Summer drought shapes grassland butterfly-flower networks more than management type in an Austrian conservation area

Erika Depisch & Konrad Fiedler

Abstract: Summer drought shapes grassland butterfly-flower networks more than management type in an Austrian conservation area. Flower-butterfly networks on three grassland types in the National Park Neusiedler See – Seewinkel were analysed, viz. (1) a fenced pasture grazed mainly by Przewalski's horses at low densities, (2) pastures grazed by non-stationary cattle and (3) meadows maintained by mowing. Sampling took place in June and July 2021 during a drought period. We observed 4,160 flower-butterfly interactions involving 27 butterfly and 59 plant species, including 147 interaction pairs not previously recorded. Species diversity and composition of interacting communities varied across the three grassland types and two survey months, with highest diversities on mown meadows. Nectar flower abundance did not differ between grassland types, but decreased from early to high summer. Network specialization H2' and modularity Q did not vary systematically between grassland types, but decreased in response to drought. All observed flower-visiting butterfly species visit multiple nectar plant species, but average species-level specialization d' was higher on meadows than on pastures and further decreased with summer drought. This suggests that partitioning of nectar sources among butterflies is more effective at times of high supply, while overlap in resource use increases during drought. These results suggest that grassland butterflies in the study area respond opportunistically to shortages in nectar flower abundance caused by summer drought, whereas extensive management by grazing vs. mowing left a rather minor signature on these ecological networks. Due to their higher nectar flower abundance mown meadows are important for maintaining butterfly diversity in this large conservation area.

Keywords: bipartite networks, flower visitors, grassland, diurnal Lepidoptera, summer drought

Introduction

In Central European lowlands, most grassland ecosystems (except for sites with specific edaphic conditions like extremely dry, saline or water-logged soils: Albert et al. 2020) are anthropogenic in origin. Anthropogenic grasslands therefore require management by grazing or mowing for maintenance to prevent shrub encroachment and, eventually,

succession towards forest as potential natural climax vegetation. At the same time, anthropogenic grasslands harbour a rich biodiversity (Cerabolini et al. 2016), especially with regard to heliophilic organisms such as butterflies and many other insects. Hence, grassland management has long been in the focus of nature conservation research and practice in Europe (Kun et al. 2021). This also applies to the management zone of the National Park Neusiedler See – Seewinkel, where only small fractions of land with saline or very wet soils are naturally free of woody vegetation (Korner et al. 2008). All other grasslands in the area were established through human land-use activities and have been maintained over time (or restored in recent decades) by means of management, i.e. grazing or mowing (Eule et al. 2014).

Mowing and grazing may favour different species assemblages (Steffan-Dewenter & Leschke 2003, Schley & Leytem 2004). As a result, on the landscape scale pluralism in management practices may foster an increased gamma diversity (Fiedler et al. 2017). Moreover, whether grazing or mowing are better suited to meet conservation goals varies between target taxa (for the study region e.g. Zulka et al. 1997, Hölzler 2008). Yet, for the functioning of ecosystems not only the organismal communities and their diversities are important. Rather, the interactions between organisms are essential for all the fluxes of energy, matter and information through an ecosystem. Prominent examples are plant-animal interactions, such as herbivory or pollination.

Globally, 87.5% of all angiosperm species, including many agricultural crops, are pollinated by animals (Ollerton et al. 2011). However, concomitant with increasing land-use intensity species richness of flower visitors is declining, which also translates into reduced complexity of biotic interactions (Weiner et al. 2011, 2014). In parallel, climate change poses a threat to pollination services (Settele et al. 2016). Besides distribution shifts of interacting species, indirect effects like phenological mismatches between pollinators and plants or the decline in quality and quantity of floral resources may occur (Memmott et al. 2007, Hegland et al. 2009). With progressing climate change, especially the occurrence and intensity of drought events will increase (Dai 2013). Drought threatens pollinators through its impact on floral resources (Thomson 2016), since plants under drought stress spend less energy in reproduction, translating into smaller flowers, less pollen and nectar (Halpern et al. 2010, Pinheiro & Chaves 2011). As plant species respond differentially to drought, the net effect of drought stress on the community level might further depend on species composition (Grime et al. 2000). Hence, understanding the response of ecological networks to drought events might become even more crucial in the decades to come (Phillips et al. 2018).

In recent years, the structure of interaction networks has gained prominence in biodiversity research (Olesen et al. 2008, Weiner et al. 2014, Zografou et al. 2020). One well established target group for that purpose are butterflies. Their distinctive appearance and moderate species richness facilitate species identification in the field, and habitat requirements of European butterfly species are well documented. Moreover, butterflies respond sensitively to environmental change (e.g. Sawchik et al. 2005). For example, Power & Stout (2011) investigated differences in flower visitor network structure between organically and conventionally managed dairy farm pastures in Britain, where the

degree of network specialisation seemed to be influenced by land-use intensities. It has been suggested that generalists in networks benefit from disturbance of their habitats, while specialists suffer (McKinney 1997, Aizen et al. 2012). However, support for this idea is not unequivocal (Memmott 1999, Pocock et al. 2012).

Ecological networks consist of "nodes" (i.e. species) connected by "links". These are analysed using a variety of quantitative metrics, some of which have only been developed during the past two decades (Dormann et al. 2009, Heleno et al. 2014). One example is network-level specialization H2' which describes the exclusiveness (or complementarity) of interactions at network level. This scaled metric is based on Shannon entropy and ranges between 0 (no specialization, viz. species interactions merely reflect the relative abundances of all players) and 1 (completely specialized network; Blüthgen 2010). Other metrics focus at the species level, such as the specialization index d'. This measure also scales from 0 to 1, with 0 indicating no specialization at all and 1 showing that a species has only one single partner in the network under consideration. Finally, some measures describe the extent of compartmentalization of networks into functional subunits, e.g. the network modularity Q, which also scales from 0 to 1. The higher the Q value, the more the network is segregated into modules. All these measures are not strongly influenced by network size or sampling intensity (Blüthgen 2010).

As seasonal changes shape flower availability and insect emergence profoundly, it is not surprising that some studies found seasonal changes in pollinator-plant networks (Souza et al. 2018). When more plants come into blossom, visitors have a greater selection to choose from and their apparent specialization might decrease. On the contrary, when flower availability is low, e.g. during a drought event, apparent specialization might increase. European flower-visiting butterflies are usually not specific to certain nectar plants (Dennis 2010). One would therefore expect apparent specialization to co-vary with local flower supply, which again is expected to vary between grassland types and over time. Even generalist butterfly species may appear rather specialized whenever they are forced to use only few available flower resources, while the same species might behave more opportunistically once a broader array of nectar sources is available.

The aim of the present study was to gain insight into flower-butterfly networks on three grassland types in the National Park Neusiedler See – Seewinkel. These grassland types are known to harbour quite different communities of flowering plants (see below), and also variation in their butterfly assemblages has earlier been documented (Fiedler et al. 2017). We therefore set out to investigate whether these differences translate into variation in the butterfly-flower networks. Specifically, we address the following research questions:

i.   Do network structures and species-level specialization vary consistently between grassland management types?

ii. Do these network structures vary between early and high summer, i.e. immediately after a severe spell of drought?

Here, we report on results aggregated according to grassland types or observation months. Detailed analyses on the site level can be found in Depisch (2022).

Methods

Study area

Data sampling took place in the management zone of the National Park Neusiedler See – Seewinkel in eastern-most Austria, situated about 2-3 km west or north-west of the village of Illmitz. Much of the area 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 only 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: 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, grazing was re-established as a means of ecological restoration (Zulka et al. 1997, Eule et al. 2014). Today, in the management zone three major types of grassland can be found: (1) Pastures with mainly Przewalski's horses grazing there, (2) pastures grazed by cattle, and (3) meadows maintained by mowing. The area is situated in the Pannonic climate region characterised by high temperatures and low precipitation during summer (Lalic et al. 2013). June 2021, however, was extreme with only 3.2 mm precipitation, while the average monthly precipitation during June was 57.2 mm since 1999 (Wasserportal Burgenland 2022).

Study sites

Six plots on the Przewalski's horse pasture were chosen, six further plots on cattle pastures and 12 plots on meadows. All plots were spaced from another by a distance of at least 200 m. This random selection of plots was based on 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 fenced Przewalski's horse pasture (total area 69.5 ha) is situated between a sandy dam and the eastern margin of Lake Neusiedl, in the so-called "Seevorgelände". The more humid parts are dominated by plant associations like *Juncetum subnodulosi* and *Schoenetum nigricantis*, whereas on the drier eastern parts the vegetation is of the *Centaureo pannonicae-Festucetum pseudovinae* type. In 2021 the area 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 the enclosure.

The cattle pasture sites were situated on the gravel terrace east of the sandy dam, around the soda pans "Kirchsee" (~46 ha) and "Zicklacke" (~27 ha). Both these temporary saline ponds (Häusler 2020) were completely dried out at the time of sampling. Two herds of cattle based in the village of Illmitz, both comprising about 100 cows with their calves, grazed the area, ranging under control by herdsmen. This pasture management was started in the 1980s and has since successfully contributed to restoration of the historical vegetation (Rechnitzer 2019). Vegetation at sampling sites showed multiple signs of disturbance by cattle, including dung deposits and gaps created by trampling. The vegetation is semi-dry grassland of the *Centaureo pannonicae-Festucetum pseudovinae* type (Korner et al. 2008).

The meadow sites, situated south of the cattle pastures, are extensively mown once or twice per year, are not fertilized and represent semi-dry calcareous, in part slightly ruderal vegetation of the *Festuco-Brometea* type. Unfortunately, no data about their exact mowing schedule in the previous years is available. For further information about the individual plots see Depisch (2022).

Field sampling

Butterfly-flower networks were sampled in June and July 2021. There were six visits to every site, separated by 1-2 weeks, three in June 2021 and three in July 2021. Beyond true butterflies (Rhopalocera) we also included flower visits by burnet moths (genus *Zygaena*) and one diurnal hawkmoth (*Macroglossum stellatarum*), but for simplicity we below use the term "butterflies" throughout. Plot size was 50 m x 50 m at each site. At each sample site all observed butterfly-plant interactions were recorded. As an interaction we only counted if the butterfly was touching the open petals of a flower. Butterfly individuals resting on plants or flying through the site were not counted. Each sample site was walked 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 nectaring, recording only took place at suitable conditions, adapted from the Butterfly Monitoring Scheme methodology (van Swaay et al. 2008): (a) plots were not walked when air temperature was below 13 °C; (b) a plot was walked only provided there was at least 60% sunshine; (c) when wind speed was above 5 on the Beaufort scale, plots were not walked; and (d) recording only took place between 9 am and 5 pm.

Butterflies which could not be identified from a distance were captured with an insect net, identified on the spot and released immediately. Species identification followed Stettmer et al. (2006) for butterflies and Fischer et al. (2008) for plants. Two sibling species pairs were scored as one operational taxonomic unit (OTU), as field identification is not reliably possible: *Zygaena purpuralis/minos* and *Colias hyale/alfacariensis*. All available potential nectar sources (i.e. flowers and flowerheads of entomophilous plant species) were counted in one randomly selected 10 x 10 m² area within each plot. Compact inflorescences like Asteraceae or Caprifoliaceae flowerheads were counted as one unit (Alarcón et al. 2008).

To characterize the range of the butterflies' nectar sources, published information on nectar plants of all butterfly species observed in 2021 was compiled from Ebert & Rennwald (1993), Hofmann (1994), Hesselbarth et al. (1995), Dennis (2010), Lafranchis et al. (2015), Gelbrecht et al. (2016) and Richert & Brauner (2018). Plant species observed to receive visitations, but which had not been mentioned in this literature for the respective species, were regarded as "novel" records.

Statistical analyses

Field data was digitized into a spread sheet software, resulting in a matrix of all observed interactions at all sampling events. This matrix was subsequently partitioned either according to the three grassland types, or the two sampling months. Network analyses were done using the R package "bipartite" (Dormann et al. 2022).

For further statistical analysis, the RStudio software version 4.1 was used (RSTUDIO TEAM 2020), and for graphical illustrations the package "ggplot2" (WICKHAM 2016). For the comparison of species diversity of flower-visiting butterflies as well as flower species visited by butterflies between the months and the grassland types, individual based accumulation curves were generated with the package "iNEXT" (HSIEH et al. 2016). As Hill number the factor q=1 was chosen, which is equivalent to the exponential Shannon species diversity, also termed "effective number of species" (CHAO et al. 2014).

Results

General observations on the butterfly-flower networks

We altogether recorded 4,160 butterfly-flower interactions in June and July 2021; 27 butterfly species and 59 plant species were involved. Eight butterfly species accounted for 92% of all interactions, while 10 species were accountable for 73% of the observed interactions from the plants' perspective (Figures 1 and 2). Six butterfly species were seen less than five times visiting a flower, and 14 plant species were visited less than five times by a butterfly. Among the butterflies, only *P. icarus* was more prevalent as flower visitor in July than in June. Late summer flowering plant species were *Ononis spinosa*, *Eryngium campestre*, *Scabiosa ochroleuca* and *Centaurea stoebe*. *Lotus corniculatus* was frequently visited in both months, whereas *Thymus serpyllum*, *Inula salicina* and *Dianthus carthusianorum* were characteristic of the early summer aspect.

All butterfly species observed in the networks were already known to visit rather broad ranges of nectar flower species (Figure 3). However, for more than half of them novel nectar plants could be added to their resource lists, with the most sizeable additions observed in *Polyommatus icarus*, *Plebejus argus* and *Coenonympha pamphilus*. In all, 147 new nectar plant records were assembled (Table 1). On average, 61 nectar plant species are now reported per butterfly species represented in the observed networks.
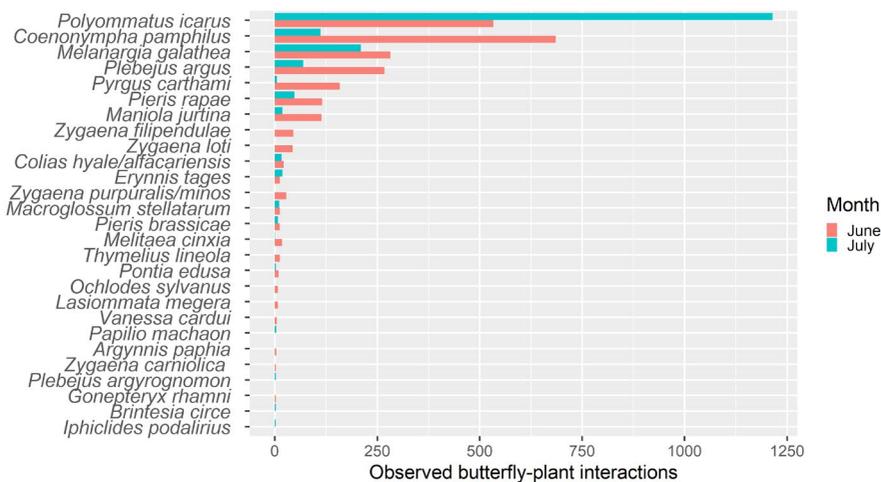

Fig. 1: Numbers of observed plant-butterfly interactions per butterfly species, segregated per observation month.

Nectar flower abundance did not significantly vary between the three grassland types (two-way ANOVA: $F_{2;72}=0.135$, $p=0.874$), but was distinctly higher in June (1.4±0.9 flowers/m²) than in July (0.85±0.56 flowers/m²; $F_{1;72}=8.447$, $p=0.005$). There was no significant month × grassland type interaction ($F_{2;72}=1.696$, $p=0.19$).

Nectar flower supply on the sites and the number of observed interactions were positively related to each other in June (Spearman rank correlation: $\rho=0.380$, $p=0.005$) and even more strongly so in July ($\rho=0.767$, $p<0.0001$), when nectar supply was lower.
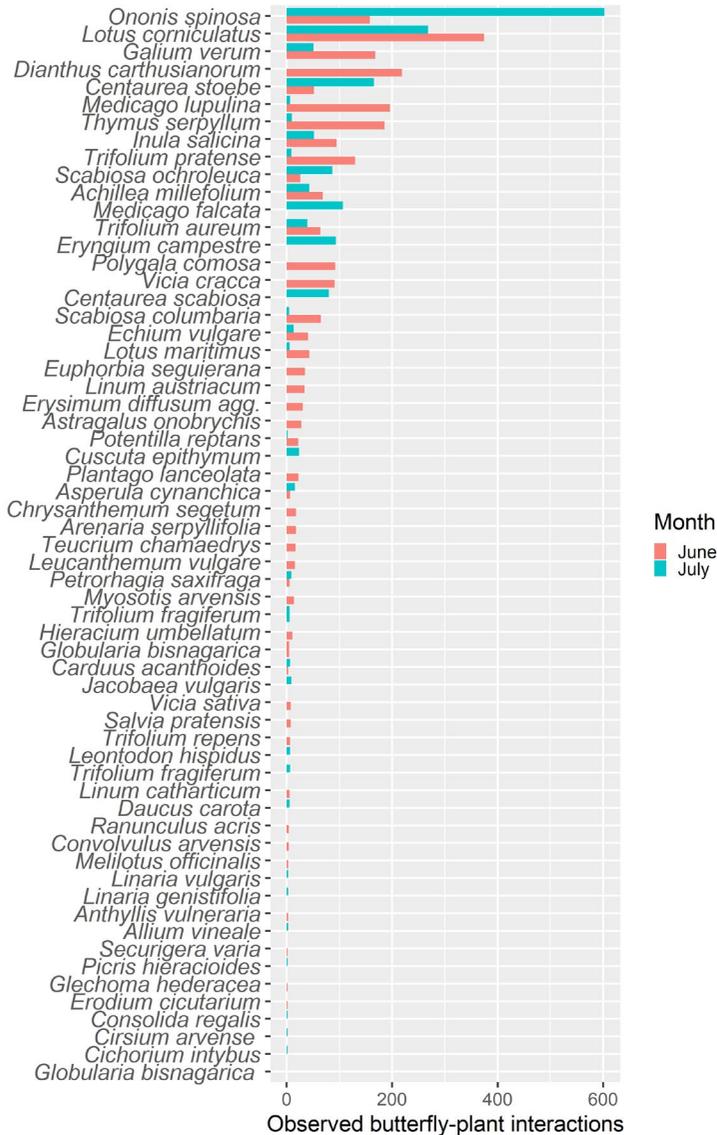

Fig. 2: Numbers of observed plant-butterfly interactions per plant species, segregated per observation month.
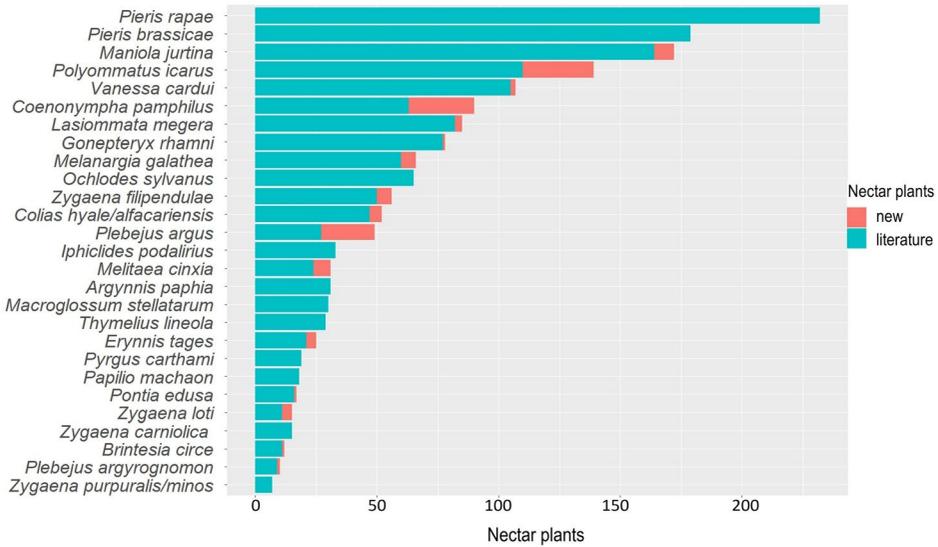
Fig. 3: Numbers of previously recorded (blue) and newly documented nectar plants (red) of the 27 observed butterfly species.

Tab. 1: Nectar plants which were not earlier mentioned in the cited literature for the respective butterfly species.

Brintesia circe	Coenonympha pamphilus	Colias hyale/alfacariensis
Ononis spinosa	Arenaria serpyllifolia	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 bisnagarica	
	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 agg.	Dianthus carthusianorum	Achillea millefolium agg.
Astragalus onobrychis	Galium verum	Dianthus carthusianorum
Galium verum	Inula salicina	Galium verum
Inula salicina	Medicago falcata	Linum austriacum
Ononis spinosa	Ononis spinosa	Medicago lupulina
Scabiosa columbaria	Securigera varia	Scabiosa columbaria
Scabiosa ochroleuca		
Thymus serpyllum		
Ochlodes sylvanus	**Plebejus argus**	**Polyommatus icarus**
Astragalus onobrychis	Achillea millefolium agg.	Achillea millefolium agg.
	Arenaria serpyllifolia	Allium vineale
	Astragalus onobrychis	Asperula cynanchica
	Centaurea stoebe	Astragalus onobrychis
	Chrysanthemum segetum	Centaurea scabiosa
	Cirsium arvense	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		

Species diversity of butterflies (Figure 4) and plants (Figure 5) in the networks was more than twice as high in June than in July. In regard to the land use types, there were differences in the ranking between plants and butterflies. In both cases the meadows revealed the highest diversity of species participating in the networks. Yet, butterfly species diversity in the networks tended to be lower on cattle pastures than at the Przewalski's horse pasture, while the reverse pattern applied to nectar plants.

Species composition of butterfly-visited flowers substantially varied between grassland types and months (two-way PERMANOVA based on a Bray-Curtis similarity matrix; grassland type: $F_{2;36}=6.165$, p<0.001; month: $F_{1;36}=6.349$, p<0.001; interaction: $F_{2;36}=2.967$, p<0.0016). Species composition of flower-visiting butterflies varied even more strongly between grassland types and months (butterfly counts square-root transformed for analysis; grassland type: $F_{2;36}=11.139$, p<0.001; month: $F_{1;36}=9.746$, p<0.001; interaction: $F_{2;36}=1.785$, p=0.046).
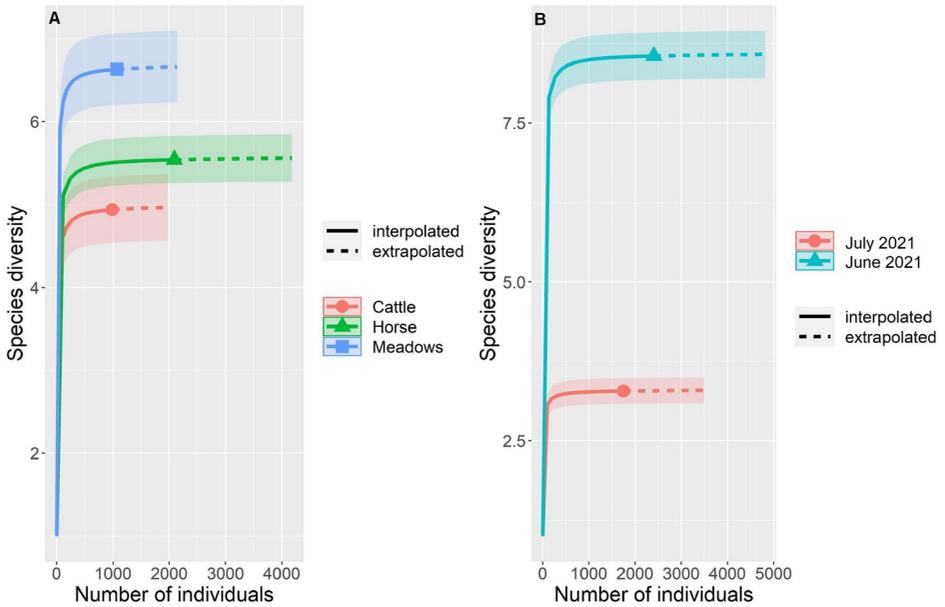
Fig. 4: Individual-based randomized diversity accumulation curves (Hill numbers, q=1) of flower-visiting butterflies (A) at the different land use types and (B) between the months. Shaded areas represent 95% confidence intervals.
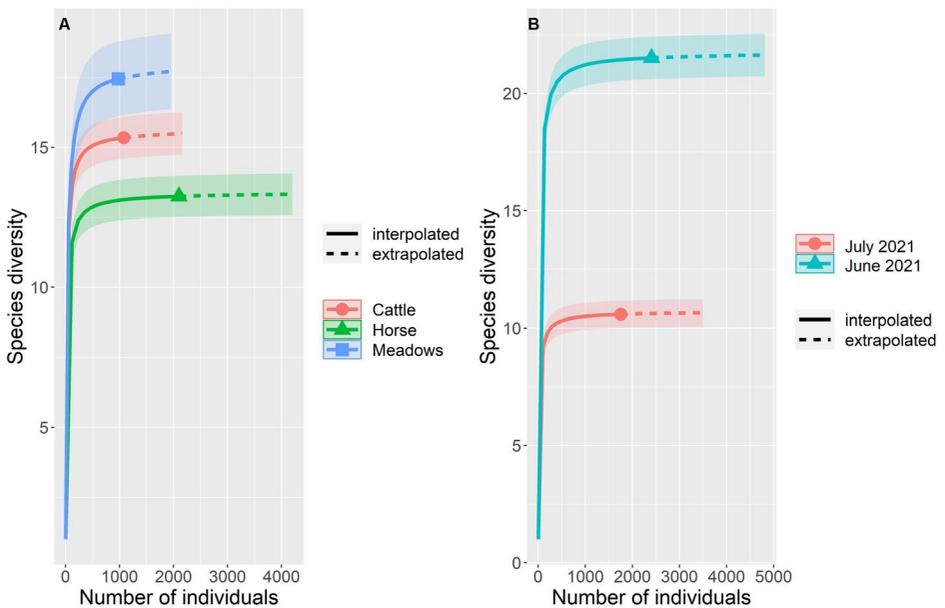

Fig. 5: Individual-based randomized diversity accumulation curves (Hill numbers, q=1) of butterfly-visited plants (A) at the different land use types and (B) between the months. Shaded areas represent 95% confidence intervals.

Network structures at land-use type and monthly levels

Butterfly-flower network structure was overall remarkably similar between the three grassland types (Figures 6, 7 and 8), despite the substantial variation in species diversity and composition of the interacting partners. Network specialization H2' was rather low in all three cases (horse pasture: 0.283; cattle pastures: 0.356; meadows: 0.356), and there was no evidence for compartmentalization. The role of individual butterfly as well as plant species varied between grassland types. In contrast, network topology varied more strongly between early and high summer in 2021 (Figures 9 and 10). In June, overall specialization was far higher (H2'=0.642) than after the onset of summer drought in July (H2'=0.250). Only three butterfly species (viz. *C. pamphilus*, *M. galathea* and especially *P. icarus*) strongly dominated the visitor networks in July, whereas visitation frequencies were more evenly distributed in June.

Network modularity Q revealed a pattern very similar to H2'. Q was lowest on the horse pasture (0.273), highest on cattle pastures (0.373) and intermediate on meadows (0.323). Moreover, Q was distinctly higher in June (0.349) than July (0.179).

Network specialization d' on butterfly species level was overall low (species mean ± SD across months: 0.344±0.162; across grassland types: 0.335±0.137) and did not significantly correlate with the number of available records per species (at monthly level: r=-0.288, p>0.07; at grassland types level: r=-0.047, p>0.73). However, species level specialization d' averaged across butterfly species differed significantly between grassland types (one-way ANOVA: $F_{2;53}$=5.425, p<0.008) as well as between months (t-test: t_{39}=2.114, p=0.041). Mean specialization d' was higher in June (0.372±0.127) than in July (0.284±0.137), and was distinctly higher on meadows (0.427±0.196) than on the two types of pasture ecosystems (horse: 0.271±0.123; cattle: 0.351±0.120). Only 9 cases involving 6 butterfly species of rather narrow flower specializations (d'>0.500) were observed: *M. stellatarum* on meadows (0.877); *P. edusa* on meadows (0.739); *V. cardui* on meadows (0.650); *Z. filipendulae* on horse pastures (0.506); *M. galathea* on cattle pastures (0.588); *M. galathea* in June (0.596); *P. edusa* in June (0.621); *V. cardui* in June (0.618); and *E. tages* in July (0.504).

Discussion

In temperate zone grasslands, mowing or grazing lead to higher diversity of plant and insect species than abandonment or intense management (HABEL et al. 2019, HANNAP-PEL & FISCHER 2020). However, it is also well known that too high land use intensity may lead to a loss of biodiversity (BLÜTHGEN et al. 2012, SOCHER et al. 2013, ALLAN et al. 2014). Therefore, using traditional agricultural methods as tool in conservation management needs to be done carefully. The highest plant species diversity involved in flower visitor networks during this study in the National Park Neusiedler See – Seewinkel was found on meadows, followed by 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 shrubs and trees start to grow, generally have a negative effect on butterfly diversity (BALMER & ERHARDT 2000). Our results support these findings partly: Meadows showed highest species diversity of
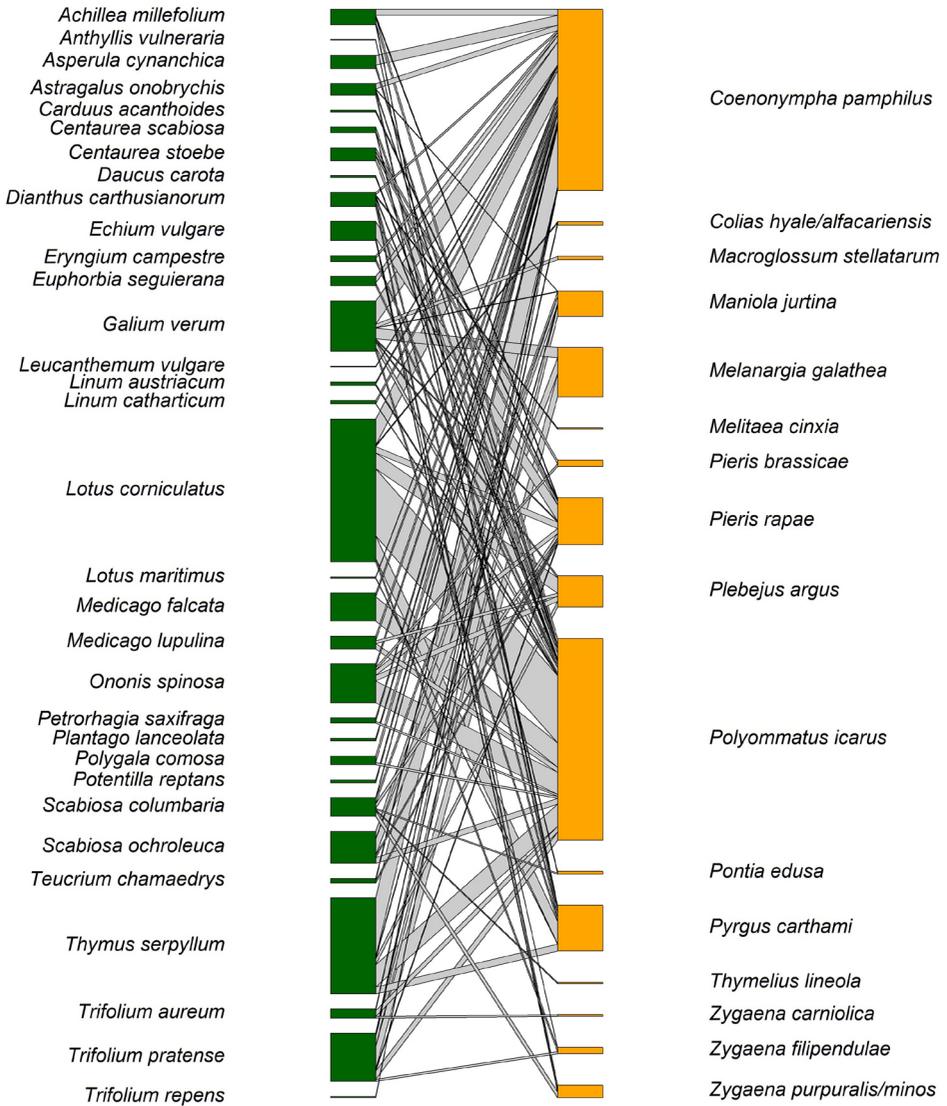
Fig. 6: Bipartite butterfly-flower networks of the cattle pastures aggregated over all replicate surveys. Nectar flowers in green, flower visiting butterflies in orange. Interactions drawn as lines, whose width is proportional to the number of observed interactions.

Fig. 7: Bipartite butterfly-flower networks of the Przewalski's horse pasture aggregated over all replicate surveys. Nectar flowers in green, flower visiting butterflies in orange. Interactions drawn as lines, whose width is proportional to the number of observed interactions.
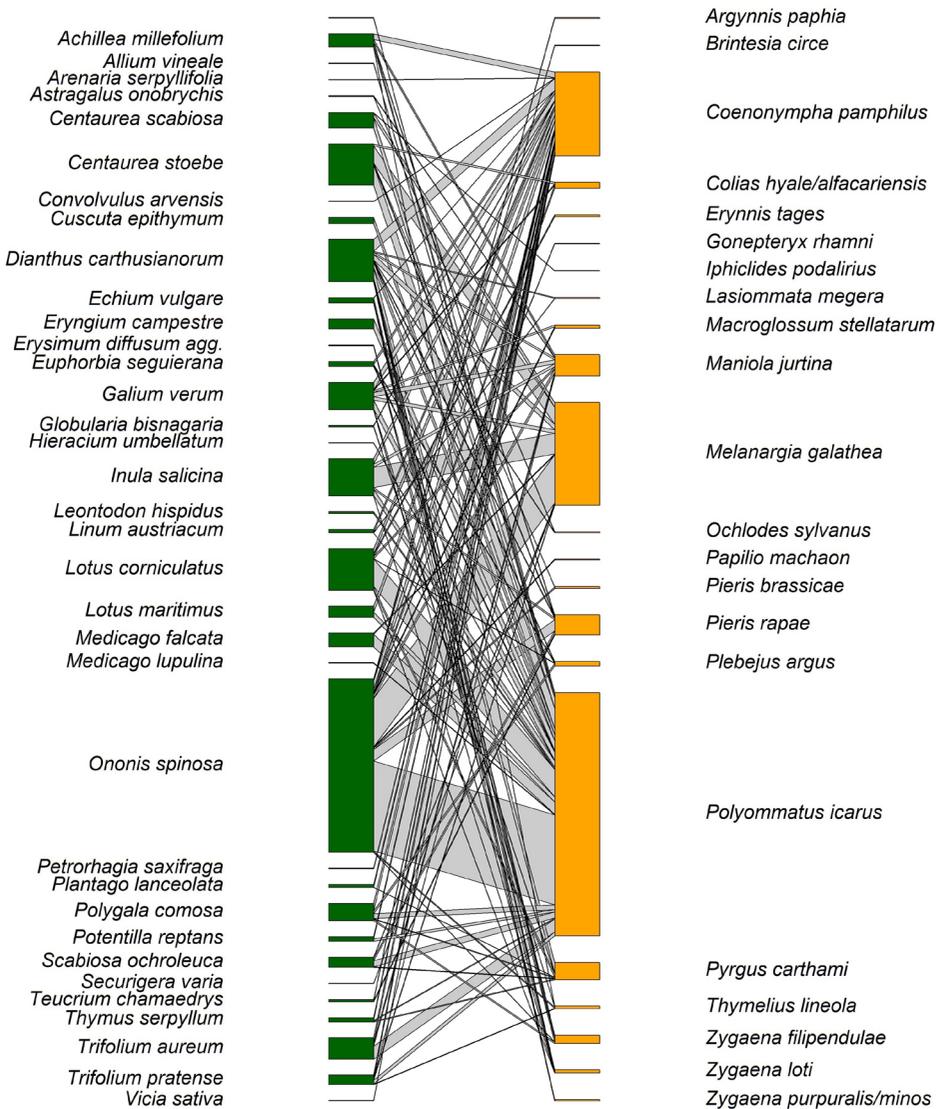
Fig. 8: Bipartite butterfly-flower networks of the meadows aggregated over all replicate surveys. Nectar flowers in green, flower visiting butterflies in orange. Interactions drawn as lines, whose width is proportional to the number of observed interactions.
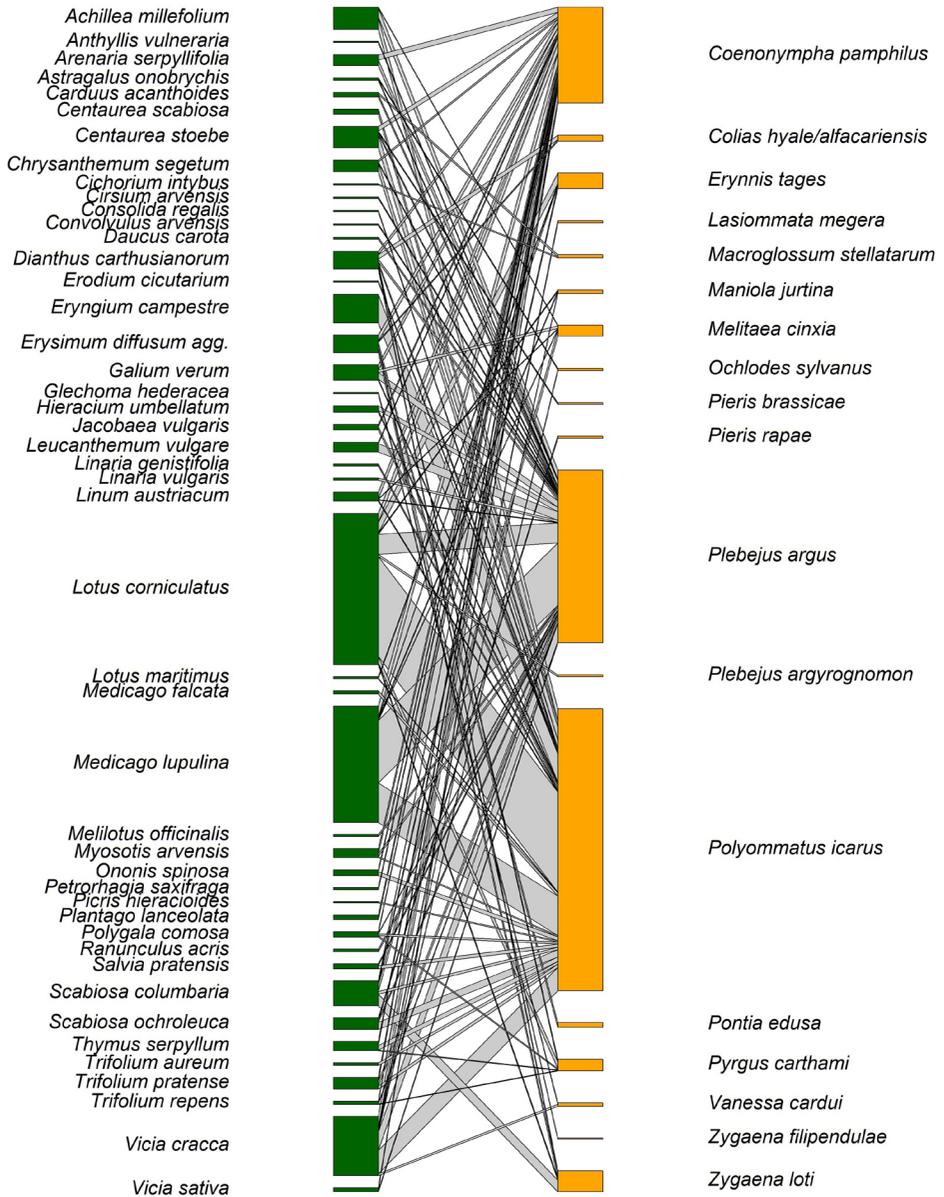
Fig. 9: Bipartite butterfly-flower networks in June, regardless of the land use type. Nectar flowers in green, flower visiting butterflies in orange.
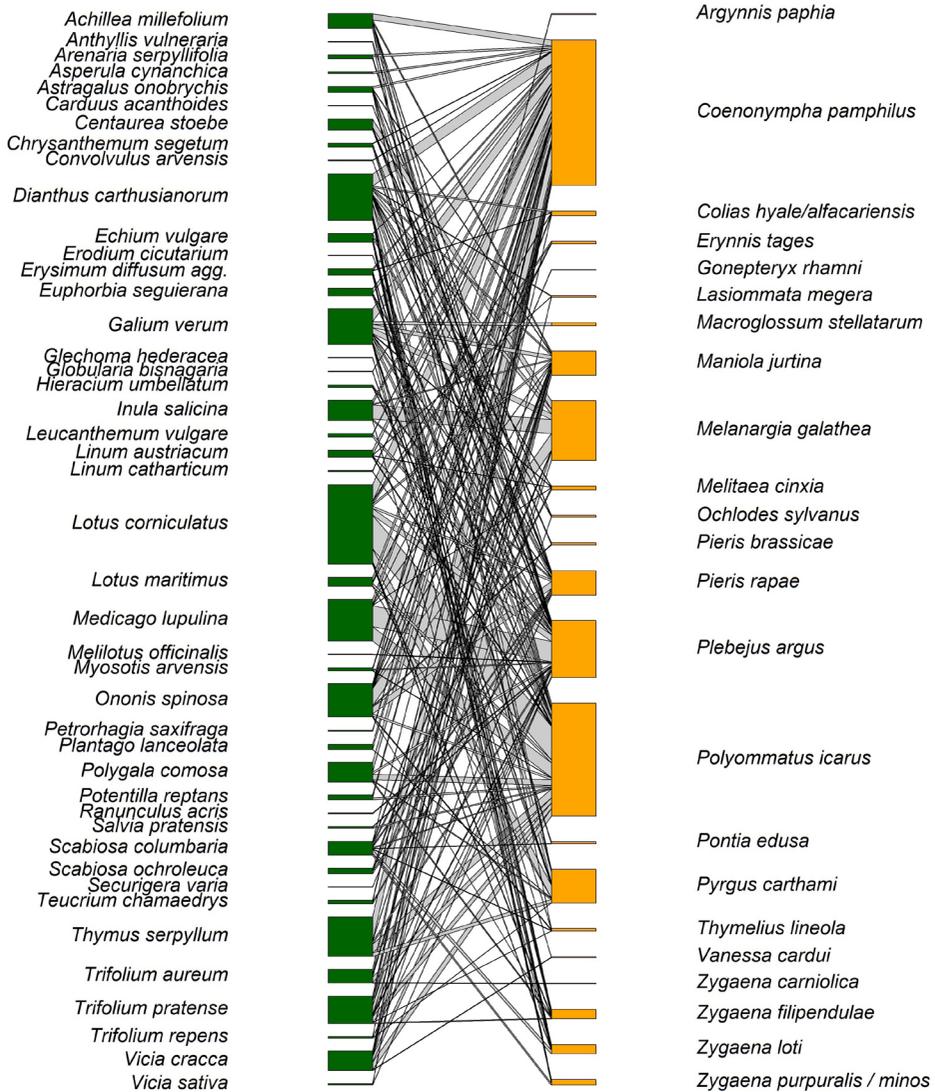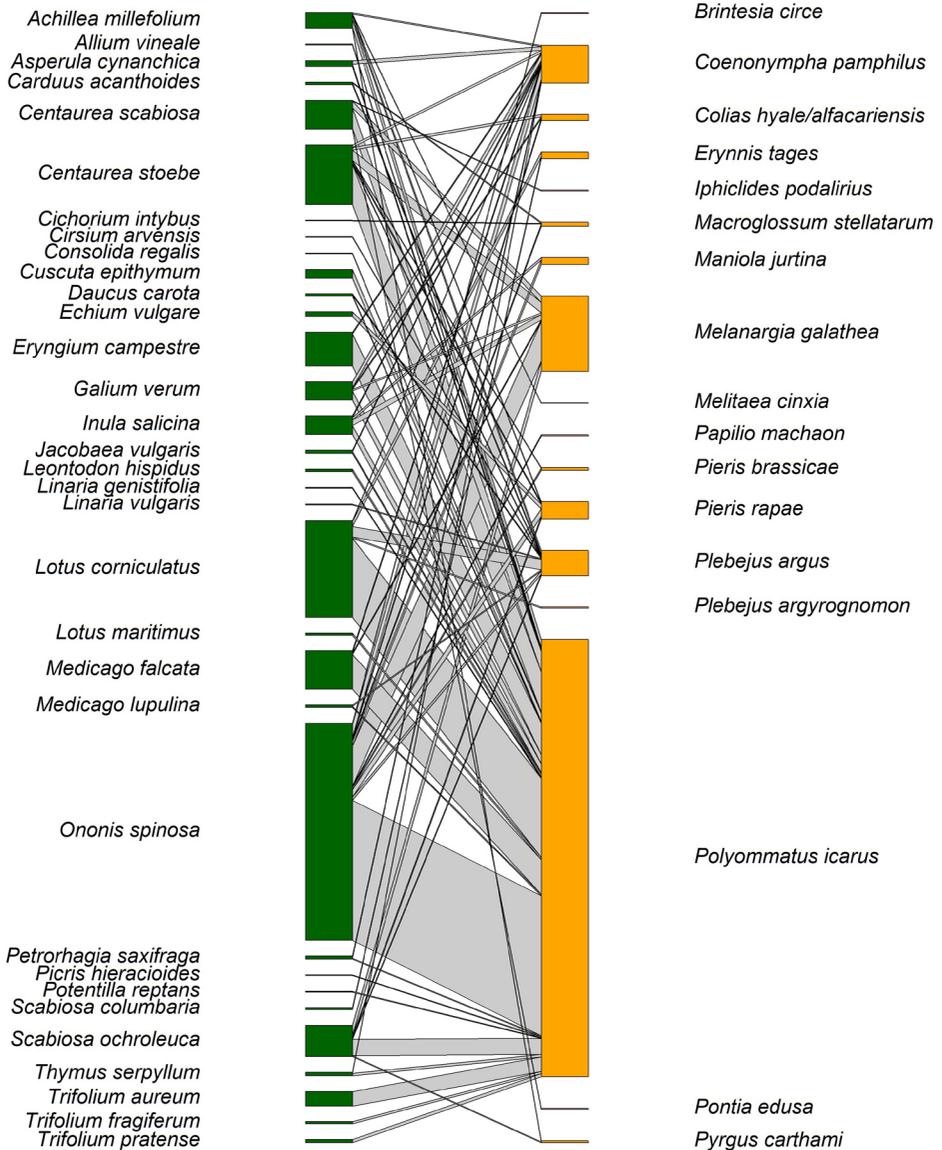
Fig. 10: Bipartite butterfly-flower networks in July, regardless of the land use type. Nectar flowers in green, flower visiting butterflies in orange.

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) also confirmed a peak of plant and butterfly species in late summer, viz. July and August. However, this pattern did not recur in our present study. Rather, the accumulation curves revealed a significant decrease of species diversity from June to July 2021. This could likely be explained by the massive summer drought in 2021 (Gao et al. 2009, Forister et al. 2018). There was a positive correlation of flower supply and visitation rate. The much tighter correlation between nectar flower abundance and observed interactions in July might also indicate a bottleneck of nectar resources in late summer due to the drought.

In contrast to their larval stages (Clarke 2022), European butterfly species are well known to utilize rather broad ranges of nectar flower species as adults, in a largely opportunistic manner (Dennis 2010). While temporary flower constancy may emerge in butterflies at the individual or population level under suitable conditions (Altermatt & Pearse 2011), flower-visiting butterflies are much less specialized than many other pollinators such as flies or wild bees. Among the latter, a sizeable fraction is oligolectic (Westrich 2019). It was therefore not surprising that we could observe a number of butterfly-flower interactions that had not previously been reported in the evaluated literature.

Nevertheless, communities of butterflies and the flowering plants they visited for nectaring differed clearly in regard to species diversity and composition between grassland types. Yet, structural differences in the resulting networks were only weakly detectable between grazed and mown grassland habitats, while differences in the networks between early and high summer were distinct. We attribute this observation to the high flexibility of butterflies when foraging for nectar, so that these insects may opportunistically switch to alternative nectar sources whenever needed. Obviously in that regard the mown or grazed grassland sites did not offer conditions so contrasting from another to stipulate repercussions on network level. One might have expected the extensively grazed grasslands to offer more favourable conditions for flower visitors, since grazing does not remove all flowers at once, as does mowing. However, at least as long as our meadow sites had not yet been mown, they even offered more nectar flower species relevant for butterflies and we observed no consistent differences between grassland types in flower abundances. To conclude, while species diversity and composition significantly differed between the land use types, these differences were not reflected by network specialisation or modularity. These metrics were unable to characterise the differences between the butterfly biocenoses in the study area well. Hence, although network measures may yield important insights about the analysed interactions, this information might be less relevant in the light of practical nature conservation.

These observations do not imply that there were no differences at all between the butterfly-flower networks in regard to individual species. Indeed, some butterfly species were more important in flower visitor networks of one grassland type than in the others. For example, *C. pamphilus* contributed a much larger share to the networks on cattle pastures, *P. argus* on meadows, and *M. galathea* on the horse pasture (Figures 6, 7 and 8). Yet,

these local "preferences" did not translate into sizeable effects on network level. It is also worth mentioning that, since our study sites were all situated in a large conservation area, land-use intensity was low, be it through grazing or mowing. Therefore, our study sites did not encompass sites under intense levels of management, in contrast for example to the study of Weiner et al. (2011).

Although in total 27 butterfly species were observed visiting 59 plant species, just 30% of the butterfly species and 15% of the plant species accounted for most of the 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. Again, only a few species built up most of the observed networks. Nevertheless, it should not be concluded that only common species are functionally important in the networks. Rare species might not play a prominent direct role in the networks, but their existence could have an indirect impact on networks. For example, an increasing number of studies suggest a link between higher biodiversity and more effective pollination services (Vergara & Badano 2009, Blitzer et al. 2016). Another line of evidence is that some members of a network might improve the effectiveness of others (Cardinale et al. 2002, Greenleaf & Kremen 2006). Diversity can also be seen as an insurance (Valone & Barber 2008). At one point in time an abundant species might dominate in flower visitor interactions, but if populations of this species are somehow affected, e.g. by climate change or other disturbances, other co-occurring species might step in.

Probably the most interesting finding was that specialization at network level as well as across butterfly species decreased substantially from June to July 2021, concomitant to the massive decrease in nectar flower abundance. We attribute these observations to the effects of the severe drought during June, which finally resulted in an almost complete lack of nectar flowers on the study sites in August (E. Depisch, personal observations). 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 our 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. This is likely due the ability of plants and pollinators to switch partners. In line with these thoughts, our results showed a low specialisation of the key players within the networks, especially among the plants.

During our observations, flower-visiting butterflies distributed more unevenly across available nectar flower species in June, when still more flowering species and flower units were available, while specialization decreased in July. Apparently, then, butterflies were forced to distribute their foraging efforts on all of the few nectar sources that were still available. Concomitantly, also network modularity was slightly higher in June than in July.

As a consequence, competition between butterfly species, but also between butterflies and other flower visitors, was likely higher after drought in July, whereas in June there was still more scope for specialization, preferences and thus resource partitioning among butterflies. If spells of drought should become more frequent in the region, along with

climate change (Dai 2013), more intense competition for the few available flowers might have repercussions on reproduction and population dynamics of butterflies. This could be especially critical in species which are known to be strongly dependent on sufficient nectar income for realizing their fecundity (Jervis & Boggs 2005, Lebeau et al. 2018).

Overall, the summer drought shaped grassland butterfly-flower networks on grassland sites in the National Park Neusiedler See – Seewinkel more strongly than the management practices that have given rise to the different grassland types. This contrasts with species diversity and composition, which significantly differed between the land use types for both groups of organisms connected in the networks. It seems that the reduction of flower supply because of a severe summer drought forced the butterflies towards a more opportunistic use of the remaining nectar sources, thereby reducing leverage for specialization and modularity at network level. Although some changes occurred between the two observation months, the importance of the partners did not change profoundly over time. Even though all observed butterflies are opportunistic flower visitors, there were preferences noticeable. Extensive mowing led to the highest species diversity in nectar plants and visiting butterflies. Species of conservation concern like *Pyrgus carthami* or *Melitaea cinxia* did not contribute high proportions of visitations to the networks.

Deutsche Zusammenfassung

Wir analysierten Netzwerke zwischen tagaktiven Faltern und Nektarblüten auf drei Typen von Grasland-Ökosystemen im Nationalpark Neusiedler See-Seewinkel: (1) eine Koppel beweidet durch Przewalski-Pferde in sehr geringer Dichte, (2) extensive Rinder-Hutweiden und (3) ungedüngte Heuwiesen. Die Datenaufnahme erfolgte im Juni und Juli 2021 während einer ausgeprägten Sommerdürre. Insgesamt wurden 4.160 Interaktionen an Blüten zwischen 27 Falter- und 59 Pflanzenarten beobachtet, darunter 147 Kombinationen, die zuvor nicht berichtet worden waren. Artdiversität und -zusammensetzung der interagierenden Gemeinschaften variierten signifikant zwischen den Graslandtypen und Erhebungsmonaten. Die höchste Vielfalt wurde auf Heuwiesen beobachtet. Nektarblüten traten in den 3 Graslandtypen in etwa gleicher Häufigkeit auf, aber das Blütenangebot nahm infolge der Dürre signifikant vom Juni zum Juli hin ab. Netzwerk-Spezialisierung H2' und -modularität Q unterschieden sich nicht in Relation zum Graslandtyp, aber nahmen im Juli deutlich ab. Alle beobachteten Blüten besuchenden Falter nutzen eine Vielzahl von Nektarquellen, aber ihr beobachteter mittlerer Spezialisierungsgrad d' war auf den Heuwiesen höher als auf beiden Typen von Weideökosystemen und nahm zudem im Zuge der Dürre deutlich weiter ab. Diese Beobachtungen zeigen, dass Grasland-Schmetterlinge opportunistisch und flexibel auf vermindertes Blütenangebot reagieren, wohingegen das extensive Grasland-Management nur wenig Einfluss auf die Netzwerkstrukturen hatte. Aufgrund ihres Blütenangebotes erwiesen sich die Heuwiesen als wichtige Lebensräume im Habitat-Mosaik des Schutzgebietes.

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