Site8	1.203	0.327	3.678	0.000	0.002
Other	Site9	0.816	0.352	2.317	0.020	0.123
Other	Site10	1.05	0.336	3.122	0.002	0.013

Table S5 The results of GLMs comparing the Shannon diversity of four main families or family groups (Noctuidae, Geometridae, Erebidae and Other) among ten study sites along the latitudinal gradients.

Family	Site	Estimate	Standard error	t-value	p value	p adjusted
Noctuidae	Site1	4.019	1.072	3.750	0.001	0.008
Noctuidae	Site2	2.685	1.750	1.534	0.139	0.557
Noctuidae	Site3	-2.206	1.750	-1.260	0.221	0.566
Noctuidae	Site4	-2.375	1.750	-1.357	0.189	0.566
Noctuidae	Site5	-1.809	1.750	-1.034	0.313	0.566
Noctuidae	Site6	4.703	1.750	2.687	0.013	0.067
Noctuidae	Site7	10.739	1.750	6.136	3.55E-06	3.20E-05
Noctuidae	Site8	15.503	1.750	8.858	1.05E-08	1.05E-07
Noctuidae	Site9	6.388	1.750	3.650	0.001	0.008
Noctuidae	Site10	8.244	1.750	4.710	0.0001	0.0009
Erebidae	Site1	2.687	0.467	5.760	2.93E-05	0.0003
Erebidae	Site2	-0.933	0.873	-1.069	0.301	1
Erebidae	Site3	-1.151	1.143	-1.007	0.329	1
Erebidae	Site4	-1.180	1.143	-1.033	0.317	1
Erebidae	Site5	-0.404	0.873	-0.463	0.650	1
Erebidae	Site6	-1.347	0.762	-1.768	0.096	0.769
Erebidae	Site7	0.013	0.762	0.017	0.987	1
Erebidae	Site8	1.169	0.762	1.534	0.145	1
Erebidae	Site9	-0.149	0.762	-0.196	0.847	1
Erebidae	Site10	5.528	0.762	7.256	1.92E-06	1.92E-05
Geometridae	Site1	2.379	1.151	2.067	0.058	0.347
Geometridae	Site2	-0.397	2.302	-0.173	0.865	1
Geometridae	Site3	-0.742	1.820	-0.408	0.690	1
Geometridae	Site4	-0.753	1.820	-0.414	0.685	1
Geometridae	Site5	-1.067	2.302	-0.464	0.650	1
Geometridae	Site6	-0.007	1.628	-0.004	0.997	1
Geometridae	Site7	3.839	1.628	2.359	0.033	0.234
Geometridae	Site8	6.218	1.628	3.820	0.002	0.017
Geometridae	Site9	6.926	1.628	4.255	0.001	0.008
Geometridae	Site10	6.043	1.628	3.713	0.002	0.019
Other	Site1	2.264	0.372	6.095	9.28E-06	7.80E-05
Other	Site2	0.368	0.607	0.606	0.552	1
Other	Site4	0.018	0.607	0.030	0.977	1
Other	Site5	-0.372	0.695	-0.535	0.599	1
Other	Site6	-0.237	0.695	-0.341	0.737	1
Other	Site7	0.941	0.607	1.551	0.138	0.692
Other	Site8	3.059	0.607	5.043	8.47E-05	0.0006
Other	Site9	1.252	0.607	2.064	0.054	0.322
Other	Site10	3.718	0.607	6.129	8.67E-06	7.80E-05

Table S6 The results of GLMs comparing the abundance of four main families or family groups (Noctuidae, Geometridae, Erebidae and Other) among ten study sites along the latitudinal gradients.

Family	Site	Estimate	Standard error	z-value	p value	p adjusted
Noctuidae	Site1	1.947	0.608	3.204	0.004	0.032
Noctuidae	Site2	2.694	0.992	2.715	0.013	0.043
Noctuidae	Site3	3.184	0.992	3.209	0.004	0.032
Noctuidae	Site4	4.472	0.992	4.508	0.000	0.002
Noctuidae	Site5	4.204	0.992	4.237	0.000	0.003
Noctuidae	Site6	2.399	0.992	2.418	0.024	0.043
Noctuidae	Site7	3.037	0.992	3.061	0.006	0.034
Noctuidae	Site8	2.761	0.992	2.783	0.011	0.043
Noctuidae	Site9	2.551	0.992	2.571	0.017	0.043
Noctuidae	Site10	2.991	0.992	3.015	0.006	0.034
Erebidae	Site1	0.895	0.460	1.945	0.070	0.487
Erebidae	Site2	1.030	0.861	1.195	0.249	1.000
Erebidae	Site3	-0.202	1.128	-0.179	0.860	1.000
Erebidae	Site4	-0.202	1.128	-0.179	0.860	1.000
Erebidae	Site5	1.593	0.861	1.849	0.083	0.498
Erebidae	Site6	-0.664	0.752	-0.884	0.390	1.000
Erebidae	Site7	0.953	0.752	1.267	0.223	1.000
Erebidae	Site8	2.117	0.752	2.816	0.012	0.099
Erebidae	Site9	2.955	0.752	3.931	0.001	0.011
Erebidae	Site10	3.421	0.752	4.550	0.000	0.003
Geometridae	Site1	1.059	0.435	2.435	0.029	0.144
Geometridae	Site2	-0.366	0.870	-0.421	0.680	1.000
Geometridae	Site3	-0.366	0.688	-0.532	0.603	1.000
Geometridae	Site4	-0.163	0.688	-0.238	0.816	1.000
Geometridae	Site5	-1.059	0.870	-1.217	0.244	0.974
Geometridae	Site6	1.844	0.615	2.997	0.010	0.058
Geometridae	Site7	2.305	0.615	3.746	0.002	0.015
Geometridae	Site8	3.620	0.615	5.883	0.000	0.000
Geometridae	Site9	3.641	0.615	5.916	0.000	0.000
Geometridae	Site10	3.736	0.615	6.071	0.000	0.000
Other	Site1	1.106	0.302	3.664	0.002	0.010
Other	Site2	0.856	0.493	1.737	0.099	0.398
Other	Site4	0.259	0.493	0.525	0.606	1.000
Other	Site5	-0.210	0.565	-0.372	0.714	1.000
Other	Site6	0.248	0.565	0.439	0.666	1.000
Other	Site7	1.825	0.493	3.702	0.002	0.010
Other	Site8	2.321	0.493	4.708	0.000	0.002
Other	Site9	1.878	0.493	3.810	0.001	0.009
Other	Site10	1.916	0.493	3.886	0.001	0.009

Table S7 Livestock numbers of each site. Data are obtained for each site from the National Statistical Office of Mongolia (*"Livestock," 2020*)

Site	Year	Camel	Cow	Goat	Horse	Sheep
1	2018	470	980	44280	2390	10370
1	2019	450	1080	49590	2680	11400
2	2018	380	250	7230	330	2760
2	2019	470	270	9740	400	3480
3	2018	4100	580	37300	1670	20360
3	2019	4280	630	39750	1880	21760
4	2018	5340	360	36740	3890	40860
4	2019	5540	370	37620	3950	39890
5	2018	80	1610	37230	6220	45050
5	2019	70	1550	38860	6450	47320
6	2018	320	3860	48170	7720	63180
6	2019	350	3610	50350	8120	64670
7	2018	0	19580	13310	5680	16800
7	2019	0	21200	15320	5970	16710
8	2018	0	4730	3830	2570	3230
8	2019	0	5500	5190	2580	3960
9	2018	0	4280	16210	3320	21000
9	2019	0	5390	20730	3870	25290
10	2018	0	6040	9700	2400	11310
10	2019	0	6200	11410	2610	12030

Table S8 Model parameters for all fitted models of relevant environmental variables for species richness, Shannon diversity, and Simpson diversity. For each environmental variables three types of model are fitted: environmental variable as a single factor, additive: environmental variable+biome (B), interaction effect: environmental variable x biome (B). For each model, model estimate- β , standard error-St.err., p value, and AIC are given in the table. The best model with the lowest AIC is marked in bold. Abbreviations of the environmental variables are as follows: Pred- predictor, P – precipitation, B- biome, Veg cov – vegetation cover, L - livestock, W – wind, A- altitude, Veg rich- vegetation richness.

Pred	Model for richness				Model for Shannon diversity				Model for Simpson diversity			
	β	St.err	p-value	AIC	β	St.err	p-value	AIC	β	St.err	p-value	AIC
B				306.940	1.639	0.21	***	84.732	1.400	0.192	***	77.364
P	0.010	0.001	***	294.470	0.012	0.001	***	66.805	0.010	0.001	***	62.341
P+B				296.370				68.805				64.341
P	0.010	0.002	***		0.012	0.003	***		0.010	0.003	***	
B	-0.121	0.369	ns		-0.003	0.397	ns		0.007	0.376	ns	
P x B	0.002	0.005	ns	298.260	-0.004	0.005	ns	70.261	-0.002	0.005	ns	66.198
Veg cov	0.020	0.005	***	324.720	0.029	0.005	***	100.767	0.026	0.005	***	88.388
Veg_cov+B				305.670				77.385				68.146
Veg cov	0.008	0.004	ns		0.015	0.005	**		0.014	0.004	**	
B	1.098	0.209	***		1.274	0.223	***		1.040	0.198	***	
Veg_cov x B	-0.006	0.009	ns	307.240	-0.011	0.010	ns	77.950	-0.010	0.009	ns	68.824
L	0.000	0.000	**	328.890	0.000	0.000	***	109.965	0.000	0.000	***	97.140
L + B				305.670				59.707				48.121
L	-8E-06	2E-06	**		-1E-05	2E-06	***		-1E-05	2E-06	***	
B	1E+00	2E-01	***		2E+00	2E-01	***		1E+00	1E-01	***	
L x B	-1E-05	5E-06	*	299.670	4E-06	5E-06	ns	60.776	6E-06	4E-06	ns	47.867
W	-9E-01	1E-01	***	299.040	-1E+00	0.134	***	84.733	-9E-01	1E-01	***	78.954
W + B				300.780				84.698				78.351
W	-1.0E+00	3.0E-01	***		-0.539	0.388	ns		-0.349	0.358	ns	

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<i>B</i>	-2.6E-01	4.8E-01	ns		0.845	0.608	ns		0.886	0.562	ns	
W x B	-1.2E+00	7.0E-01	ns	299.750	-2.800	0.759	***	73.862	-2.790	0.679	***	64.968
A	-1.1E-03	2.5E-04	***	320.410	-0.001	0.000	***	110.627	-0.001	0.0003	**	101.310
A + B				308.500				86.575				79.127
A	-0.0002	0.0003			0.0001	0.0003	ns		0.000	0.0003	ns	
<i>Biome</i>	1.152	0.256	***		1.717	0.295	***		1.487	0.268	***	
A x B	-0.001	0.001	*	304.940	-0.002	0.001	***	76.427	-0.002	0.0005	***	68.857
Veg rich	0.065	0.009	***	306.590	0.072	0.011	***	94.650	0.063	0.010	***	83.678
Veg rich+B				296.890				77.600				69.472
<i>Veg rich</i>	0.039	0.010	***		0.036	0.012	**		0.034	0.011	**	
<i>B</i>	0.773	0.204	***		1.163	0.245	***		0.221	0.221	***	
Veg rich x B	-0.024	0.025	ns	298.010	0.019	0.028	ns	79.070	0.028	0.025	ns	70.073

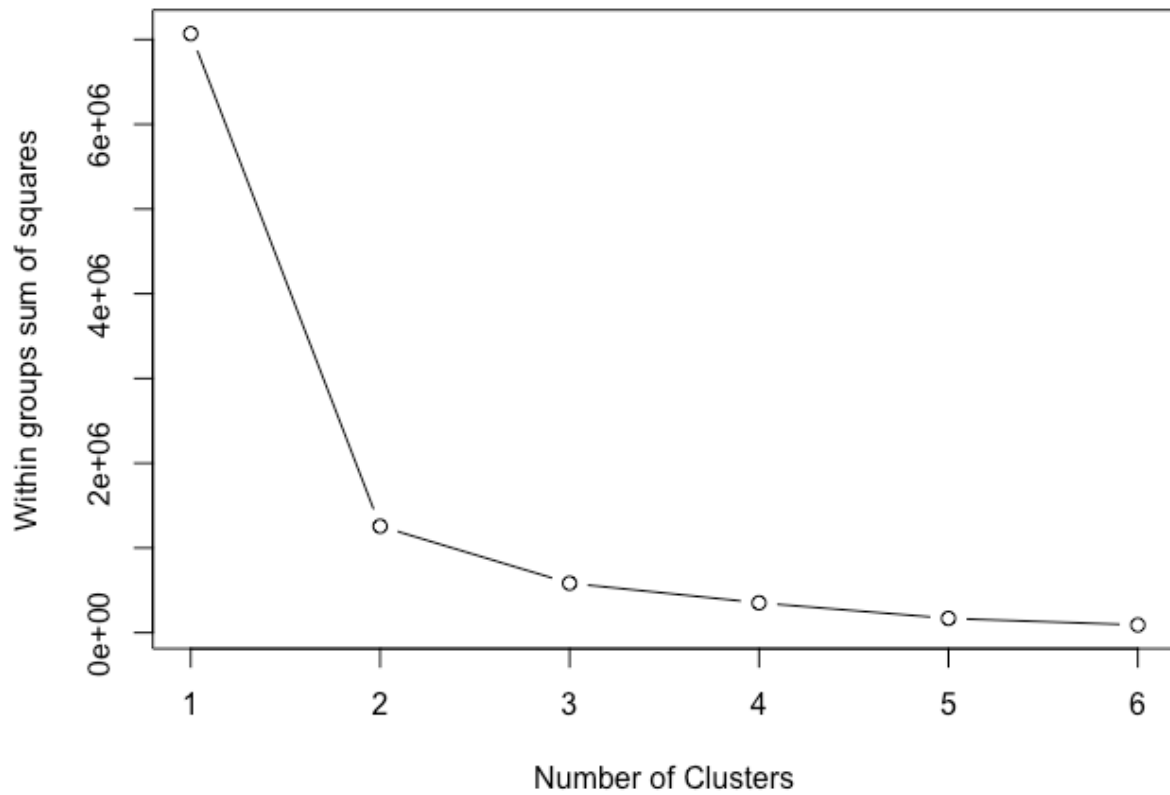


Figure S1 Scree plot shows the suitable number of clusters for ten sites. Optimal number of clusters corresponds to the elbow location (2), thus indicating two groups, southern (desert) and northern sites (grassland).

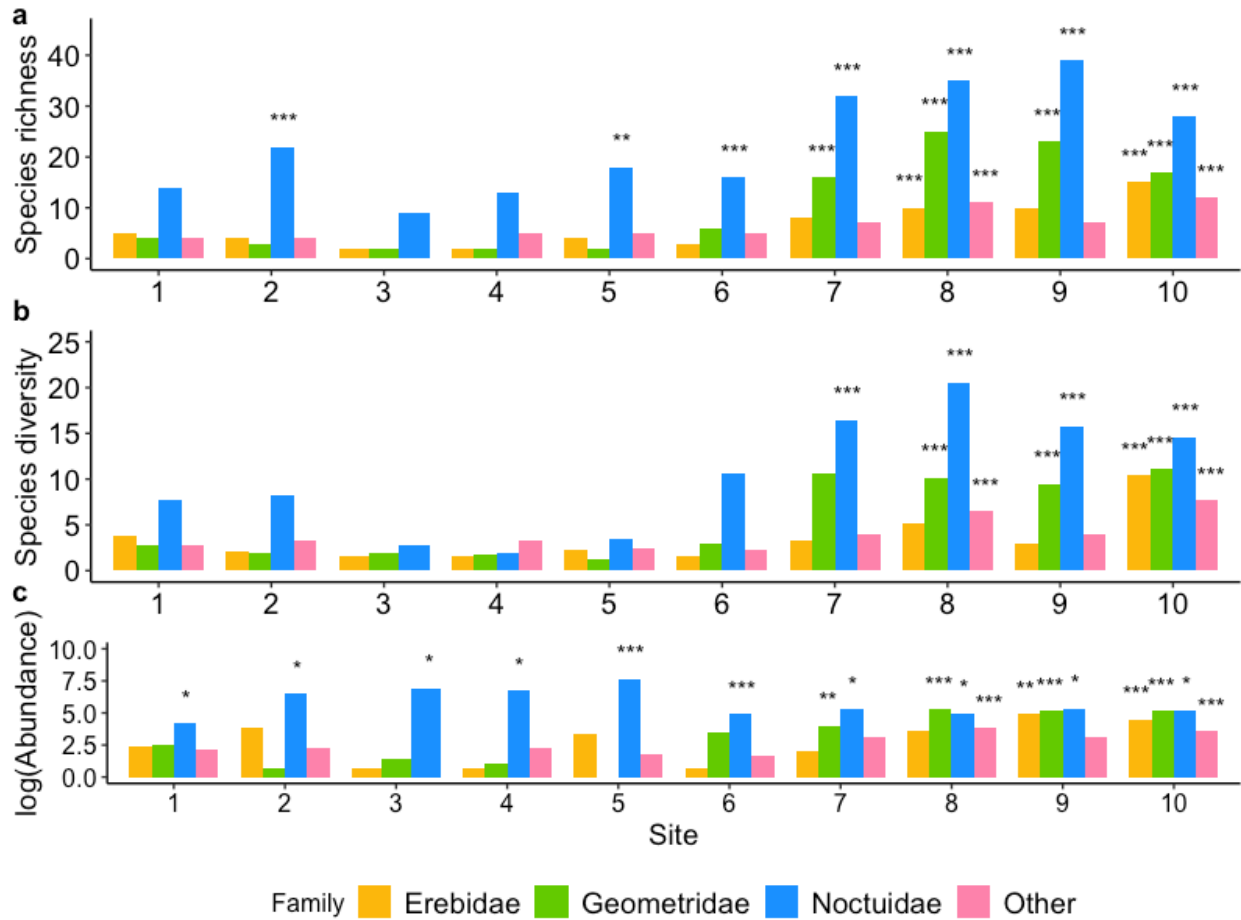


Figure S2 Species richness, species diversity and abundance (Hill numbers) of Noctuidae, Geometridae, Erebidae and other families of each site. (Compared with GLM).

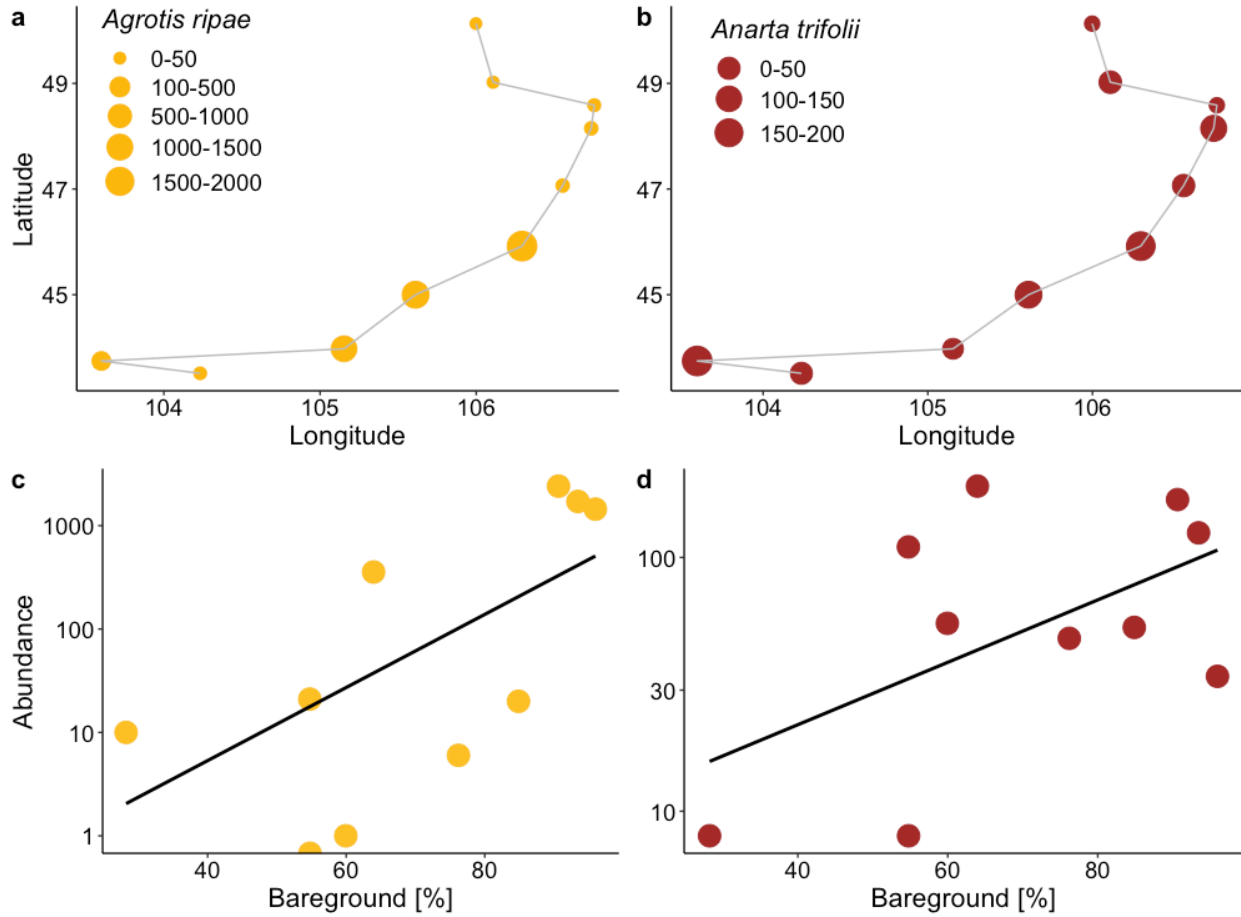


Figure S3 Abundance of two most dominant species *Agrotis ripae* (left) and *Anarta trifolii* (right) along the latitudinal gradient. a) Abundance of *Agrotis ripae*, b) Abundance of *Anarta trifolii*. Correlation of the percentage of Bareground with Abundance of c) *Agrotis ripae* and d) *Anarta trifolii* after log10 transformation. GLM line was fitted to each correlation graph to show the response of Abundance to Bareground.

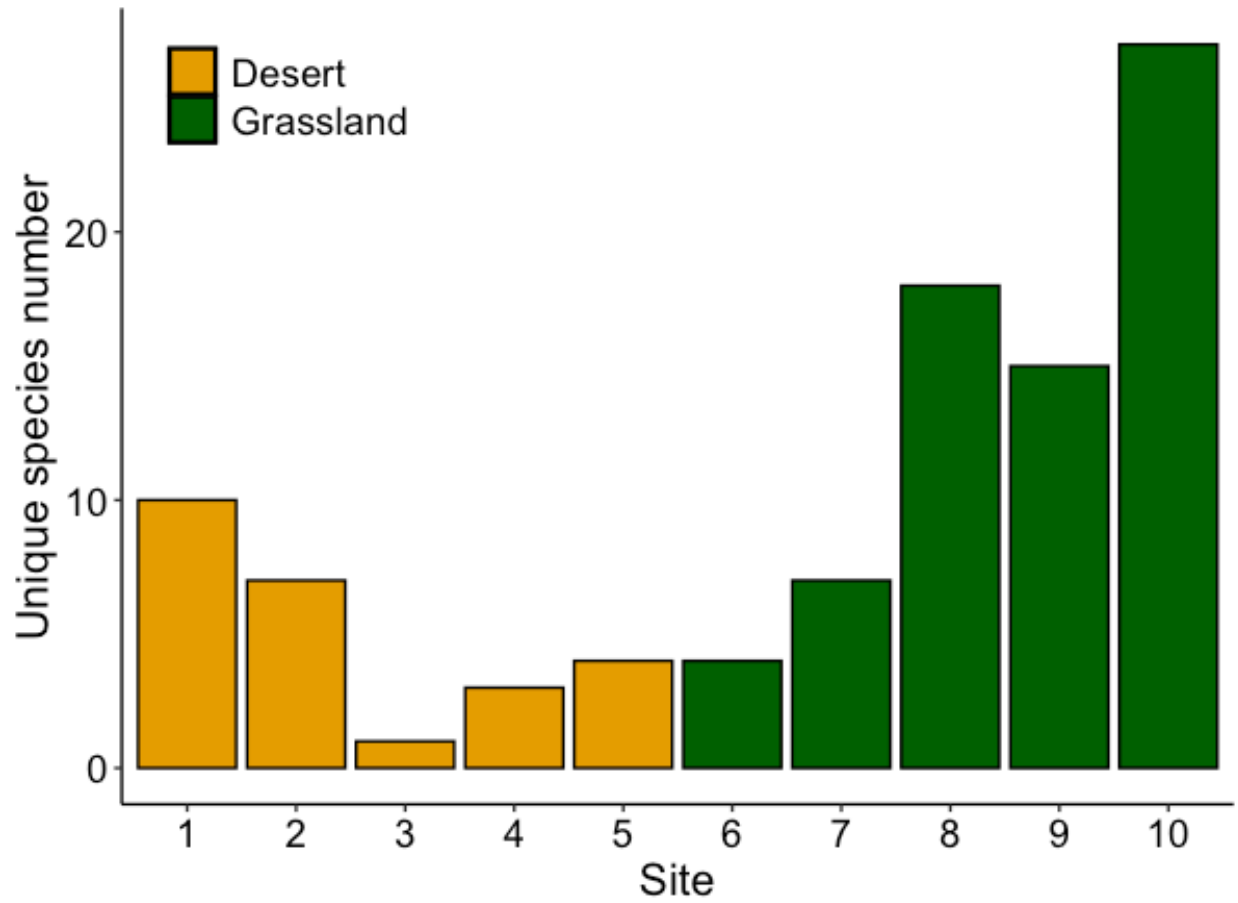


Figure S4 Number of unique species per site. These species occurred only in one site. Site three had only one unique species, whereas site 10 had 27 unique species.

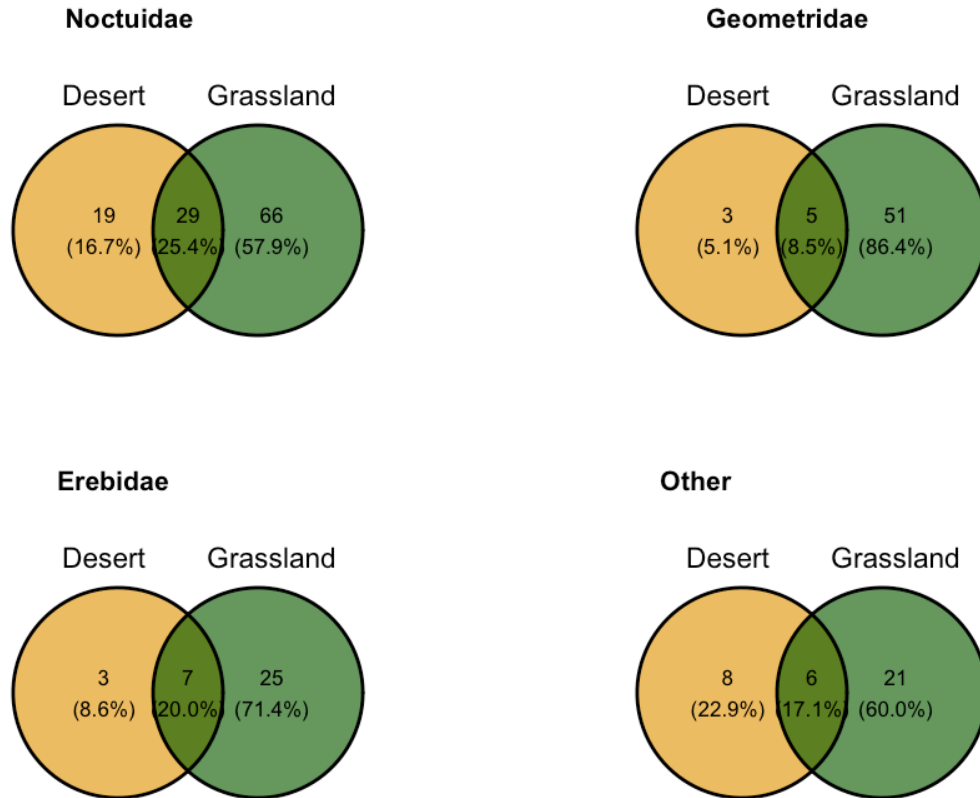


Figure S5 Venn diagrams showing the species overlaps of assemblages by main groups. a) Noctuidae, b) Geometridae, c) Erebidae, and d) Other

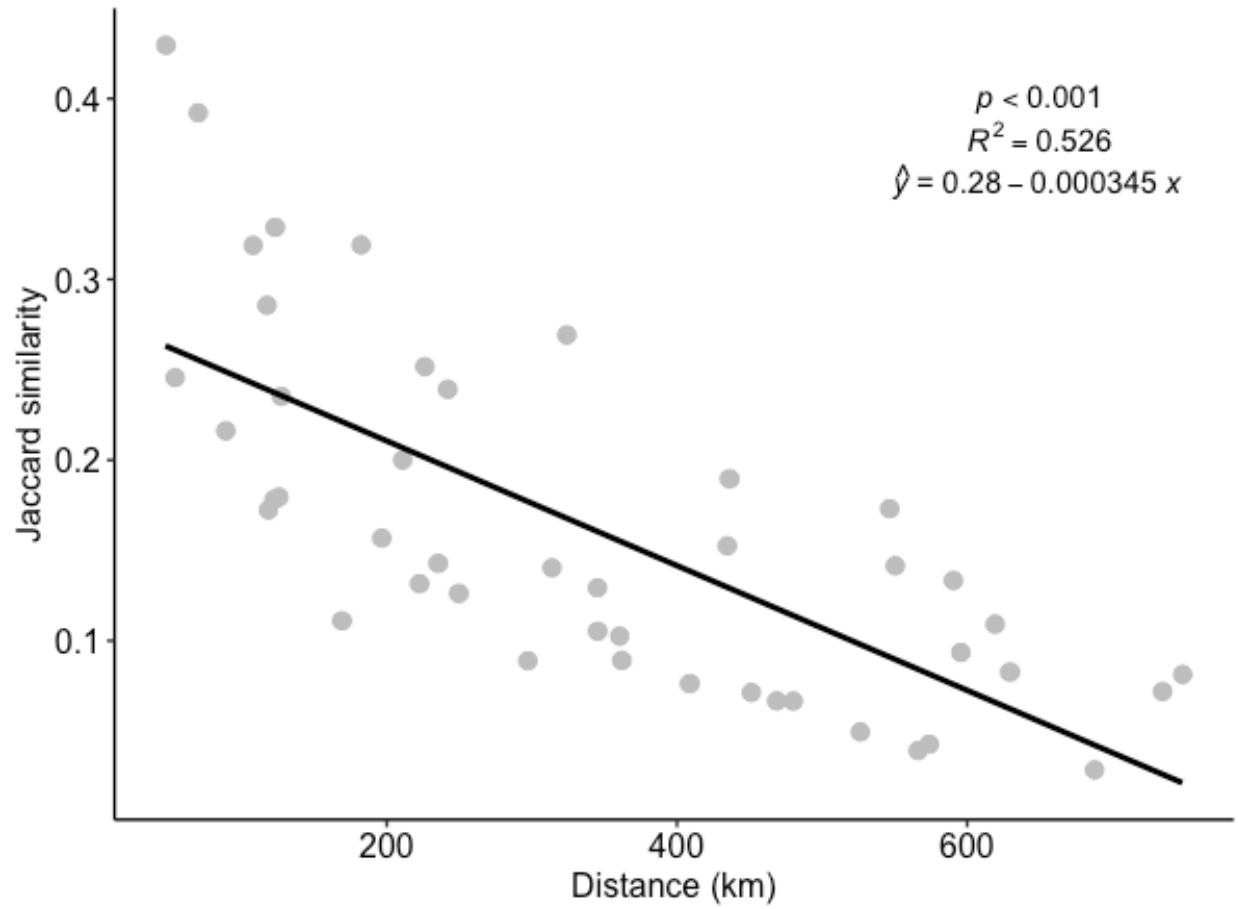


Figure S6 Distance-decay relationship for Mongolian moth assemblages. Shown is pairwise Jaccard similarity of all sites plotted against the pairwise distance in km.

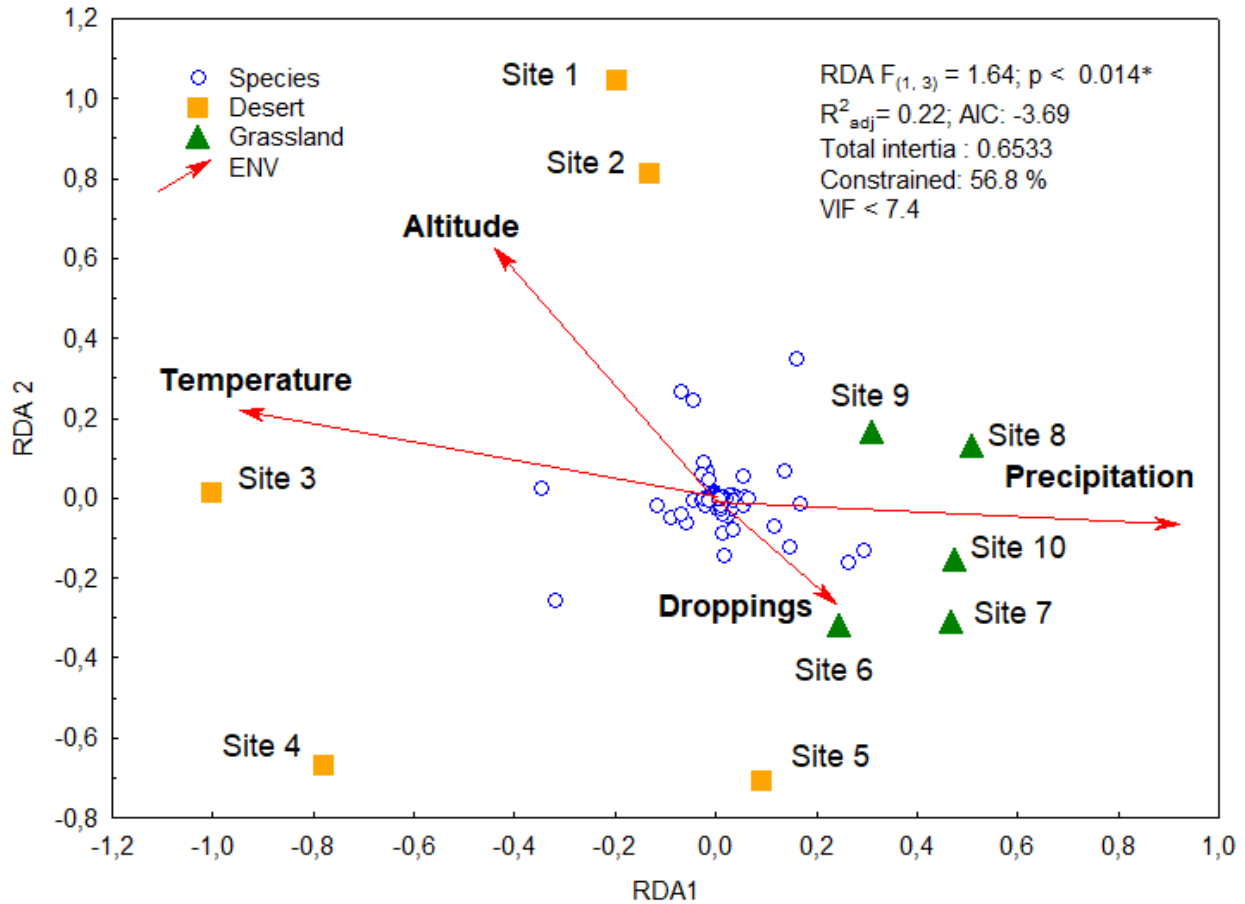


Figure S7 Parsimonious RDA of the plant communities. Four parameters explained 22% of the variation. Z-standardized environmental parameters had variance inflation factors (VIF) < 7.4. Species data were Hellinger-transformed prior to analysis. While site 5 is intermediate in plant species composition, the plots of plant communities in desert and grassland are clearly separated and differ significantly in RDA1 (U-test, $U = -2.61$, $p < 0.009$).

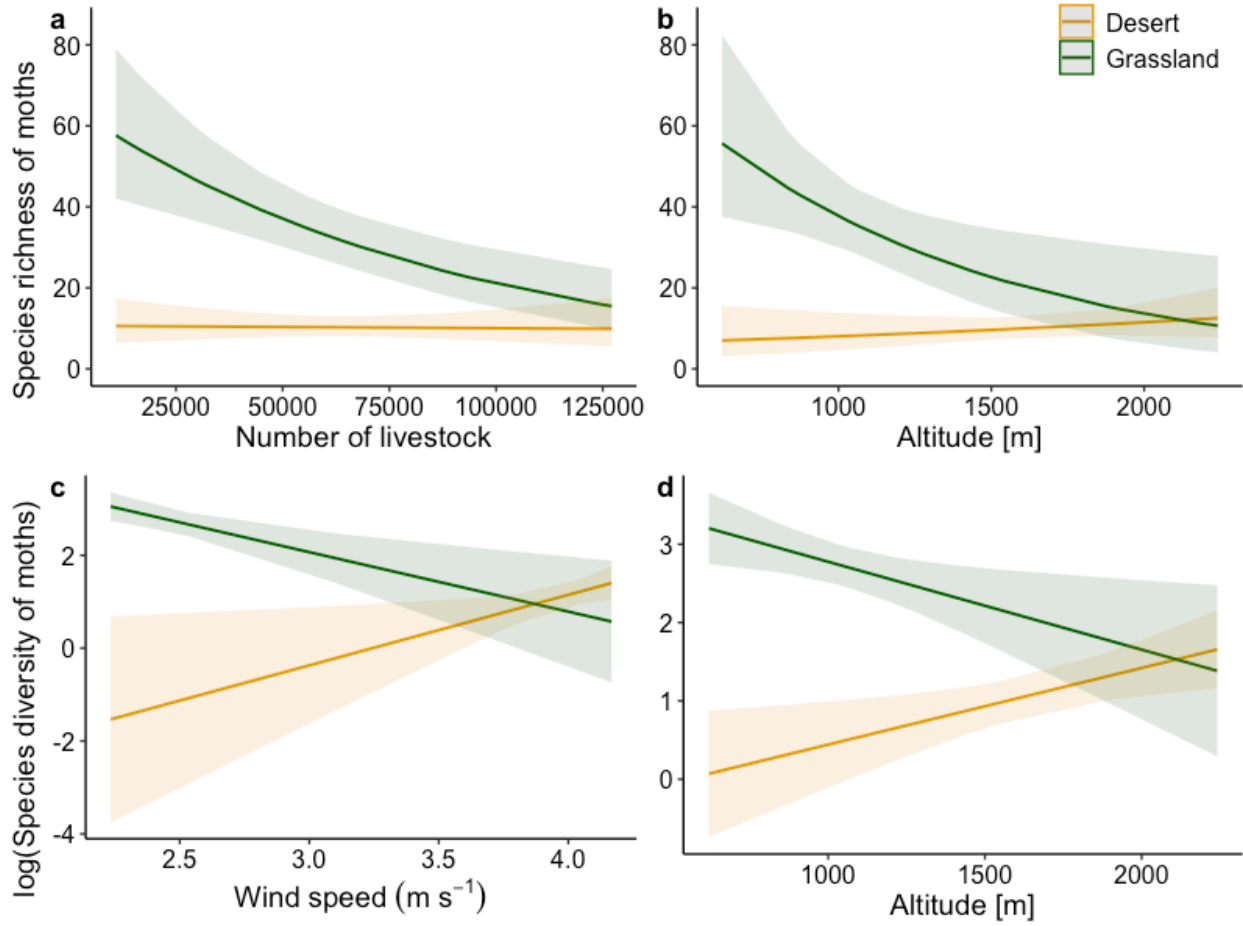


Figure S8 Interaction effects of environmental variables and biome type on the species richness and the diversity of macro-moths. a) Number of livestock x Biome, b) Altitude, c) Wind speed, d) Altitude.

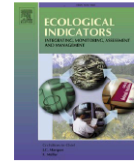
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Effects of grazing on macro-moth assemblages in two different biomes in Mongolia

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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 kiti*, *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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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, species richness of both specialist and generalist moths did not differ between grazed and less grazed plots; in contrast, in grassland, species richness of both groups was higher in less grazed plots. We found two indicator species of grazing in the desert: *Hyles chivilini* 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.

Key words: Lepidoptera, livestock, habitat disturbance, diversity, gradient, specialist, generalist, functional trait, beta diversity

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 interaction between species, while land-use change leads to population declines and species losses (Kadlec et al., 2009). 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 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 is steadily increasing since the privatization of livestock sector after socialism (Lkhagvadorj et al., 2013). In 2020, the total number of livestock was 67 068 486 (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 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 important 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 are responding differently to grazing. For example, generalist species are benefiting, while specialists are suffering (Warren et al., 2001), especially moths in grasslands and arid lands (Wagner et al., 2021). (But see Schwarz & Fartmann: 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 short time period.)

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). Another review shows that moths and butterflies are dispersing to higher latitudes due to climate change and habitat degradation (Warren et al., 2001). In Great Britain, it was reported that ranges of cold-adapted species shrank and populations declined due to habitat modification and climate change; 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, 2019). 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 response to grazing. According to the dynamic equilibrium model, in arid areas (non-equilibrium), grazing impact on plant diversity is weaker compared to climate variables such as low precipitation. In contrast, in wetter areas (equilibrium), grazing impact on plant diversity is relatively stronger compared to climate variables (Wang et al., 2017). In a study of

vegetation (Ahlborn et al., 2020), effects of precipitation were stronger than effects of livestock grazing (Wesche et al., 2010) in arid areas. The effects of livestock grazing made some species more tolerant to this impact, and generally, the species composition of plants did not differ much between grazing intensities in wetter areas. Since moth species are dependent on specific plants as food resource, they could show a similar response to grazing in arid and wetter biomes. Moreover, revealing how moth species composition changes between intensively and lesser grazed plots with different plant species richness is crucial from the conservation point of view. If moth species composition of grazed and less grazed pastures differs due to spatial turnover (i.e., species replacement), this indicates grazed and less grazed pastures have distinct species compositions, and therefore, both pastures should be managed in a different way. If the difference between grazed and less grazed pastures is due to nestedness (i.e., species gain or loss), they can be regarded as similar pastures and they can be managed in a similar way. In a previous study on moths along the latitudinal gradient, moth community composition broke down in two groups that differed significantly 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 in two contrasting biomes and to reveal indicator species for grazing pattern and along the latitudinal gradient.

We hypothesized:

1. Moth species richness and diversity are higher in less grazed plots than in grazed plots.
2. Moth species composition is different between grazed and less grazed plots.
3. At grazed plots, generalized traits of moths will be dominant in the population over specialized traits.
4. 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.
5. 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) (Figure 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). Along the latitudinal climatic gradient, they established a 600 km long transect 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). 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).

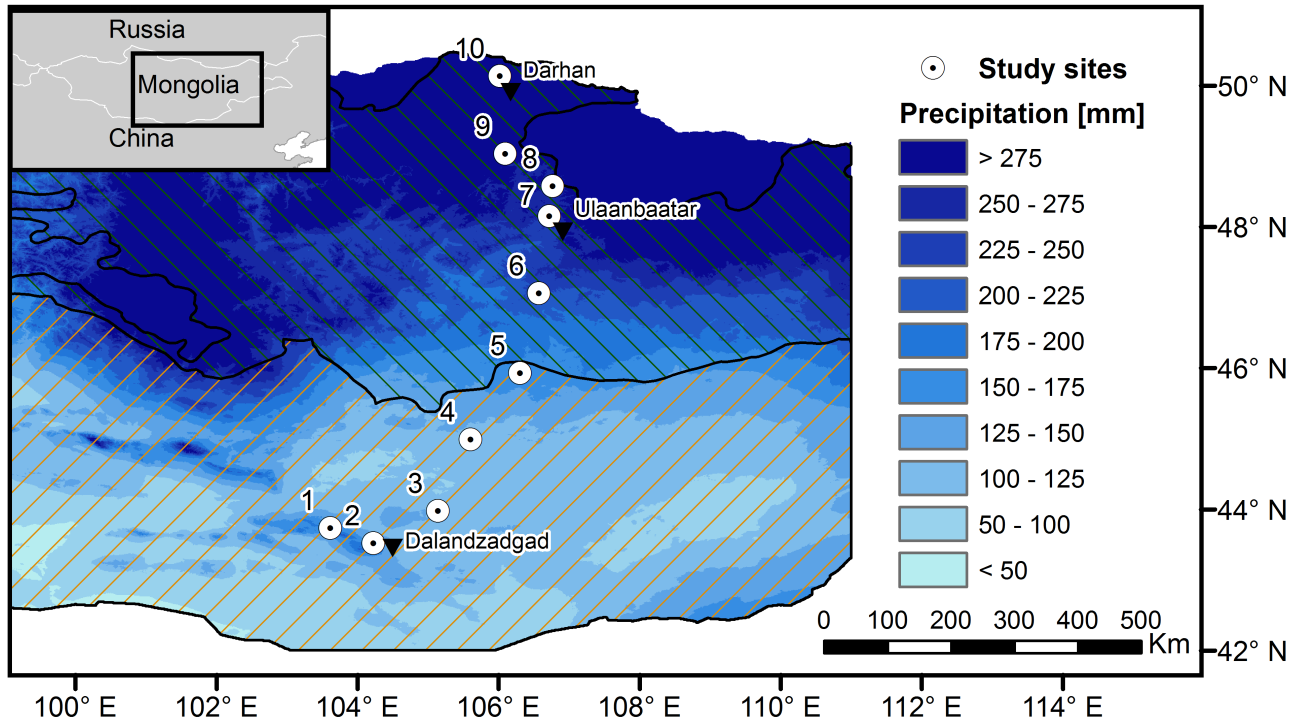


Figure 1 Study area along the rainfall gradient in Mongolia (Lang et al., 2019 and Ahlborn et al., 2020). Dark green hashed area represents Desert and xeric shrublands biome and orange hashed area represents Temperate grasslands, savannas & shrublands biome.

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.s.l. 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).

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 powerbank batteries (EasyAcc 26 Ah), (Brehm, 2017), inside light "towers" (Bioform: Large R. Müller light trapping tower, mesh size 1mm, 70 cm diameter, 180 cm high). Moths were manually sampled using collecting jars. In the field, we sorted and identified all individual moths at 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 9–12 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, 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., 2021b, 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 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., 2019) and *purrr* (Henry et al., 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 11117 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).

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

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 (Figure 2 a-i). All metrics in the 'Other' group (remaining assemblage) did not differ significantly between grazed and less grazed plots (Figure j-l).

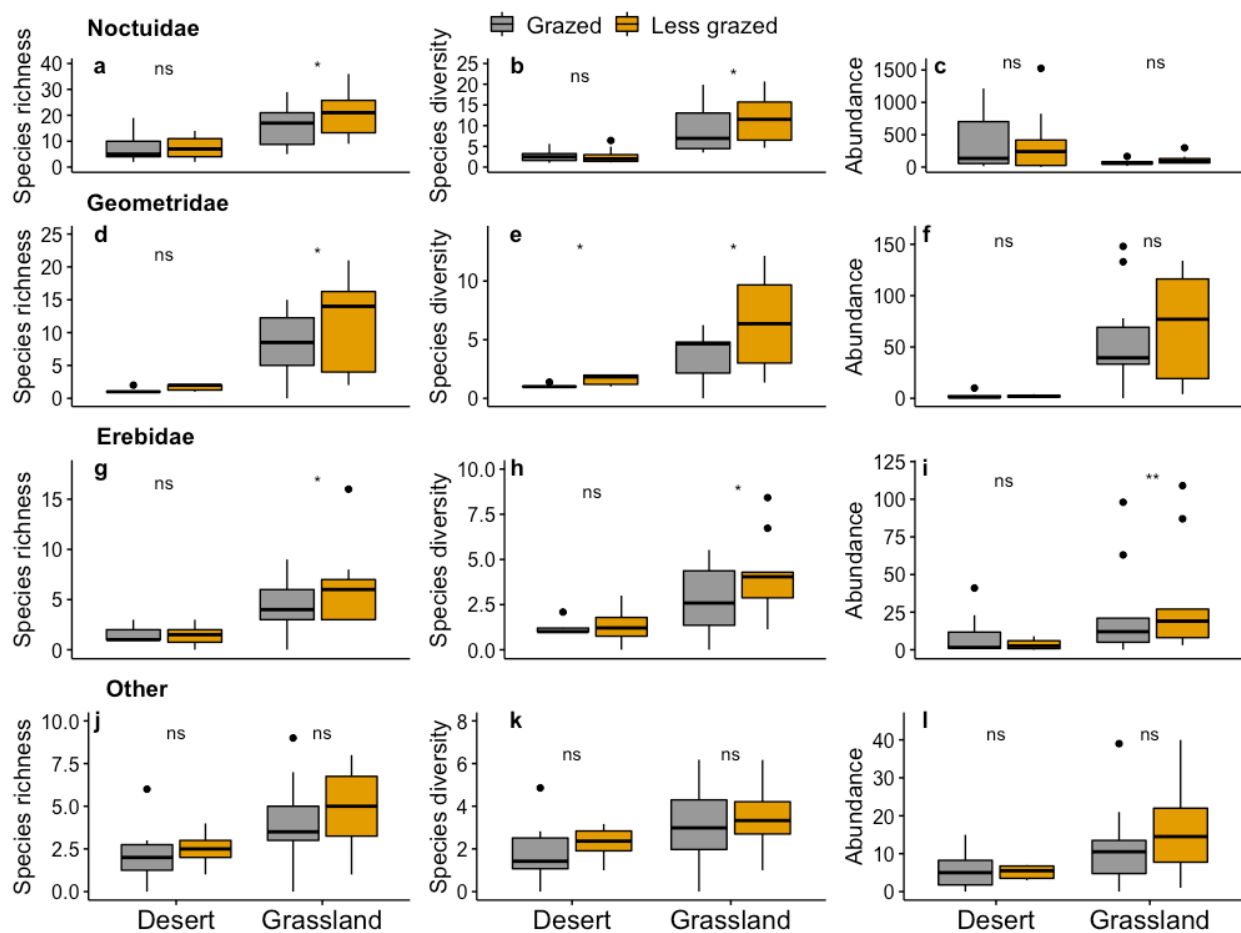


Figure 2 Comparisons of species richness, species diversity, abundance (aggregated from 5 sites x 6 nightly samples in each biome) (a-c), Noctuidae (d-f), Geometridae (g-i), Erebidae (j-l), 'Other' for each

Results

biome under different grazing regimes. Significant differences are represented by stars: * $p < 0.05$, ** $p < 0.01$, ns = non-significant.

3.2 Species composition

Venn diagrams show that the number of overlapping species between grazed and less grazed plots differed in the two biomes (Figure 3 and Figure 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'.

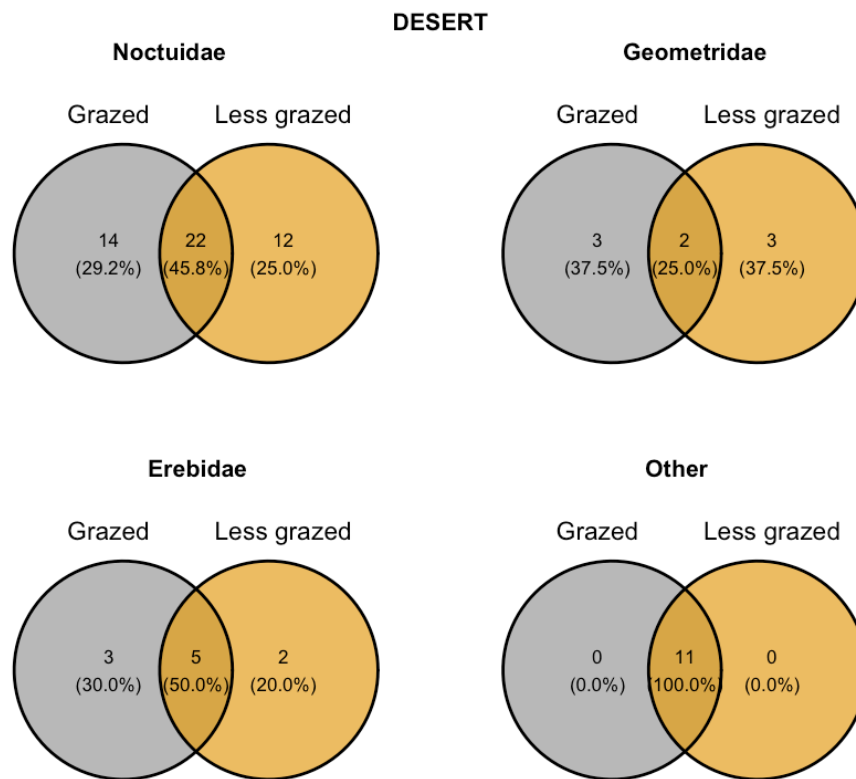


Figure 3 Venn diagrams of desert biome demonstrate the overlapping of unique species between grazed and less grazed plots in the families of Noctuidae, Geometridae, Erebidae and group 'Other'. No unique species were found in both Grazed and Less grazed plots in the group 'Other'.

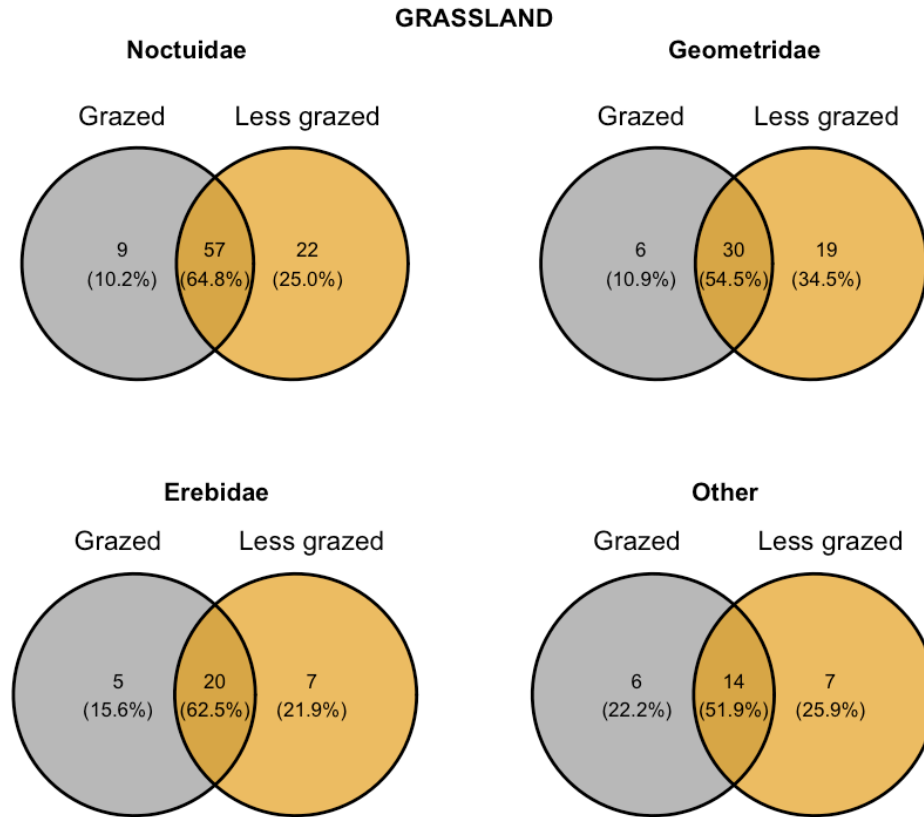


Figure 4 Venn diagrams of grassland biome demonstrate the overlapping of unique species between grazed and less grazed plots in the families of Noctuidae, Geometridae, Erebidae and group 'Other'.

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 (Figure 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 (Figure 5b). Lastly, we checked if vegetation species richness differs in grazed and less grazed plots in both biomes (Figure 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.

Results

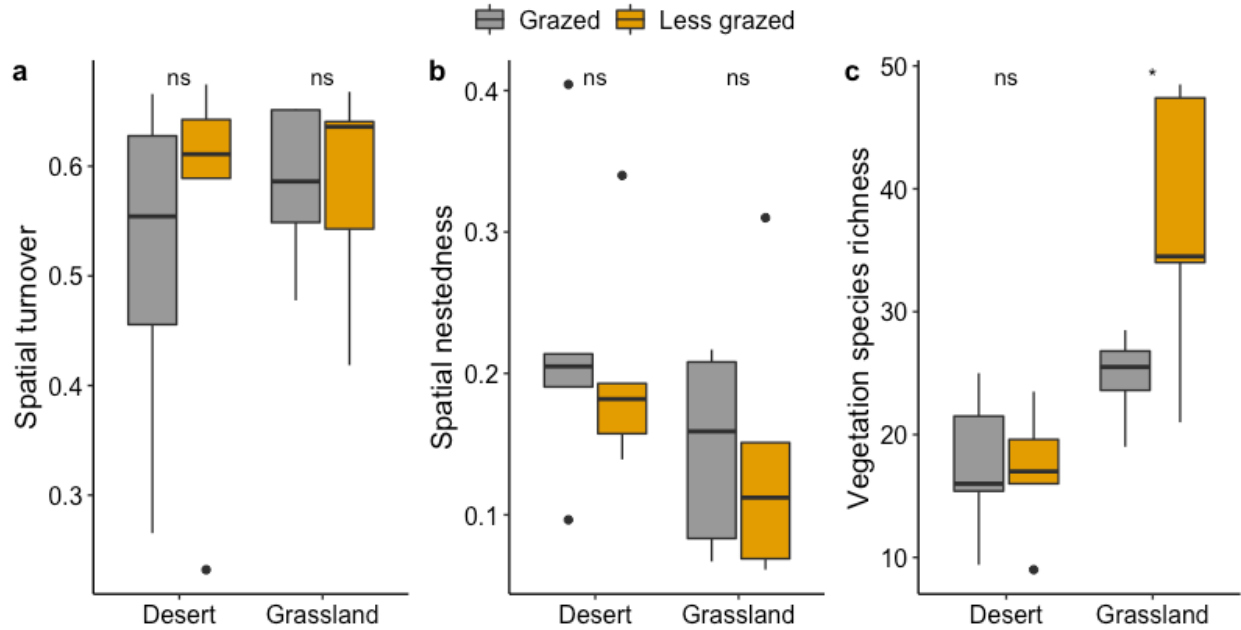


Figure 5 a) Spatial turnover, b) spatial nestedness, and c) vegetation species richness under different grazing regimes in desert and grassland. Dots represent outliers, significant differences are represented by stars: * $p < 0.05$, ns = non-significant.

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

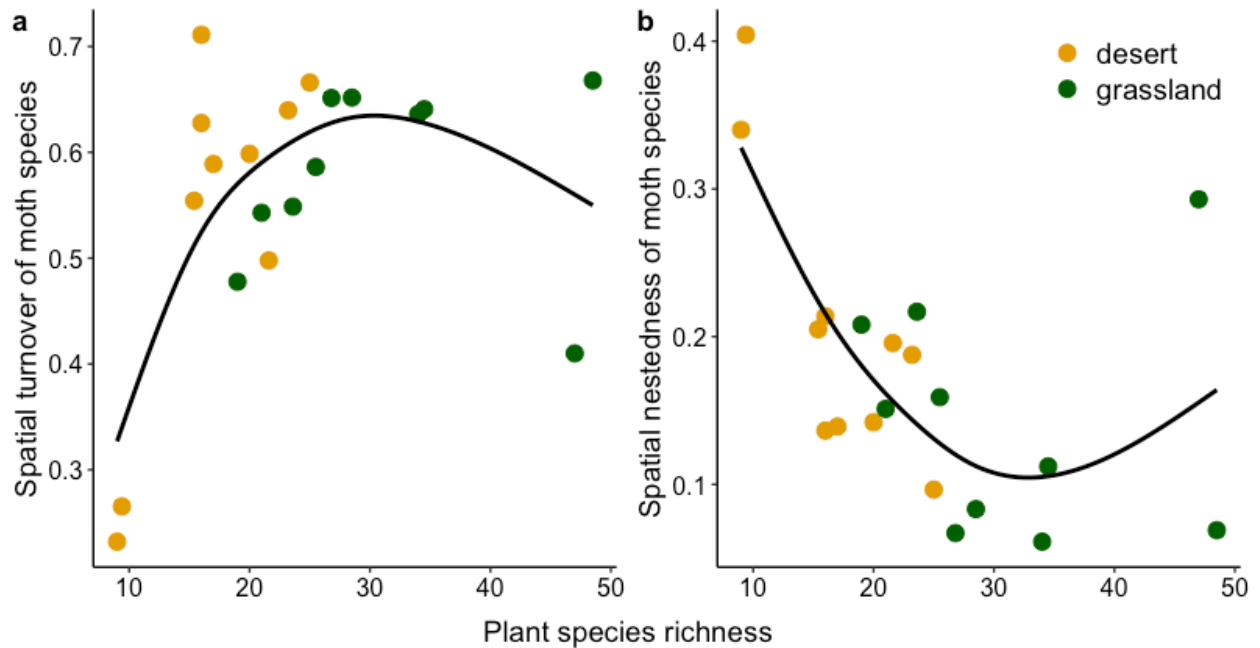


Figure 6 Relationship between a) spatial turnover of moth species (between grazed and less grazed plots) and vegetation species richness, and b) along grazing nestedness and vegetation species richness. Orange circles indicate desert, green circles indicate grassland.

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 (Figure 7).

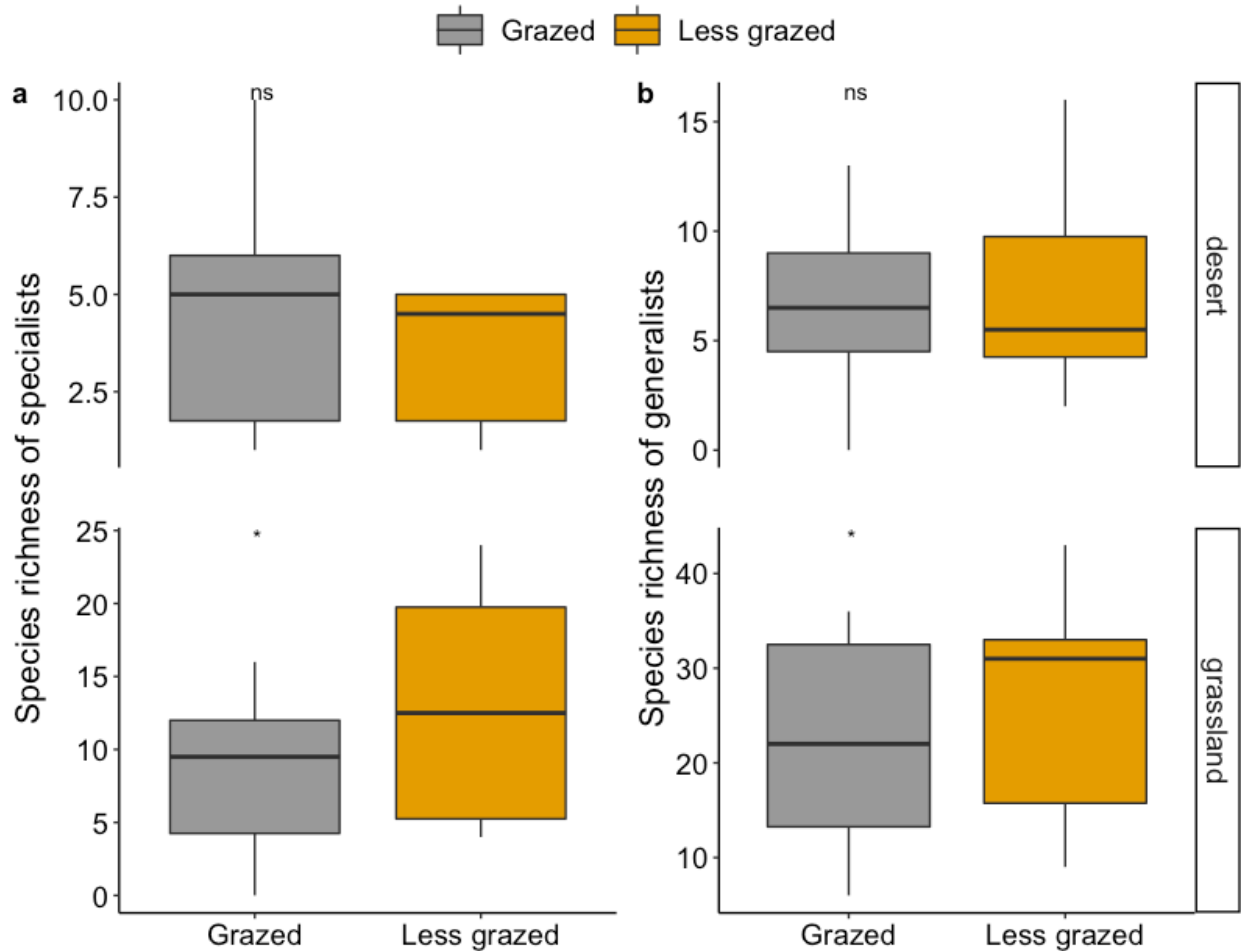


Figure 7 Species richness of a) specialist and b) generalist moths in grazed and less grazed plots in two distinct biomes: desert and grassland as compared by T-test. Significant differences are represented by stars: * $p < 0.05$, ** $p < 0.01$, ns = non-significant.

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) (Figure 8).

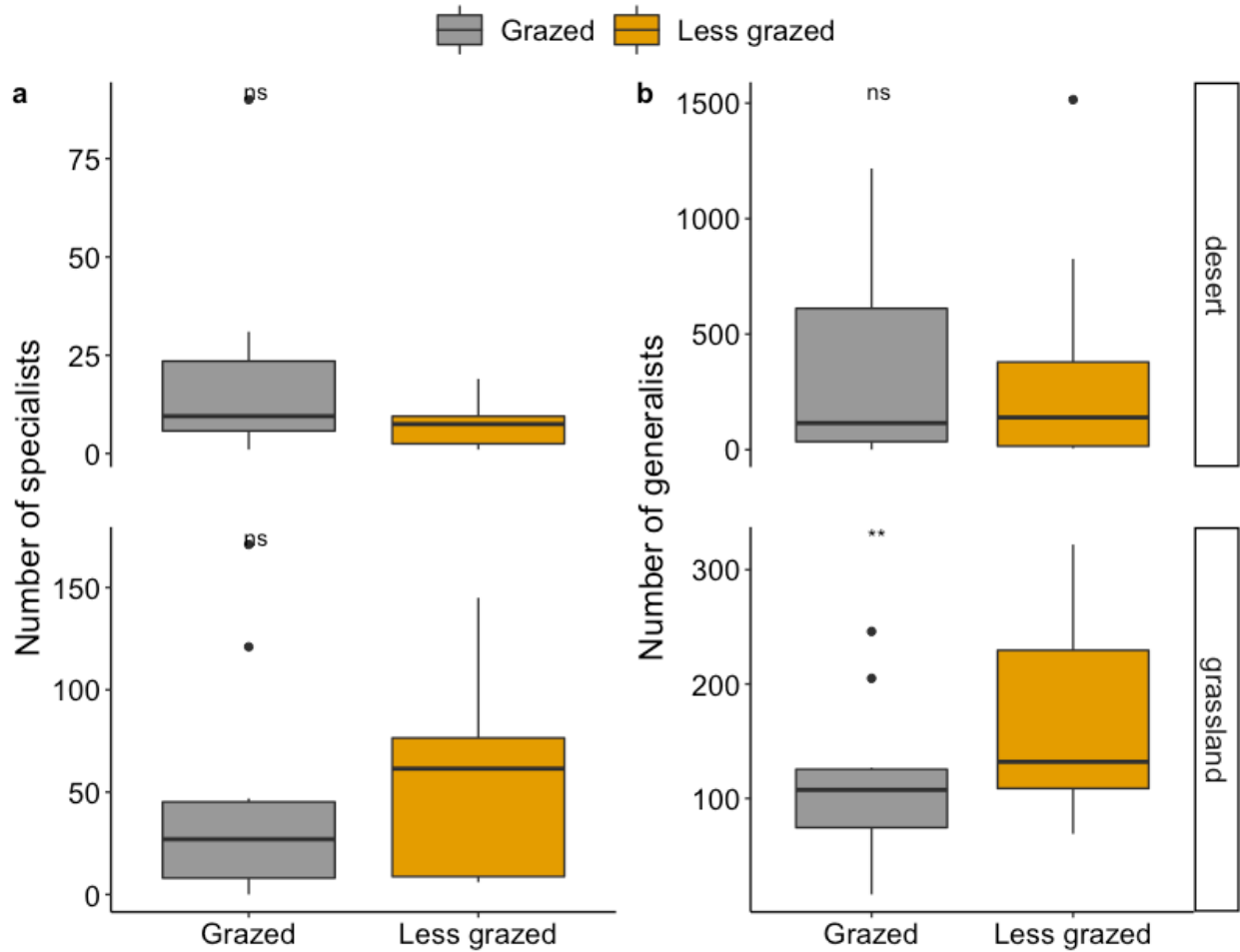


Figure 8 Numbers of a) specialist and b) generalist moth individuals in grazed and less grazed plots in two distinct biomes: desert and grassland. Significant differences are represented by stars: * $p < 0.05$, ** $p < 0.01$, ns = non-significant.

Against our expectation, species richness of generalists correlated stronger with species richness of vegetation than that of the specialists (Figure 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: $r=0.50$, $p < 0.001$).

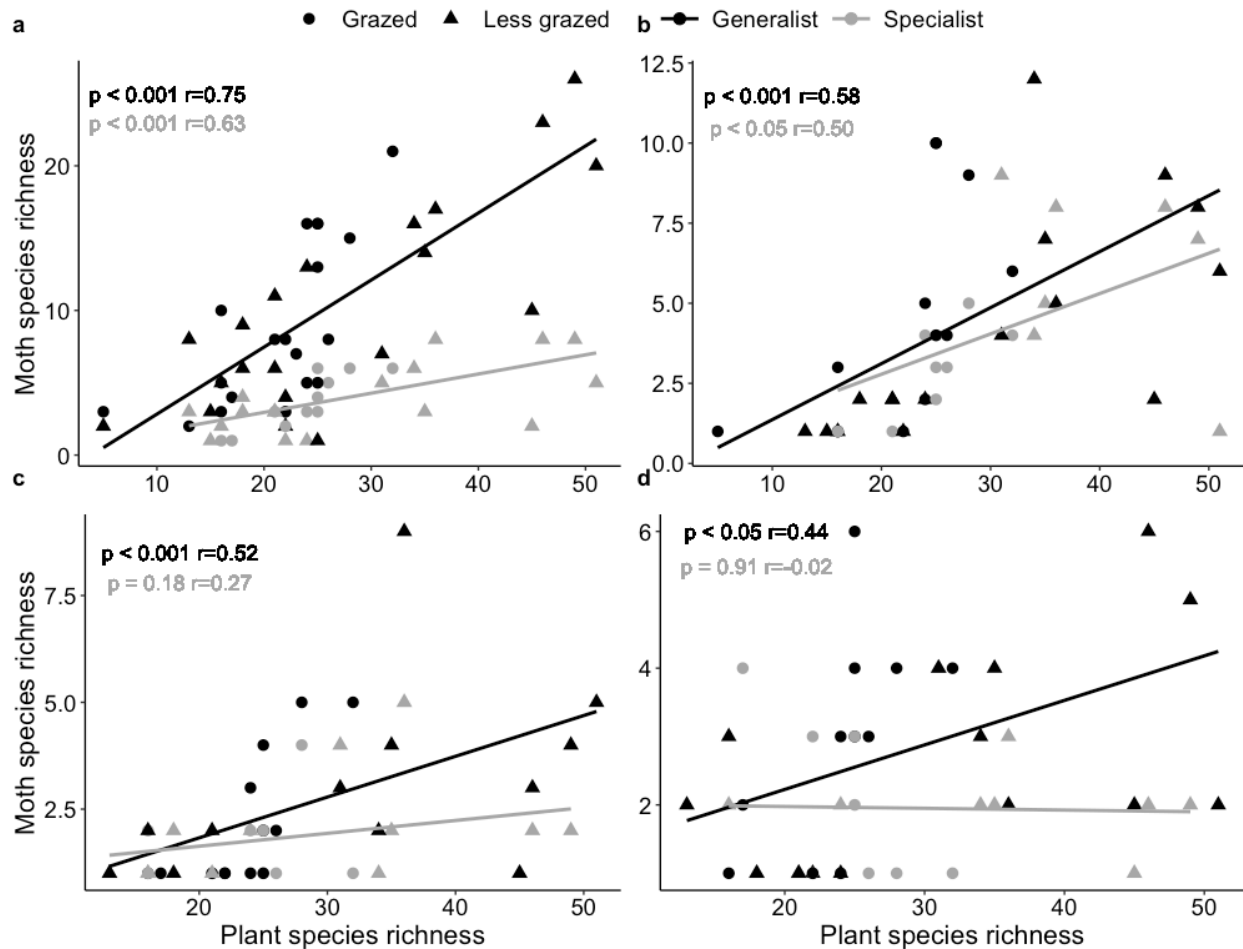


Figure 9 Relationship between moth species richness and vegetation species richness for Generalists (black line) vs. Specialists (grey line). a) Noctuidae, b) Geometridae, c) Erebidae, d) 'Other'. Grazed and less grazed plots have been pooled for each of both groups.

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.

Results

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	<i>Catarhoe cuculata</i>	Specialist	0.894	0.0473											
2019	2	Noctuidae	<i>Cucullia splendida</i>	Specialist	0.873	0.0418	■	■									
2019	1	Noctuidae	<i>Euxoa ochrogaster</i>	Generalist	0.882	0.0467						■	■				
2018, 2019	1	Sphingidae	<i>Hyles chivilini</i>	Generalist	0.894	0.0455	■										
2019	1	Noctuidae	<i>Lacanobia thalassina</i>	Generalist	0.777	0.0224											
2019	1	Geometridae	<i>Megalycinia strictaria</i>	Not clear	0.787	0.0093											
2018, 2019	1	Noctuidae	<i>Mythimna comma</i>	Generalist	0.814	0.0004											
2019	1	Noctuidae	<i>Polia bombycina</i>	Generalist	0.776	0.0327											
2018, 2019	1	Noctuidae	<i>Rhyacia simulans</i>	Generalist	0.913	0.0148											
2019	1	Noctuidae	<i>Sideridis kitti</i>	Specialist	0.777	0.0338											
2019	1	Noctuidae	<i>Sideridis egena</i>	Specialist	0.913	0.016											
2018, 2019	1	Sphingidae	<i>Smerinthus caecus</i>	Specialist	0.894	0.0465											

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* (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).

Results

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	<i>Actebia fennica</i>	1	0.8333	0.913	0.0003
2018	6	Noctuidae	<i>Actebia poecila</i>	0.8537	0.6667	0.754	0.0013
2018	7+8	Noctuidae	<i>Agrotis clavis</i>	0.918	0.8182	0.867	1.00E-04
2018	4+5	Noctuidae	<i>Agrotis ripae</i>	0.941	1	0.97	0.0001
2018	4+5	Noctuidae	<i>Anarta stigmosa</i>	1	0.8182	0.905	0.0001
2018	10	Geometridae	<i>Arichanna sinca</i>	1	0.6667	0.816	0.0004
2018	9+10	Erebidae	<i>Calyptra thalictri</i>	1	0.5	0.707	0.0028
2018	10	Erebidae	<i>Catocala deuteronympha</i>	1	0.8333	0.913	0.0003
2018	10	Erebidae	<i>Catocala pacta</i>	1	0.8333	0.913	0.0003
2018	8	Erebidae	<i>Chelis dahurica</i>	0.8951	1	0.946	0.0001
2018	10	Noctuidae	<i>Cosmia puralina</i>	1	0.6667	0.816	0.0008
2018	10	Noctuidae	<i>Cucullia scopariae</i>	0.95	0.6667	0.796	0.0008
2018	10	Erebidae	<i>Euproctis similis</i>	1	0.5	0.707	0.0099
2018	8+9+10	Lasiocampidae	<i>Gastropacha quercifolia</i>	1	0.5	0.707	0.0033
2018	8	Noctuidae	<i>Hada plebeja</i>	1	0.5	0.707	0.0086
2018	10	Noctuidae	<i>Ipimorpha retusa</i>	1	0.6667	0.816	0.0002
2018	9+10	Geometridae	<i>Isturgia arenacearia</i>	0.9839	0.8333	0.905	0.0001
2018	8	Noctuidae	<i>Lacanobia thalassina</i>	1	0.6667	0.816	0.0002
2018	7+8	Noctuidae	<i>Lasionhada proxima</i>	0.9474	0.7273	0.83	4.00E-04
2018	10	Erebidae	<i>Leucoma candida</i>	0.88	0.8333	0.856	0.0003
2018	9+10	Erebidae	<i>Lygephila lubrica</i>	0.9176	0.8333	0.874	0.0001
2018	7	Erebidae	<i>Lygephila vicae</i>	0.7598	1	0.872	0.0003
2018	10	Erebidae	<i>Lymantria dispar</i>	1	0.6667	0.816	0.0006
2018	10	Noctuidae	<i>Mythimna conigera</i>	1	0.5	0.707	0.01
2018	9+10	Noctuidae	<i>Mythimna velutina</i>	1	0.5	0.707	0.0109
2018	10	Noctuidae	<i>Polia bombycina</i>	0.9643	0.6667	0.802	0.0003
2018	6+7	Noctuidae	<i>Rhyacia simulans</i>	0.9217	0.7273	0.819	9.00E-04
2018	10	Geometridae	<i>Scopula decorota przewalskii</i>	0.9444	0.8333	0.887	1.00E-04
2018	10	Geometridae	<i>Scopula rubiginata</i>	1	0.5	0.707	0.0089
2018	8	Geometridae	<i>Scotopteryx chenopodiata</i>	1	0.8333	0.913	0.0005
2018	10	Sphingidae	<i>Smerinthus caecus</i>	1	0.5	0.707	0.0087
2018	10	Geometridae	<i>Thetidia chlorophyllaria</i>	0.913	0.8333	0.872	0.0001
2019	7+8	Noctuidae	<i>Agrotis clavis</i>	0.925	0.5833	0.735	0.0085
2019	7+8+9	Noctuidae	<i>Agrotis exclamationis</i>	0.8889	0.6667	0.77	0.001
2019	8	Erebidae	<i>Autographa buraetica</i>	0.6364	0.8333	0.728	0.002
2019	7+10	Geometridae	<i>Biston betularia</i>	0.8958	0.9	0.898	1.00E-04
2019	10	Sphingidae	<i>Callambulyx tatarinovii</i>	0.7895	0.75	0.769	0.0012
2019	10	Erebidae	<i>Catocala bella</i>	1	0.5	0.707	0.0138

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2019	10	Erebidae	<i>Catocala deuteronympha</i>	0.8824	0.75	0.813	0.0012
2019	1	Noctuidae	<i>Dichagyris vallesiaca</i>	0.8621	0.6667	0.758	0.0031
2019	1	Cossidae	<i>Eogystia hippophaecolus</i>	1	0.6667	0.816	0.0013
2019	1	Noctuidae	<i>Euxoa cursoria</i>	0.9489	0.8333	0.889	0.0006
2019	8+10	Lasiocampidae	<i>Gastropacha quercifolia</i>	0.8111	0.9	0.854	1.00E-04
2019	7	Noctuidae	<i>Heliothis ononis</i>	0.75	0.6667	0.707	0.0068
2019	2	Sphingidae	<i>Hyles chivulini</i>	0.7059	0.8	0.751	0.0007
2019	9+10	Geometridae	<i>Isturgia arenacearia</i>	0.9087	1	0.953	1.00E-04
2019	7+8+9	Noctuidae	<i>Lacanobia thalassina</i>	1	0.6111	0.782	0.0015
2019	7+8	Noctuidae	<i>Lasionhada proxima</i>	1	0.6667	0.816	0.0004
2019	9	Erebidae	<i>Lygephila lubrica</i>	0.8944	1	0.946	0.0002
2019	7	Erebidae	<i>Lygephila vicae</i>	0.9773	1	0.989	0.0001
2019	8	Noctuidae	<i>Malacosoma castrensis</i>	0.9091	0.8333	0.87	0.0001
2019	10	Sphingidae	<i>Marumba gaschkewitschii</i>	1	0.5	0.707	0.014
2019	8+10	Geometridae	<i>Megaspilates mundataria</i>	1	0.7	0.837	2.00E-04
2019	2	Noctuidae	<i>Panchrysia ornata</i>	1	0.6	0.775	0.0017
2019	9	Geometridae	<i>Pelurga comitata</i>	1	0.5	0.707	0.0063
2019	8+9	Geometridae	<i>Phibalapteryx virgata</i>	0.9077	0.75	0.825	0.0003
2019	8+9+10	Noctuidae	<i>Polia bombycina</i>	0.9672	0.625	0.778	0.0012
2019	9	Geometridae	<i>Scopula virgulata</i>	0.5882	0.8333	0.7	0.0098
2019	8+9	Geometridae	<i>Scotopteryx chenopodiata</i>	0.9167	0.5833	0.731	0.0019
2019	8	Sphingidae	<i>Sphinx ligustri</i>	1	0.6667	0.816	0.0017
2019	8+9+10	Geometridae	<i>Thetidia chlorophyllaria</i>	1	0.6875	0.829	0.0001

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 (Figure 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.

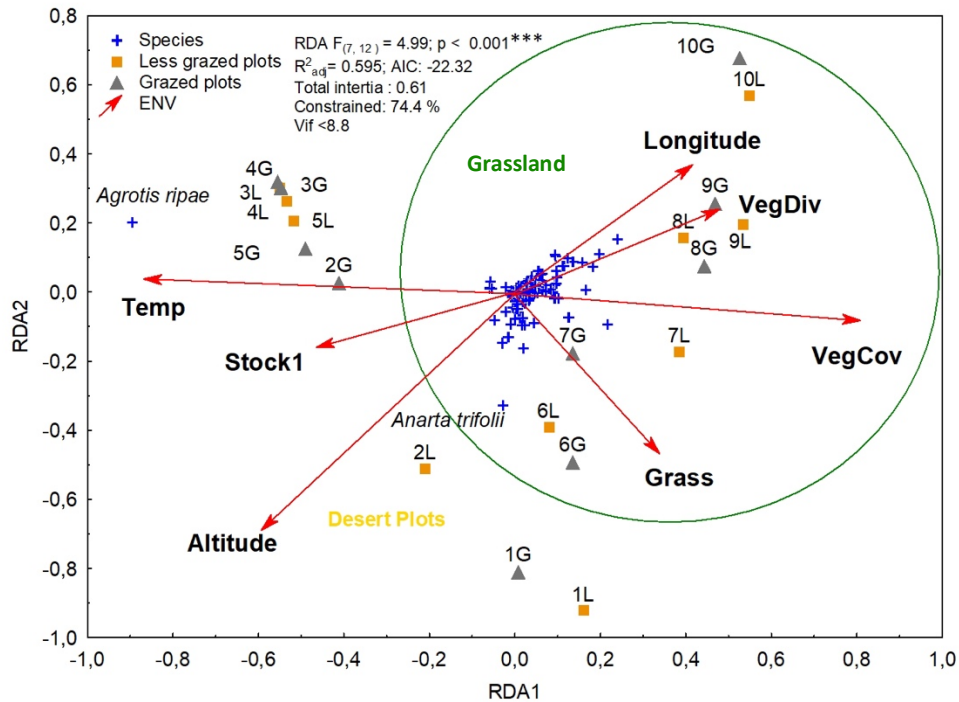


Figure 10 Parsimonious redundancy analysis (RDA) based on the composition of macro-moth assemblages of grazed and less grazed plots at ten sites along our transect. Grassland plots within the green disk. Seven environmental factors explained 60 % of the model variation: mean annual temperature (Temp), 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 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 ($p < 0.001$).

Lastly, we aimed to study how vegetation species richness was responsible for 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 trifolii*, 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 chivilini* 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. chivilini* 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 (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.

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 (Poyry 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.

Declaration of Competing interests

The authors declare no competing interests.

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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.

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Supplementary material

Table S1 Summary of 10 study sites which comprises 20 study plots. Odd numbers of codes represent heavily grazed area, even numbers represent slightly grazed areas. Here are shown Location name in detail, Coordinates, Altitude, Sampling time period, Grazing type, Number of trap nights and Biome. Biome data derived from (“WWF - Endangered Species Conservation,” 2020)

Sites	Location	Coordinates	Altitude	Time period	Grazing type	No of trap nights	Biomes
1	Umnugobi Aimag, Dalanzadgad, Shatiin am	43.52048 104.22263	1875	June 2018, August 2019	Grazed	7	Desert and Xeric Shrublands
	Umnugobi Aimag, Dalanzadgad, Shatiin am	43.51139 104.23272	1916	June 2018, August 2019	Less grazed	7	
2	Umhubobi Aimag, Bayandalai Soum, Khuv, Khaalganii khuudas	43.73480 103.61254	2241	June 2018, August 2019	Grazed	5	
	Umhubobi Aimag, Bayandalai Soum, Khuv, Khaalganii khuudas	43.74442 103.59985	2163	June 2018, August 2019	Less grazed	5	
3	Umnugobi Aimag, Tsogtovoo Soum, Khetsuu khoshuu	43.97874 105.13784	1518	June 2018, July, August 2019	Grazed	5	
	Umnugobi Aimag, Tsogtovoo Soum, Khetsuu khoshuu	43.97555 105.15340	1542	June 2018, July, August 2019	Less grazed	5	
	Dundgobi Aimag, Khuld Soum, Dov Dev	44.99017 105.60041	1196	June 2018,	Grazed	6	

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				July 2019			
4	Dundgobi Aimag, Khuld Soum, Dov Dev	44.99908 105.61159	1218	June 2018, July 2019	Less grazed	6	
	Dundgobi Aimag, Saintsagaan Soum, Khargim	45.92816 106.30558	1459	June 2018, July 2019	Grazed	5	
5	Dundgobi Aimag, Saintsagaan Soum, Limbet	45.91909 106.29333	1471	June 2018, July 2019	Less grazed	5	
	Tuv Aimag, Bayan- Unjuul Soum, Khalzan Ukhaa	47.06146 106.57088	1430	July 2018, June 2019	Grazed	6	Temperate Grasslands, Savannas & Shrublands
6	Tuv Aimag, Bayan- Unjuul Soum, Khalzan Ukhaa	47.06541 106.55341	1439	July 2018, June 2019	Less grazed	6	
	Tuv Aimag, Ulaanbaatar city, Songinokhairkhan district, 21th khoroo, Partizan, Tsagaan chuluutiin am	48.15344 106.71899	1240	July 2018, July 2019	Grazed	6	
7	Tuv Aimag, Ulaanbaatar city, Songinokhairkhan district, 21th khoroo, Partizan, Tsagaan chuluutiin am	48.14886 106.73609	1283	July 2018, July 2019	Less grazed	6	
	Selenge Aimag, Tunkhel village, Khailaast	48.57911 106.7648	1028	July 2018, July	Grazed	6	

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8	Selenge Aimag, Tunkhel village, Khailaast	48.58620 106.75533	1070	2019	Less grazed	6
				July 2018, July 2019		
9	Selenge aimag, Baruun kharaa soum, Bayangol	49.03340 106.09534	877	2019	Grazed	6
				July 2018, July 2019		
10	Selenge aimag, Baruun kharaa soum, Bayangol	49.02225 106.10812	834	2019	Less grazed	6
				July 2018, July 2019		
10	Selenge Aimag, Zuunburen Soum, Gangiin tokhoi	50.13868 106.01599	619	2019	Grazed	5
				July 2018, July 2019		
10	Selenge Aimag, Zuunburen Soum, Gangiin tokhoi	50.13164 105.99805	619	2019	Less grazed	5
				July 2018, July 2019		

Table S2 Species list of two biomes under different grazing regimes.

#	Biome	Family	Species	Desert		Grassland	
				Grazed	Less grazed	Grazed	Less grazed
1		Cossidae	<i>Acossus sp</i>	1	1	0	0
2		Cossidae	<i>Catopta sp1</i>	1	2	0	0
3		Cossidae	<i>Cossid sp5</i>	0	0	1	0
4		Cossidae	<i>Cossidae sp1</i>	1	0	0	0
5		Cossidae	<i>Cossidae sp2</i>	1	0	0	0
6		Cossidae	<i>Eogystia hippophaecolus</i>	20	5	0	0
7		Cossidae	<i>Eogystia sibirica</i>	1	0	0	3
8		Drepanidae	<i>Drepana falcataria</i>	0	0	0	1

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9	Drepanidae	<i>Tethea ocularis</i>	0	0	1	1
10	Drepanidae	<i>Thyatira batis</i>	0	0	1	0
11	Erebidae	<i>Arctia flavia</i>	0	0	2	2
12	Erebidae	<i>Arctia matronula</i>	0	0	1	2
13	Erebidae	<i>Atolmis rubricollis</i>	0	0	1	2
14	Erebidae	<i>Callistege fortalitium</i>	0	0	1	0
15	Erebidae	<i>Calyptra thalictri</i>	0	1	2	6
16	Erebidae	<i>Catocala bella</i>	0	0	4	1
17	Erebidae	<i>Catocala deuteronympha</i>	0	0	46	38
18	Erebidae	<i>Catocala fulminea</i>	0	0	0	1
19	Erebidae	<i>Catocala nupta japonica</i>	0	0	15	16
20	Erebidae	<i>Catocala pacta</i>	0	0	9	7
21	Erebidae	<i>Chelis daturica</i>	0	0	21	31
22	Erebidae	<i>Chelis mongolica</i>	2	0	1	2
23	Erebidae	<i>Chrysothrum flavomaculata</i>	0	0	1	8
24	Erebidae	<i>Diacrisia purpurata</i>	0	0	0	2
25	Erebidae	<i>Diacrisia sannio</i>	0	0	0	2
26	Erebidae	<i>Dicallomera angelus</i>	1	1	1	1
27	Erebidae	<i>Drasteria chinensis</i>	69	17	6	0
28	Erebidae	<i>Drasteria rada</i>	2	1	1	0
29	Erebidae	<i>Eilema flavociliata</i>	0	0	0	1
30	Erebidae	<i>Emmelia trabealis</i>	0	0	1	2
31	Erebidae	<i>Epatolmis caesarea</i>	1	2	0	0
32	Erebidae	<i>Eublemma rosea</i>	1	3	1	2
33	Erebidae	<i>Eublemma sp</i>	1	0	0	0
34	Erebidae	<i>Euproctis similis</i>	0	0	2	4
35	Erebidae	<i>Hypena obesalis</i>	0	2	0	0
36	Erebidae	<i>Ivela ochropoda</i>	0	0	0	4
37	Erebidae	<i>Leucoma candida</i>	0	0	11	15
38	Erebidae	<i>Lygephila ludicra</i>	0	0	85	124
39	Erebidae	<i>Lymantria dispar</i>	1	0	4	13
40	Erebidae	<i>Polypogon tentacularia</i>	0	0	1	0
41	Erebidae	<i>Setina irrorella</i>	0	0	1	2
42	Erebidae	<i>Spiris bipunctata</i>	0	0	1	1
43	Erebidae	<i>Spiris striata</i>	0	0	1	0

Conclusion

44	Erebidae	<i>Stigmatophora flava</i>	0	0	0	3
45	Erebidae	<i>Stigmatophora micans</i>	0	0	0	6
46	Geometridae	<i>Abraxas grossulariata</i>	0	0	0	2
47	Geometridae	<i>Alcis sp1</i>	0	0	1	0
48	Geometridae	<i>Arichanna melanaria</i>	0	0	2	6
49	Geometridae	<i>Aspitates curvaria</i>	1	0	0	0
50	Geometridae	<i>Biston betularia</i>	0	0	43	79
51	Geometridae	<i>Cabera leptographa</i>	0	0	0	1
52	Geometridae	<i>Catarhoe cuculata</i>	0	0	8	19
53	Geometridae	<i>Chiasmia clathra</i>	0	0	4	5
54	Geometridae	<i>Deileptenia sp</i>	0	0	0	1
55	Geometridae	<i>Digrammia rippertaria</i>	0	0	0	1
56	Geometridae	<i>Epirrhoe pupillata</i>	0	0	0	2
57	Geometridae	<i>Epirrhoe supergressa</i>	0	0	0	4
58	Geometridae	<i>Euphyia unangulata</i>	0	0	1	2
59	Geometridae	<i>Eupithecia centaureata</i>	0	0	1	0
60	Geometridae	<i>Eupithecia intricata</i>	0	1	0	0
61	Geometridae	<i>Eupithecia laricata</i>	0	0	0	1
62	Geometridae	<i>Eupithecia subumbrata</i>	0	0	0	3
63	Geometridae	<i>Gagitodes sagittata</i>	0	0	0	1
64	Geometridae	<i>Geometra rana</i>	0	0	8	3
65	Geometridae	<i>Hemistola veneta</i>	0	0	27	41
66	Geometridae	<i>Hylaea fasciaria</i>	0	0	0	1
67	Geometridae	<i>Hypomecis punctinalis</i>	0	0	0	1
68	Geometridae	<i>Hypomecis roboraria</i>	0	0	2	1
69	Geometridae	<i>Idaea serpentata</i>	0	0	1	0
70	Geometridae	<i>Idaea straminata</i>	0	0	0	2
71	Geometridae	<i>Isturgia arenacearia</i>	0	0	131	103
72	Geometridae	<i>Isturgia kaszabi</i>	0	0	1	2
73	Geometridae	<i>Jankowskia athleta</i>	0	0	0	19
74	Geometridae	<i>Juxtephria consentaria</i>	0	0	3	8
75	Geometridae	<i>Lampropteryx sp1</i>	0	0	0	1
76	Geometridae	<i>Lithostege sp2</i>	9	3	143	180
77	Geometridae	<i>Macaria AH01Mg</i>	0	0	1	1
78	Geometridae	<i>Macaria alternata</i>	0	0	0	1
79	Geometridae	<i>Macaria artesiaria</i>	0	0	0	1
80	Geometridae	<i>Macaria sp 2</i>	0	0	1	0
81	Geometridae	<i>Macaria sp 3</i>	0	0	0	1

Conclusion

82	Geometridae	<i>Macaria wauaria</i>	0	0	2	21
83	Geometridae	<i>Megalycinia strictaria</i>	1	0	1	38
84	Geometridae	<i>Megaspilates mundataria</i>	0	0	8	19
85	Geometridae	<i>Odontopera bidentata</i>	0	0	2	2
86	Geometridae	<i>Pelurga comitata</i>	0	0	3	3
87	Geometridae	<i>Phibalapteryx virgata</i>	1	0	64	28
88	Geometridae	<i>Rheumaptera hastata</i>	0	0	1	0
89	Geometridae	<i>Rhodostrophia jacularia</i>	5	7	1	4
90	Geometridae	<i>Rhodostrophia vibicaria</i>	0	0	5	4
91	Geometridae	<i>Schistostege nubilaria</i>	0	0	1	7
92	Geometridae	<i>Scopula albiceraria</i>	0	0	3	1
93	Geometridae	<i>Scopula decorota przewalskii</i>	0	0	8	12
94	Geometridae	<i>Scopula immorata</i>	0	0	0	1
95	Geometridae	<i>Scopula rubiginata</i>	0	0	23	8
96	Geometridae	<i>Scopula subpunctaria</i>	0	1	8	4
97	Geometridae	<i>Scopula virgulata</i>	0	0	15	28
98	Geometridae	<i>Scotopteryx chenopodiata</i>	0	0	28	12
99	Geometridae	<i>Spargania luctuata</i>	0	0	0	1
100	Geometridae	<i>Stamnodes danilovi</i>	0	1	0	0
101	Geometridae	<i>Thalera chlorosaria</i>	0	0	1	0
102	Geometridae	<i>Thetidia chlorophyllaria</i>	0	0	1	8
103	Geometridae	<i>Thetidia smaragdaria</i>	0	0	2	11
104	Lasiocampidae	<i>Dendrolimus superans</i>	0	0	2	14
105	Lasiocampidae	<i>Gastropacha populifolia</i>	0	0	1	0
106	Lasiocampidae	<i>Gastropacha quercifolia</i>	0	4	12	37
107	Lasiocampidae	<i>Malacosoma castrensis</i>	1	1	6	6
108	Lasiocampidae	<i>Malacosoma neustria transmongolicum</i>	1	0	0	0
109	Lasiocampidae	<i>Phyllodesma ilicifolia</i>	0	1	0	0
110	Noctuidae	<i>Abrostola tripartita</i>	0	0	1	1
111	Noctuidae	<i>Actebia fennica</i>	1	0	8	5
112	Noctuidae	<i>Actebia poecila</i>	1	7	5	4
113	Noctuidae	<i>Actebia praecox</i>	0	0	1	1
114	Noctuidae	<i>Actebia squalida</i>	6	1	0	1
115	Noctuidae	<i>Agrotis clavis</i>	0	0	21	42

Conclusion

116	Noctuidae	<i>Agrotis exclamationis</i>	0	0	16	24
117	Noctuidae	<i>Agrotis ipsilon</i>	1	2	0	1
118	Noctuidae	<i>Agrotis ripae</i>	3206	2728	28	24
119	Noctuidae	<i>Agrotis segetum</i>	5	0	0	1
120	Noctuidae	<i>Amphipoea fucosa</i>	0	0	0	4
121	Noctuidae	<i>Anaplectoides prasina</i>	0	0	0	1
122	Noctuidae	<i>Anarta stigmosa</i>	21	18	0	0
123	Noctuidae	<i>Anarta colletti</i>	0	1	0	0
124	Noctuidae	<i>Anarta trifolii</i>	231	336	84	150
125	Noctuidae	<i>Apamea lateritia</i>	26	2	4	10
126	Noctuidae	<i>Apamea maillardi</i>	0	0	2	0
127	Noctuidae	<i>Autographa buraetica</i>	2	0	7	4
128	Noctuidae	<i>Bryophila orthogramma</i>	0	0	0	1
129	Noctuidae	<i>Calamia decipiens</i>	0	1	0	0
130	Noctuidae	<i>Caradrina montana</i>	20	18	2	2
131	Noctuidae	<i>Caradrina sp2</i>	16	7	0	0
132	Noctuidae	<i>Cardepia sociabilis</i>	0	1	0	0
133	Noctuidae	<i>Chersotis ocellina</i>	0	0	0	2
134	Noctuidae	<i>Chilodes repeteki</i>	0	1	0	0
135	Noctuidae	<i>Coenobia rufa</i>	4	0	0	0
136	Noctuidae	<i>Conisania arida</i>	0	0	1	5
137	Noctuidae	<i>Cosmia pyralina</i>	0	0	1	12
138	Noctuidae	<i>Cryptocala chardinyi</i>	0	0	1	1
139	Noctuidae	<i>Cucullia absinthii</i>	0	1	0	0
140	Noctuidae	<i>Cucullia argentea</i>	0	0	3	6
141	Noctuidae	<i>Cucullia artemisiae</i>	0	0	2	0
142	Noctuidae	<i>Cucullia biradiata</i>	1	0	0	2
143	Noctuidae	<i>Cucullia cineracea</i>	0	0	0	5
144	Noctuidae	<i>Cucullia dracunculi</i>	1	0	2	3
145	Noctuidae	<i>Cucullia fraudatrix</i>	0	0	0	1
146	Noctuidae	<i>Cucullia scopariae</i>	1	1	6	18
147	Noctuidae	<i>Cucullia sp2</i>	0	0	0	1
148	Noctuidae	<i>Cucullia splendida</i>	11	9	10	12
149	Noctuidae	<i>Cucullia umbratica</i>	0	0	3	4
150	Noctuidae	<i>Diachrysis stenochrysis</i>	0	0	0	1
151	Noctuidae	<i>Dichagyris kaszabi</i>	0	3	0	0
152	Noctuidae	<i>Dichagyris musiva</i>	0	0	0	1

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153	Noctuidae	<i>Dichagyris sp</i>	1	0	0	0
154	Noctuidae	<i>Dichagyris vallesiaca</i>	12	5	0	0
155	Noctuidae	<i>Energia paleacea</i>	0	0	1	6
156	Noctuidae	<i>Eremohadena sp</i>	1	0	0	0
157	Noctuidae	<i>Euchalcia mongolica</i>	0	0	2	3
158	Noctuidae	<i>Euchalcia renardi</i>	0	0	0	2
159	Noctuidae	<i>Eurois occulata</i>	0	0	0	1
160	Noctuidae	<i>Euxoa basigramma</i>	1	0	0	0
161	Noctuidae	<i>Euxoa cursoria</i>	11	83	0	1
162	Noctuidae	<i>Euxoa decorans</i>	0	6	0	0
163	Noctuidae	<i>Conisania sp</i>	3	3	23	37
164	Noctuidae	<i>Euxoa ochrogaster</i>	61	69	129	173
165	Noctuidae	<i>Euxoa oranaria</i>	0	1	0	0
166	Noctuidae	<i>Euxoa sp</i>	0	1	0	0
167	Noctuidae	<i>Euxoa tritici</i>	0	0	14	4
168	Noctuidae	<i>Feltia nigrita</i>	0	0	1	0
169	Noctuidae	<i>Hada plebeja</i>	0	0	2	5
170	Noctuidae	<i>Hadena aberrans</i>	0	0	2	1
171	Noctuidae	<i>Hadena corrupta</i>	0	0	1	1
172	Noctuidae	<i>Hadena variolata</i>	1	1	1	4
173	Noctuidae	<i>Heliiothis adauca</i>	0	0	1	1
174	Noctuidae	<i>Heliiothis ononis</i>	0	0	3	11
175	Noctuidae	<i>Hoplodrina octogenaria</i>	0	0	0	4
176	Noctuidae	<i>Hyssia cavernosa</i>	0	0	1	3
177	Noctuidae	<i>Ipimorpha retusa</i>	0	0	76	22
178	Noctuidae	<i>Lacanobia aliena</i>	0	0	5	12
179	Noctuidae	<i>Lacanobia contigua</i>	0	0	5	11
180	Noctuidae	<i>Lacanobia thalassina</i>	0	0	12	39
181	Noctuidae	<i>Lasionycta imbecilla</i>	0	0	1	3
182	Noctuidae	<i>Lasionycta proxima</i>	0	0	14	32
183	Noctuidae	<i>Lygephila pastinum</i>	0	0	1	0
184	Noctuidae	<i>Lygephila viciae</i>	0	0	18	66
185	Noctuidae	<i>Mamestra brassicae</i>	10	9	0	1
186	Noctuidae	<i>Mythimna albiradiosa</i>	2	2	0	1
187	Noctuidae	<i>Mythimna comma</i>	1	0	70	67
188	Noctuidae	<i>Mythimna conigera</i>	0	0	3	5
189	Noctuidae	<i>Mythimna opaca</i>	0	0	1	4
190	Noctuidae	<i>Mythimna oxygala</i>	0	0	1	6

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191	Noctuidae	<i>Mythimna pallens</i>	0	0	5	5
192	Noctuidae	<i>Mythimna separata</i>	0	1	0	0
193	Noctuidae	<i>Mythimna velutina</i>	0	0	16	48
194	Noctuidae	<i>Naenia contaminata</i>	0	0	0	1
195	Noctuidae	<i>Ochropleura plecta</i>	0	0	0	1
196	Noctuidae	<i>Panchrysia dives</i>	0	0	2	0
197	Noctuidae	<i>Panchrysia ornata</i>	5	1	0	0
198	Noctuidae	<i>Plusia putnami</i>	0	0	1	0
199	Noctuidae	<i>Polia altaica</i>	1	0	2	5
200	Noctuidae	<i>Polia bombycina</i>	0	0	15	42
201	Noctuidae	<i>Polia nebulosa</i>	0	0	3	3
202	Noctuidae	<i>Prognorisma albifurca</i>	0	0	1	1
203	Noctuidae	<i>Protoschinia scutosa</i>	1	1	0	1
204	Noctuidae	<i>Pyrrhia umbra</i>	0	0	1	0
205	Noctuidae	<i>red_noc</i>	0	0	1	0
206	Noctuidae	<i>Resapamea mammuthus</i>	0	0	1	5
207	Noctuidae	<i>Resapamea vulpecula</i>	7	0	1	3
208	Noctuidae	<i>Rhyacia ledereri</i>	0	0	2	7
209	Noctuidae	<i>Rhyacia lucifera</i>	0	1	0	0
210	Noctuidae	<i>Rhyacia simulans</i>	1	4	19	58
211	Noctuidae	<i>Sideridis egena</i>	9	10	11	43
212	Noctuidae	<i>Sideridis kitti</i>	0	0	5	15
213	Noctuidae	<i>Sideridis turbida</i>	0	0	0	3
214	Noctuidae	<i>Simyra nervosa</i>	1	0	1	19
215	Noctuidae	<i>Syngrapha ain</i>	0	0	2	5
216	Noctuidae	<i>Xestia kollari</i>	0	0	2	0
217	Noctuidae	<i>Xestia versuta</i>	0	1	1	0
218	Notodontidae	<i>Clostera albosigma</i>	0	0	7	4
219	Notodontidae	<i>Clostera anachoreta</i>	0	0	0	1
220	Notodontidae	<i>Furcula furcula</i>	0	0	1	0
221	Notodontidae	<i>Nerice davidi</i>	0	0	0	2
222	Notodontidae	<i>Notodontid sp1</i>	0	1	1	1
223	Notodontidae	<i>Phalera bucephala</i>	0	0	1	0
224	Notodontidae	<i>Ptilodon kuwayamae</i>	0	0	1	0
225	Sessidae	<i>Sessidae sp1</i>	0	0	0	2
226	Sphingidae	<i>Callambulyx tatarinovii eversmanni</i>	0	0	1	6

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227	Sphingidae	<i>Deiliphila sp</i>	0	0	1	1
228	Sphingidae	<i>Hyles chivulini</i>	6	16	1	1
229	Sphingidae	<i>Hyles gallii</i>	0	0	51	49
230	Sphingidae	<i>Hyles hippophaes</i>	1	0	0	0
231	Sphingidae	<i>Laothoe amurensis</i>	0	0	22	19
232	Sphingidae	<i>Marumba gaschkewitschii</i>	0	0	1	1
233	Sphingidae	<i>Smerinthus caecus</i>	0	0	1	9
234	Sphingidae	<i>Sphinx ligustri</i>	0	0	7	7
235	Sphingidae	<i>Sphinx morio</i>	1	0	0	3
236	Zygaenidae	<i>Jordanita sp1.</i>	0	0	0	2

Table S3 Comparison of diversity metrics (species richness, species diversity, and abundance) between grazed and less grazed plots in the families of Erebidae, Geometridae, Noctuidae, and 'Other'

Family	Biome	Diversity metrics	Group1	Group2	p-value	p.adjusted
Erebidae	desert	species richness	Grazed	Less grazed	0.796	0.8
Erebidae	grassland	species richness	Grazed	Less grazed	0.016	0.031
Geometridae	desert	species richness	Less grazed	Grazed	0.029	0.029
Geometridae	grassland	species richness	Less grazed	Grazed	0.012	0.024
Noctuidae	desert	species richness	Grazed	Less grazed	0.828	0.83
Noctuidae	grassland	species richness	Grazed	Less grazed	0.026	0.053
Other	desert	species richness	Less grazed	Grazed	0.66	0.93
Other	grassland	species diversity	Less grazed	Grazed	0.47	0.93
Erebidae	desert	species richness	Grazed	Less grazed	0.598	0.6
Erebidae	grassland	species richness	Grazed	Less grazed	0.034	0.068
Geometridae	desert	species richness	Less grazed	Grazed	0.076	0.076
Geometridae	grassland	species richness	Less grazed	Grazed	0.035	0.07

Conclusion

Noctuidae	desert	species richness	Grazed	Less grazed	0.932	0.93
Noctuidae	grassland	species richness	Grazed	Less grazed	0.018	0.035
Other	desert	species richness	Less grazed	Grazed	0.87	0.87
Other	grassland	species richness	Less grazed	Grazed	0.18	0.35
Erebidae	desert	abundance	Grazed	Less grazed	0.196	0.2
Erebidae	grassland	abundance	Grazed	Less grazed	0.0093	0.019
Geometridae	desert	abundance	Less grazed	Grazed	0.67	0.67
Geometridae	grassland	abundance	Less grazed	Grazed	0.25	0.49
Noctuidae	desert	abundance	Grazed	Less grazed	0.794	0.79
Noctuidae	grassland	abundance	Grazed	Less grazed	0.055	0.11
Other	desert	abundance	Less grazed	Grazed	0.81	0.81
Other	grassland	abundance	Less grazed	Grazed	0.14	0.28

Table S4 Plant community dissimilarity between grazed and less grazed plots. Jaccard diversity is partitioned into spatial turnover (i.e., species replacement) and spatial nestedness (i.e., species loss or gain)

Biome	Site	Jaccard	Turnover	Nestedness
Desert	1	0.417	0.364	0.053
Desert	2	0.417	0.222	0.194
Desert	3	0.200	0.000	0.200
Desert	4	0.556	0.500	0.056
Desert	5	0.313	0.154	0.159
Grassland	6	0.586	0.571	0.015
Grassland	7	0.786	0.647	0.139
Grassland	8	0.782	0.647	0.135
Grassland	9	0.705	0.629	0.076
Grassland	10	0.707	0.647	0.060

Conclusion

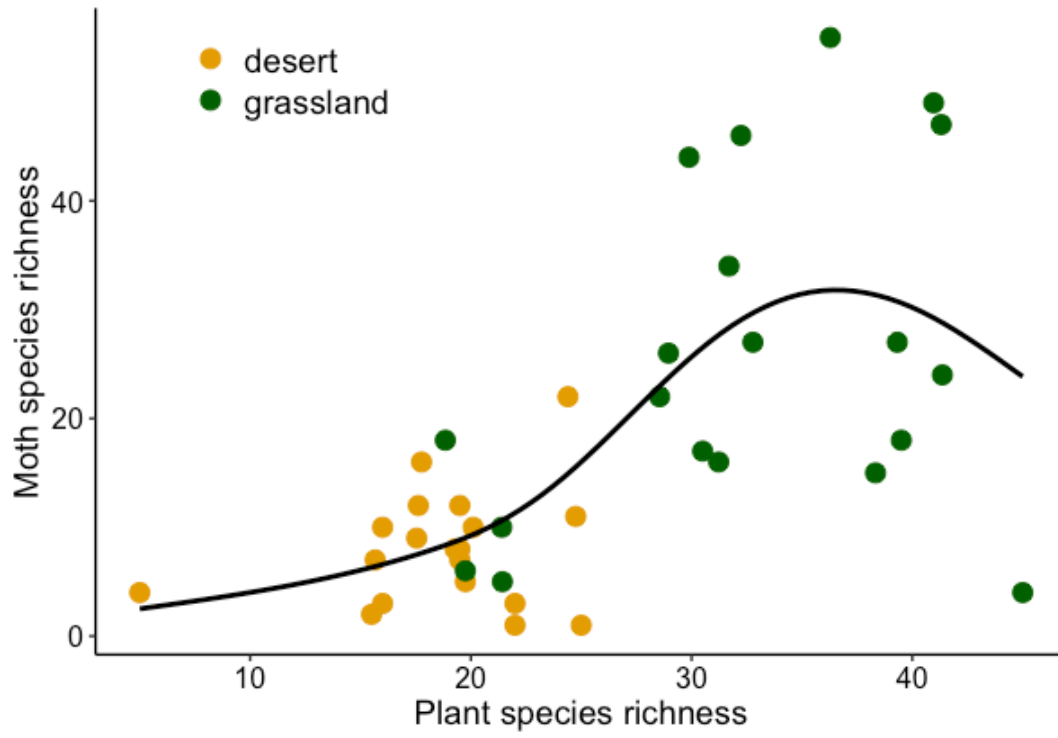


Figure S1 Relationship between moth species richness and vegetation species richness

Declaration of contributions of authors

Manuscript I

Title: Diversity and Distribution Patterns of Geometrid Moths (Geometridae, Lepidoptera) in Mongolia.

Authors: Khishigdelger Enkhtur, Boldgiv, Bazartseren, Martin Pfeiffer

Journal: **Diversity** 12 (2020), 186

Personal contribution: data collection: 100%, data analysis and figures: 100%, writing: 90%, idea and concept: 90%, corresponding author

Manuscript II

Title: Alpha and beta diversity patterns of macro-moths reveal a breakpoint along a latitudinal gradient in Mongolia

Authors: Khishigdelger Enkhtur, Gunnar Brehm, Boldgiv, Bazartseren, Martin Pfeiffer

Journal: **Scientific Reports** 11 (2021), 15018

Personal contribution: data collection: 100%, data analysis and figures: 95%, writing: 90%, idea and concept: 95%, corresponding author

Manuscript III

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

Authors: Khishigdelger Enkhtur, Gunnar Brehm, Boldgiv, Bazartseren, Martin Pfeiffer

Journal: **Ecological Indicators** 133 (2021), 108421

Personal contribution: data collection: 100%, data analysis and figures: 95%, writing: 90%, idea and concept: 95%, corresponding author

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Appendix

Publications included in the thesis

Enkhtur, K., Boldgiv, B., & Pfeiffer, M. (2020). Diversity and Distribution Patterns of Geometrid Moths (Geometridae, Lepidoptera) in Mongolia. *Diversity*, 12(5), 186. <https://www.mdpi.com/712808>

Enkhtur, K., Brehm, G., Boldgiv, B., & Pfeiffer, M. (2021). Alpha and beta diversity patterns of macro-moths reveal a breakpoint along a latitudinal gradient in Mongolia. *Scientific Reports*, 11(1), 1-13. <https://www.nature.com/articles/s41598-021-94471-3>

Enkhtur, K., Brehm, G., Boldgiv, B., & Pfeiffer, M. (2021). Effects of grazing on macro-moth assemblages in two different biomes in Mongolia. *Ecological Indicators*, 133, 108421. <https://www.sciencedirect.com/science/article/pii/S1470160X21010864>

Other publications

Enkhtur, K., Pfeiffer, M., Lkhagva, A., & Boldgiv, B. (2017). Response of moths (Lepidoptera: Heterocera) to livestock grazing in Mongolian rangelands. *Ecological indicators*, 72, 667-674.

Enkhtur, K., Munkhbat, U., Boldgiv, B., Pfeiffer, M., (2021) Diversity of moths (Lepidoptera: Heterocera) in north-central Mongolia” *Erforschung biologischer Ressourcen der Mongolei*, Martin-Luther-Universität Halle-Wittenberg. Band 14. <https://digitalcommons.unl.edu/biolmongol/263/>

Conference contributions

Enkhtur*, K., Pfeiffer, M., Lkhagva, A., & Boldgiv, B. "Response of moths (Lepidoptera: Heterocera) to livestock grazing in Mongolian rangelands" poster presented in *Programm zum 56. Bayerischen Entomologentag "Entomologie der Zukunft – Zukunft der Entomologie" am 9. und 10. März 2018 in München.*

Khishigdelger Enkhtur*, Martin Pfeiffer, Bazartseren Boldgiv. „Diversity of moths (Lepidoptera: Heterocera) in north-central Mongolia" poster presented in *Programm zum 57. Bayerischen Entomologentag "Insekten vor dem Aus!?" am 8. und 9. März 2019 in München.*

Khishigdelger Enkhtur*, Martin Pfeiffer, Bazartseren Boldgiv. "Spatial pattern of geometrid moth community in Mongolia and the potential distribution of some endemic species of Geometridae" poster presented in *AK Biogeographie in Frankfurt am Main 2019*

Khishigdelger Enkhtur*, Bazertseren Boldgiv, Martin Pfeiffer. „Diversity and distribution pattern of geometrid moths (Geometridae, Lepidoptera) in Mongolia" poster presented in *Bayceer Workshop 2018.*

Khishigdelger Enkhtur*, Gunnar Brehm, Bazertseren Boldgiv, Martin Pfeiffer. „Response of diversity of moths to bioclimatic zones in Central Asia" poster presented in *Bayceer Workshop 2020*

Khishigdelger Enkhtur*, Gunnar Brehm, Bazartseren Boldgiv & Martin Pfeiffer "Alpha and beta diversity patterns of macro-moths reveal a breakpoint along a latitudinal gradient in Mongolia" talk presented in Lepidopterist's Society: 69th Annual Meeting, 18th-20th, August 2021

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