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Butterfly-flower networks in different grassland types in the National Park Neusiedler See / Seewinkel

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Abstract

The flower-butterfly networks of different land use types of grassland in the "National Park Neusiedler See - Seewinkel" were analysed. The land use types were (1) pastures with mainly Przewalski's horses grazing there, (2) pastures grazed by ranging non-stationary cattle and (3) meadows maintained without large grazing animals. Data sampling took place in June and July 2021 during a drought period. Overall, 4160 flower-butterfly interactions involving 27 butterfly and 59 plant species, were observed. Besides the description of the overall network structure, network metrics such as specialisation H2 and vulnerability were calculated. At species level, specialisation d' and species strength were computed for the most often visited plants and butterflies, respectively. Additionally, 15 years of observation data was used to compare the relative abundance of butterfly species with their observed frequency in flower-butterfly interactions. Network specialisation H2 did not correlate with flower supply and varied also not systematically between land use types but was influenced by the interaction of land use type and observation month. Vulnerability decreased with lower land use intensity. Species diversity of plants and butterflies involved in networks was highest on meadows. At all three land use types diversity of interacting species decreased from early to high summer due to drought. No plant or butterfly species in the more detailed analyses showed a high specialisation or strength. Floral colour, nectar amount, and inflorescence type had a significant impact on visitation rate, whereas UV patterns did not have an effect. Overall, butterflies preferred yellow flowers, a high nectar amount, and racemes and composite inflorescences over single flowers. Although the more detailed analysed species *Polyommatus icarus*, *Plebejus argus*, *Coenonympha pamphilus* and *Melanargia galathea* were opportunistic regarding their flower visits, preferences in colour, corolla tube length and nectar amount were observed. Contrary to the overall trend, *M. galathea* preferred violet blossoms with a low nectar reward. *Coenonympha pamphlilus* and *Plebejus argus* tended to visit plants with corollas under 5 mm, whereas *Polyommatus icarus* and *Melanargia galathea* preferred corolla tubes longer than 10 mm.

Zusammenfassung

Diese Arbeit befasst sich mit Blüten-Schmetterlings-Netzwerken von verschiedenen Landnutzungstypen des Graslandes im Nationalpark Neusiedlersee Seewinkel. Die bearbeiteten Flächen waren (1) eine extensive beweidete Przewalski-Pferde-Koppel, (2) Hutweiden, die von Rindern in Begleitung eines Hirten beweidet wurden, und (3) gemähte Wiesen ohne Beweidung. Die Datenakquise erfolgte im Juni 2021 bis Juli 2021 während einer ungewöhnlichen Dürreperiode. Insgesamt wurden 4160 Interaktionen zwischen 27 tagaktiven Falterarten und 59 blühenden Pflanzenarten beobachtet. Neben der allgemeinen Beschreibung der Netzwerkstrukturen wurde die Indizes „H2“ und „vulnerabilty“ berechnet. Auf der Ebene der Arten wurden die Spezialisierung „d‘“ und „species strength“ für die häufigsten Arten betrachtet. Zusätzlich wurde aus Beobachtungsdaten über 15 Jahre das durchschnittliche Vorkommen der Falter berechnet und damit verglichen, wie oft die betreffenden Arten in Interaktionen mit Blüten beobachtet wurden. Die Netzwerkspezialisierung H2 korrelierte nicht mit dem Blühangebot, war aber beeinflusst von einer statistischen Interaktion zwischen Beobachtungsmonat und Landnutzungstyp. „Vulnerability“ sank mit sinkender Landnutzungsintensität. Die höchst Artendiversität an Pflanzen und Tieren in den Netzwerken wurde auf den Wiesen vorgefunden. Auf allen Landnutzungstypen wurde eine Reduktion der Diversität im Laufe des Sommers beobachtet. Keine der näher betrachteten Pflanzen- oder Tierarten zeigte eine hohe Spezialisierung oder „species strength“. Farbe, Nektarmenge und Type der Blüten hatten eine signifikante Auswirkung auf die Besucherhäufigkeit, wobei UV-Muster keine Auswirkung hatten. Die beobachteten Schmetterlinge präferierten gelbe Blüten, eine hohe Nektarmenge und Blütenstände in Form von Trauben bzw. Körben. Obwohl die näher beschriebenen Arten *Polyommatus icarus*, *Plebejus argus*, *Coenonympha pamphilus* und *Melanargia galathea* sehr opportunistisch bezüglich ihrer Blütenbesuche waren, konnten Präferenzen für Farbe, Blütenkronenlängen und Nektarmenge beobachtet werden. *M. galathea* bevorzugte entgegen des allgemeinen Trends violette und nektararme Blüten. *Coenonympha pamphlilus* und *Plebejus argus* tendierten zu Blüten mit einer Blütenkelchlänge unter 5 mm, wogegen *Polyommatus icarus* und *Melanargia galathea* häufiger Blütenkelche die länger als 10 mm waren besuchten.

Introduction

Pollination is one of the many ecosystem services provided by nature. The importance of this service is enormous: 87.5% of the angiosperm species, including many agricultural crops, are pollinated by animals (Ollerton et al., 2011). The linkage of pollination services to the world food production leads to a huge economical value of this ecosystem service (Hanley et al., 2015). Although the importance of pollination mediated by animals is beyond dispute, there is an ongoing threat due to land-use intensification and climate change. Concomitant with increasing land-use intensity species richness of flower visitors is decreasing, which also translates into a loss off the complexity of biotic interactions (Weiner et al., 2014). In recent years, investigating the structure of interactions between species has gained prominence in biodiversity research. The exploration of pollination networks is a prime example (Olesen et al., 2008). The analysis of networks in ecological communities, however, poses a challenge for research due to the high complexity and wide diversity of species and their interactions. Nevertheless, applied to a subset of the community network analysis can lead to new insights without grappling with sheer insoluble complexity (Weiner et al., 2014; Zografou et al., 2020). One well established group for investigation of ecological questions are butterflies. On the one hand their distinctive appearance and moderate species richness facilitates their identification in the field (in most cases even to species level). On the other hand, their life-cycles entail close interactions with plants, both as a larva as well as during the adult stage. Hence, butterflies are known to respond sensitively to environmental changes (Sawchik et al., 2005). Therefore, the observation of butterflies and their interaction networks can draw a picture of the condition of the whole ecosystem.

Besides land-use change, also climate change can pose a threat to pollination services. It is predicted that climate change will cause several effects on pollinators and especially on plant-pollinator interactions (Settele et al., 2016). Besides direct effects like distribution shifts of species, indirect effects like a phenological mismatch between pollinators and plants or the decline in quality and quantity of floral resources can occur (Hegland et al., 2009; Jane Memmott et al., 2007). One aspect which is going to increase with ongoing climate change is the occurrence and intensity of drought events in some regions of the world (Dai, 2013). Drought acts as a threat for pollinators primarily through its impact on floral resources, especially nectar (Thomson, 2016). One main problem in this regard is reduced photosynthesis. Hence, the plants can spend less energy in reproduction which leads to smaller flowers, less pollen and nectar (Pinheiro & Chaves, 2011; Carroll et al., 2001; Halpern et al., 2010). Also the quality of floral resources can decline, like lower sugar concentration in nectar (Wyatt, 1992). If drought is severe, it will not only reduce flower size or the number of flowers per plant, it will also lead to a massive decline in plant numbers. For butterflies this means not only the food resource as adults will be threatened but also their herbivorous juveniles may be affected. As drought responses depend on the species, the overall effect of a drought on the community level might depend on the species composition (Grime et al., 2000). Although this topic was investigated in some studies, an understanding of the response of network structures and species to drought events might become even more crucial in the coming decades, as more droughts are likely to occur (Phillips et al., 2018).

Land use intensification is often connected to severe biodiversity decline (Oliver & Morecroft, 2014). However, the remaining species-rich habitats in Central Europe are often strongly modified by human hand and often times (e.g. pastureland) have only come into existence through human activities. As all European ecosystems have been shaped by humans since the last glacial period their character is somehow adapted to human impact. Especially agriculture before the agro-industrial revolution with its extensive methods led to a process of diversification. This laid the foundation of a diverse cultural landscape in Central Europe comprising a mosaic of different land-use types and intensities (Schmitzberger et al., 2005). This landscape, even though it was shaped by human hand, was characterised by a high diversity of species as well as habitats. The massive changes of agricultural practices, which started in Austria mostly after the end of World War II, have largely put an end to this kind of landscape. However, as some of these former agricultural methods are known to promote biodiversity, landscape preservation measures which simulate them started to become a tool in conservation management (Waitzbauer, 2008). As ‘nature’ in Central Europe should not be equated with pristine wilderness without human impact, the question arises which type of management actions are appropriate for the purpose of biodiversity conservation.

One example is the "National Park Neusiedler See - Seewinkel" in eastern-most Austria. National parks have the goal to protect natural diversity and its ecological structure and ecosystem processes. So, the interest of how certain networks look like should be given (Crofts et al., 2020). Although there are a few studies which investigated pollinator-plant interactions in national parks in Austria (Neumüller et al., 2018), no study was conducted in the area of the National Park Seewinkel yet. Today in the management zone of the NP Neusiedler See - Seewinkel three major types of grassland ecosystems can be found, in relation to their management regimes, viz. pastures mainly grazed by Przewalski’s horses, pastures grazed by cattle, and meadows maintained by mowing, without grazing animals. These management regimes have an impact on species composition of butterflies (Fiedler et al., 2017). Although there are studies which showed similar results for other organisms in the same region, e.g. Apoidea and Arachnida, the question of which extent of grazing is optimally shaping the species composition has not been answered unambiguously (Hölzler, 2008; Steffan-Dewenter & Leschke, 2003; Schley & Leytem, 2004; Zulka et al., 1997). Therefore, the question arises whether these different management regimes not only govern species compositions but also the resulting butterfly-flower networks. There are suggestions that this is the case: Power et al. (2011) investigated if there are differences in the network structure between organically and conventionally managed dairy farm pastures in Britain. Conventional pastures are expected to be managed more intensively than organic ones. Although both types of habitats are heavily altered by human hand, organic farmers are not allowed to use chemical fertilizers or pesticides and their pastures tend to have lower grazing intensity. While the authors found nearly the same number of insect species on both farm types, the networks looked quite different. As there were more generalist species on organic farmland, the mean number of interactions per pollinator species was significantly higher. The degree of network specialisation seemed to be influenced by land-use intensities. It has been suggested that generalists benefit from disturbance, while specialists suffer (McKinney, 1997; Aizen et al., 2012). However, there are studies which observed the opposite (J. Memmott, 1999; Pocock et al., 2012). This might be the case because the degree of interaction specialisation is often expressed in a binary way and this way of recording is particularly prone to sampling bias and might neglect interaction strength (Blüthgen & Menzel, 2006).

It is well known that plants have evolved attributes to increase the visitation by pollinators. For example butterflies tend to have a colour preference for purple, pink, red and yellow flower colours (Dafni et al., 2005). It is known that insects have different visual spectra than humans and mostly possess good visual capacity in the UV range (Willmer, 2011). Therefore, UV patterns on the surface of blossoms might have an influence on insect visitors as well. Also the clustering of multiple flowers in inflorescences seems to have an impact, since this reduces sampling costs for flying insects (Corbet, 2000). Flower nectar is an important reward for animals in order to promote pollination (Willmer, 2011). Hence, the quantity of it should increase visitation rates. Flowers nectars essentially contain carbohydrates as sucrose, glucose, and fructose in concentrations of on average 40% (Westrich, 2019). It is suggested that long tubular, nectar rich and massed flowers might be the ideal nectar source for butterflies (Corbet, 2000).

Pollinators are known to influence the evolution of their visited plants and vice versa . (Johnson & Anderson, 2010). Therefore, plant families, as their mirror phylogenetic relationships, might be a predictor for visitation rate. However, it is observed, that unrelated plants share similar pollinators and similar morphological features and reward patterns (Baker et al., 1972). This observation led to the concept of pollination syndromes. Although the history of this theory started 150 years ago and was prominent in its role of studying the organisation of plant-pollinator interactions, it is still not quite clear whether this concept is really fruitful (Ollerton et al., 2009; Willmer, 2011). Besides morphological features and phylogenetic relationships, it is observed that abundance of animal pollinated plant is mirrored by its interaction frequency (Weiner et al., 2011).

Ecological bipartite networks are today analysed using a variety of mathematical metrics, some of which have only been developed during the past two decades (Heleno et al., 2014). The base of these metrics is a network, where “nodes” are connected by “links”. In the case of this study, the “nodes” are the plant and butterfly species and the interactions between them are the “links”. There are different approaches how to quantify topology of a network. One example is H2 (or d’ at species level) which describe the exclusiveness of an interaction at network level. This metric is based on the Shannon diversity. It ranges between 0 (no specialisation) and 1 (completely specialized network). A high H2 value shows a specialised network, suggesting that the interacting species are specialised and interact only with a subset of other species. This suggests a high niche differentiation (Blüthgen, 2010). While there are metrics which describe the whole network, there are also some others which look at the species level. Aside from d’, which was mentioned above, there is the index ‘species strength’. It shows how many plant species are dependent on a visitor species and can therefore draw a picture about the importance of individual species in the network (Dormann et al., 2009). Among this plethora of metrics, the weighed mean number of visitors (butterflies) per plant species is represented by the index ‘vulnerability’ (Dormann et al., 2009). Thus, a higher vulnerability shows that a plant species receives more different species as visitors (Alarcon, 2010). It has been shown in grassland ecosystems in Germany that variation in management intensity had an impact on species composition and diversity of flowering plants and their visitors (Weiner et al., 2011). This leads to the suggestion that land use intensity might impact this vulnerability index as well. A study by Power et al. (2011) supports this idea as they have shown that vulnerability was higher on pastures which were organically managed in comparison to conventionally managed ones.

All interactions between species are influenced by variation in their environment. As seasonal changes shape the landscape profoundly, it is not surprising that some studies found seasonal changes in pollinator-plant networks as well (Souza et al., 2018). As soon as more plants come into blossom, visitors will have a greater selection to choose from and their apparent specialisation might decrease. Additionally, as sampling for my own thesis took place during a time period with nearly no precipitation the effect of drought might amplify this pattern of apparent specialization. For instance Souza et al. (2018) found an increased specialization in flower visitation during periods of reduced flower supply in the dry season in Central Brazil. Hence, I hypothesized that with the beginning of the vegetation period and the first limited flower supply even quite opportunistic butterfly species will appear rather specialised as they are forced to use the few available flower resources. As a corollary, the same butterfly species might behave more opportunistically once a broader array of nectar sources becomes available.

The aim of the present study was to gain insights into flower-insect interactions on three grassland types in the National Park Seewinkel. It was focused only on butterfly-plant interactions due to limitations in the ability to achieve species-level identification of flower visitors in speciose taxa like Diptera, Coleoptera or Hymenoptera. Specifically, the following research questions were formulated:

i. Is the average abundance of a certain species reflected by its interaction frequency?
ii. Are there differences in network indices and structures between early and high summer, and are these patterns influenced by the land use?
iii. Does the role of individual species vary between months or land use types?
iv. Are the numbers of butterfly visitors influenced by certain traits of the plants?
v. Are there flower preferences of particular butterfly species?

Methods

Study area

Data sampling took place in the management zone ("Bewahrungszone") of the National Park "Neusiedler See – Seewinkel" in eastern-most Austria. This National Park, which was founded in 1993, is located in an area which had traditionally been grazed by large domestic herbivores for centuries, while parts of the landscape were mowed for hay production. Apart from these open grasslands rather small areas were historically devoted to usage as crop fields, and forest cover was negligible (Schmitzberger et al., 2005). After the middle of the 20th century profound changes in the landscape have occurred: the pastures nearly vanished, instead intense viniculture and croplands took over. As negative effects of too low grazing intensities on various biota of conservation concern were detected, a grazing program was re-established as a means of ecological restoration (Zulka et al., 1997; Waitzbauer, 2008). Today, in the management zone of the NP Neusiedler See – Seewinkel, three major types of grassland ecosystems can be found in relation to their management regimes: (1) Pastures with mainly Przewalski's horses grazing there, (2) pastures grazed by cattle and (3) meadows maintained without large grazing animals. To prevent forest succession these meadows are mown. For detailed information on the treatment of the study plots 2021 see Table A11. The area of the National Park Neusiedler See - Seewinkel is influenced by the pannonic climate, which is characterised by high summer temperatures and low precipitation quantity (Lalic et al., 2013). June 2021, however, was an extreme case as there was only 3.2 mm precipitation, while the average monthly precipitation during June is 57.2 mm since 1999 (Wasserportal Burgenland, 2022). As my study was conducted between May and August 2021, the data was gained during a time period with exceptionally low precipitation.

Study sites

Six plots on the Przewalski's horse pasture were chosen, 6 plots on the pastures with cattle and 12 plots on meadows. The base of this random selection of plots was a land use map provided by the National Park administration. Too sandy areas with very sparse vegetation cover were avoided, as were sites directly adjacent to soda pans. The Przewalski's horse pasture (total area 69,5 ha) is situated between a sandy dam and the eastern lakeside of Lake Neusiedel, in the so-called "Seevorgelände". Large areas of the Przewalski's horse pasture are influences by the sandy dam, therefore the soil tend to be dry. It has been established 2001. The whole area is dominated by *Junco obtusiflori* and *Schoenetum nigricantis.* In the direction of the lake the reed belt starts, whereas eastern a *Centaureo pannonici-Festucetum pseudovinae* population start. In 2021 it was grazed by 13 Przewalski's horses the whole year. During autumn there were additionally 110 cows with their calves held for 3 months in that enclosure. The cattle pasture sites were situated on the gravel terrace east of the sandy dam, in the area of the "Kirchsee" (~ 46 ha) and the "Zicklacke" (~ 27 ha). Both these temporary saline ponds situated in soda pans (Häusler, 2020) were completely dried out at the time my sampling took place. Two herds of cattle based in the village of Illmitz, both containing about 100 cows with their calves, grazed the area, ranging under control by herdsmen. Therefore, they were not kept in fenced enclosures. This pasture management was started in the 1980ies and has since successfully contributed to restoration of a historical vegetation type, the "Illmitzer Sandpuszta" (Rechnitzer, 2019). The vegetation is characterised by the feeding of the cattle, input of nutrients by dung and urine and gap creating by trampling. This led to mosaic of small-scaled nutrient rich and nutrient poor habitats, which result structural heterogeneity. The vegetation" is a semi-arid grassland, with the plant community of *Centaureo pannonici-Festiicetiim pseudovinae* (Korner et al., 2008). The differences between cattle pastures and Przewalski's horse pasture result on the one hand due to higher grazing intensity at the cattle pastures. On the other hand, cattle use their tongue to graze which effect a lower vegetation than horses, which use their teeth.

Finally, the meadow sites were situated further south. These meadows are extensively used, the plant community is *Festuco-Brometea.* Unfortunately, no data is available about the exact mowing treatment in the previous years and about the fate of the hay. For detailed information about the individual plots see Table 11A in the Appendix. In Figure 1 the spatial configuration of the plots is shown.

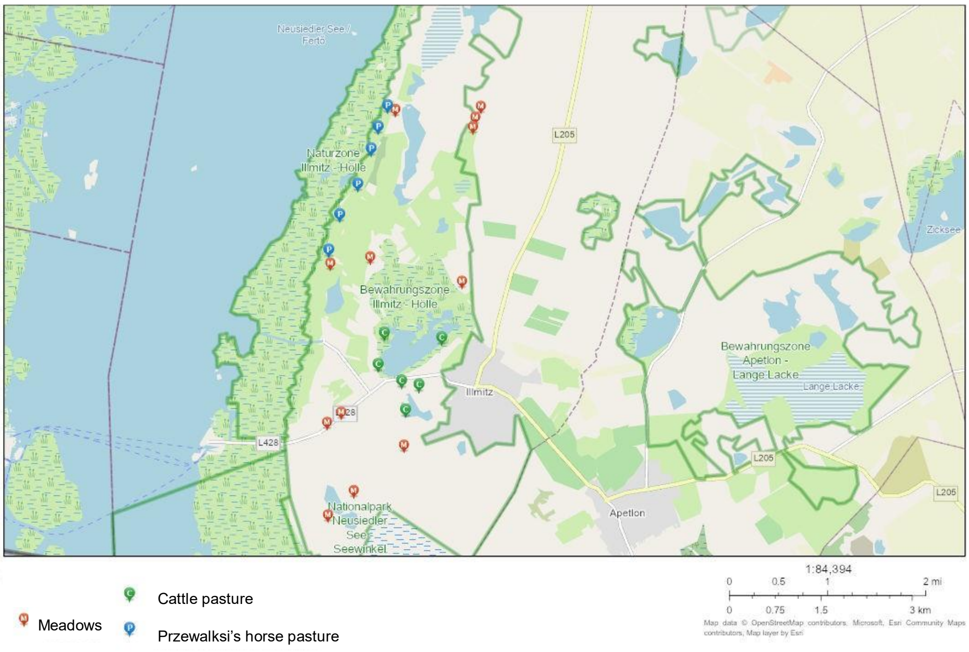


Figure 1: Map of the study area. Blue: 6 plots on the Przewalksi's horse pasture; green: 6 plots at cattle pastures: red: 12 plots at meadows. For further information see Table 1A in the Appendix.

Field sampling

Butterfly-flower networks were sampled in June and July 2021. There were six sampling events at every site, three in June 2021 and three in July 2021. The exact coordinates were noted in the program ArcGIS Pro 2.4.0. The program was connected to the app ArcGIS Field Maps, which guaranteed that exactly the proper spots were visited every time.

Beyond true butterflies (superfamily Papilionoidea) I also counted burnet moths (Zygaenidae) and one diurnal species of Sphingidae (*Macroglossum stellatarum*). The plot size was 50m x 50m at each site. A standardised data sheet was filled out during each survey. At each sample site all observed butterfly-plant interactions were recorded. As an interaction I only counted if the butterfly was touching the open petals of a flower. Butterfly individuals which were only sitting on non-reproductive plant organs or were flying through the site were not counted. The flowering plants and their visiting butterflies were recorded to the lowest taxonomic level possible. For data collection, the sample site was walked by me in a meandering pattern, in an attempt to cover all potentially available nectar flowers as exhaustively as possible. The survey was finished either if 60 butterfly-plant interactions had been observed or otherwise was terminated after one hour. As butterflies prefer warm, windless and sunny weather for their nectaring activities, sampling only took place at suitable conditions, adapted from the Butterfly Monitoring Scheme methodology (van Swaay et al., 2008).

I. Plots were not walked when the temperature was below 13°C.
II. A plot was walked only provided there was at least 60% sunshine.
III. When wind speed was above 5 on the Beaufort scale, plots were not walked.
IV. Sampling only took place between 9 am and 5 pm.

Butterflies which I could not identify from a distance I captured with an insect net. Species identification of butterflies followed Stettmer et al. (2006) and for plants Fischer et al. (2008). The identification of the Zygaenidae happened with the help of Konrad Fiedler. Two species pairs were counted as one operational taxonomic unit (OTU), as field identification is not reliable: *Zygaena purpuralis/minos* and *Colias hyale/alfacariensis*. All potentially available nectar sources (flowers and flowerheads of plant species that are insect-pollinated) were counted in 10 m^2 areas within the plot. Compact inflorescences like Asteraceae flowerheads were counted as one flowering unit (Alarcón et al., 2008). Wind pollinated flowers were excluded from this census.

Additional data

An average annual abundance index of grassland butterflies around Illmitz was calculated from observation data provided by Konrad Fiedler (pers. communication). This data was collected during a student field course which took place in one week in June every year (except 2010 and 2011) from 2005-2021. This course was held in largely the same area as this study. Therefore, the data can be used as a rough proxy of the relative abundance of the observed butterfly species in early summer at a landscape level. The sum of observation per species over the years was divided by all observations to achieve the relative proportion of the species.

The distinction between the colours of inflorescences followed Arnold et al. (2010). The described colours refer to the perception visible for the human eye. In addition, information on UV patterns and flower syndromes was collected from the Bioflor database (Klotz et al., 2002). Here, I distinguished between inflorescences with exposed nectar (A), inflorescences with partly hidden nectar (AB), inflorescences with completely covered nectar (B), inflorescences targeted at Hymenoptera (H) and those targeted at Lepidoptera (F) and flowers which are essentially wind-pollinated but were occasionally visited by butterflies (W). The rewards offered by the flowers were categorized in three groups: low amount of nectar/pollen, medium amount of nectar/pollen and high amount of nectar/pollen. Information on nectar and pollen amounts were mainly taken from Maurizio and Grafl (1982), supplemented by Pritsch (2018). The inflorescence type was separated into the following groups: composite, loose, panicle and racemes. Finally, data on corolla tube length was taken from Fischer et al. (2008).

The nectar plants were taken from Dennis (2010), Ebert and Rennwald (1993), Gelbrecht et al. (2016), Richert and Brauner (2018), Hesselbarth et al (1995) and Lafranchis et al. (2015). Plants which were observed to receive visitations by a certain butterfly species, but which were not mentioned by name were declared as new.

Network analysis

Field data was digitized into a spread sheet using Microsoft Office Excel version 2019. The data matrix contained all observed interactions of all sampling events. For further analysis a distinction was made between the months June (early summer) and July (high summer). For the analysis of the network structures the R package ‘bipartite’ was utilized. The visualizations of the web contain on the one hand all observed interactions per month separated by land use type and on the other hand all observed interactions per month, regardless of the land use type. The line thickness is proportional to the interaction strength (Dormann et al., 2009).

Blüthgen and Menzel (2006) proposed that analyses based on binary data have serious shortcomings and that they are strongly influenced by sampling effort, the size of the investigated networks and the decision if a species should be excluded.

Accordingly, they introduced two metrics which are based on interaction frequencies to measure the degree of specialisation: d' (standardized Kullback-Leibler distance) describes the degree of specialisation at species level (which can be calculated from the perspective of each insect as well as plant species). Additionally, H2 (standardized two-dimensional Shannon entropy) describes the degree of specialisation in the entire network (Dormann et al., 2009). It has been shown that H2 is not (strongly) influenced by network size or sample intensity (Blüthgen, 2010).

From the multiple indices available in the output of analyses using the ‘bipartite’ package to describe a network, I therefore selected the following:

I. H2
II. Vulnerability: It is calculated as the mean number of butterfly species per plant species (Tiedeken & Stout, 2015).
III. d‘ for selected (sufficiently common) species
IV. Species strength for selected species. It shows how many plants are connected with this butterfly species (Dormann et al., 2009).

Statistical analyse

For further statistical analysis the RStudio software version 4.1 was used and $p < 0.05$ was defined as the threshold value for significance (RStudio Team, 2020). To graphically illustrate results the package ‘ggplot2’ was used (Wickham, 2016). Scatterplots were drawn to illustrate the average relative abundance of butterfly species on the landscape level in comparison to the relative proportion of the same species in flower interactions during my study.

To compare the chosen indices between the months, first a matrix of their Euclidean distances was calculated. Afterwards a PERMANOVA with 999 permutations was conducted in the package ‘vegan’ (Oksanen et al., 2020). Within the three different land use types a comparison with FDR correction (False discovery rate) was used (Pike, 2011). For answering the question if there is a correlation between flower supply and overall interaction frequency at the community level Spearman's rank correlation coefficient was computed. For the comparison of species richness between the months and the land use types, an individual based species accumulation curve was calculated with the package ‘iNEXT’ (Hsieh et al., 2016). As Hill number the factor one was chosen, which is equivalent to the exponential Shannon diversity, also termed ‘effective number of species’ (Chao et al., 2014).

To test for relationships between plant traits and visitation rate Generalized Linear Mixed Model analyses (GLMMs) with the package ‘lme4’ were conducted (Bates et al., 2015). The land use type and the month were set as random variable, and the respective plant trait was modelled as fixed factor. Additionally, the conditional (R^2c) and marginal coefficient of determination (R^2m) was calculated with the package ‘MumIn’ (Barton, 2009). R^2c shows the variance which can be explained by fixed and random factors combined, whereas R^2m indicates the variance explained by only the fixed factors. Afterwards an ANOVA and Tukey HSD post-hoc test was performed. Beforehand, the proportion of visitation was logit-transformed.

The colour preferences and corolla tube length, and the proportion of observed visitations of the four common each butterfly species was documented. To illustrate results histograms were drawn. For the two most commonly observed butterfly species *Polyommatus icarus* and *Coenonympha pamphilus* enough data was available for more detailed analyses. Here a distinction was further made between the land use types as well. For all other butterfly species this distinction was impossible due to insufficient data.

Results

General observations on the butterfly-flower networks

In June and July 2021, I altogether recorded 4160 butterfly-flower interactions: 27 butterfly species and 59 plant species were part of the networks. Eight butterfly species accounted for 92% of all interactions, while 10 species were accountable for 73% of the observed interactions from the plants’ perspective (Figure 2). Six butterfly species were seen less than five times visiting a flower, and 14 plant species were only visited less than five times by a butterfly (Figure 2). Among the butterflies, only *P. icarus* was more prevalent as flower visitor in July than in June. Late flowering plant species were *Ononis spinosa, Eryngium campestre, Scabiosa ochroleuca* and *Centaurea stoebe. Lotus corniculatus* was in both months often visited, whereas *Thymus serpyllum, Inula salicina* and *Dianthus carthusianorum* were species of the early summer.

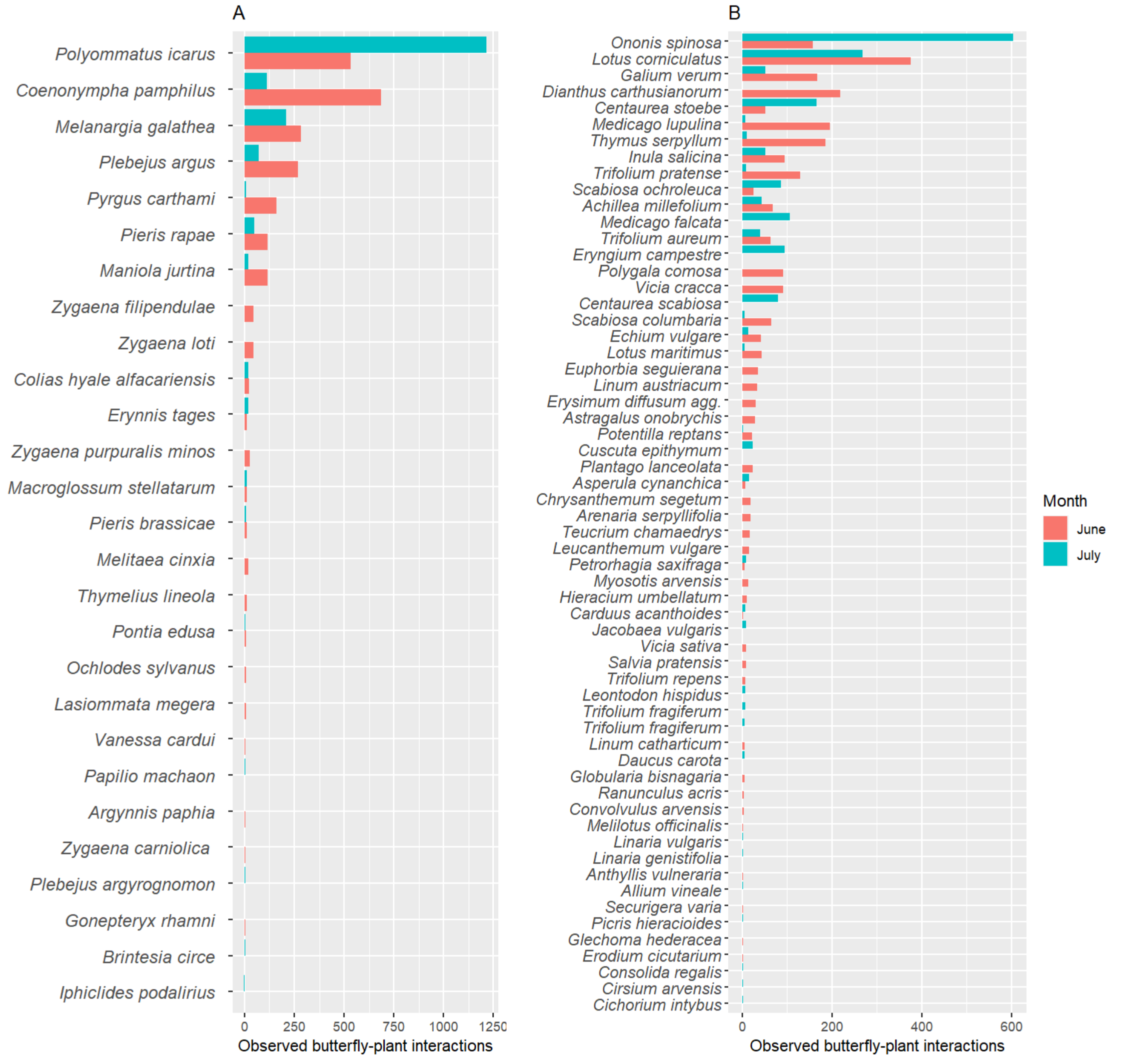


Figure 2: Numbers of observed plant-butterfly interactions per (A) butterfly species and (B) plant species.

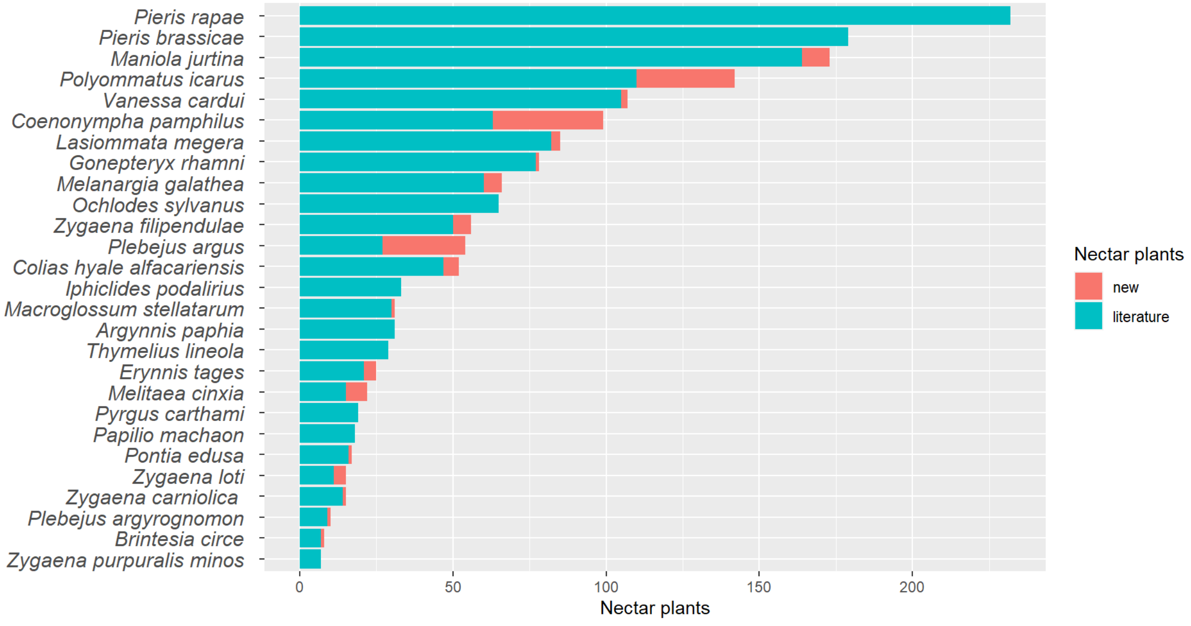


Figure 3: Numbers of recorded and new nectar plants of the 27 observed butterfly species.

Figure 3 shows the nectar plants of the 27 observed butterfly species. The plants which were observed during an interaction with a certain butterfly species, but which are not listed in the cited literature are listed in Table A41. On average there are 61 nectar plants per species. The accumulation curves paint a clear picture of differences in species diversity between early summer (June) and high summer (July). For the plants in flower as well as the visiting butterflies, species diversity in the networks was more than twice as high in June. In regard to the different land use types there were differences between the plants and the butterflies. In both cases the meadows had the highest species diversity in networks. However, butterfly species diversity in the networks tended to be lower at the cattle pastures than at the Przewalski's horse pasture. In contrast, plant diversity in the networks was significantly lower at the Przewalski's horse pasture compared to the cattle pastures (Figure 4 and Figure 5).

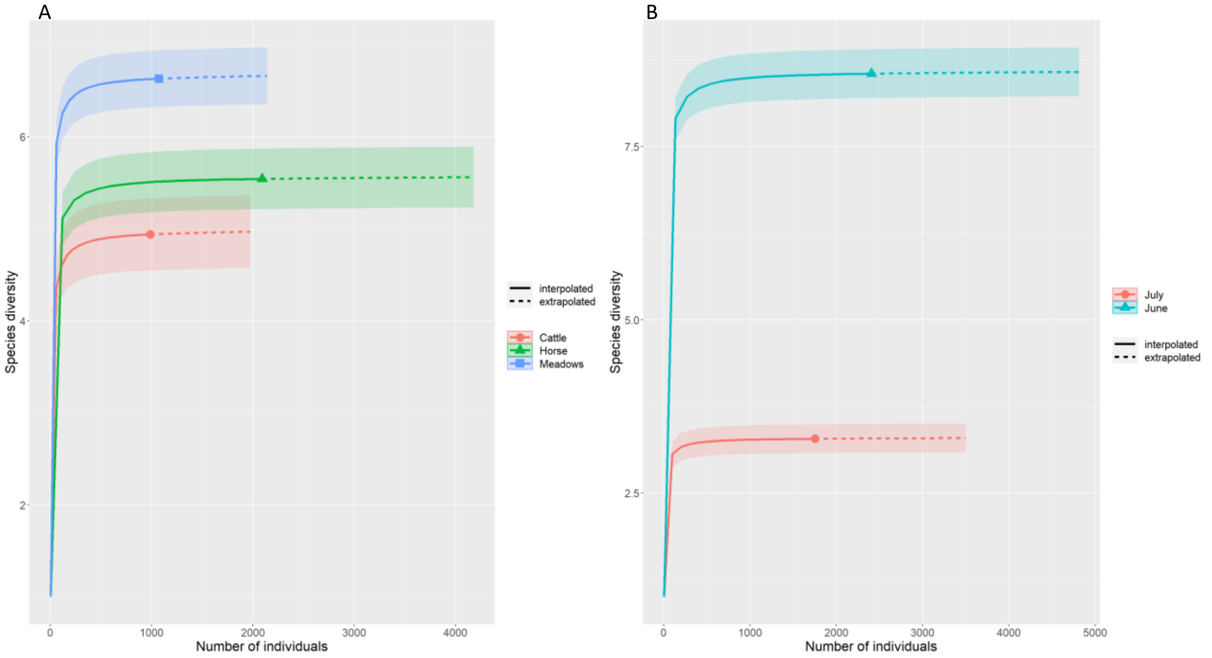


Figure 4: Individual based randomized diversity accumulation curves (Hill numbers, q=1) of butterflies (A) at the different land use types and (B) between the months. The shaded areas represent 95% confidence intervals.

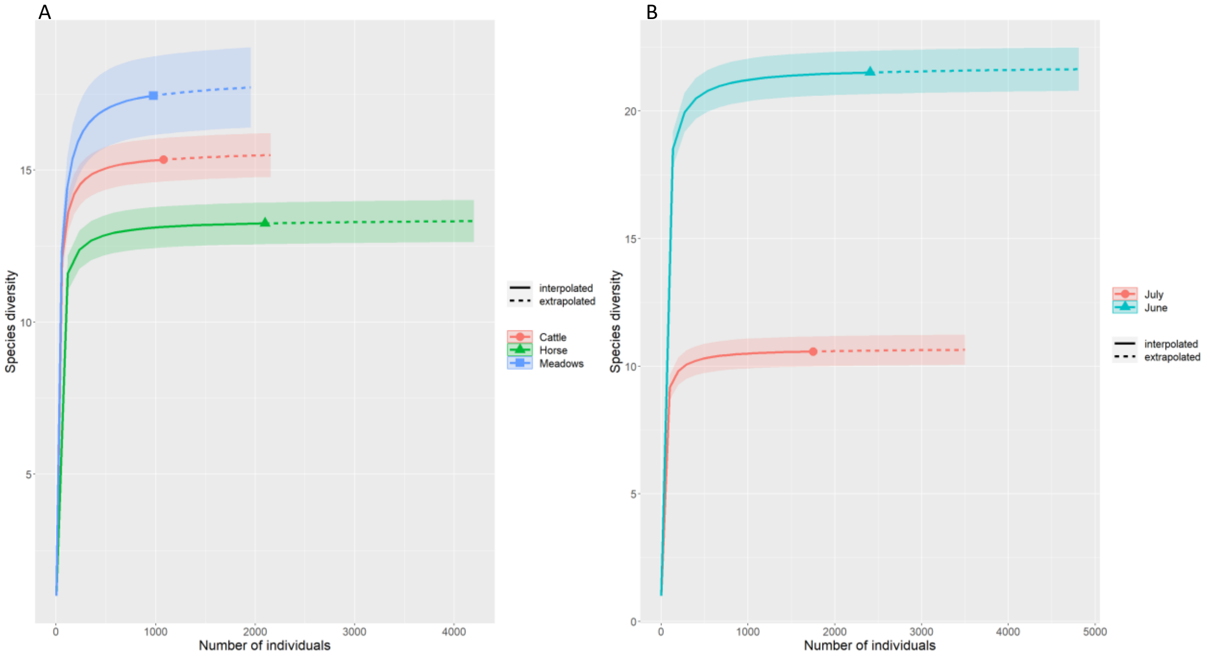


Figure 5: Individual based randomized diversity accumulation curves (Hill numbers, q=1) of plants (A) at the different land use types and (B) between the months. The shaded areas represent 95% confidence intervals.

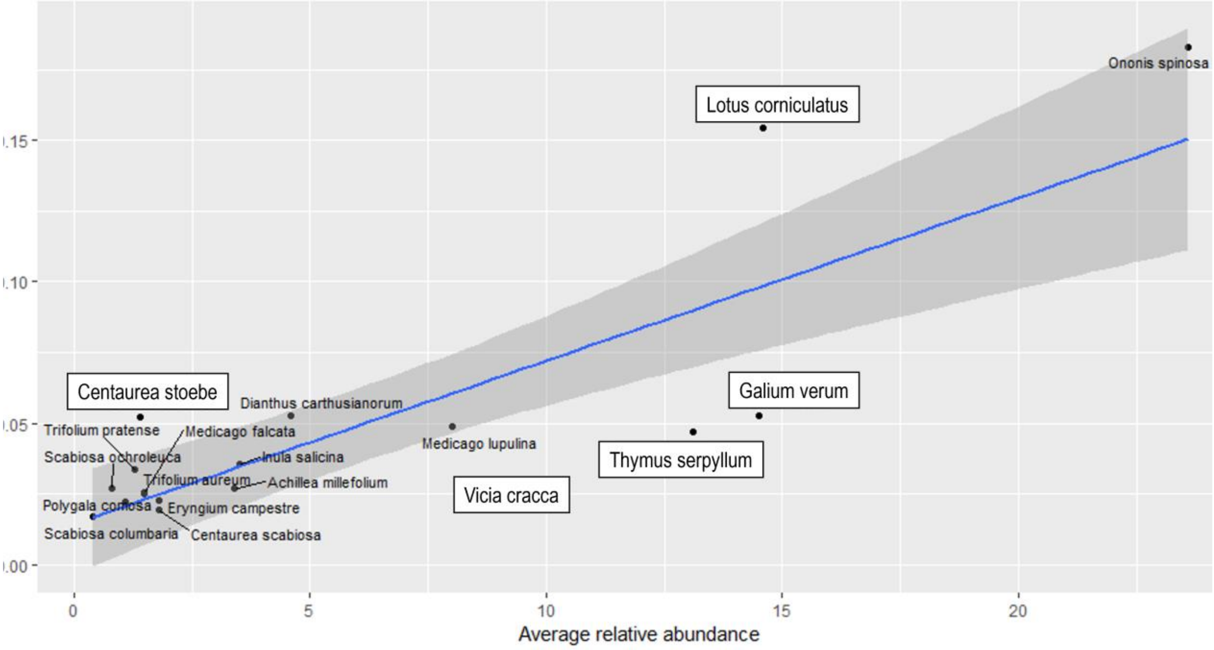


Figure 6: Proportion of butterfly flower visits relative to the average abundance of these flower species across all surveys. For visual clarity, only the 18 most abundant plant species were included. The shaded area reveals a confidence interval of 95%, the blue line represents an ordinary least squares regression line.

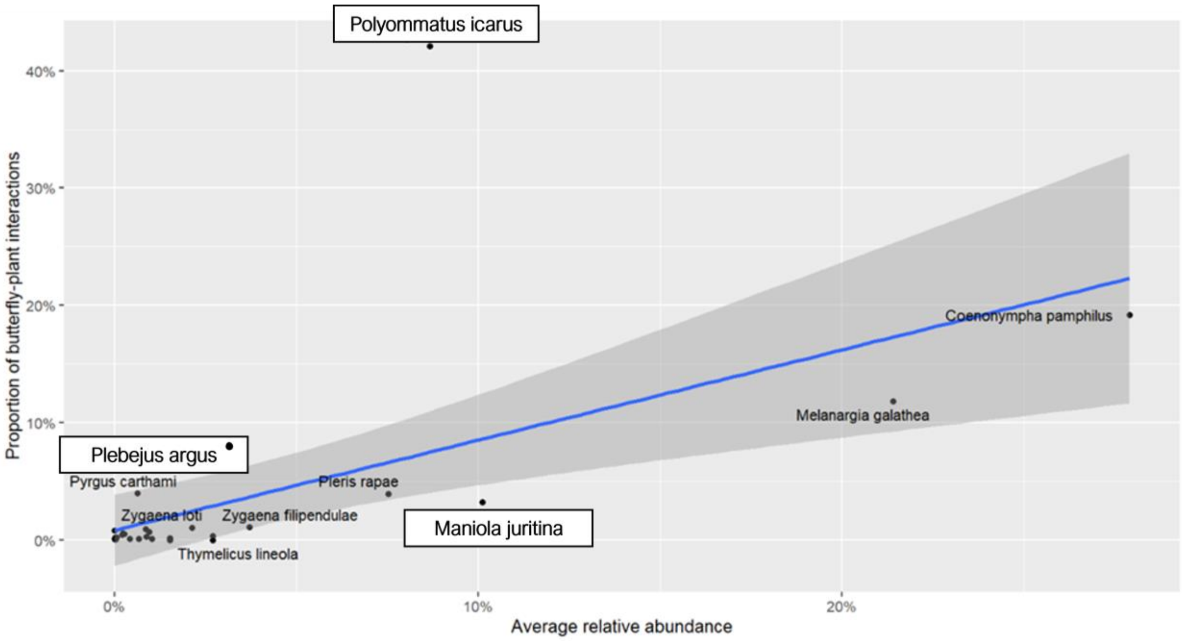


Figure 7: Proportion of 17 butterfly species observed visiting flowers in 2021, relative to their average occurrence at the landscape level in the years 2005-2021. The shaded area is the 95% confidence interval, the blue line represents an ordinary least squares regression line.

There was a strong positive correlation between the mean frequency of butterflies in the landscape and their proportion among observed flower interactions (ρ=0.679, p=0.003; Figure 7). Similarly, there was a positive correlation between the average abundance of the flowers at the sites and the proportion of butterfly visitations they received (ρ=0.619, p=0.006; Figure 6). Hence, overall the contribution of commonly visited flowering plant species mirrored their abundance on the plots. However, some plant species deviated substantially from that pattern. For example, *Galium verum* was generally abundant but was comparatively not often visited by butterflies. The same applied to *Vicia cracca* and *Thymus serpyllum.* On the other hand, *Lotus corniculatus* and *Centaurea stoebe* were disproportionately often visited. *Polyommatus* *icarus* was far more often observed during an interaction with a flower than its average abundance would have suggested. The same can be said about *Plebejus argus*, although it was not so pronounced. Although the average abundance of *Maniola juritina* indicates otherwise, this species was more rarely observed visiting flowers than expected. Plant species which contributed less than 1% to the overall interactions were excluded from the graph due to better legibility. However, in all cases visits at the excluded flower species laid in the range as expected from their abundance.

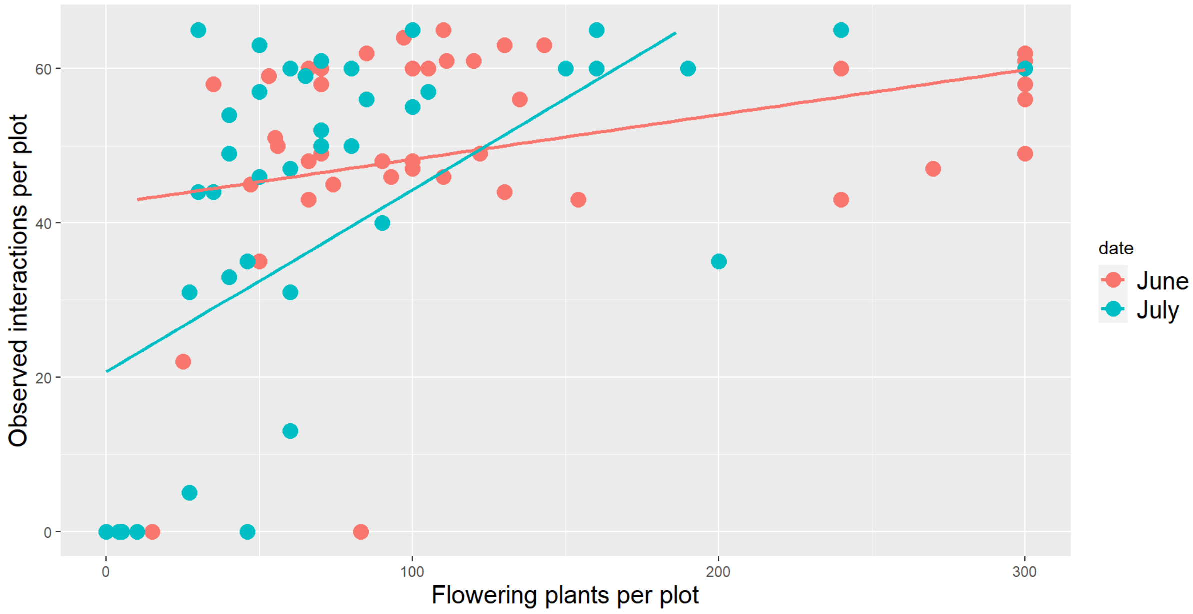


Figure 8: Relationship between the number of observed interactions per plot and the number of flowering plant individuals per 10mx10m area within the plot (n_{June}= 53, n_{July} = 46 surveys).

Nectar flower supply on the sites and the number of observed interactions were highly positively related to each other in June (ρ=0.380, p=0.005 as well as in July (ρ=0.767, p<0.0001; Figure 8).

Network structures at land-use type and monthly levels

At the Przewalski's horse pasture in June the plant species with the most interactions was *Dianthus carthusianorum*, for the butterflies it was *Coenonympha pamphilus*. Additional to *Dianthus carthusianorum*, there were nine further species across which most of the remaining interactions were rather evenly distributed. However, there were many flowering plant species which contributed only a small proportion to the overall observed interactions. In June for the butterflies there were clearly three main species involved in the interactions, namely *Coenonympha pamphilus*, *Melanargia galathea* and *Polyommatus icarus*. In comparison to July, the whole network showed a more diverse set of interactions. In July the most important plant was by far *Ononis spinosa*, followed with some distance by *Centaurea stoebe*. The most visiting butterfly was *Polyommatus icarus*, followed by *Melanargia galathea*. The observed interactions were mostly distributed on the mentioned species, although this pattern was more pronounced for the butterflies. *Coenonympha pamphilus*, which contributed most of the interactions in June, played a very minor role in July. By far the most interactions were made between *Polyommatus icarus* and *Ononis spinosa*. Though, most of these interactions happened in July. Network diversity H2 halved from June to July and also network vulnerability V decreased (Figure 9/A).

The most important plants in June at the cattle pastures were *Lotus corniculatus*, *Thymus serpyllum*, *Trifolium pratense* and *Galium verum*. *Coenonympha pamphilus* and *Polyommatus* *icarus* contributed by far the most observed interactions. However, the remaining interactions were primarily distributed between *Pyrgus carthami*, *Maniola jurtina, Plebejus argus*, *Melanargia galathea* and *Pieris rapae*. The interactions in July were more evenly distributed on the plants, however, there was a decrease of participating plant species as well. There was no plant more excessively visited than the rest, the three most visited were *Lotus corniculatus*, *Medicago falcata* and *Ononis spinosa*. Among the butterflies *Polyommatus icarus* was responsible for over 50% of the observed interactions. In contrast to the Przewalski's horse pasture, the interactions of *Polyommatus icarus* were not primarily with *Ononis spinosa*. Participating butterflies decreased from 17 species to 7 from June to July. Diversity H2 showed a trend for increase from June to July, whereas vulnerability V was decreasing (Figure 9/B).

In June at the meadows the most visited plant was *Medicago lupulina,* followed by *Lotus corniculatus* and *Vicia cracca.* The three main visitors were *Coenonympha pamphilus, Polyommatus icarus* and *Plebejus argus*. In contrast to the Przewalski's horse pasture and the cattle pastures no single sighting of *Melanargia galathea* during an interaction with a flower occurred. In July the proportion of interactions shifted towards *Polyommatus icarus,* although *Coenonympha pamphilus* and *Plebejus argus* remained the second-most important visitators. In July *Medicago lupulina* lost its dominating role, it was replaced by *Lotus corniculatus*. *Eryngium campestre*, *Centaurea stoebe* and *Achillea millefolium* received most of the remaining visits in July. Like for the cattle pastures, the network diversity H2 was decreasing, and the network vulnerability V was increasing (Figure 9/C).

Regardless of the land use type, the most visited plants were *Lotus corniculatus* in June, followed by *Dianthus carthusianorum* and *Medicago lupulina. Polyommatus icarus* and *Coenonympha pamphilus* were the most observed butterflies in June. In July the most important plant was by far *Ononis spinosa*, followed by *Lotus corniculatus* and *Centaurea stoebe*. Most interactions were made by *Polyommatus icarus*, mostly with *Ononis spinosa*. Besides *Polyommatus icarus, Coenonympha pamphilus* and *Melanargia galathea* contributed most to the remaining fraction of observed interactions. H2 stayed nearly the same, vulnerability decreased (Figure 10). *Galium verum* and *Ononis spinosa* experienced an increased specialisation of their visits from June to July, whereas *Centaurea stoebe* and *Ononis spinosa* showed a decrease. *Dianthus carthusianorum* only flowered in June. Except for *Polyommatus icarus* and *Melanargia galathea*, most observed butterflies tended to show an increasing specialisation in their flower visits. None of the most frequent plants showed a high specialisation, especially not in July (Table 1).

Table 1: The development of the network specialization index d' for the five most often observed butterfly and plant species from June to July. Red indicates a decrease in specialisation, green an increase.

	Species	June	July		Species	June	July
1	*Polyommatus icarus*	0.25	0.17	1	*Centaurea stoebe*	0.56	0.10
2	*Coenonympha pamphilus*	0.26	0.44	2	*Dianthus carthusianorum*	0.30	-
3	*Melanargia galathea*	0.66	0.35	3	*Galium verum*	0.21	0.26
4	*Plebejus argus*	0.48	0.56	4	*Lotus corniculatus*	0.28	0.29
5	*Pyrgus carthami*	0.38	0.67	5	*Ononis spinosa*	0.55	0.25

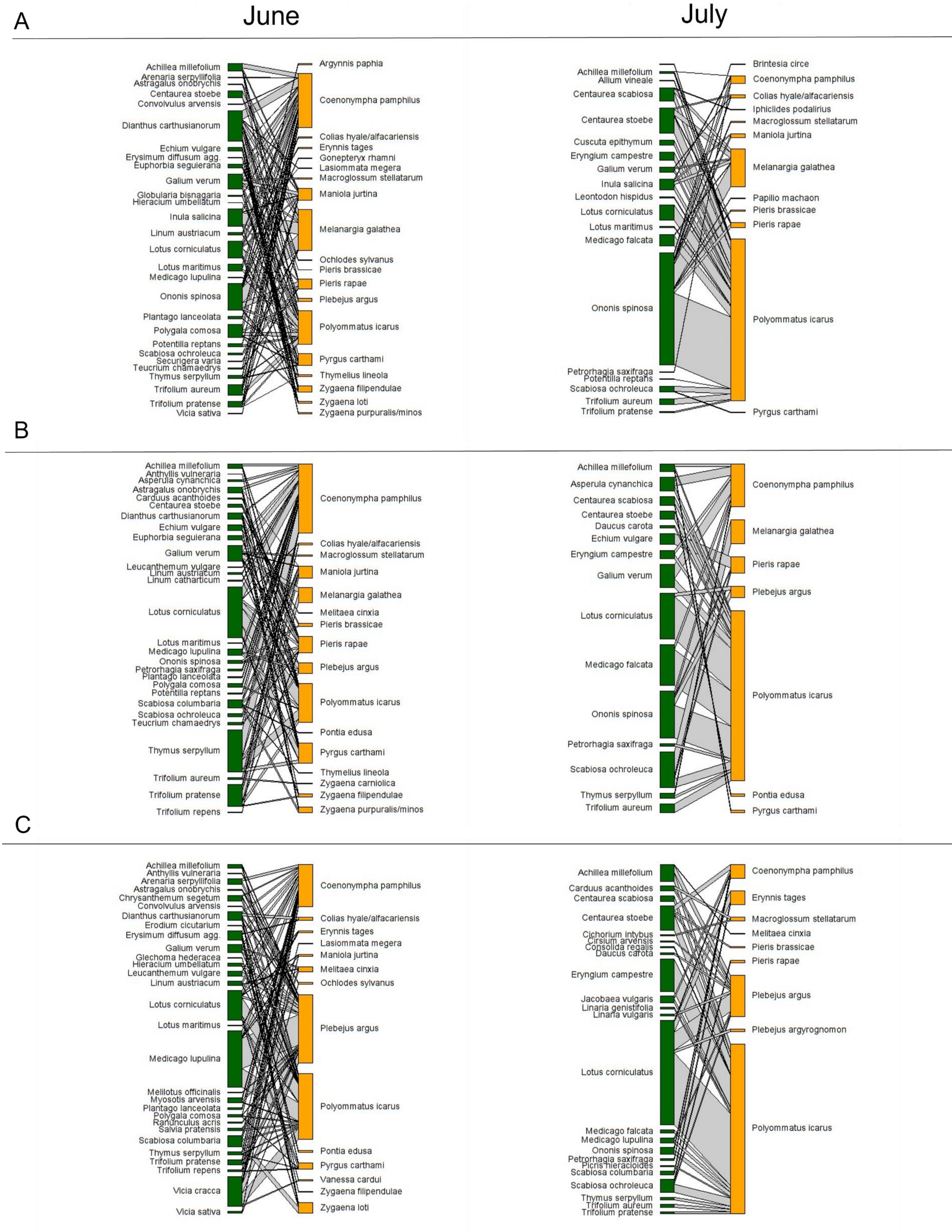
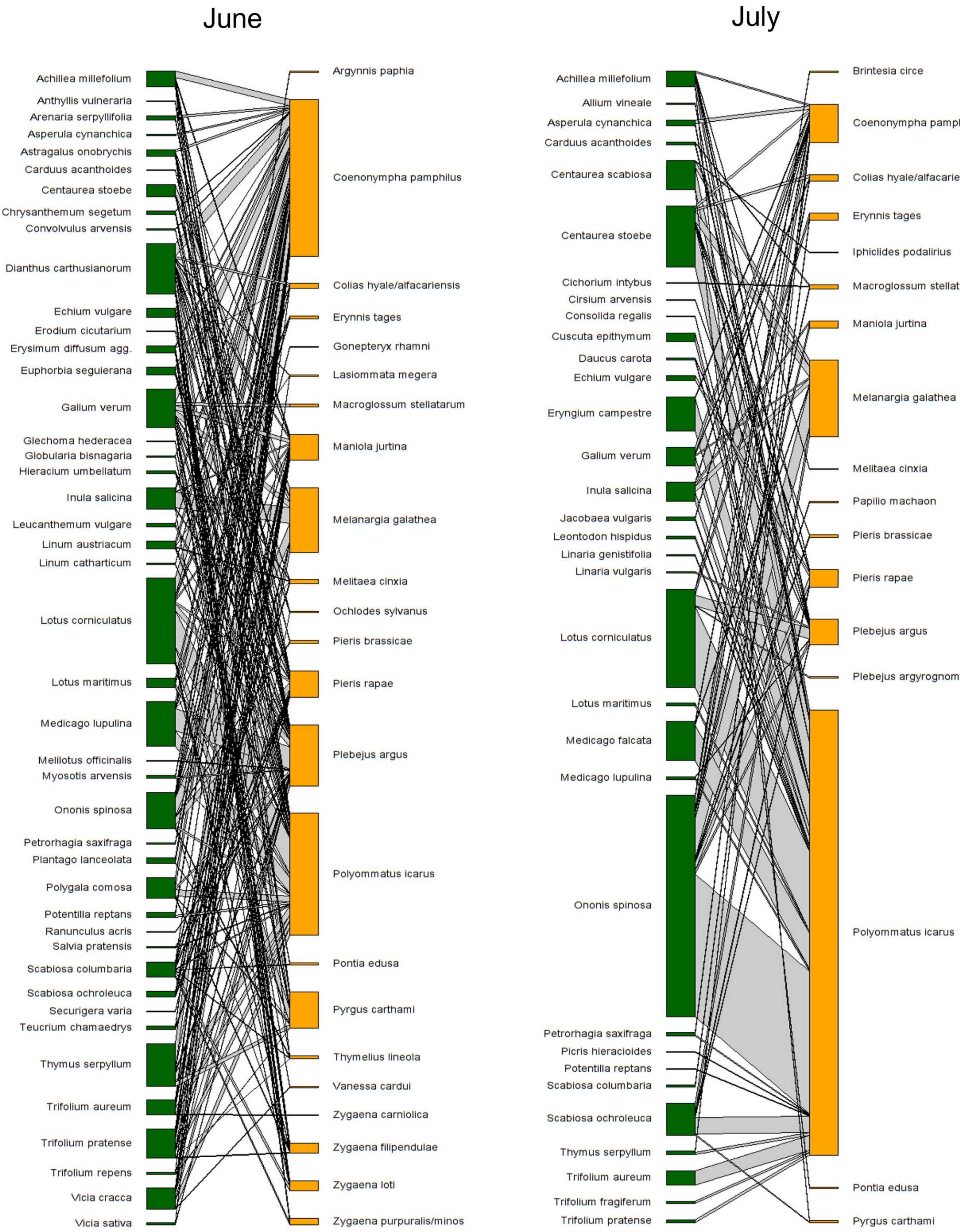


Figure 9: Cumulative bipartite butterfly-flower networks in June and July of the (A) Przewalski’s horse pasture, (B) cattle pastures and (C) meadows. The interactions are drawn as lines, whose width is proportional to the number of interactions between the interacting species.



June

July

Figure 10: Cumulative bipartite butterfly-flower networks in June and July, regardless of the land use type. The interactions are drawn as lines, whose width is proportional to the number of interactions between the interacting species.

Network level patterns across individual surveys

Following the exploration of butterfly-flower networks aggregated at the level of survey months or land-use types, I further compared networks among individual plot visits. The PERMANOVA revealed a significant impact of the interactions between survey month and land use type on the butterfly-flower network diversity. Furthermore, the pairwise comparisons showed a significant decrease of H2 at the Przewalski's horse pasture from June to July, whereas no such difference was observed at the cattle pastures and meadows. In July, H2 was significantly higher on the cattle pastures than on the Przewalski's horse pasture.

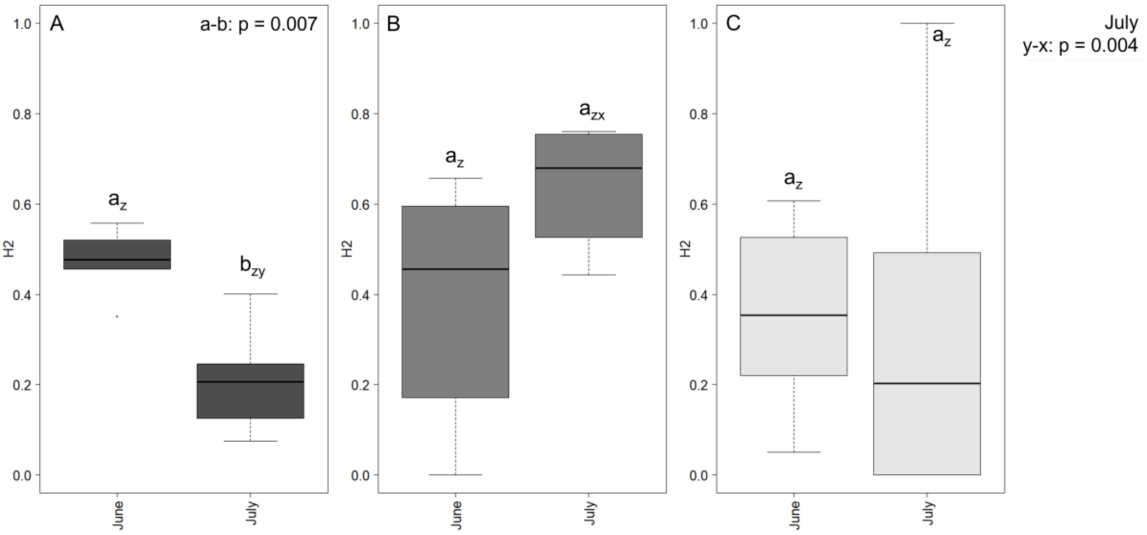


Figure 11: Boxplots showing the development of butterfly-flower network diversity (H2) from June to July on to (A) Przewalski's horse pasture, (B) cattle pastures and (C) meadows. Small letters indicate significant differences ($p<0.05$) between the months. Subscript letters indicate significant differences between the land use types within the months (PERMANOVA using FDR correction, $p<0.05$).

Table 2: Results of a two-factorial PERMANOVA of network diversity H2. The used factors are land type and month and their interaction. Significant results ($p<0.05$) are printed in bold face.

	Df	Sum of Squares	R²	F	p
Land use type	2	0.18	0.06	1.63	0.221
Month	1	0.02	0.01	0.41	0.522
Land type:Month	2	0.38	0.13	3.51	**0.043**
Residual	42	2.29	0.80		
Total	47	2.87	1.00		

Network vulnerability was significantly influenced by the factors month and land use type. It significantly decreased between the months at the Przewalski's horse pasture and the meadows. The same trend was detected at the cattle pastures but was not significant there. Network vulnerability was at the Przewalski's horse pasture significantly higher than at the meadows in June as well as in July (Figure 12, Table 3).

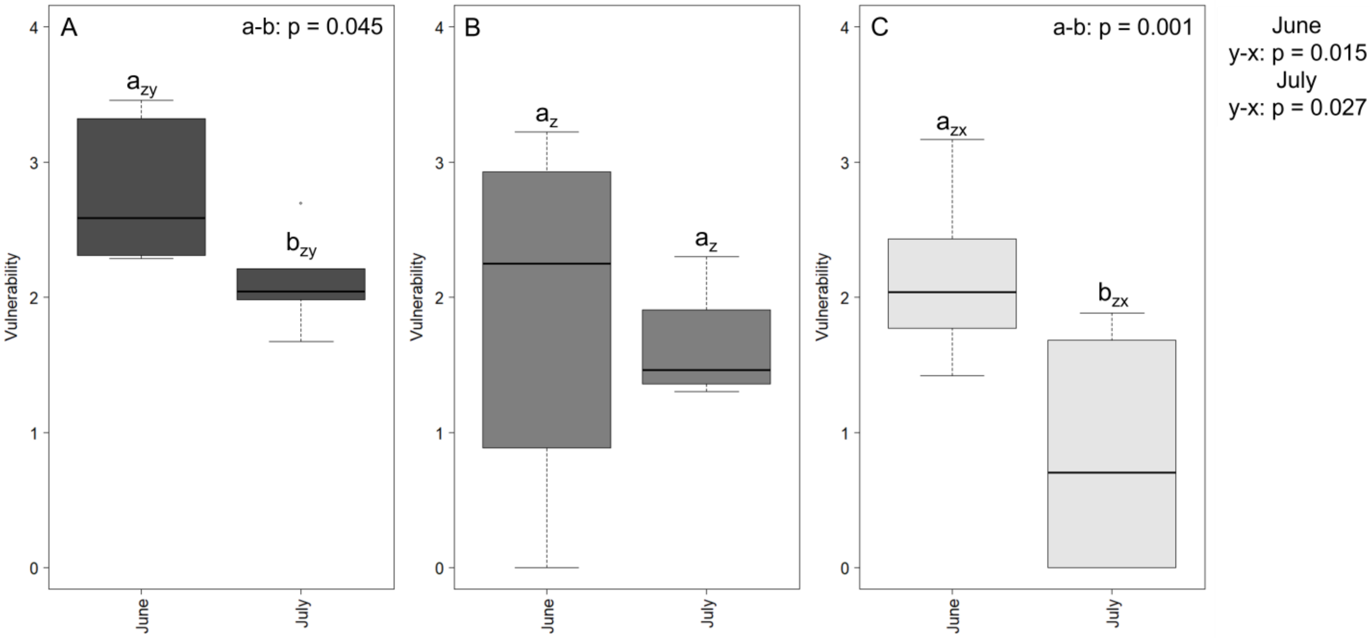


Figure 12: B: Boxplots showing the development of network vulnerability from June to July on to (A) Przewalski's horse pasture, (B) cattle pastures and (C) meadows. Small letters indicate significant differences ($p<0.05$) between the months. Subscript letters indicate significant differences between the land use types within the months (PERMANOVA using FDR correction, $p<0.05$).

Table 3: Results of a two-factorial PERMANOVA of network vulnerability. The used factors are land type, month and their interaction. Significant results ($p<0.05$) are printed in bold face.

	Df	Sum of Squares	R²	F	p
Land type	2	7.36	0.17	6.11	**0.005**
Month	1	9.24	0.21	15.35	**0.001**
Land type:Month	2	2.05	0.05	1.70	0.177
Residual	42	25.28	0.58		
Total	47	43.93	1.00		

Vulnerability was significantly influenced by the factors month and land-use type, whereas network diversity was affected by the interaction of them. Network vulnerability decreased in all three land use types from June to July. Network diversity showed a trend for decreasing over the time at the Przewalski's horse pasture an the meadows, whereas the cattle pastures tended to increase.

Butterfly interaction in relation to flower supply

The flower supply was significantly influenced by the factor month (Table 4). There was a trend for decreasing flower supply from June to July at all three land use types observable, but only at the meadows this was significant. In June, there were no differences of flower supply detectable between the land use types. However, in July the meadows had significantly fewer blossoming flowers than the pastures (Figure 13).

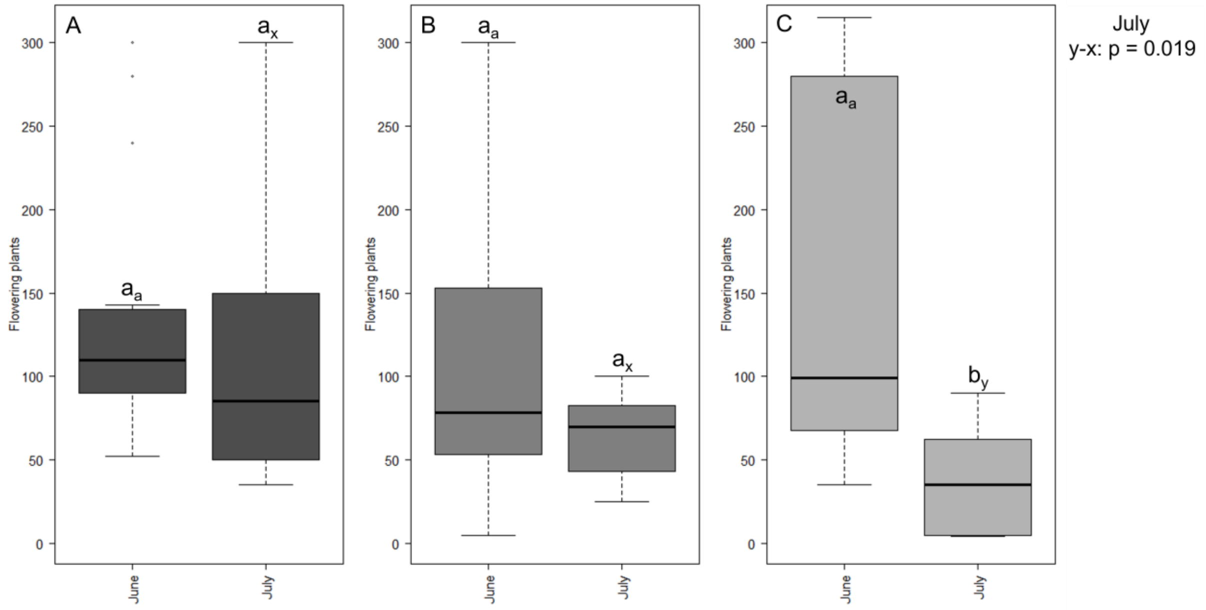


Figure 13: Boxplot showing the number of flowering plants in 10 m x 10 m areas within the plots from June to July according to (A) Przewalski's horse pasture, (B) cattle pastures and (C) meadows. Small letters indicate significant differences ($p<0.05$) between the months using FDR correction. The subscripts indicate significant differences between the land use types within the months using FDR correction ($p<0.05$).

Table 4: Statistical results of two-factorial PERMANOVA of flower supply. The used factors are land use type and month. Significant results ($p<0.05$) are printed in bold face.

	Df	Sum of Squares	R^2	F	p
Land type	2	7444.67	0.01	0.61	0.571
Month	1	76083.81	0.13	12.41	**0.002**
Land type:Month	2	32408.02	0.05	2.64	0.064
Residual	79	484273.19	0.81		
Total	84	600209.69	1.00		

Nectar flower supply on the sites and the network specialisation H2 only showed a weak trend for negative correlation, however, these results are not significant (ρ= - 0.114, p=0.484, Figure 14)

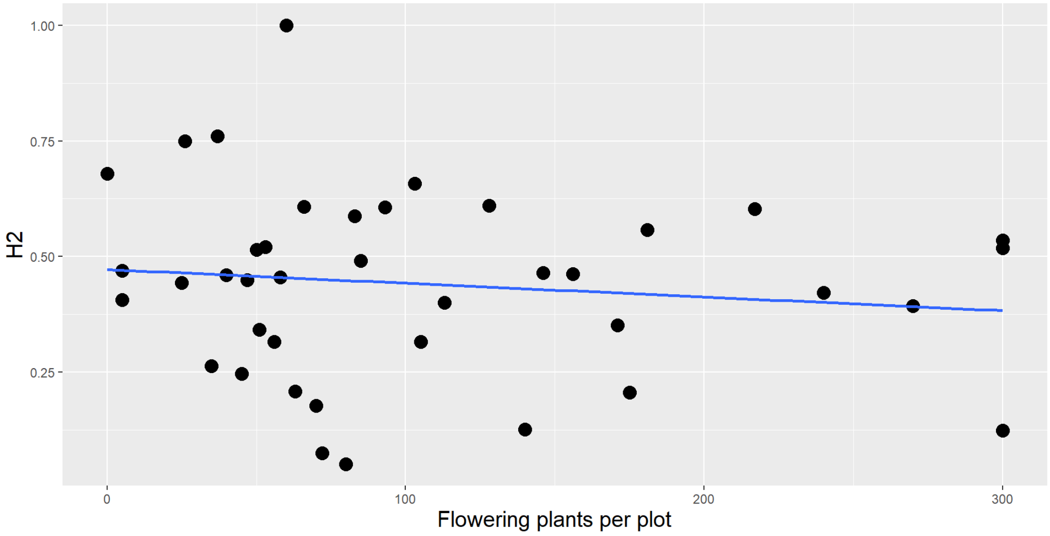


Figure 14: Relationship between the mean network specialisation H2 per plot and the mean number of flowering plant individuals per 10mx10m area within the plot (n = 99 surveys).

Butterfly interactions in relation to plant characteristics

Figure 15 shows the relative proportion of visited inflorescences according to their colours. Meadows and cattle pastures revealed a similar distribution as yellow was the most visited floral colour, followed by violet and purple. At the Przewalski's horse pasture, in contrast, purple was the most frequently visited colour, followed by yellow. Blue was in all three cases the least visited floral colour. A Chi² test corroborated an association between land use type and visited inflorescence colour (Table 5).

Figure 15: Histogram showing the relative proportions of visited inflorescence colours at (A) Przewalski's horse pasture (n_{horse} = 2100), (B) cattle pastures (n_{cattle} = 1071) and (C) meadows (n_{meadow} = 986).

Table 5: Contingency table showing the frequencies of the combination of land use type and inflorescence colour. Significant results are printed in bold.

	Przewalski's horse pasture	Cattle pastures	Meadows	χ²
blue	19	6	32	
purple	195	77	138	
violet	1050	405	141	
white	103	75	84	
yellow	733	508	591	
p				**< 0.0001**

On all three land use types flowers of Fabaceae (e.g. *Ononis spinosa* and *Lotus corniculatus*) were the most often visited plant family (Figure 16). At the Przewalski's horse pasture and the meadows the second-most frequently visited plant family were Asteraceae, especially *Centaurea stoebe* and *Inula salicina.* At the cattle pastures, however Lamiaceae like *Thymus serpyllum* were the second-most frequently visited plant family, followed by Asteraceae. The other 13 observed plant families played a minor role (Figure 16). A Chi² test revealed that the chosen plant families were not independent of the land use type (Table 6).

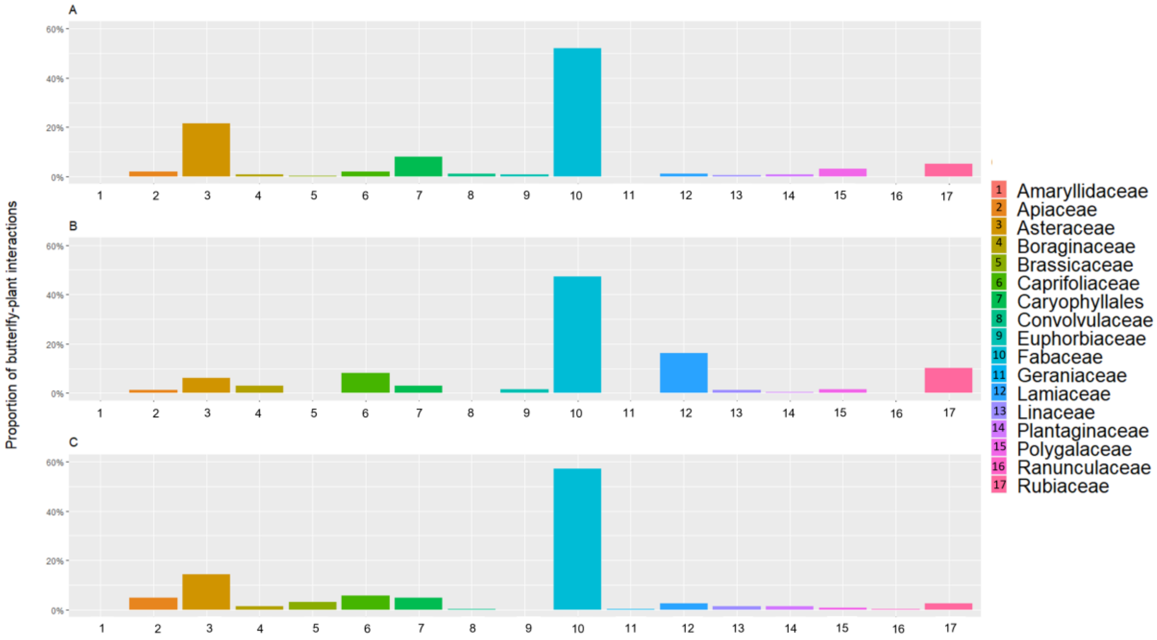


Figure 16: Histogram showing the relative proportions of visited plant families of the 14 most frequent visited plants at (A) Przewalski's horse pasture (n_{horse} = 1741), (B) cattle pastures (nc_{attle} = 814) and (C) meadows (n_{meadow} = 514).

Table 6: Contingency table showing the frequencies of the combination of land use type and plant families. Significant results are printed in bold.

	Przewalski's horse pasture	Cattle pastures	Meadows	χ²
Amaryllidaceae	3	0	0	
Apiaceae	40	13	47	
Asteraceae	451	67	140	
Boraginaceae	21	33	14	
Brassicaceae	4	0	31	
Caprifoliaceae	40	87	56	
Caryophyllales	172	33	47	
Convolvulaceae	26	0	2	
Euphorbiaceae	19	16	0	
Fabaceae	1091	507	562	
Geraniaceae	0	0	2	
Lamiaceae	26	173	24	
Linaceae	14	12	14	
Plantaginaceae	16	5	13	
Polygalaceae	69	15	8	
Ranunculaceae	0	0	2	
p				**< 0.0001**

At all three land use sides the most frequently visited flower type were representatives of so-called 'Hymenoptera flowers', followed by inflorescences with completely covered nectar. Only at the Przewalski's horse pasture inflorescences putatively addressing Lepidoptera as a syndrome were visited more often than inflorescences with exposed nectar. Inflorescences with partly hidden nectar and wind pollinated flowers played in all three land use type a minor role (Figure 17). The flower syndrome seemed to be associated with the land use type (Table 7).

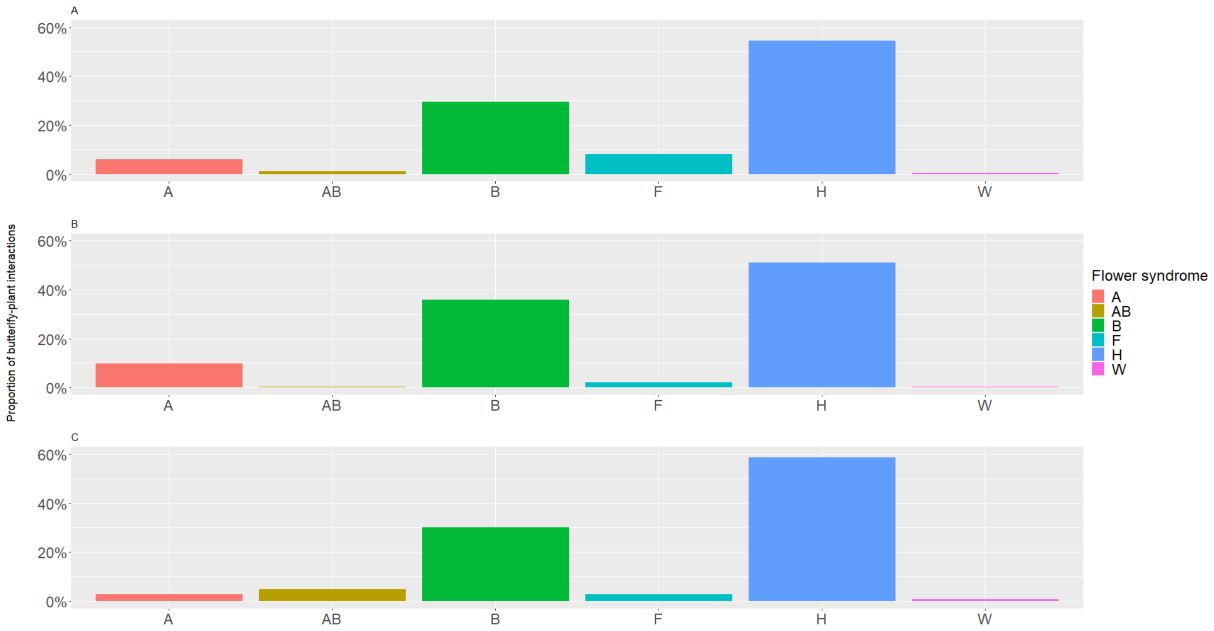


Figure 17: Histogram showing the relative proportions of visited flower syndromes at (A) Przewalski's horse pasture ($n_{horse} = 1741$), (B) cattle pastures ($n_{cattle} = 814$) and (C) meadows ($n_{meadow} = 514$).

Table 7: Contingency table showing the frequencies of the combination of land use type and flower syndromes. Significant results are printed in bold.

	Przewalski's horse pasture	Cattle pastures	Meadows	χ^2
A	127	106	27	
AB	24	5	48	
B	620	383	297	
F	173	24	27	
H	1145	548	580	
W	11	5	7	
p				**< 0.0001**

There were significant differences in the visitation rate of butterflies between the inflorescence colours (Figure 18/B), nectar amount (Figure 18/D) and inflorescence type (Figure 18/A) of the plants. Violet and yellow flowers attracted the highest fraction of interactions. Plant species known to offer high nectar amounts tended to get more often visited by butterflies. Racemes and composite inflorescences seemed to be preferred by butterflies. Concerning the UV patterns on the flowers (Figure 18/B) the ANOVA revealed no significant difference (Table 8). However, even if statistically significant, all observed effects were weak, as evidenced by the very low R^2 values.

Table 8: Results (F- and p-values) of GLMMs and ANOVAs on the proportion of butterfly flower visits according to various floral types. Significant results ($p<0.05$) are printed in bold.

Trait	den.d.f.	F	p	R^2m	R^2c
Flower colour	344	3.03	**0.02**	0.03	0.03
Inflorescence	344	2.99	**0.02**	0.03	0.03
Nectar amount	344	4.16	**0.02**	0.02	0.02
UV patterns	344	2.73	0.10	0.01	0.01

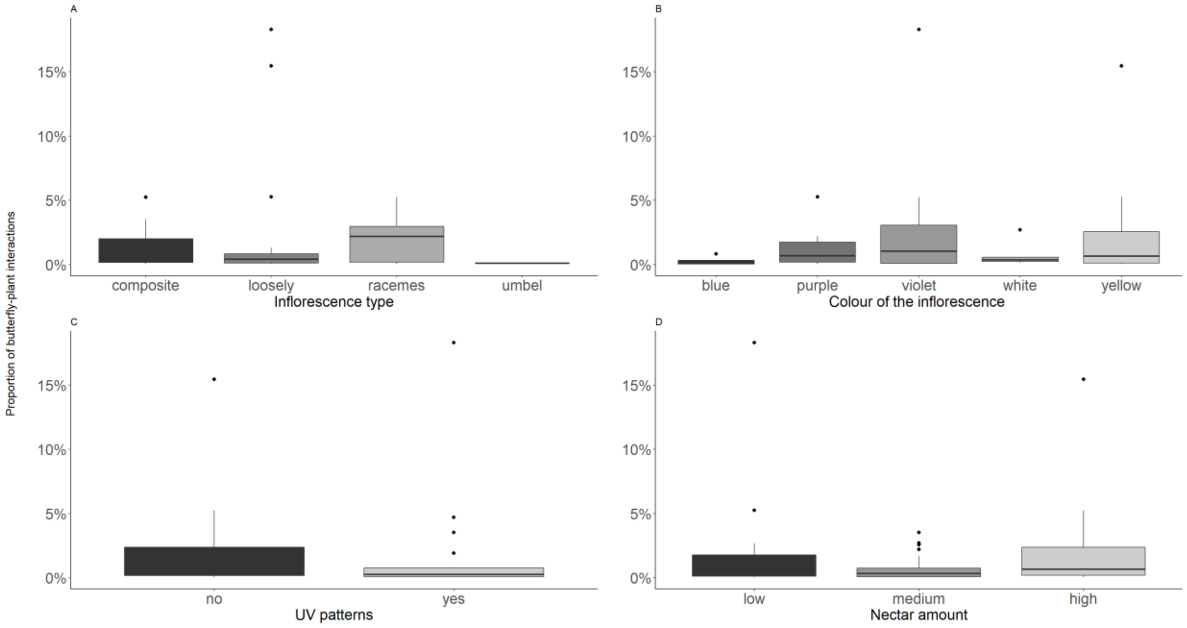


Figure 18: Proportions of butterfly visits to flowers per survey according to (A) inflorescence type, (B) colour of the inflorescence, (C) existence of UV patterns on the blossoms and (D) nectar amount.

Preferences on butterfly species level

For only four species of butterflies, I obtained sufficiently large numbers of observations allowing for a more detailed exploration of possible resource preferences and specializations across the three grassland types. The selection criteria were at least 70 observed interaction per month.

Polyommatus icarus

The common blue butterfly accounted for the largest fraction of all observed flower visits. *P. icarus* mostly visited *Ononis spinosa* and *Lotus corinculatus* (Table 9), which also serve as important larval host plants of that species. These butterflies visited 41 plant species in total. They occurred in all grassland types and on all 24 study plots.

Table 9: The five most often visited nectar plants of *Polyommatus icarus*. In total 1751 interactions were observed.

	Plant species	Interactions	Proportion
1	*Ononis spinosa*	399	23%
2	*Lotus corniculatus*	379	22%
3	*Centaurea stoebe*	113	6%
4	*Medicago falcata*	97	6%
5	*Eryngium campestre*	89	5%

Strength of this butterfly species in visitation networks generally increased from June to July, with but minor differences between the three grassland types (Figure 15, Table 6). Species strength was only slightly higher than in *C. pamphilus*. Network specialization d’ was similarly low as in *C. pamphilus*, but with less variation between sites, and did not reveal strong differences between months and land-use types, except in July between meadows and the Przewalski’s horse pasture (Figure 19). The factor month had a significant impact on species strength whereas specialisation was influenced by the land use type (Table 10).

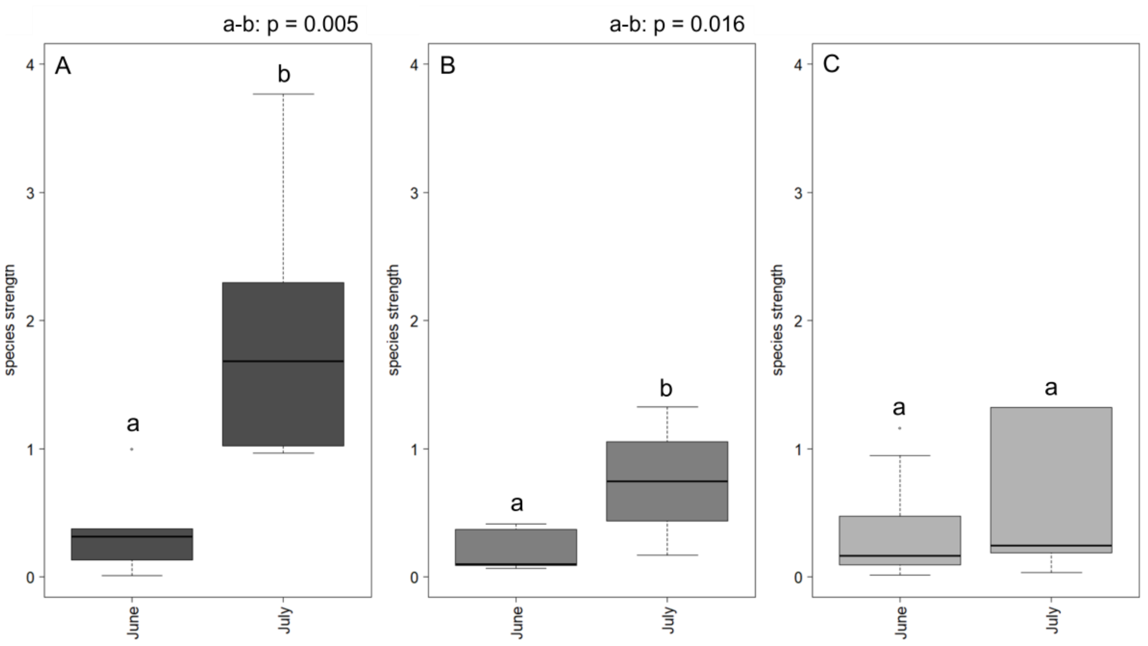


Figure 19: Boxplot showing species strength of *Polyommatus icarus* in flower visitor networks from June to July according to (A) Przewalski's horse pasture, (B) cattle pastures and (C) meadows. Small letters indicate significant differences ($p<0.05$) between the months using FDR correction.

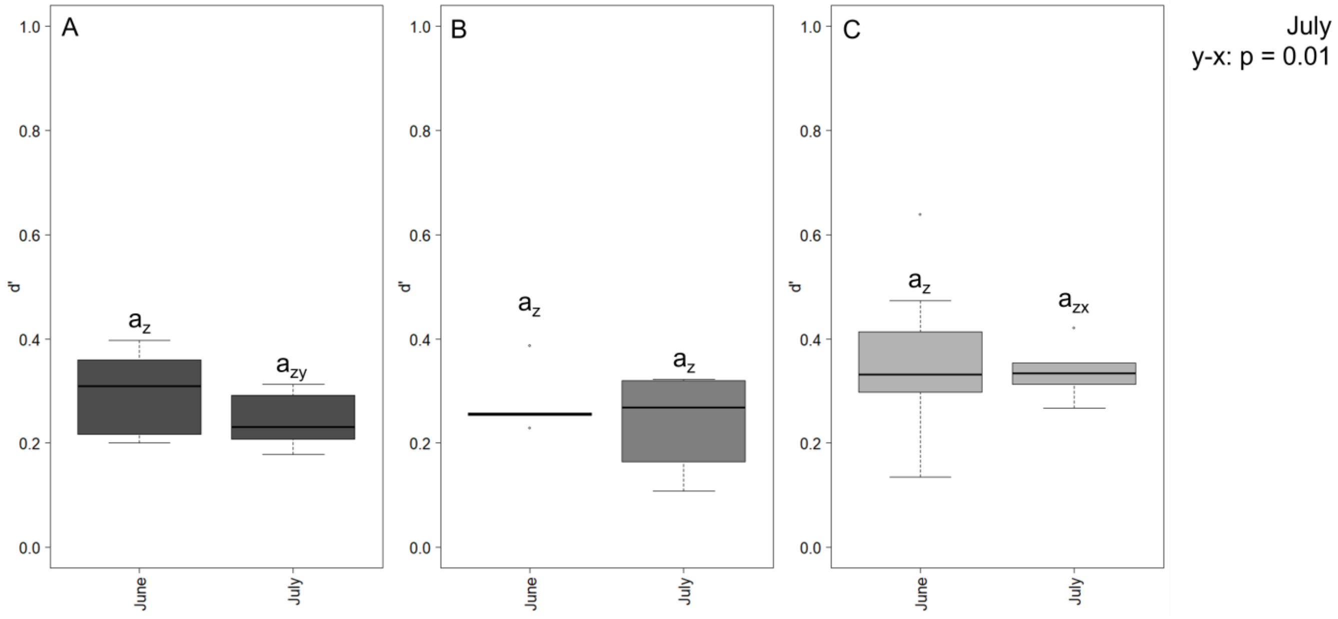


Figure 20: Boxplot showing the development of the index d' for *Polyommatus icarus* from June to July according to (A) Przewalski's horse pasture, (B) cattle pastures and (C) meadows. Small letters indicate significant differences ($p<0.05$) between the months using FDR correction. The subscripts indicate significant differences between the land use types within the months using FDR correction ($p<0.05$).

Table 10: Statistical results of two-factorial PERMANOVA of species strength and network specialisation d' for *Polyommatus icarus*. The used factors are land use type and month. Significant results ($p<0.05$) are printed in bold face.

species strength					
	Df	Sum of Squares	R²	F	p
Land type	2	3.33	0.09	2.49	0.071
Month	1	8.43	0.23	12.59	**0.001**
Land type:Month	2	1.62	0.04	1.21	0.310
Residual	34	22.77	0.63		
Total	39	36.16	1.00		

d'					
	Df	Sum of Squares	R^2	F	p
Land type	2	0.07	0.18	3.95	**0.028**
Month	1	0.01	0.03	1.20	0.280
Land type:Month	2	0.00	0.01	0.18	0.852
Residual	34	0.29	0.78		
Total	39	0.37	1.00		

The most frequently visited flower colours were yellow and violet. The remaining 10% were either purple or white, only a small fraction had blue inflorescences (Figure 25/B). Over 50% of the visited flowers have a corolla tube length of 6-10 mm, while about 30% of the visitations belonged to flowers with a short corolla, and 10 % had a medium long corolla (Figure 26/B). The distribution of visitation regarding nectar amount was similar to *C. pamphilus*: About 50% were flowers with high nectar, 40% little and the remaining 10% had moderate quantities (Figure 27/B).

Plebejus argus

The silver-studded blue butterfly was also relatively common as flower visitor. It occurred in all grassland types and was seen on 14 of 24 sites. The observations revealed *Medicago lupulina* as most visited nectar plant of *P. argus*, followed by *Lotus corniculatus* (Table 11). Again, both these preferred nectar plants also serve as important larval host plants. Overall, flower visitation patterns differed between the two syntopic and abundant Lycaenidae species *P. argus* and *P. icarus* (Table A31).

In total 338 interactions of *Plebejus argus* were observed with 31 different plants. 60% of the interactions occurred with yellow flowers, the remaining 40% were uniformly distributed among purple, violet, and white flowers. Blue blossoms only received a small fraction of visits (Figure 25/C).

Table 11: The five most visited nectar plants of *Plebejus argus*. In total, 338 interactions were observed.

	Plant species	Interactions	Proportion
1	*Medicago lupulina*	101	30%
2	*Lotus corniculatus*	60	18%
3	*Vicia cracca*	28	8%
4	*Achillea millefolium*	14	4%
5	*Galium verum*	13	4%

In *P. argus*, like in *P. icarus*, species strength as well as specialization in the networks tended to be higher in high than in early summer (Figure 21, Table 12). The category “medium” of the corolla tube length received about 10% of visits by *Plebejus argus.* The most frequently visited flower category was “short” with regard to corolla length, followed by the category “long” (Figure 26/C). Nearly 60% of the visitation went to blossoms with a high nectar amount. The remaining 40% were nearly evenly distributed on the other two categories.

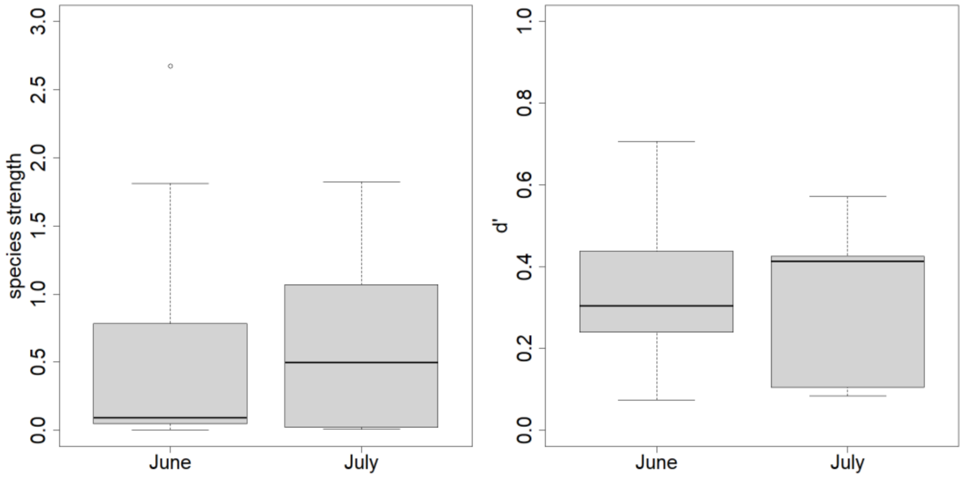


Figure 21: Boxplot showing the development of the index (A) species strength and (B) d’ for *Plebejus argus* from June to July regardless to the land use type.

Table 12: Statistical results of PERMANOVA of the index species strength and d’ for *Plebejus argus* with 999 permutations using the months June and July as grouping factor. Significant results with p<0.05 are printed in bold face. No differentiation between land use types is made.

	species strength						**d'**					
	Df	Sums of Sqs	Mean Sqs	F-Model	R2	Pr(>F)	Df	Sums of Sqs	Mean Sqs	F-Model	R2	Pr(>F)
Month	1	0.01	0.01	0.01	0.00	0.90	1	0.00	0.00	0.02	0.00	0.87
Residuals	17	11.70	0.69		1.00		17	0.56	0.03		1.00	
Total	18	11.70			1.00		18	0.57			1.00	

Coenonympha pamphilus

The small heath butterfly, *C. pamphilus,* occurred at all sites and was involved in 768 interactions with flowers of 38 plant species (Figure 10). *Thymus serpyllum* was the most frequently visited plant species (Table 13).

Table 13: The five nectar plant species most frequently visited by *Coenonympha pamphilus*. In total 768 interactions at 38 plant species were observed.

	Plant species	Interactions	Proportion
1	*Thymus serpyllum*	118	15%
2	*Lotus corniculatus*	81	10%
3	*Galium verum*	77	10%
4	*Dianthus carthusianorum*	56	7%
5	*Polygala comosa*	44	6%

Species strength of *C. pamphilus* in the networks tended to be higher in June than July and was particularly low on Przewalski’s horse pasture in July (Figure 22, Table 14). In contrast, specialization d’ of *C. pamphilus* in the networks did not vary according to month or land-use type (Figure 14, Table 14). Overall, specialization of this butterfly species was low compared to the other species. A two-factorial PERMANOVA revealed that the factor month had a significant impact on the species strength of *C. pamphilus*. No significant impact was found for its network specialisation.

It is worth noting that *Coenonympha pamphilus* was the only butterfly which was observed serval times visiting inflorescences of the anemophilic plant *Plantago lanceolata*.

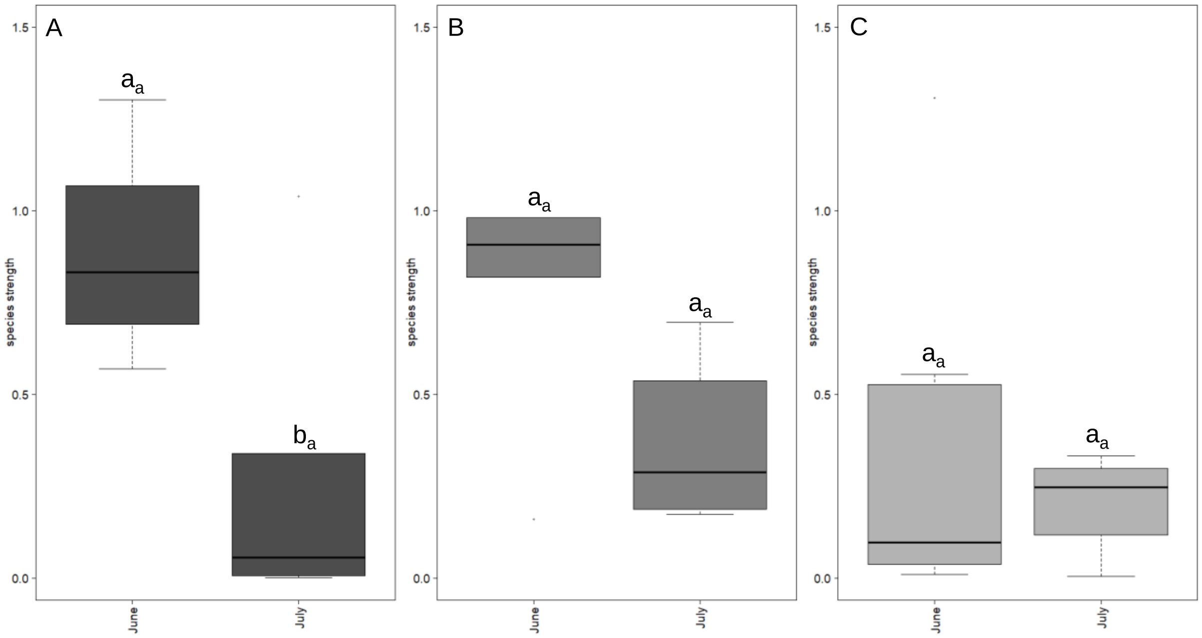


Figure 22: Boxplot showing the species strength of *Coenonympha pamphilus* in flower networks from June to July according to (A) Przewalski's horse pasture, (B) cattle pastures and (C) meadows. Small letters indicate significant differences ($p<0.05$) between the months using FDR correction. The subscripts indicate significant differences between the land use types within the months using FDR correction ($p<0.05$).

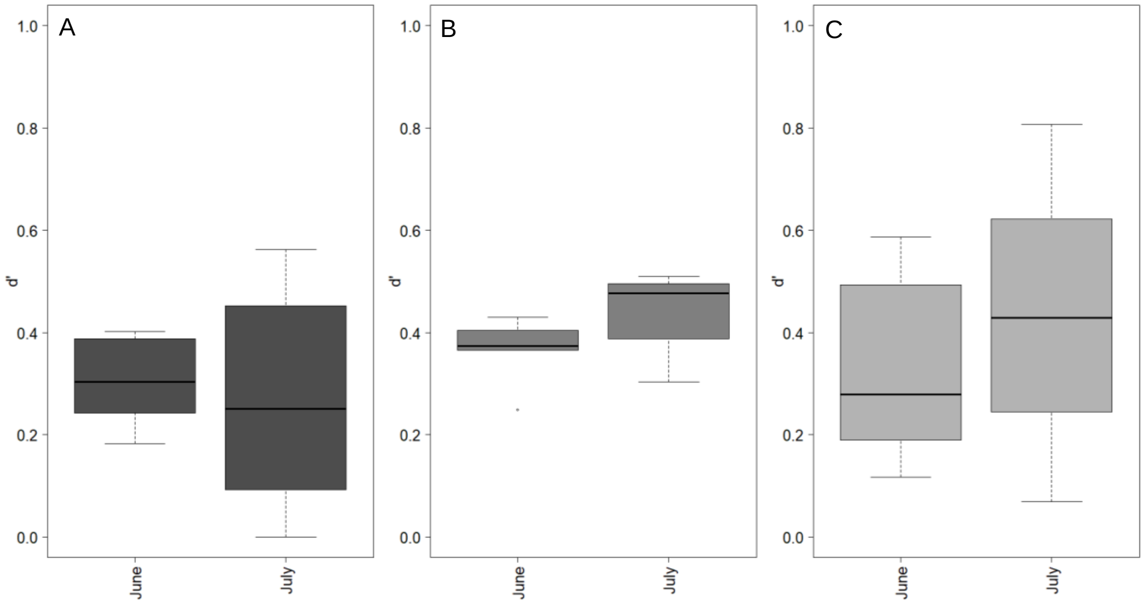


Figure 23: Boxplot showing the specialization d' of *Coenonympha pamphilus* in flower networks from June to July according to (A) Przewalski's horse pasture, (B) cattle pastures and (C) meadows.

Table 14: Statistical results of two-factorial PERMANOVA of species strength and species strength and network specialisation d' for *Coenonympha pamphilus*. The used factors are land use type and month. Significant results ($p<0.05$) are printed in bold face.

species strength					
	Df	Sum of Squares	R^2	F	p
Land type	2	1.37	0.17	4.62	0.015
Month	1	1.53	0.19	10.27	**0.004**
Land type:Month	2	0.55	0.07	1.86	0.175
Residual	32	4.76	0.58		
Total	37	8.22	1.00		

d'					
	Df	Sum of Squares	R^2	F	p
Land type	2	0.07	0.07	1.26	0.30
Month	1	0.02	0.02	0.62	0.44
Land type:Month	2	0.03	0.03	0.56	0.57
Residual	32	0.90	0.88		
Total	37	1.01	1.00		

Figure 25/A reveals that the most often visited blossom colour was yellow, closely followed by violet, while purple, white and blue flowers attracted few *C. pamphilus* butterflies. About 55% of the visited flowers had short corolla tubes. The observed visitations for blossoms with a corolla longer than 10 mm are about 30%. The remaining 10% are among the medium long tubes (Figure 26/A). About 50% of the visited flowers had a high nectar amount, nearly 40% had little nectar. This pattern is similar to *Polyommatus icarus* (Figure 27/A).

Melanargia galathea

Finally, the marbled white butterfly was a common component of the flower visitor networks. This species occurred only at the Przewalski’s horse pasture and the cattle pastures. There it was seen on 10 of 12 sites.

Ononis spinosa was by far the most frequently visited nectar plant of *Melanargia galathea*. Compared to *Ononis spinosa, Inula salicina* was over 20% less frequently visited, followed by *Centaurea stoebe* (Table 15).

Table 15: The five most frequently visited nectar plants of *Melanargia galathea*. In total 492 interactions were observed.

	Plant species	Interactions	Proportion
1	*Ononis spinosa*	192	39%
2	*Inula salicina*	81	16%
3	*Centaurea stoebe*	68	14%
4	*Trifolium pratense*	43	9%
5	*Galium verum*	32	7%

Species strength did not differ between surveys in June and July, whereas network specialization d’ clearly decreased with the progress of summer (Figure 24, Table 16).

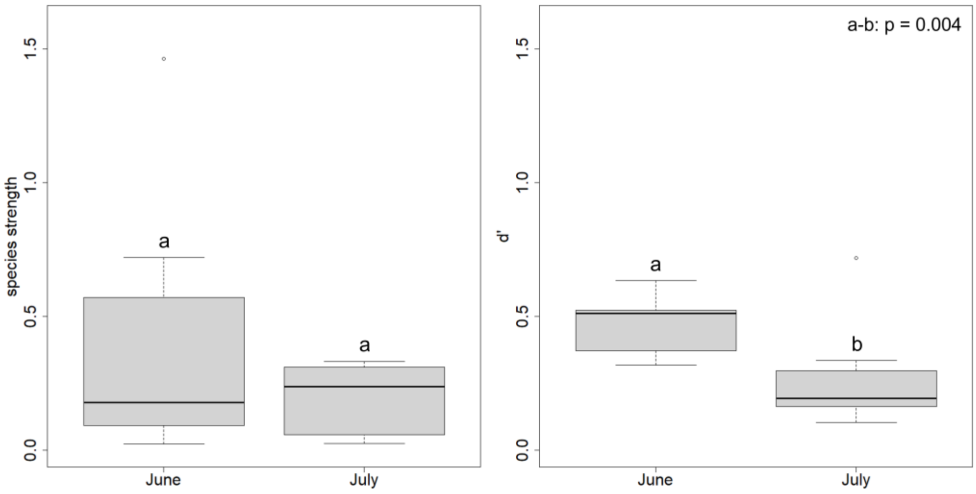


Figure 24: Boxplot showing the development of the index (A) species strength and (B) d' for *Melanargia galathea* from June to July regardless to the land use type. Small letters indicate significant differences ($p<0.05$).

About 50% of the visited plants had violet blossoms, followed by yellow with a total amount of about 30% of all visited inflorescences (Figure 25/D). The most often visited corolla length type with over 50% of the total number of all interactions belonged to the category "long" (Figure 26/C). 50% of the visitation went to flowers with low nectar amount. The other half is evenly distributed on the two other categories (Figure 27/C).

Table 16: Statistical results of PERMANOVA of the index species strength and d' for *Melanargia galathea* with 999 permutations using the months June and July as grouping factor. Significant results with $p<0.05$ are printed in bold face. No differentiation between land use types is made.

	species strength							**d'**					
	Df	Sums of Sqs	Mean Sqs	F-Model	R2	Pr(>F)		Df	Sums of Sqs	Mean Sqs	F-Model	R2	Pr(>F)
Month	1	0	0.12	0.95	0.06	0.41		1	0	0.18	7.31	0.33	**0.03**
Residuals	15	2	0.13		0.94			15	0	0.02		0.67	
Total	16	2			1.00			16	1			1.00	

Comparison

Figure 25 shows that there were slightly different preferences regarding the blossom colour of the four most observed butterfly species. For *C. pamphilus, P. icarus* and *P. argus* yellow was the most visited floral colour followed by violet. *M. galathea* provided an exception as most interactions were observed with violet flowers. *M. galathea* butterflies were also never observed visiting a white or blue flower. Although white was quite seldom visited by *P. icarus* as well, *C. pamphilus* and *P. argus* were observed comparatively quite frequently with white blossoms. *P. icarus* and *M. galathea* showed a preference for corolla tubes longer than 10 mm, whereas *C. pamphilus* and *P. argus* seemed to prefer short corolla tubes. All four species have in common that medium long corolla tubes were the rarest to be visited. In regard to the nectar amount, *C. pamphilus, P. icarus* and *P. argus* tended to preferentially visit plants with a high nectar amount, whereas surprisingly *M. galathea* showed a preference for flowers with little nectar supply.

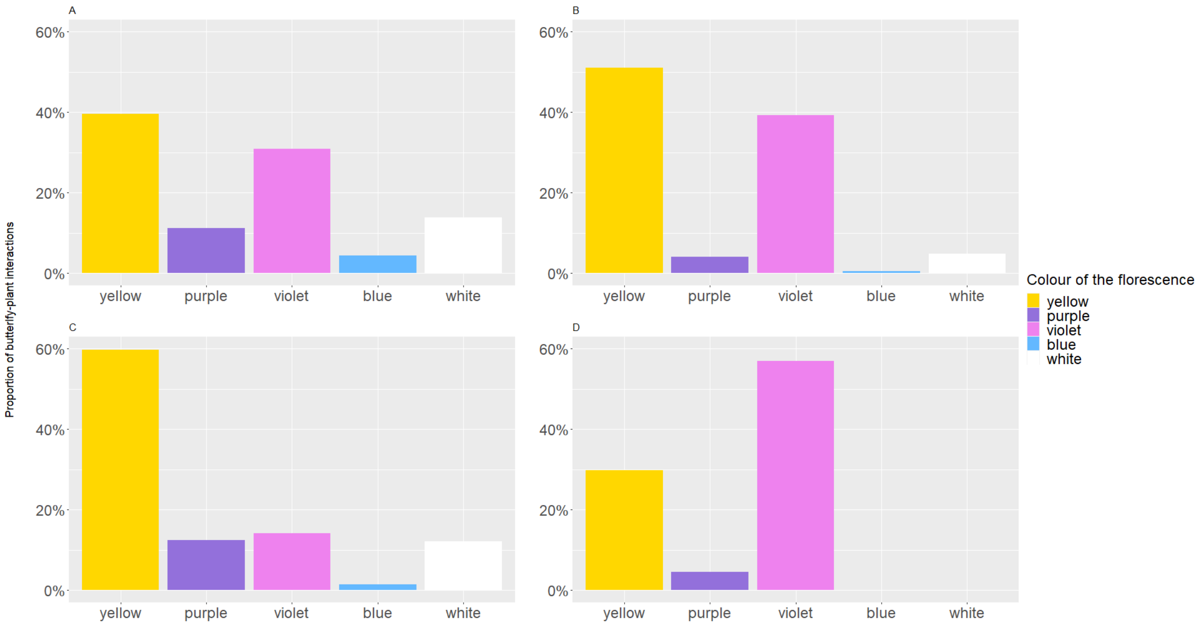


Figure 25: Histogram showing the relative proportions of visited florescence according to their colours of (A) *Coenonympha pamphilus* (n_{total} = 768), (B) *Polyommatus icarus* (n_{total} = 1751), (C) *Plebejus argus* (n_{total} = 338) and (D) *Melanargia galathea* (n_{total} = 492)

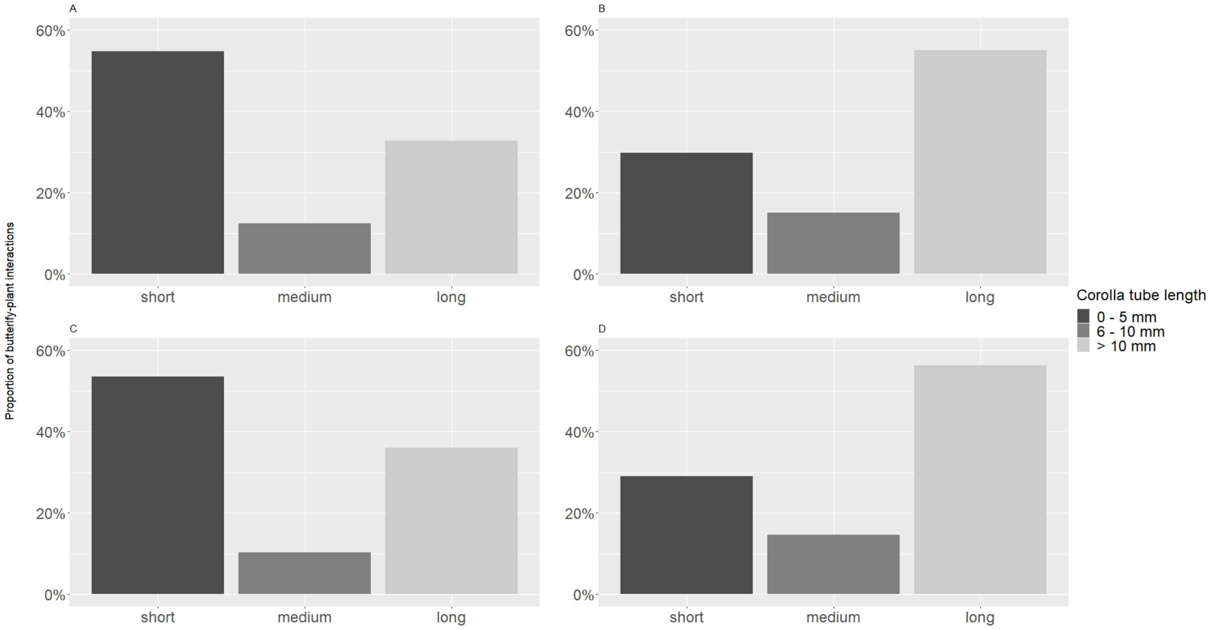


Figure 26: Histogram showing the fraction of visitations according to the corolla tube lengths of visited plants of (A) *Coenonympha pamphilus* (n_{total} = 768), (B) *Polyommatus icarus* (n_{total} = 1751), (C) *Plebejus argus* (n_{total} = 338) and (D) *Melanargia galathea* (n_{total} = 492).

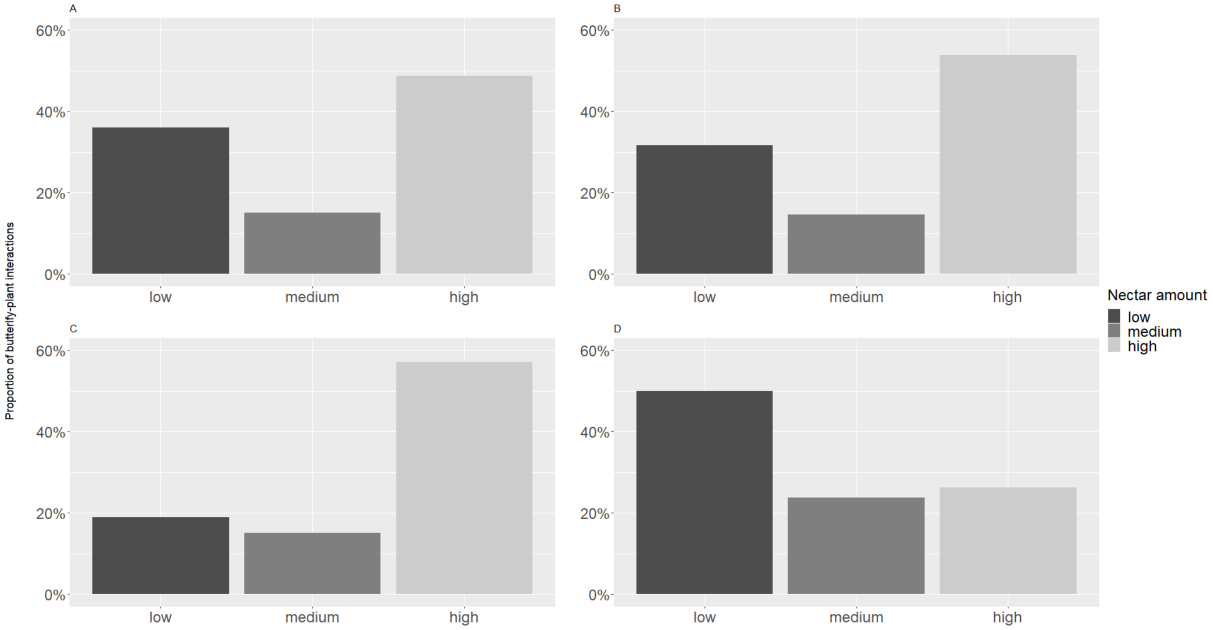


Figure 27: Histogram showing the fraction of visitations according to nectar amount of visited plants of (A) *Coenonympha pamphilus* (n_{total} = 768), (B) *Polyommatus icarus* (n_{total} = 1751), (C) *Plebejus argus* (n_{total} = 338) and (D) *Melanargia galathea* (n_{total} = 492).

Discussion

i. Is the average abundance of a certain species reflected by its interaction frequency?

Overall, the abundance of a butterfly species at the landscape scale was mirrored by its flower interaction frequency in 2021. However, some species deviated substantially from this pattern, like *Maniola jurtina*. Although the Meadow Brown butterfly is still very common in the western Palaearctic and also in grassland habitats in the NP Neusiedler See - Seewinkel, it was underrepresented in this study. This might be explained by its ecology: As a strictly univoltine species, it is adapted to use the resources of its habitat optimally (Danks, 2006; Kostál, 2006). One strategy to bypass reduced availability of larval host plants for oviposition in hot and dry periods is summer dormancy. This means that especially the females perform an aestivation until autumn when rainfall brings back the growth of grasses, which are the larval host plants (Grill et al., 2013). During aestivation, *Maniola* butterflies usually hide in the shade of hedgerows or trees during daytime and only briefly forage for nectar in late afternoon hours. Therefore, *Maniola jurtina* might have largely been dormant during my sampling period due to the weather conditions which has led to its underrepresentation in the pollination networks. Although population from Centra or Northern Europe normally do not show this behaviour, it had been shown that populations of the study region also react with summer dormancy. However, dormancy is photoperiodically induced in this butterfly species. As drought does not alter day length, it seems unlikely that lack of rainfall alone can induce summer dormancy in *Maniola jurtina* (Haeler et al., 2014). Though, it is still unclear how the ability of summer dormancy is regulated as Mediterranean and Central European population are genetically nearly not distinguishable (Grill et al., 2013). Further studies are needed to examine these questions.

Polyommatus icarus was by far more often observed in interactions with flowers in the summer 2021 than its average abundance over the years would have indicated. An explanation might be that both species use some of their larval host plants also as a nectar resource. Most of the female butterflies have to deal with the possible conflict to fulfil their nutritional demands as adults, which can be done by searching and visiting appropriate nectar plants or the search and the evaluation of oviposition sites. These needs are not often provided by the same plant species. Therefore, for female butterflies a trade-off arises: The time which is used for the search of nectar sources happens at the expense of the exploration of larval host plants. Hence, strategies have evolved to bypass this conflict. One example is *P. icarus*, which obtain food and larval hosts from the same plant species. It was shown that *P. icarus* preferred *L. corniculatus* with open flowers for nectaring for oviposition over plants with no flowers (Janz, 2005). Therefore, *P. icarus* is able to search for host plants and simultaneously keep a high nutritional state. The reduced search time seems to be a greater advantage than the drawback that this strategy is a compromise as the nutritional demands of the adults might be prioritized and not its properties as larval host (Janz, 2005). However, this efficiency in time could lead to the increased interaction frequency as the females do not have to additionally search for oviposition plants. Male butterflies might use the larval host plants for the search for females. This can explain why also males were seen primarily with an interaction with a larval host plant. According to my observations *L. corniculatus, Ononis spinosa* and *Medicago falcata* served as important nectar plants, which are also documented larval host plants (Ebert et al., 1993). The same applied also to *Plebejus argus:* For the silver-studded blue butterfly *Medicago lupulina*, followed by *Lotus corniculatues*, were the most important nectar plants which are also important larval host plants of this species (Ebert et al., 1993; Pendl et al., 2013). This might be an explanation of the overall high visitation rate of *L. corniculatus* since *P. icarus* as well *P. argus* utilize *L. corniculatus* as both, nectar plant and larval host plant. Though *Securigera varia* is also a known larval host plant for these two lycaenid species, no interaction was observed. Nevertheless, it should be noted, that *Securigera varia* was comparatively rarely in flower during my observation period. *Medicago lupulina* received only 4% of the total visitations of *P. icarus*. This plant was common on my study sites and is considered to be an important larval host plant of *P. icarus* but compared to *Ononis spinosa* (23%) it was rather rarely visited, even though *M. lupulina* gives a higher nectar reward than *O. spinosa*. Though*, O. spinosa* was more abundant than *M. lupulina*. Therefore, it seems that another important factor of the choice of visitation is the abundance of the plant. In general, my data shows that the abundance of the plants on the sites is mirrored by their visitation rates, which accords with Weiner et al. (2011).

Vicia cracca was among the plants which were less often visited by butterflies than expected from its floral abundance. Dennis (2010), studying British butterflies, also showed that *V. cracca* was visited by far fewer butterfly species than expected. *V. cracca* is often used as a nectar source by bumble bees. Short-tongued bumble bees are known to rob nectar by biting holes in the corolla of longer-tubed flower. For example, for *Bombus terrestis* it is documented that over 85% of visitations of *Viccia faba* in Chile were nectar robbery (Smith et al., 2021). This kind of nectar collecting leads to permanent floral damage. Additionally to the primary robbery, the resulting hole in the corolla enable others to steal nectar as well (Willmer, 2011). As it is known that *Bombus terrestris* tends to often steal nectar from *V. cracca* this way (Newton & Hill, 1983), visiting *V. cracca* might not be so profitable for butterflies as the nectar has often already been robbed.

Centaurea stoebe also got high visitation rates. This coincides with the findings of Jennersten (1984) at the closely related *C. jacea*. Although *Thymus serpyllum* is a recorded host plant and nectar plant (Wiklund, 1984; Brommer & Fred, 1999*)*, it was less often visited in this dataset than its abundance was suggesting. Though, of the 27 observed butterfly species only *Zygaena minos/purpuralis* feed on *T. serpyllum.* Additionally, *T. serpyllum* was only very abundant at some plots in June. As the mean floral abundance was used in my analyses, this could lead to the biased picture of reduced visitation. *Galium verum* was also less often visited than expected from its floral abundance, but it was still the third most often visited plant. This stands in strong contrast to the findings of Jennersten (1984), who reported *G. verum* as a common flower, which was never visited by any butterflies. One explanation might be that the drought had reduced the overall flower quality and quantity, therefore the butterflies were forced to use resources which will not be utilized during normal conditions.

Apart from the already discussed plants, *Dianthus carthusianorum* and *Trifolium pratense* were also important plants in the observed networks. Both are known to be often visited nectar plants (Willmer, 2011; Lebeau et al., 2017).

Although 27 butterfly species and 59 plant species were observed during interactions, only 30% of the butterfly species and 15% of the plant species accounted for most of the 4160 observed interactions. This pattern complies with Zografou et al. (2020) who analysed butterfly-plant networks over eleven years from five grassland sites in southwestern Pennsylvania. Only a few species built up most of the observed networks. Compared with the butterfly observation data collated in Illmitz over 15 years, a high proportion (53%) of these species was never observed during a flower interaction in the summer 2021. This can be explained by several reasons: First of all, the species which were not observed during an interaction in 2021 were generally relatively rare in the study region. Therefore, it is not surprising that the sampling time might have been insufficient to observe flower visits of these species. Furthermore, the month of June 2021 was a severe exception in regard to precipitation. Some of the missing species might have experienced difficulties to deal with these extreme weather conditions which lead to decimated numbers of individuals. *Aglais io Cupido argiades* and *Zygaena transalpina* were species which were observed over 100 times during the 15 years of observations. However, those species were never observed within an interaction 2021. Though, most of the observations of the peacock butterfly were made in 2007 and 2012, the other years this species was also mostly not seen. It is surprising that *Cupido argiades* was also almost not counted the previous year 2021, as the species is known to increase its frequency (Landeck et al, 2013). However, the missing of these two species might be due to the natural fluctuations of abundance which most species are subject to (Zografou, 2012). *Zygaena transalpina* is similar in its appearance to *Z. filipendulae* and therefore my data might be biased because of inaccuracy in species determination.

Nevertheless, it should not be concluded that only a few species are important in the networks. The others might not play a prominent direct role in the networks, but their existence could have an indirect impact on network. As mentioned before, pollination as ecosystem service is of great interest. An increasing number of studies suggest a link between higher biodiversity and more effective pollination services (Blitzer et al., 2016; Hölzler, 2008; Vergara & Badano, 2009). Blitzer et al. (2016) observed a relationship between increased biodiversity and pollination services of bees. A higher functional diversity in bees led to higher seed sets in apple orchards, although 50% of the collected bee individuals were just honeybees. One explanation for this relationship are functional traits of the species: More diverse pollinator communities comprise species with different body sizes or levels of sociality, contributing to niche partitioning which can provide more pollination service (Hölzler, 2008). Another line of evidence is that some members of a network might improve the effectiveness of the others (Cardinale et al., 2002). Greenleaf and Kremen (2006) supported this idea with their study about pollination efficiency in hybrid sunflowers. Although 72% of the observed visitations were by honeybees, it was shown that honeybee pollination increased with wild bee richness. Diversity can also be seen as an insurance (Valone & Barber, 2008). At one moment an abundant species might dominate in flower interactions, but if populations of this species are somehow affected, e.g. by climate change or other disturbances, the other co-occurring species might step in. Although it seems that most butterfly species did not play an important role in the insect-flower networks that I observed, this might not directly apply for the ecosystem service of pollination. For example, some butterflies may act as nectar thieves rather than legitimate pollinators (Jennersten, 1984). Moreover, the aforementioned studies are mainly about Hymenoptera, especially bees. These are known to feed primarily on nectar and pollen, even in their larval stages. This is an exception in the world of insects, as many flower-visiting insects feed on these resources as adults, but not as larvae. Therefore, the demand of bees for nectar and pollen is enhanced as they rely heavily on floral resources (Goulson, 2010).

ii. *Are there differences in network indices and structures between early and high summer, and are these patterns influenced by the land use?*

It has been shown that in temperate grasslands, mowing or grazing lead to higher diversity of plant species than abandonment or intense management (Hannappel & Fischer, 2020; Habel et al., 2019). However, it is also well known that too high land use intensity can lead to a loss of biodiversity (Socher et al., 2013; Allan et al., 2014; Blüthgen et al., 2014). Therefore, the use of traditional agricultural methods as tool in conservation management should be used carefully. The highest plant species diversity involved in flower visitor networks during my study in the National Park Neusiedler See - Seewinkel was found on the meadows, followed by the pastures grazed by cattle. As most of the time only 13 horses grazed on 69.5 ha in the 'Seevorgelände' in 2021, this might indicate too low grazing intensity. Ecological successions at later stages, when scrubs and trees start to grow, have generally a negative effect on butterfly diversity (Balmer & Erhardt, 2000). My results support these findings partly: Meadows showed the highest species diversity of flower-visiting butterflies. Even though the pastures with ranging cattle had a higher plant diversity, butterfly diversity was still slightly higher at the Przewalski's horse pasture. Jennersten (1984) showed, that under normal weather conditions the peak of butterfly species diversity among North European butterflies occurs in July. Zografou et al. (2020) confirmed a peak of plant and butterfly species in late summer, viz. July and August. However, this did not occur in my study. Rather, the species accumulation curves revealed a significant decrease of species diversity from June to July. This could be explained by the massive summer drought in 2021, as drought is known to reduce the species diversity of plants and butterflies (Gao et al., 2009; Forister et al., 2018). There is a positive correlation of flower supply and visitation rate. The much tighter correlation in July might indicate a bottleneck of nectar resources due to the drought.

Although, species diversity is linked to higher aboveground productivity (Isbell & Wilsey, 2011), the more important tool to promote grassland resistance and resilience after a drought is a low mowing frequency (Vogel et al., 2012). This should be taken into account considering nature conservation management, as droughts may occur more often in future (Grillakis, 2019). While the species diversity was significantly different between the months and the land use types, these differences were not reflected by network specialisation. H2 was unable to characterise the differences of the butterfly biocenosis in the study area well, whereas the calculated species diversity did illustrate the existing variations. Although network specialisation may give insights about the analysed network, the information might be impractical in the light of nature conservation. Overall, the factor month had a significant impact on network specialisation. However, the hypothesis that along with reduced flower availability network specialisation would increase could not be supported. At the Przewalski's horse pasture, there was even a significant decrease of network specialisation observable. This stands in contrast to results of other studies indicating that drought leads to higher network specialisation (Souza et al., 2018; Balmaki et al., 2022). As fire in grasslands may be somewhat comparable in its impacts to an extreme form of a drought, the findings of Da Silva Goldas et al. (2022) might help to interpret my results. This study looked at plant-pollinator networks after a fire for a period of two years.

Their results indicate a high stability of the network, with an overall ability of the plants and pollinators to adjust after such a severe disturbance. It is suggested this is due the ability of plants and pollinators to switch partners. My results showed a low specialisation of the key players within the networks, especially among the plants. Additionally, my data revealed a mean network specialisation of 0.45, which is similar to a freshly burnt grassland (Da Silva Goldas et al., 2022). However, more data, especially in a year without drought, is needed to examine the impact of these extreme weather conditions more precisely.

I assume mowing to be a single disturbance event, where the whole flower supply vanishes at one time, whereas grazing is a continuous and spatially heterogeneous process. Due to their low numbers, the grazing intensity of the Przewalski horses was far lower than on the pastures with cattle. However, it should be noted that the cattle were not fenced, therefore grazing pressure was also reduced as they can move more freely. Therefore, I assume the meadows experienced the highest land use intensity, followed by the cattle pastures. Weiner et al. (2011) analysed 40 grasslands in Germany, which were either managed at low or high intensity. They observed a higher flower specialisation of butterflies at the low intensity meadows. Although in this study the land use type had a significant impact on network specialisation, higher land use intensity did not result in lower network specialisation. Although my study plots varied in land use intensity, differences might have been too small to detect a decrease in network specialisation. However, an analysis of 119 grasslands with varying management regimes also revealed no consistent relation of land use and network specialisation (Weiner et al., 2014). Therefore, the link between land use intensity and flower visitor network specialisation needs to be further examined.

An 11-year study in Pennsylvania, USA revealed the highest network specialisation to occur in September, assuming the reduced flower availability led to an apparent specialisation (Zografou et al., 2020). However, in this present study overall flower supply only decreased at the meadows significantly in July, and the land type did not have a significant impact on flower supply, only the month. The meadows were mowed in the middle of June, this was mirrored by the lower flower supply. Too little water can reduce plant growth, therefore the drought slowed down the process of regrowth and minimized the flower supply later on. Moreover, drought is known to not only alter the quantity of flower supply, but also its quality (Wyatt, 1992). Therefore, even if there was no significant difference in counted inflorescences, the quality of the flower nectar supply might have decreased. However, no correlation of network specialisation and flower supply was detected. H2 is either not influenced by provided floral resources or the scoring of flower supply in the field was too coarse to detect possible correlations.

Overall, network vulnerability decreased from June to July. Vulnerability is a description for how diverse the sets of pollinators for the plants are. As there were significantly fewer butterfly species on the wing in July than in June, the observed decrease of vulnerability is not surprising. Power et al. (2011) found out, that the network structure of dairy farm pastures in Britain was altered by agricultural methods. Organically managed farms, which are considered as less intensely managed than conventionally ones, tended to show a higher network vulnerability. This trend of lower land use intensity and higher vulnerability corresponds with my results: The Przewalski's horse pasture had a significantly higher vulnerability in June as well as in July compared to the meadows. This is especially interesting considering the significantly lower species diversity at the Przewalski's horse pasture.

Hardy et al. (2007) accumulated a nectar database with over 10 000 nectar feeding records of butterflies on the British Isles. They calculated for each species a score of relative nectar feeding specialism. This was obtained as residuals from a regression of the availability of nectar sources relative to the observed nectaring records. According to this score *P. argus*, *P. icarus* and *C. pamphilus* are feeding generalists (positive residuals) while *M. galathea* is a feeding specialist (negative residual). My results partly confirm this assertion: With an average specialisation d' on under 0.5 *P. argus*, *P. icarus* and *C. pamphilus* can be considered as flower generalists. However, *M. galathea* did not show a higher specialisation during my observations. Therefore, according to my results, all four species should be considered as generalists. The minor discrepancies might be explained by the different geographical locations, weather conditions, different mode of calculation, or insufficient data sampling.

Only in *M. galathea* I observed a significant shift in flower specialization between June and July. An explanation could be that the Marbled White is the only univoltine species of the four more detailed analysed species. One explanation might be as there are quite long long-living (Pendl et al., 2013) and there was a compositional turnover of plants within a relatively short time, *M. galathea* might be adapted to changing nectar sources.

Species strength in the networks only varied between the months, but the land use type had no impact. Although the identity and the frequency of the visited plants changed, the overall dependency of plants on certain butterfly species did not change profoundly. Species strength was generally low and did not differ profoundly between the species. This could indicate that butterflies were not that important as pollinators, as these low values imply low dependence of plants. The role of butterflies within the plant-pollinator network is debatable. On the one hand there is evidences that butterflies mainly act as nectar robbers because they mostly do not carry enough pollen to ensure a successful pollination (Morse, 1982; Lazri & Barrows, 1984). As visitation does not inevitably imply pollination (Ne'eman et al., 2010), it may be invalid to infer pollination services from network metrics. On the other hand, some butterflies are important players within plant-pollinator networks (Murphy, 1984; Bloch et al., 2006). However, in order to explore pollinator performance, the visitation frequency, the pollen load and pollen deposition have to be observed (Dafni et al., 2005).

iii. Does the role of individual species vary between months or land use types?

The butterfly species with the most flower visits remained more stable over land use and month than the highly ranked plants, which varied more between the land use types. As the flower interaction frequency was correlated with the abundance of a plant and plants react differently to land use intensities, it is not surprising that there were differences between the visited plant families as well. For example, *O. spinosa*, which was an important partner at the pastures, did not play an important role at the meadows. *O. spinosa* is protected against grazing through its spines and therefore thrives on pastures, especially at the Przewalski's horse pasture with its low grazing intensity. However, it is sensitive to mowing and therefore almost never occurred at the meadows (Licht, 2022). As plants are sessile, the land use intensity has a direct effect on them, whereas butterflies are mobile and therefore mowing or grazing have more indirect influence, by changing the plant communities. However, the differences between the land use types in visited plant families were not pronounced. This is unexpected as it is shown that these different management regimes differ in species compositions (Fiedler et al., 2016). One explanation might be that the search for preferred nectar sources was not restricted by natural barriers like hills or a forest. As the butterflies are quite mobile, the differences in plant species compositions might be too small scaled. This suggests that the identity of adult nectar resources do not shape the butterfly-plant visitations profoundly. It seems that the quantity of floral resources and their accessibility is more important than the identity. This is emphasized by the high number of documented nectar plants per butterfly species, which draws a picture of a high generalism regarding nectar plants. Though, my data suggest the existence of preferences for certain plant traits. This stands in contrast to other insects which use floral resources much more specialised, e.g., bees. There are estimations that a third of all bee species are monolectic or oligolectic in regard to pollen (Bogusch et al., 2020). From a nature conservation point of view, it seems that in order to support butterfly species, the amount of nectar plants is important, but not the identity of the plant species. Whereas for bees, e.g., the species composition of the pollen resources is a crucial factor if the bee species can occur. For butterflies, the identity of plants plays an important role only for the larvae, as they are much more specific regarding their host plants (Dennis, 2010). This may be the main driver of different butterfly assemblages to be observed at different grassland management types in my study region, despite the lack of pronounced barriers in the landscape (Fiedler et al., 2017).

Plebejus argus was only infrequently observed at the Przewalski's horse pasture. Further *P. argus* is an obligate myrmecophilous species with only *Lasius niger* or *Lasius alienus* ants as partners (Seymour et al., 2003; Jordano & Thomas; 1992). Silver-studded blue butterflies need these ant species for their reproductive success, but the Przewalski's horse pasture seems to be too overgrown for ants, which might led to fewer sightings.

iv. Are the numbers of butterfly visitors influenced by certain traits of the plants?

The most visited plant family in all three cases was Fabaceae, at the cattle pasture Lamiaceae was second most visited. At the Przewalski's horse pasture and the meadows, this rank was taken by Asteraceae instead. These results are similar to those reported by Dennis (2010). However, it is to question if plant families are a useful level for analysing flower visitation rates. Unrelated plants which share similar pollinators often have similar morphological features and reward patterns (Baker et al., 1972). This has led to the – debated – concept of pollinator syndromes, which groups plants according to their traits instead of their phylogenetic relationships. According to the pollination's syndrome concept, butterfly-pollinated flowers have the following traits in common: They are mainly red, orange or yellow in colour, the inflorescences are shaped to provide a sufficient landing platform and the nectar sites are usually concealed. The individual flowers are often small, long tubed and slightly scented (Willmer, 2011). However, my observational data does not corroborate this classification. Rather, so-called 'Lepidoptera flowers' only received a minor fraction of observed visitations. This coincides with the overall sceptical discussion whether classification of flowers into pollination syndromes is really fruitful (Ollerton et al., 2009; Willmer, 2011; Johnson & Steiner, 2000).

Although pollination syndromes did not predict observed flower visitation patterns well, a look at individual plant species traits provided better explanations for apparent preferences. Floral colour is known to be an advertising signal and animals capable of colour vision may evolve colour preferences. Butterflies are known to learn associations with a colour due to rewards. Favoured floral colours are red, pink, purple and yellow (Willmer, 2011). This corresponds with my results, except of red. Though no plant flowered red, hence no visitation could be made. This is not surprising, since there are nearly no red flowering plants in Central Europe.

The differences between the land use type especially regarding violet are related to *Onois spinosa*, which was only abundant at the pastures. In contrast to results reported by Jennersten (1984) and Tiple et al. (2005) blue flowers did not receive many visitations. Though, throughout the study region only a small fraction of plants flowered blue, therefore the low sighting rate might be due to the lack of blue flowers rather than a lack of preference. However, colour choice in butterflies seem to vary strongly, even within a species (Weiss, 2001). Additionally, there are many factors which influence the effect of floral colours. Not only the colour of the background plays a role, also the age of the inflorescence or the number and intensity of other signals can have an impact (Dafni et al., 2005). As a result, discrepancies between studies can occur. Although UV patterns have been found to be important in plant-pollinator interactions (Dafni et al., 2005), the existence of UV patterns on the flowers had no detectable influence on visitation rates during my observations.

Floral colour and UV patterns work as attractors, like an advertisement, but nectar is a nutritious reward offered by flowering plants for pollination. Nectar is often the main reason for an animal visiting a flower. Nevertheless it is worth mentioning that there are other rewards as well, like the provision of breeding sites (Sakai, 2002). Therefore, it is not surprising that nectar is a crucial factor shaping plant-pollinator interactions (Willmer, 2011; Schmidt-Lebuhn et al., 2007). My results suggest a trend, whereby flowers with putatively high nectar reward receive more visitors. However, nectar quality much more complex than the literature-based classification into low, medium and high reward may indicate. Not only the volume per flower is crucial, but also the chemical composition of the sugars, amino acids, and other components. Additionally, the actual nutrient concentration and viscosity are also important (Dafni et al., 2005; Willmer, 2011). To receive a complete picture of the influence of nectar on the observed plant-butterfly networks, all these parameters should be included. This lack of information in the statistical analyses might explain the weakness of observed links between nectar amount and visitation rate. Nevertheless, as nectar is the primary energy source of butterflies, flower selection should aim to maximise the net energy gain. The number of flowers exploited per time unit depends on handling time and time to get to a new inflorescence. As flying costs more energy than walking, plants which have densely crowded flowers should be preferred by butterflies (Corbet, 2000). I found a weak effect of the inflorescence type, with a trend of composite inflorescences and racemes preferred by butterflies. Although my results suggest a difference in preference between the butterflies, an important factor is not taken into account: The energetic cost of flying for each species. It has been shown that the energy demand increases with mass per unit of wing area, also known as wing load (Heinrich, 1993). Corbet (2000) observed that butterfly species which have a high wing loading tend to feed on massed flowers, which are nectar rich. Additionally, Dennis (1992) reported that species with low wing loading tended to feed on solitary inflorescences. Therefore, it seems that solitary flowers are not excluded per se by foraging butterflies, but their choice is influenced by the actual costs of flight.

Butterflies were frequently observed on flowers which exceeded their mean proboscis length. This result stands in contrast to Corbet (2000), who reported that no butterfly was ever seen to feed on flowers with a deeper corolla than the mean proboscis length. On the one hand, this could be explained by the definition of a flower visit in this study: In contrast to my study, where a visitation would be counted if a butterfly was touching the reproductive part of the plant, here it would only be recorded if the butterfly probed a flower. Additionally, as we deal with average values it is possible that I recorded individuals which deviated from the mean body size and tongue length and were therefore capable to reach the nectar. On the other hand, Tiple et al. (2009) reported that the corolla depth was not such a strict limitation as considered by Corbet (2000). They also observed several butterflies feeding on flowers wit corollas longer than their proboscis. Though, I cannot tell from my observations if all feeding attempts were successful. However, there were butterflies observed that probed their head deeply into the corolla tube, which will expand the reach of their proboscis. Although I did not make such observations this emphasizes that limitations based solely on corolla depth or proboscis length might not be that strict. Although long tubular, nectar-rich and massed flowers might be the ideal nectar source for butterflies (Corbet, 2000), my data also revealed a high visitation rate at shallow and inflorescences putatively low in nectar. One explanation might be competition among the butterflies and also with other flower visitors. Having a smaller size, shorter proboscis and lower energy cost, it might be more favourable to feed rapidly on shallow and nectar-low flowers than competing with larger flower visitors (Tiple et al., 2009). Within butterfly families, *M. galathea* as well as *P. icarus* are larger than *C. pamphilus* and *P. argus,* respectively. The larger two showed a preference for flowers with deep corollas, whereas the smaller two were mostly seen on shallow ones. However, the preferred nectar amount deviates from the previous suggestion. For example, *M. galathea* was observed mainly on low-nectar plants, although it had a preference for deep corollas. This could indicate a niche partitioning as the other three more abundant species did not show this trend.

v. Are there flower preferences of particular butterfly species?

None of the 27 butterfly species that I observed visiting flowers during my study is a true specialist with regard to its adult nectar sources. The numbers of reported flower species to be visited in Britain and Central Europe alone is on average 61 plant species for the 27 observed butterfly species of my study. However, even though these butterflies are opportunistic about their flower visits, local or temporary preferences have been frequently observed. For example, my study revealed differences between preferred flower colour, nectar amount and corolla tube length between the four in more detailed analysed species.

During my study, I observed *P. icarus* visiting flowers of 41 plant species which indicate a high flexibility regarding the nectar source. This flexibility is supported by Dennis (2010) which recorded over 100 nectar plants. Its average proboscis length of about 8 mm stands in contrast to the preferred corolla length of over 10 mm (Corbet, 2000). *Polyommatus icarus* showed an increasing species strength with progress of the summer, regardless of the land use type. Therefore, it gained in importance for the plants. Even though P. icarus is a generalist in regard to its nectar plants, there are clear preferences: The preferred colour that I observed (viz. yellow) coincided with results by Yurtsever et al. (2010), whose study was based on 1329 field observations.

Vicia cracca is also mentioned in the literature as an nectar plant for *P. argus*, which my findings can support (Straka, 2005; Ebert and Rennwald, 1993). However, with 8% of the total visitations it is far from being the most visited plant as Odette et al. (2014) reported. Similar to Straka (2005) and Dennis (2010) I observed over thirty nectar plants being utilized. Among them, 22 are not mentioned in the cited literature. Also the findings about yellow as preferred colour correspond with Straka (2005), although my findings cannot confirm visitations of red flowers. With a mean proboscis length of only 7 mm (Herrera, 1988) *Plebejus argus* preferred a short corolla tube length (<5 mm); however, it was also seen on flowers which corolla length longer than 10 mm, which exceeded its proboscis length. *P. argus* and *P. icarus* are ecologically similar, but my results suggest that they use different nectar resources if they co-occur together.

Except of *Lotus corniculatus*, the most visited nectar plants of *C. pamphilus* did not correspond with those reported by Dennis (2010). Ebert et al. (1993) mentioned that *Thymus serpyllum* gained in importance in September, especially at mowed meadows and sheep pastures. My results suggest the importance of *T. serpyllum* is not limited to September. A long term study, which took place in northeast Spain, confirm *T. serpyllum* as preferred nectar plant of the small heath butterfly (Stefanescu & Traveset, 2009). *C. pamphilus* was observed to feed on inconspicuous, small flowers (Ebert and Rennwald, 1993). In this study the small heath butterfly was the only species which also visited *P. lanceolata* flower heads, although this plant is generally known to be wind pollinated. However, there are observations which confirmed that *P. lanceolata* can be insect pollinated as well. For example Cliffford (1962) reported honey bees foraged for pollen *P. lanceolata* during warm weather conditions. Ebert and Rennwald (1993) described several species which visited *P. lanceolata*, inter alia *C. pamphilus.*

The trend of *C. pamphilus* to prefer short corolla tubes and plants offering a high nectar amount is similar to *P. icarus*. But besides *L. corniculatus,* they visited different plants regularly. This might indicate a way of niche partitioning. The decrease of species strength of *C. pamphilus* over time could suggest a higher impact of the drought on *C. pamphilus* than on the other species analysed in more detail, which did not show such a trend. Maybe the reduced flower availability led to higher competition between the flower visitors and *C. pamphlilus* was forced to use other nectar plants. However, Ebert and Rennwald (1993) reported that there were fewer individuals observed in July compared June, although the second generation already started. Therefore, as abundance was correlated with visitation rate, the reduced species strength could mirror this. No overlap of the larval host and adult nectar plants occurred, as the larvae feed on grasses. *C. pamphilus* is throughout the literature described as food generalist (van Swaay, 2002; Tudor et al., 2004). Willmer (2011) described Satyrinae to prefer yellow flowers, which coincides with my findings.

The importance of *C. jacea* and *C. scabiosa* as nectar plants of *M. galathea* has been described throughout the literature (Rennwald, 1986; Sonntag, 1983; Steffny et al., 1984). However, my findings confirmed the related *C. stoebe* only on the third rank, far behind *O. spinosa*. Also, the other frequently mentioned plants like *Scabiosa columbaria* or *Cirsium sp.* were not often visited during this study. However, Ebert and Rennwald (1993) reported over 60 nectar plants for *M. galathea*, yet stressed that this species had a narrow nectar plant spectrum due to the similarity of the visited plants. Most of them blossom in violet, offer a sufficient landing platform and produce massed flowers, such that *M. galathea* butterflies can walk from blossom to blossom. This did not coincide with my results. Although violet was the most visited colour, 50% of the interactions happened with differently coloured flowers. This is a vast difference to Ebert and Rennwald (1993). They mentioned only 1% of all visitations occurring at flowers of a different colour than violet. *M. galathea* showed a trend towards flowers with long corollas and low nectar amount. This could indicate a resource partitioning as the other three more abundant species did not show this trend. In contrast to *Polyommatus icarus* and *Plebejus argus* the mean proboscis length of 13 mm was longer than the visited corollas (Bloch & Erhardt, 2008). The larval host plants are grasses; therefore, nectar plants and host plants do not overlap.

Conclusion

Overall, the land use type as well month of observations had an impact on the structure of the butterfly-flower networks on grassland sites in the National Park Neusiedler See - Seewinkel. Though, the differences depended on the network metrics considered and were overall quite subtle. This contrasts with species diversity, which was significantly different between the land use type and between early and high summer. Whereas network specialisation, although influenced by the interaction of land use and month, remained relatively stable, vulnerability changed more profoundly. The hypothesis that network vulnerability decreases with lower land use intensity could be confirmed. The role of individual partner species varied more often among the plants than the butterflies. Some plants are sensitive to mowing and therefore only occurred at the pastures, where there were often visited. Although some changes occurred between the two observation months, the importance of the partners did not change profoundly over time. Even though they are all opportunistic flower visitors, there were preferences of the four most frequently observed butterfly species (*Polyommatus icarus*, *Plebejus argus*, *Coenonympha pamphilus* and *Melanagria galathea*) noticeable regarding floral colour, corolla length, inflorescence type, nectar amount and nectar plant species identity. Yellow and violet flowers were by far the most visited. Flower colour, inflorescence type and nectar amount had a weak influence on visitation rates, whereas floral UV patterns did not alter the choice of butterflies significantly. However, in the light of nature conservation it seems more important to provide a high amount of nectar plants with preferred traits than certain plant species. Though, the much higher host specificity of the larvae should be taken into account. The pollination syndrome classification did not provide a good prediction of visitation frequency. Extensive mowing led to the highest species diversity in nectar plants and visiting butterflies. Species of conservation concern did not contribute a high proportion of visitations to the networks.

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Appendix

Table A11: Geographic coordinates of study sites near Illmitz (Austria)

Plot ID	**Coordinates**		**Mowing status**
C01	16,7859928°E	47,7579136°N	-
C02	16,7888447°E	47,7615596°N	-
C04	16,7850965°E	47,7622018°N	-
C06	16,7799813°E	47,7645754°N	-
C05	16,7813621°E	47,7691712°N	-
C03	16,7937495°E	47,7684885°N	-
H01	16,7690974°E	47,7814411°N	-
H02	16,7715893°E	47,7866212°N	-
H03	16,7754230°E	47,7910724°N	-
H04	16,7784225°E	47,7962965°N	-
H05	16,7799888°E	47,7995209°N	-
H06	16,7820325°E	47,8026009°N	-
M01	16,7687118°E	47,7561769°N	Mown
M02	16,7718612°E	47,7576792°N	Mown
M03	16,8023762°E	47,8026521°N	Mown
M04	16,8012905°E	47,8010803°N	Mown
M05	16,7737795°E	47,7469074°N	Mown
M06	16,7863268°E	47,7527301°N	Mown
M07	16,7689724°E	47,7429483°N	Not mown

M08	16,8006118°E	47,7996739°N	Not mown
M09	16,7836453°E	47,8021553°N	Not mown
M10	16,7695218°E	47,7796271°N	Not mown
M11	16,7781522°E	47,7805306°N	Not mown
M12	16,7983436°E	47,7768796°N	Not mown

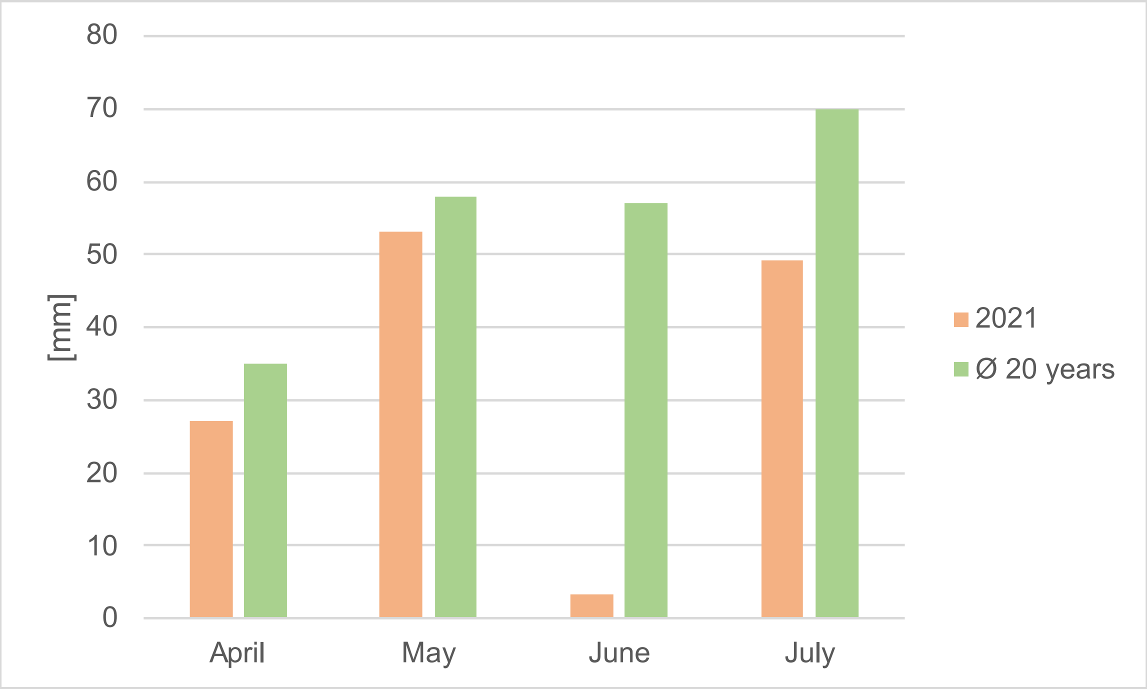

Figure A21: Precipitation in the region Illmitz. Orange stands for the rainfall in 2021, green for the average precipitation of 2000-2020 (Wasserportal Burgenland, 2022).

Table A31: Contingency table showing the frequencies of the combination of the species *Polyommatus icarus* and *Plebejus argus* and their visited plants.

Plant species	***Polyommatus icarus***	***Plebejus argus***
Achillea millefolium	43	14
Allium vineale	3	0
Anthyllis vulneraria	0	2
Arenaria serpyllifolia	0	9
Asperula cynanchica	6	0
Astragalus onobrychis	2	2
Carduus acanthoides	0	4
Centaurea scabiosa	57	0
Centaurea stoebe	113	3
Chrysanthemum segetum	13	2
Cirsium arvensis	0	2
Consolida regalis	2	0
Convolvulus arvensis	0	2
Cuscuta epithymum	24	0
Daucus carota	3	3
Dianthus carthusianorum	28	7
Erodium cicutarium	2	0
Eryngium campestre	89	0
Euphorbia seguierana	11	3

Galium verum	46	13
Hieracium umbellatum	4	7
Inula salicina	25	0
Jacobaea vulgaris	5	0
Leontodon hispidus	7	0
Leucanthemum vulgare	0	13
Linaria genistifolia	3	0
Linaria vulgaris	0	3
Linum austriacum	6	1
Linum catharticum	1	0
Lotus corniculatus	379	60
Lotus maritimus	21	0
Medicago falcata	97	0
Medicago lupulina	72	101
Melilotus officinalis	0	3
Myosotis arvensis	2	4
Ononis spinosa	399	9
Petrorhagia saxifraga	3	0
Picris hieracioides	2	0
Polygala comosa	26	11
Potentilla reptans	10	0
Ranunculus acris	0	4
Salvia pratensis	5	3
Scabiosa columbaria	4	0
Scabiosa ochroleuca	45	4
Thymus serpyllum	49	10
Trifolium aureum	65	0
Trifolium pratense	41	7
Trifolium repens	0	2
Vicia cracca	36	28
Vicia sativa	0	2

Table A41: Nectar plants which are not mentioned in the cited literature and therefore labelled as “new”.

Coenonympha pamphilus	***Brintesia circe***	***Colias hyale/alfacariensis***
Arenaria serpyllifolia	*Ononis spinosa*	*Centaurea stoebe*
Asperula cynanchica		*Dianthus carthusianorum*
Astragalus onobrychis		*Erysimum diffusum agg.*
Chrysanthemum segetum		*Galium verum*
Convolvulus arvensis		*Ononis spinosa*
Dianthus carthusianorum		
Echium vulgare		
Eryngium campestre		
Erysimum diffusum agg.		
Euphorbia seguierana		
Galium verum		
Globularia bisnagaria		
Inula salicina		

Jacobaea vulgaris		
Leucanthemum vulgare		
Linum austriacum		
Linum catharticum		
Lotus maritimus		
Myosotis arvensis		
Ononis spinosa		
Petrorhagia saxifraga		
Plantago lanceolata		
Polygala comosa		
Potentilla reptans		
Teucrium chamaedrys		
Vicia cracca		
Vicia sativa		
Erynnis tages	***Gonepteryx rhamni***	***Lasiommata megera***
Lotus corniculatus	*Ononis spinosa*	*Dianthus carthusianorum*
Lotus maritimus		*Linum austriacum*
Medicago lupulina		*Vicia cracca*
Scabiosa columbaria		
Maniola jurtina	***Melanargia galathea***	***Melitaea cinxia***
Achillea millefolium	*Dianthus carthusianorum*	*Achillea millefolium*
Astragalus onobrychis	*Galium verum*	*Dianthus carthusianorum*
Galium verum	*Inula salicina*	*Galium verum*
Inula salicina	*Medicago falcata*	*Galium verum*
Ononis spinosa	*Ononis spinosa*	*Linum austriacum*
Scabiosa columbaria	*Securigera varia*	*Medicago lupulina*
Scabiosa ochroleuca		*Scabiosa columbaria*
Thymus serpyllum		
Ochlodes sylvanus	***Plebejus argus***	***Polyommatus icarus***
Astragalus onobrychis	*Achillea millefolium*	*Achillea millefolium*
	Arenaria serpyllifolia	*Allium vineale*
	Astragalus onobrychis	*Asperula cynanchica*
	Centaurea stoebe	*Astragalus onobrychis*
	Chrysanthemum segetum	*Centaurea scabiosa*
	Cirsium arvensis	*Centaurea stoebe*
	Convolvulus arvensis	*Chrysanthemum segetum*
	Daucus carota	*Consolida regalis*
	Dianthus carthusianorum	*Cuscuta epithymum*
	Euphorbia seguierana	*Daucus carota*
	Galium verum	*Erodium cicutarium*
	Hieracium umbellatum	*Eryngium campestre*
	Linaria vulgaris	*Euphorbia seguierana*
	Linum austriacum	*Galium verum*
	Melilotus officinalis	*Hieracium umbellatum*
	Myosotis arvensis	*Inula salicina*
	Ononis spinosa	*Jacobaea vulgaris*

	Polygala comosa	*Leontodon hispidus*
	Ranunculus acris	*Linaria genistifolia*
	Salvia pratensis	*Linum austriacum*
	Trifolium pratense	*Linum catharticum*
	Vicia sativa	*Myosotis arvensis*
		Petrorhagia saxifraga
		Picris hieracioides
		Polygala comosa
		Potentilla reptans
		Salvia pratensis
		Scabiosa columbaria
		Scabiosa ochroleuca
Pontia edusa	***Vanessa cardui***	***Zygaena filipendulae***
Erysimum diffusum agg.	*Glechoma hederacea*	*Dianthus carthusianorum*
	Vicia cracca	*Echium vulgare*
		Erysimum diffusum agg.
		Lotus corniculatus
		Ononis spinosa
		Polygala comosa
Zygaena loti		
Erysimum diffusum agg.		
Galium verum		
Inula salicina		