BACHELOR’S THESIS

Species assemblage and trait distribution of diurnal Lepidoptera at a dry levee subdividing a floodplain area, compared intra- and inter-annually

Melanie Haidvogl

12234718

12234718@univie.ac.at

Supervisor: Univ.-Prof. Mag. Dr. Konrad Fiedler

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Abstract

Lepidoptera are one intensively studied order of insects and known for their ability to reflect environmental alterations, especially with ongoing global warming. In Europe, grasslands offering warm and dry conditions are valuable habitats for butterfly populations and communities. The Marchfeldschutzdamm runs through the National Park Donau-Auen and, because of its artificial construction, mainly consists of such xerothermic conditions. In 2023, species richness and functional diversity as well as trait distribution of diurnal Lepidoptera species at the levee from early to high summer were investigated. These circumstances now lead us to another review in 2025, examining species assemblage and traits from mid to high summer and, additionally, comparing our findings with those from 2023. My main topics were whether assemblage composition and traits of species would differ due to inter-annual fluctuations. Furthermore, I tested if changes in assemblage and trait distributions would occur in line with the phenological species turnover from mid to high summer. Regarding species assemblage compared between both years significant changes in variation of abundance as well as trait distributions were observed. Especially *Cupido minimus*, *Leptidea sinapis/juvernica*, *Maniola jurtina* and *Melanargia galathea* were more common in 2023, whereas *Colias hyale/alfacariensis*, *Polyommatus icarus* and *Issoria lathonia* were clearly more prominent in 2025. The traits voltinism, specialization status and wetland preference reached higher values in 2025, while the preference for xerothermic habitats declined. Based on this short window of merely two years, such variation most likely happened by reason of annual fluctuations and local marginal conditions rather than climate change. At the same time, a species turnover resulting in variable trait distributions along the season was partially met. Concerning this matter, grass feeders were most common and especially present at the end of June, host plant specialization fluctuated across all survey rounds, multivoltine forms predominated and arose with round second and xerothermic habitat preferences still clearly accounted for the majority. A significant shift of species over the summer was shown.

Keywords: Lepidoptera, butterflies, diurnal moths, species assemblage composition, trait distribution, seasonal shift, inter-annual fluctuations

Zusammenfassung

Lepidoptera sind eine intensiv studierte Ordnung der Insekten und bekannt für ihre Fähigkeit, Umweltschwankungen zu reflektieren, insbesondere durch fortschreitenden globalen Klimawandel. Trockene und warme Graslebensräume erweisen sich dabei in Europa als wertvolle Habitate für Populationen und Gemeinschaften insbesondere tagaktiver Schmetterlinge. Als Beispiel eines solch xerothermen Areals gilt der Marchfeldschutzdamm, der durch den Nationalpark Donau-Auen verläuft und durch den Menschen künstlich geschaffen wurde. Bereits im Jahr 2023 wurde an diesem Damm eine Untersuchung von Artenreichtum, funktionaler Diversität und der Verteilung spezifischer Eigenschaften tagaktiver Lepidoptera von Früh- bis Hochsommer vollzogen. Die Wiederholung dieser Studie setzte sich nun das ähnliche Ziel, sowohl die Artenzusammensetzung als auch die Verteilung repräsentativer funktioneller Eigenschaften von Mittsommer bis Hochsommer zu untersuchen und zusätzlich Vergleiche mit den Ergebnissen aus 2023 herauszuarbeiten. Wesentliche Themen beinhalteten zum einen, ob Artenzusammensetzung und Eigenschaften aufgrund von zwischenjährlichen Schwankungen Unterschiede aufweisen, und zum anderen, ob Variationen dieser Faktoren infolge eines Arten-Turnovers von Mittsommer bis Hochsommer auftreten. Zwischen beiden Jahren wurden signifikante Differenzen bezüglich der Artenzusammensetzung und der Verteilung von Eigenschaften beobachtet. Besonders *Cupido minimus*, *Leptidea sinapis/juvernica*, *Maniola jurtina* und *Melanargia galathea* traten im Jahr 2023 häufiger auf, während *Colias hyale/alfacariensis*, *Polyommatus icarus* und *Issoria lathonia* im Jahr 2025 deutlich prominenter vertreten waren. Multivoltine Arten, der Grad der Spezialisierung und die Bevorzugung nasser Standorte erreichten höhere Werte im Jahr 2025, während die Präferenz für xerotherme Habitate zurückging. Hinsichtlich des kurzen Zeitfensters von nur zwei Jahren sind derartige Fluktuationen höchstwahrscheinlich auf jährliche Schwankungen und lokale Randbedingungen, jedoch nicht auf Auswirkungen des Klimawandels zurückzuführen. Die Verlagerung der Spezies, endend in variablen Verteilungen der Arteigenschaften entlang der Saison, wurde teilweise gezeigt. Diesbezüglich waren Grasfresser die meisten Vertreter und besonders Ende Juni vorhanden, Wirtspflanzen-Spezialisierung schwankte über die Runden hinweg, multivoltine Formen überwiegten ab dem zweiten Durchgang und Präferenzen für xerotherme Habitate machten die klare Mehrheit aus. Eine signifikante Artenverschiebung trat über den Sommer auf.

Schlüsselwörter: Lepidoptera, Tagfalter, tagaktive Motten, Artenzusammensetzung, Verteilung der Eigenschaften, saisonale Verschiebung, zwischenjährliche Schwankungen

Introduction

The Marchfeldschutzdamm, running from the eastern margin of Vienna to the mouth of river Morava into the Danube, characterizes a levee constructed in favour of the Vienna Danube regulation. It was already built in 1884, i.e. approximately 150 years ago (Almásy et al., 2021), and passes through the National Park Donau-Auen on its way from Vienna to Marchfeld (Nationalpark Donau-Auen GmbH, n.d.). Originally, this area featured wetland characteristics, offered by hydrological regimes and backwater floods, which flood regulation schemes act against (Reckendorfer et al., 2013). Since its formation, the levee serves flood control and influences its environment in form of extensive sun exposure and drought due to sedimental structure. This influence ensures a valuable xerothermic vegetation (Wesner, 1995) responsible for faunal conditions, comprising a similar value. Moreover, the protection of species usually is consistent with various monitoring projects that aim to be considerate of appearing subjects of protection (Nationalpark Donau-Auen GmbH, n.d.).

Due to the high richness of butterfly species on European grasslands (van Swaay, 2002), such habitats possess great potential to contribute to preserving butterfly ensembles of the area. In fact, Lepidoptera are faunistically and ecologically well studied. Since they may be conveniently identified and monitored in the field, they usually are used as indicators for environmental changes (Lang et al., 2016). In this regard, butterfly monitoring represents a relevant method for depicting the state of biodiversity and to inform conservation management (Sevilleja et al., 2019). Globally, butterfly monitoring contributes to documenting climate change influences on individual species and entire communities (e.g. Zografou et al., 2014, Habel et al., 2021).

A trait, expressing itself physically, biochemically, behaviourally or temporally, refers to a specific characteristic of one individual and possibly impacts its performance and fitness. Thus, from an ecological point of view, species can be seen as assemblages of individuals sharing behavioural and phenotypic traits, possibly affecting their existence among each other (Cadotte et al., 2011). Species coexisting in analogue environments with similar climatic conditions therefore are characterized by similar traits, while changes in environmental states usually trigger transformation of trait distribution (Leingärtner et al., 2014).

Looking at climate change, butterfly community composition may be affected in a broader period but not necessarily concerning short periods of time (Zografou et al., 2014). Thus, differences in this regard may likely emerge due to annual abundance fluctuations which are common among insects (Franzén et al., 2013; Uhl et al., 2022). Nevertheless, any ecological changes may be reflected in alterations in community composition as well as in trait distributions, since these two factors seem to be linked (Eskildsen et al., 2015).

In 2023, species richness and the community structure of diurnal Lepidoptera regarding ecological traits and functional diversity were already surveyed from early to high summer at the same part of the Marchfeldschutzdamm (Hiel, 2023; Scanferla, 2023). For further investigation and evaluation of potential changes in assemblage and trait distribution since 2023, this survey was now repeated under approximately similar conditions, focusing on species assemblage composition as well as ecological trait distribution in 2025. In this regard, my hypotheses were as follows:

a) Trait distribution of diurnal Lepidoptera at the levee differs between mid and high summer due to seasonal species turnover.

b) Species assemblage at the levee differs between all survey rounds due to seasonal species turnover.

c) Both ecological trait distribution and species assemblage composition might show significant changes between 2023 and 2025 due to inter-annual abundance fluctuations.

Materials and Methods

Study site

The study sites were selected along the Marchfeldschutzdamm, more specifically inside the Nationalpark Donau-Auen, with our area reaching from Orth an der Donau across Eckartsau, almost until Witzelsdorf (for coordinates see Table 4 in the Appendix). Since the levee comprises dry and meadow-like vegetation (Almásy et al., 2021), all our survey area represents grassland. Centrally on top of the levee, an asphalted bicycle path runs along the dam, while meadows on both sides are affected by differences in slope inclination. Our sampling sites were restricted to the northern side, facing away from the Danube and containing a central dirt road.

Sampling

Data collection focussed on species belonging to the superfamily Papilionoidea plus diurnal moths, referred to as Lepidoptera or simply butterflies hereafter. Surveys occurred along 20 chosen transects, each comprising a length of about 100 m. At the beginning of our survey period, due to different mowing stages along the dam, only sections not mowed recently and therefore showing high vegetation height were picked. Distances between the transects varied from approximately 400 to 1800 m (Figure 1). Butterfly recording largely followed the principle of 'Pollard walks' (Barkmann et al., 2023) and occurred at a slow and steady pace along each transect, while butterflies up to five metres in front of the observer were registered. In this regard, the area for counting ranged from the upper edge (where the cycling path runs) to the lower edge of the dam (at the forest margin). If species identification was not possible by observation from a distance, butterflies were netted and released after. Individuals not identifiable in the field were photographed and identified later. Appropriate literature was used for identification (Slamka, 2004; Ulrich, 2018). The two pairs of sibling species *Colias hyale/alfacariensis* and *Leptidea sinapis/juvernica* were treated as operational taxonomic units, since their correct differentiation in the field is almost impossible.

Figure 1: 20 transects monitored in 2025 located along the dam (created in ArcGIS and edited in Inkscape, Photo source: ESRI 8/2025)

Sampling occurred in four survey rounds, the first of which was conducted in June and the remaining three in July. Each round was completed in one to four days (depending on weather). Data were collected between 10:00 and 17:00 h CEST. To ensure suitable weather conditions only days with no rain, heavy wind or unusually low temperatures were chosen. Additionally, the parameters cloud coverage (visually estimated on a scale between 1/8 to 8/8), wind speed (measured through the Beaufort rank scale from 0 = no wind to 5 = moving branches and trees, audible wind), vegetation height (< 10; 10-30; 30-70; > 70 cm) and flower availability, measured on a rank scale from 1 to 5 (1 = no flowers available, 5 = very high flower density), were noted.

Species trait data

Examined species traits included: Poaceae as larval host plant family; larval host plant specialization; voltinism; and preferences for xerothermic or wetland habitats. Further information on each trait can be found in Table 1. In general, most species in our list had been monitored in 2023 already and therefore, a huge amount of trait information from this data base (Hiel, 2023; Scanferla, 2023) could be transferred and re-used directly. Missing ecological trait data for newly monitored species was adjusted by Konrad Fiedler, using faunal monographs. For larval host plant specialization, mean pairwise phylogenetic distances (MPD values) of documented hosts for Papilionoidea were extracted from an independent source (Seifert & Fiedler, 2024).

Statistical analysis

Compiled data was analysed using the two programs Jamovi 2.7.4 (The Jamovi Project, 2025) and PAST 5.2.2 (Hammer et al., 2001). In PAST, non-metric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA) for both the comparison of species assemblage between years as well as between survey rounds of 2025 was performed. Multivariate comparisons were based on pairwise Bray-Curtis similarities. The four monitoring rounds were further differentiated into mid and high summer. Consequently, survey round one and two refer to midsummer while the remaining two were labelled as high summer. In the inter-annual comparison, indicator species (following the concept of Dufrêne & Legendre (1997)) were also determined, leaving out species rather irrelevant for the outcome (total number of sightings < 15, only exception: *Argynnis pandora*). Concerning the NMDS for species assemblage scattered over the 20 transects and compared between all survey rounds, vegetation height and flower availability were included as possible explanatory variables, additionally checking their relationship with a Spearman correlation. Also, since a strong outlier occurred in the ordination of raw observation data, a "dummy species" (with abundance N = 1 for each transect per round) was added (Clarke et al., 2006).

Jamovi software was used for one-way analyses of variance (ANOVAs) as well as generalised linear models (GLMs), specifically beta regression, when examining trait distributions of diurnal Lepidoptera (see Table 1 for further description). Regarding ANOVA, the trait Poaceae as larval host plant family was compared only between monitoring rounds of 2025, while wetland was included for the inter-annual comparison only. For GLM analysis, rounds only were associated with the traits Poaceae as larval host plant family and xerothermic habitats, whereas for comparisons between years no traits except for xerothermic and wetland habitats were included.

To address trait compositions, community weighted means (CWMs) (see Lepš & de Bello (2023) for further explanation) of each trait, either grouped according to survey rounds or years, were calculated in a spreadsheet software. For modelling through beta regression, data points constituting the exact values of zero or one had to be adjusted (zero then equals 0.001 and one equals 0.999).

For the association of both survey years in their species assemblage as well as the comparison of the trait distribution between 2023 and 2025, exclusively data collected of Papilionoidea was used, since moth data from 2023 was not available. Furthermore, the database for examining the trait larval host plant specialization by using the mean pairwise phylogenetic distance (MPD) (Seifert & Fiedler, 2024) also only contained data for Papilionoidea. This implicates that both survey round and year comparison are restricted to this group, since for most diurnal moths such information was not accessible.

All graphs, either created in Jamovi or PAST, underwent some additional editing in Inkscape 1.4.2 (https://inkscape.org).

Table 1: Description of examined species traits.

Larval host plant family: Poaceae	Functional affinity of larvae to hostplants in the family Poaceae: 0 - larvae not associated with Poaceae, 1 - larvae feed on graminoid hosts (Poaceae, rarely Cyperaceae)
Larval host plant specialization	Mean pairwise phylogenetic distance (MPD): higher value - broader larval host plant niche, lower value - larval host plant niche rather narrow

Voltinism	Number of generations per year in Eastern Austria: 1 - one generation per year, 1.5 - possibly partial second generation, 2 - two generations per year, 2.5 - possibly partial third generation, 3 - three or more generations per year
Xerothermic habitats	Presence of species in xerothermic habitats: 0 - not present, 0.5 - occasionally present, 1 - species bound to warm or dry habitats
Wetland habitats	Presence of species in wetland habitats: 0 - not present, 0.5 - occasionally present, 1 - species bound to wetland habitats

Results

In total, a number of 1353 individuals from 51 species across 12 families were sighted. Out of these individuals, 1270 (roughly 94 %) proved to be representatives of Papilionoidea and only 83 were diurnal moths.

Species assemblage

The species assemblages of the years 2023 and 2025 differed markedly (Figure 2). A one-way PERMANOVA (9999 permutations) showed that this difference was highly significant (Total sum of squares: 3.549; Within-group sum of squares: 2.641; $F = 12.03$; $p < 0.0001$). Additionally, an indicator species analysis (Figure 3) gives insight into species that contributed the most to variation between assemblages. *Cupido minimus*, *Leptidea sinapis/juvernica*, *Maniola jurtina* and *Melanargia galathea* were characteristically more common in 2023, while for 2025 these were *Colias hyale/alfacariensis*, *Polyommatus icarus* and, as the one with the highest significance, *Issoria lathonia*. Four butterfly species, namely *Anthocharis cardamines*, *Lysandra coridon*, *Ochlodes sylvanus* and *Pyrgus malvae*, observed in 2023 did not show up in the 2025 data. Conversely, four species were newly seen in 2025, namely *Argynnis pandora*, *Cupido argiades*, *Pararge aegeria* and *Vanessa cardui*.

The assemblage of species across all four survey rounds within 2025 (Figure 4) shows the phenological species turnover beginning with round one at the end of June, consecutively over round two and three until round four at the end of July. Again, these differences were highly significant (One-way PERMANOVA; Total sum of squares: 9.216; Within-group sum of squares: 6.467; $F = 10.77$; $p < 0.0001$). In the ordination plot, vegetation height and flower availability are turning towards the same negative direction and even possess similar lengths, which is supported by a Spearman correlation between both parameters (Spearman's *Rho* =

0.725, $p < 0.0001$). Butterfly assemblages in June were associated with high vegetation and larger numbers of nectar flowers available, as opposed to the situation in July (after mowing).

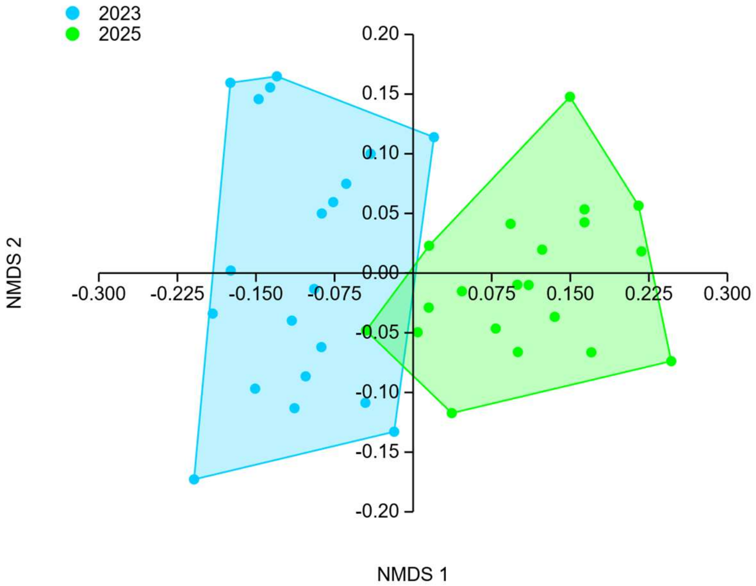

Figure 2: Total butterfly species assemblages at the levee compared between 20 transects each in 2023 and 2025 (Stress: 0.2422).

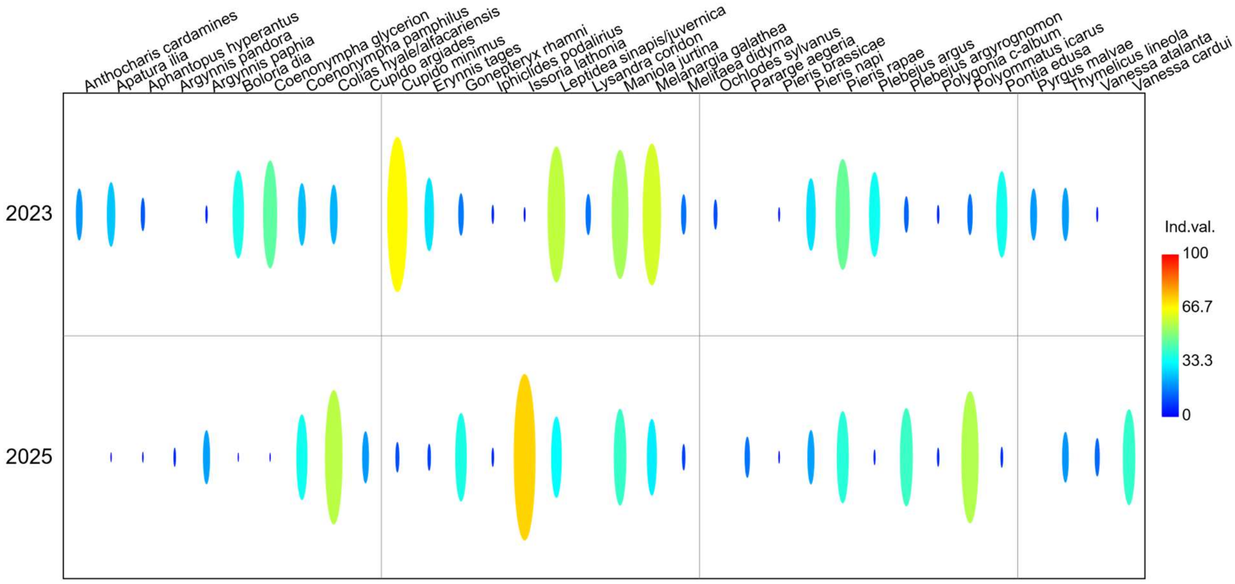

Figure 3: Indicator values of monitored butterfly assemblages compared between 2023 and 2025, excluding (for clarity) species scoring below 15 for both years (exception: *Argynnis pandora*).

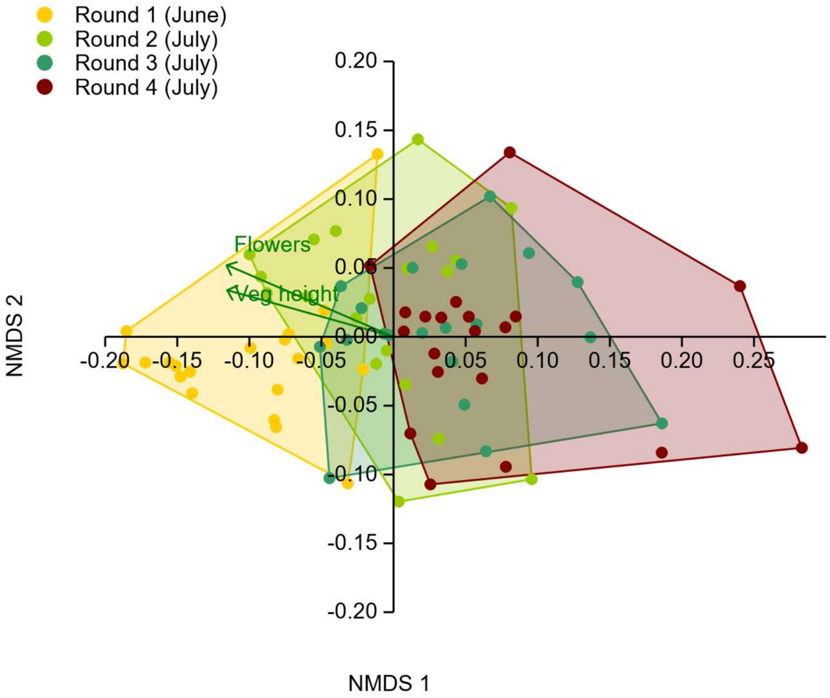

Figure 4: Butterfly assemblages of all survey rounds in 2025. Overlaid on the ordination plots are nectar flower availability (Flowers) and vegetation height (Veg height) as putative drivers of species composition.

Trait distribution

One-way ANOVAs for all analysed traits showed significant differences in their distributions compared between the two years, while all traits as well differed significantly in their frequency across the four survey rounds within 2025 (results shown in Table 2, Figure 5 and Figure 6). Butterflies associated with Poaceae as their host plant family, besides of representing the majority (CWM > 0.5), were especially prevalent in the first round (i.e. midsummer). Results for larval host plant specialization showed that the second and fourth round each differed significantly from the first and third round, whereas apparently, round two and four represent higher MPD values. Butterfly assemblages exhibited significantly higher scores regarding host plant niche breadth in 2025 than in 2023. For voltinism, univoltine species or those with a partial second generation occurred mostly in the first round, while forms of voltinism with more than one generation per year appeared in the remaining rounds more frequently. By comparing both years in terms of voltinism, it becomes obvious that in 2025 multivoltine species were more prevalent than in 2023. Preference for xerothermic habitats accounted for half or even more of all recorded butterflies in each of the survey rounds. Looking at both years, in 2023 sampling resulted in slightly, but significantly, more butterflies which prefer warm and dry environments than in 2025. On the other hand, the preference for wetland habitats remained much lower than for xerothermic habitats, and did not notably fluctuate throughout the rounds, but with a slightly higher score in 2025.

Several GLM analyses were performed (Table 3), for instance Poaceae as larval host plant family compared between the survey rounds in 2025. This specific model explains 22.4 % of the variance in the data, while its significance only accounts for the first round in contrast to the remaining three and therefore indicates a conspicuously higher incidence at the end of June. For xerothermic habitats, 11.1 % of the variance is allegeable, whereas wetland merely could reach for 2.46 %. For both these traits no significance was stated.

Table 2: Results of one-way ANOVAs for examined Lepidoptera traits at the levee, separately compared between survey rounds of 2025 and both years.

one-way ANOVA			
survey rounds			
	df	*F*	*p*
Larval host plant family: Poaceae	3; 40	13.4	**<0.001**
Larval host plant specialization	3; 38.5	8.36	**<0.001**
Voltinism	3; 40.4	15.9	**<0.001**
Xerothermic habitats	3; 41.1	6.93	**<0.001**
years			
	df	*F*	*p*
Larval host plant specialization	1; 48.0	42.1	**<0.001**
Voltinism	1; 34.6	14.5	**<0.001**
Xerothermic habitats	1; 77.7	15.4	**<0.001**
Wetland habitats	1; 77.8	9.27	**0.003**

Table 3: Results of GLM analyses (with beta distribution for the error structure) for examined Lepidoptera traits, separately compared between survey rounds of 2025 and both years.

GLM (beta)				
survey rounds				
	R^2	Contrast	Estimate	*p*
Larval host plant family: Poaceae	0.224	Round 2 - 1	-0.214	**0.003**
		Round 3 - 1	-0.282	**<0.001**
		Round 4 - 1	-0.286	**<0.001**
Xerothermic habitats	0.111	Round 2 - 1	-0.033	0.342
		Round 3 - 1	0.058	0.095
		Round 4 - 1	-0.035	0.321
years				
	R^2	Contrast	Estimate	*p*
Xerothermic habitats	0.165	2025 - 2023	-0.036	**0.009**
Wetland habitats	0.106	2025 - 2023	0.0359	**0.04**

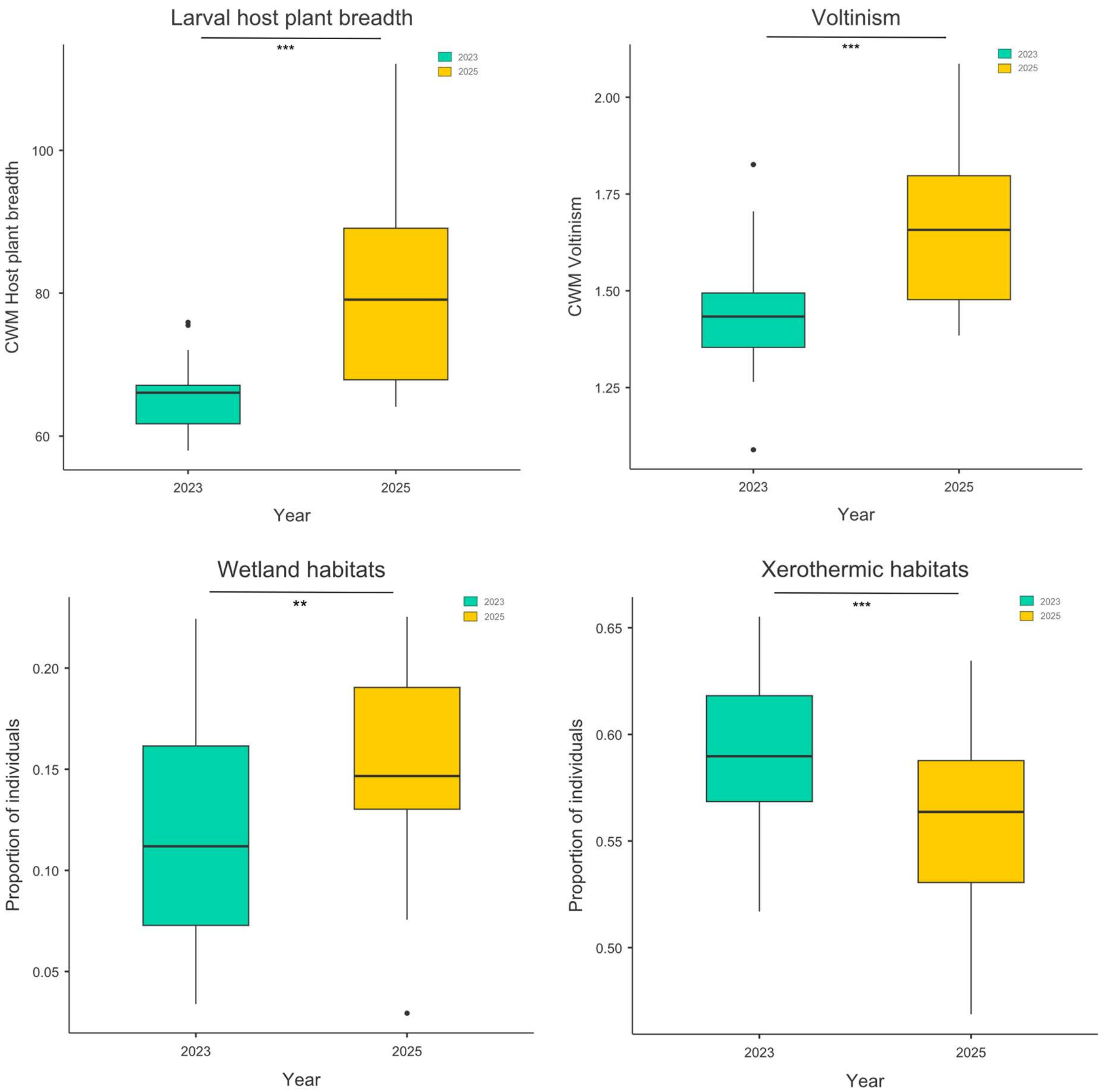

Figure 5: Distribution of the traits larval host plant breadth, voltinism, wetland preference and xerothermic preference, presented as CWMs, compared between 2023 and 2025.

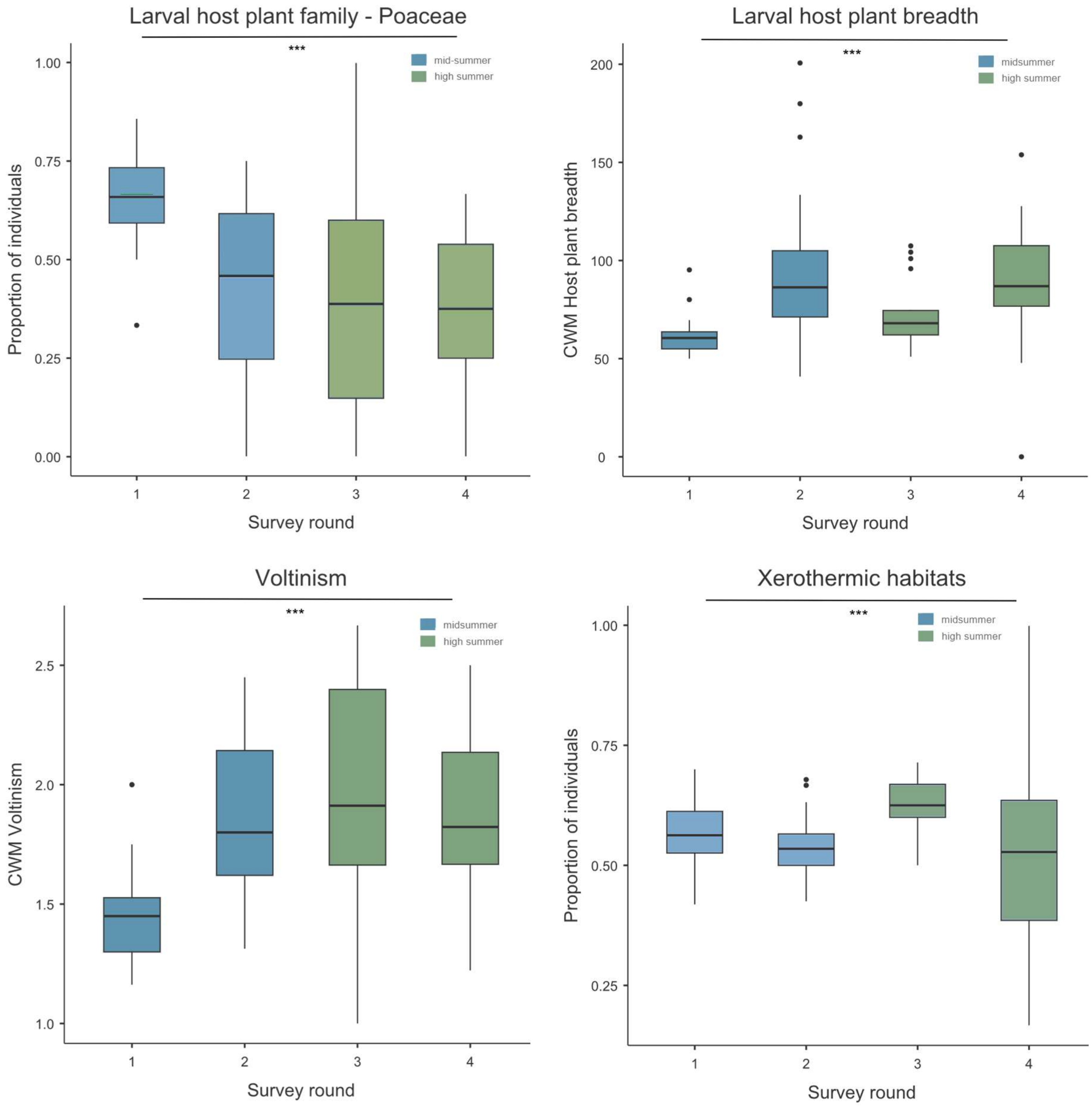

Figure 6: Temporal change of the distribution of the traits larval host plant family (Poaceae), larval host plant breadth, voltinism and xerothermic habitats, expressed as CWMs, over the four survey rounds in 2025.

Discussion

General issues with data collection period and Pollard walks

Through the present study, I showed significant differences in the composition of species assemblages at the levee between 2023 and 2025. These changes were mirrored in marked differences in the distribution of functionally important species traits. First, it should be noted that the period when transects were inspected varied, since sampling in 2023 already started in May, while this present analysis was only initiated at the end of June. Hence, phenological differences in generations of butterfly species could be responsible for missing species in only one of the two survey years. The univoltine species *Anthocharis cardamines* can be found as adult in May only until June and *Pyrgus malvae*, undergoing a spring generation, can be also found in May (Slamka, 2004), possibly responsible for their absence in 2025. However, all other species not recorded in 2025 (*Lysandra coridon*, *Ochlodes sylvanus*) are usually active as adults in July as well. This pattern may be explained by inter-annual fluctuations of compositions of species assemblages (Uhl et al., 2022), but might also have occurred due to inconvenient weather conditions like rain in July 2025 (GeoSphere Austria, 2025). Furthermore, the transects were mowed in July and therefore reduced in their nectar availability, leading butterfly individuals to leave or causing direct mortality (Cizek et al., 2012). Second, our sampling method, transect counts or also called Pollard walks, tends to gain ever more interest among butterfly sampling methods (Sevilleja et al., 2019). Unfortunately, this convenient method reveals problematic biases such as species remaining undetected, the presence of adult individuals due to space or time, while also their colour, size and behaviour influences data recordings (Dennis et al., 2006). These circumstances lead to the possibility, that some individuals potentially representing even additional species were missed during sampling, consequently affecting our results. Because especially moths are prone to attract less attention due to their unobtrusive colours and appearance, this might be the reason why much less moths were recorded compared to species of Papilionoidea. For this present analysis, all observers involved in both investigations for 2023 and 2025 used the same sampling method and exhibited low experience in terms of butterfly sampling, enabling unproblematic year comparison. On the other hand, butterfly numbers on a daily scale are displayed by relative abundance indices, which transect counts can account for (Nowicki et al., 2008) and in comparison with more comprehensive area-time counts, transect counts yielded analogue results (Barkmann et al., 2023). Furthermore, statistical agents help with the usage of long-term transect data regarding life history or occupancy (Kral et al., 2018).

Species assemblages of both years

By inspecting the assemblage of species compared between 2023 and 2025, a clear difference can be observed, and looking at the indicator species analysis provides information about those dominant species in both survey years which were mostly responsible for the observed inter-annual differences. However, 26 species and by far the most part, independent from their number of occurrences, remained similar. One plausible explanation for the variation in dominant species might be population fluctuations happening annually (Uhl et al., 2022), which correlates with the fact that with its xerothermic character among floodplain areas, the levee inhabits localized resources that are inevitable for the formation of such compositions of species. Then, this dependence on resources would lead to more susceptibility to fluctuations (Franzén et al., 2013). Concerning the indicator species analysis, *Argynnis pandora* holds an indication value below 15, that would be too low for including it into the graphic representation. However, this butterfly happens to be a rare migrant species in eastern Austria and hence emerged as a truly remarkable finding (Höttinger, 2018), which is why I included it in Figure 2. *A. pandora* had also not been observed in the study area before (e.g. Fies et al. 2016).

Species assemblages of survey rounds in 2025

As shown in the results, species composition of butterflies during all rounds ranging from June to the end of July happened to be significantly different from each other. Clearly, this picture can be seen as reflecting the species turnover from mid to high summer, since a change in abundant species took place because of variable flight periods (Altermatt, 2012). Vegetation height and nectar flower availability correlated strongly along the first coordinate of the ordination, since mowing events started at our second site inspection and gradually expanded over all transects. Additionally, the inter-correlation between both variables confirms the expected decline of flower availability with reduced vegetation height. According to the controversial aspects of mowing regimes (Fies, 2014), this could have made an impact on sampling outcome as well. These include the support of dispersal of butterflies from their habitat (Popović & Nowicki, 2023) and mortality caused by mowing in early hours, when butterfly individuals are still inactive (Cizek et al., 2012). Moreover, heterogeneous mowing strategies seem more attractive for butterflies than homogeneous forms of mowing and support the diversity of invertebrate assemblages in general (Cizek et al., 2012).

Trait distributions

Strikingly, grass feeding butterflies reached the highest prevalence in the first survey round, significantly different from the remaining others. The levee as grassland habitat comprising dry conditions was expected to primarily support species feeding on grasses, especially the northern side which is less prone to floods (Fies et al., 2016). Still, the high occurrence at the end of June in contrast to July leaves the question, which factor was responsible for such a strong variability. Looking into the data sets of all survey rounds more precisely, there are a few grass-feeder species that mainly or even solely occurred during our first survey round.

The two main species were *Melanargia galathea*, which indeed still appeared in round two to four but on much fewer transects, and *Thymelicus lineola*, disappearing at all after the first round. Usually, these species would occur through July, even until August (Slamka, 2004), but again, July comprised rainy conditions above-average (GeoSphere Austria, 2025), potentially responsible for this pattern of occurrence. Despite the visible significance, larval Poaceae feeders apparently tend to represent larger parts of the local community, already shown in the past (Fies et al., 2016).

Differences in the degree of larval host specialization over all rounds, as well as with larval Poaceae feeders, likely are due to some species occurring more frequently in the second and fourth sampling round. For instance, by looking deeper into the sampling data, *Argynnis paphia*, which possesses a high MPD value of approximately 232 and therefore rather acts as a generalist, only was present several times in round two and four. This species normally inhabits woodland and visits meadows rather temporarily (Cizek et al., 2012), hence likely contributing to the shown fluctuations with its mobile behaviour. Instead of a distinct difference between mid and high summer, this temporal range therefore seems to be marked by fluctuations of species abundance potentially caused by different flight periods through both seasonal stages (Altermatt, 2012). The significantly higher result in 2025 compared to 2023 could of course be another outcome resulting from annual fluctuations (Uhl et al., 2022). However, since specialist species commonly seem to react more sensitively to environmental changes one could carefully assume, that this pattern reflects consequences of climate change (Diamond et al., 2011; Uhl et al., 2022). Observing the development over the last decades, specialists even underwent higher degrees of populational declines than generalized species (Uhl et al., 2022). On the other hand, as mentioned before, this comparison ranges over a time of two years only, which makes a statement about ecological changes resulting from climate change rather difficult (Zografou et al., 2014). Despite global warming, local phenomena like transect mowing, the unfavourable weather conditions or general impact of flood control schemes on floodplain areas (Reckendorfer et al., 2013) are likely to have caused changes in distributions.

With voltinism, like larval Poaceae feeders, only the first round differed significantly from all other rounds and by trend included rather univoltine species, whereas round two to four comprised more butterflies with more than one generation per year. This pattern can be explained by several univoltine indicator species, like *Gonepteryx rhamni*, *Thymelicus lineola*, *Melanargia galathea*, *Zygaena filipendulae* and *Zygaena loti* which mainly or solely were represented in the first round. The other way round, *Polyommatus icarus* as multivoltine species arose only a few times at the end of June but emerged more frequently in July. Hence, once again this trait gets affected by the species turnover through summer (Altermatt, 2012). The comparison between both years reveals high significance with a trend towards more generations per year in 2025. Very carefully, this picture could be interpreted as a response to climate change, as with host plant specialization above. Accordingly, increasing temperature causes accelerated metabolism and therefore development, which supports growth and might lead to a gain of yearly generations (Altermatt, 2009; Zeuss et al., 2017). However, such shifts in voltinism, for instance 'increasing voltinism' (Wepprich et al., 2025), would acquire further examination of species altering their number of generations, which this analysis was not longing for. We simply found an increase in multivoltine forms, which still could have evolved through inter-annual species fluctuations (Uhl et al., 2022).

Across all survey rounds, xerothermic habitat preferences turned out to be the most common attribute amongst butterfly species thriving at the levee. This leaves no surprises, since the dam is characterised by dry conditions in general (Nationalpark Donau-Auen GmbH, n.d.) and was previously described regarding this topic (Fies et al., 2016). Still, as a dry environment among floodplain areas, the levee forms a habitat for species that would otherwise not be able to live in this specific area, making this result especially remarkable. In contrast, the distributions in round three, and therefore at the beginning of high summer, comprise the highest value, which again might occur because of a shift in species (Altermatt, 2012), mowing regimes (Cizek et al., 2012; Popović & Nowicki, 2023) or weather conditions (GeoSphere Austria, 2025). Year comparison shows, that even though warm and dry habitat preferences were slightly more common in 2023, this habitat type correlates strongly with the preferred environmental conditions of most species in both years. In contrast, by looking at the distribution of wetland preferences, the low share of both years represents a clear statement: Due to the xerothermic environment, the portion of species favouring wet habitats tends to narrow. Nevertheless, a significance difference regarding both traits, xerothermic and wetland habitats, between both years was depicted. This variation could be the consequence of annual fluctuations (Franzén et al., 2013; Uhl et al., 2022) or a changing environmental structure due to flood control (Reckendorfer et al., 2013).

To conclude, observed differences in assemblages and trait distributions of butterflies mirror their ability to reflect environmental change and furthermore, their use for improvement of nature conservation (Lang et al., 2016; Sevilleja et al., 2019). Interestingly, the results of 2025 in contrast to 2023 showed a significant prevalence of species with more than one generation per year and generalists. At the same time, the preference for xerothermic habitats declined significantly. If, and only if, this pattern did not just occur due to described inter-annual fluctuations or local marginal conditions, this would imply problematic changes in the value of nature conservation, at least at this specific site in the National Park Donau-Auen. Independent of the true reason causing this outcome, the levee generates a unique habitat for xerothermic organisms among a floodplain environment, worth of protecting.

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Supplementary Information

Table 4: Coordinates of the 20 transects used for Lepidoptera species recordings.

Transect ID	**Coordinates (starting points of the transects)**
T01	48.1342763N, 16.6802611E
T02	48.1342279N, 16.6850470E
T03	48.1340517N, 16.6914759E
T04	48.1339927N, 16.6960850E
T05	48.1339852N, 16.7002930E
T06	48.1339595N, 16.7075755E
T07	48.1339803N, 16.7130853E
T08	48.1339447N, 16.7189101E
T09	48.1339552N, 16.7248545E
T10	48.1339199N, 16.7337360E
T11	48.1339299N, 16.7446531E
T12	48.1338412N, 16.7596610E
T13	48.1338300N, 16.7646764E
T14	48.1338379N, 16.7837099E
T15	48.1337199N, 16.7951675E
T16	48.1336390N, 16.8006794E
T17	48.1343678N, 16.8247041E
T18	48.1347606N, 16.8298152E
T19	48.1357333N, 16.8421488E
T20	48.1364022N, 16.8474902E

Table 5: Sightings of butterflies and diurnal moths per transect of each recorded species in 2025

Species/Transect	**T01**	**T02**	**T03**	**T04**	**T05**	**T06**	**T07**	**T08**	**T09**	**T10**	**T11**	**T12**	**T13**	**T14**	**T15**	**T16**	**T17**	**T18**	**T19**	**T20**	**Total result**
Acontia trabealis	2					1		1	1					1							6
Aglais io					2																2
Amata phegea	1	1							1		1										4
Apatura ilia	1				1																2
Aphantopus hyperantus				1																	1
Apoda limacodes															1						1
Araschnia levana				1																	1
Argynnis pandora						1															1
Argynnis paphia		2	3	1	3			7		2					3						21

Autographa gamma	5		2	1		2				1							1				12
Boloria dia																		1			1
Coenonympha glycerion											2										2
Coenonympha pamphilus		1		1	1	1			1	1	3	1	1		2	1	3	1	1	1	20
Colias hyale/alfacariensis	3	3	3	5	9	5	5	5	5	7	5	3	5	8	3	9	9	2	11	11	116
Cupido argiades					1	1							1	1							4
Cupido decolorata																	1				1
Cupido minimus	5	2	2	4	2	1			1				1			2	1				21
Ematurga atomaria	5		1	3		1				1				1					1		13
Erynnis tages						1				1			2				1	1			6
Euclidia glyphica										1								1			2
Gonepteryx rhamni	2	1	2	1	1		1	1	1	2	1		6		1		2	1			23
Idaea rufaria					1															2	3
Idaea serpentata	7	4			1	1				1											14
Iphiclides podalirius		1																1		1	3
Issoria lathonia		2	4	2	1	6	1	6	3	5	2		3	9	3	6	6	8	6	5	78
Leptidea sinapis/juvernica	9	5	3	7	9	3	3	3	1	3	4	1	7	3		8	2	2	2		75
Macroglossum stellatarum	1	1								1			4								7
Maniola jurtina	46	55	21	52	43	40	15	18	15	31	27	16	25	9	11	29	5	26	19	13	516
Melanargia galathea	10	2	10	20	16	42	6	1	5	5	18	7	11	4			6	3	2	4	172
Melitaea didyma	2		1			2					1			1							7
Minoa murinata	1																				1
Pararge aegeria						1						1		1							3
Paratalanta pandalis							1				1										2
Penthophera morio									1												1
Pieris brassicae						1															1
Pieris mannii				2																	2
Pieris napi		2	2		2	3	2	1	4				1	1	2						20
Pieris rapae	1	1	4	1	1	5	2	2		3		1	2	1	1	3	4	2	2	4	40
Plebejus argus										1					1	1					3
Plebejus argyrognomon		2	2		1		2			2		2	1	7	2	1	3	2	2	4	33
Polygonia c-album	1	1	1			1															4
Polyommatus icarus	1	5	8	4	1	1	1	3	3	1	1		4	3	1	1	3	3	2	4	50
Polypogon tentacularia		1																			1
Pontia edusa					1											1			2	3	7
Spialia sertorius												1							1		2
Thymelicus lineola	1	1	1	3					1	1			1		1	1				2	13
Tyta luctuosa		1							1												2
Vanessa atalanta			3	1	1	1															6
Vanessa cardui			3	2	1	3		1		1		1		1							13
Zygaena filipendulae		1	1		3	2							1								8
Zygaena loti		1		2				1			1		1								6