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Changes in butterfly and burnet moth communities in a steppe habitat over 140 years

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1. Zusammenfassung

Steppentrockenrasen zählen zu den am stärksten gefährdeten Lebensräumen Europas und beherbergen hochspezialisierte Schmetterlingsgemeinschaften, die sensibel auf Landnutzungsänderungen, Nährstoffeinträge und klimatische Veränderungen reagieren. Auf Grundlage eines Langzeitdatensatzes analysiert diese Arbeit Veränderungen der Tagfalter- und Widderchen-Gemeinschaften im pannonischen Sandsteppen-Naturschutzgebiet „Sandberge Oberweiden“ (Niederösterreich) über einen Zeitraum von mehr als 140 Jahren.

Historische Nachweise ab 1883 wurden aus Datenbanken und Literaturquellen zusammengestellt und durch standardisierte Freilanderhebungen im Jahr 2024 ergänzt. Die Analyse erfolgte anhand von Präsenz-Absenz-Daten und umfasste Artenzusammensetzung sowie funktionelle Merkmalsstruktur auf Gemeinschaftsebene über vier Zeitperioden. Zur Anwendung kamen Community Weighted Means (CWMs), nicht-metrische multidimensionale Skalierung (NMDS) sowie permutationsbasierte Tests. Veränderungen wurden im Kontext von Landbedeckungsveränderungen interpretiert, welche anhand von historischen Karten und Orthofotos analysiert wurden.

Insgesamt wurden 90 Arten mit belastbarer zeitlicher Zuordnung berücksichtigt. Die Artenzusammensetzung zeigte einen ausgeprägten Turnover (mittlere Sørensen-Dissimilarität = 0,49), gekennzeichnet durch den Rückgang xerothermophiler Arten und dispersionslimitierter Arten sowie die Zunahme mobiler und habitatgeneralistischer Arten. Die merkmalsbasierte Analyse zeigt eine Verschiebung von der Nutzung offener Bodenstellen und niedrigwüchsiger Krautschichten hin zu gras- sowie strauch- und baumassoziierten Traits, wobei der funktionelle Turnover geringer ausfiel als der Arten-Turnover. Auf Gemeinschaftsebene nahm der Anteil multivoltiner Arten im Zeitverlauf zu. Ebenso konnte eine Verlängerung des Aktivitätsfensters festgestellt werden. Landnutzungsvariablen erklärten nur einen geringen Anteil der funktionellen Veränderungen.Die Erhebungen im Jahr 2024 zeigten deutliche Unterschiede zwischen den Habitattypen: Beweidete und strukturell heterogene Flächen wiesen eine höhere Artenzahl und funktionelle Diversität auf als gemähte Flächen.

Insgesamt weisen die Ergebnisse auf einen langfristigen Verlust spezialisierter Arten trockener Grassteppen sowie auf eine zunehmende funktionelle Homogenisierung der Schmetterlingsgemeinschaften hin.

2. Abstract

Dry steppe grasslands are among the most threatened habitats in Europe, hosting highly specialized butterfly assemblages sensitive to land-use change, nutrient enrichment and climate change. Using a unique long-term dataset, this study investigates changes in butterfly and burnet moth communities in the Pannonian sand steppe nature reserve “Sandberge Oberweiden” (Lower Austria) over more than 140 years. Historical records dating back to 1883 were compiled from databases and literature and complemented with standardized field surveys conducted in 2024. Species composition and community-level functional trait structure (were analyzed across four time periods using community weighted means (CWMs), non-metric multidimensional scaling (NMDS), and permutation-based statistical tests. Changes were assessed in relation to land-cover change derived from historical maps and aerial images.

A total of 90 species with reliable temporal information were recorded. Species composition showed pronounced turnover (mean Sørensen dissimilarity = 0.49), with a decline in xerothermophilic and sedentary species and an increase in mobile and habitat-generalist species. Trait-based analyses revealed a vertical shift from bare ground and short herb utilization towards grass and shrub/tree associated traits, although functional turnover was not as pronounced as species turnover. Community-level voltinism and flight length increased over time, indicating a growing dominance of multi-voltine species with extended activity periods. Land use variables explained little of the observed trait turnover.

The 2024 survey demonstrated strong differences among habitat types with grazed and structurally heterogenous sites supporting higher species richness and functional diversity than areas managed by mowing. Overall, the results highlight

long-term loss of dry grassland habitat specialists and functional homogenization of butterfly communities over the past 140 years.

3. Introduction

Butterflies are important pollinators and serve as valuable indicators of broader environmental health, contributing significantly to ecosystem functioning and human wellbeing (Thomas, 2005). They can be surveyed by applying non-invasive methods and their ecology is well known (Fumy & Fartmann, 2023). Butterflies react quickly to changes in climate and land use, and their presence and abundance do not simply follow vegetation-based indicators (Warren et al., 2001). Additionally, butterflies serve as suitable indicators for general invertebrate diversity in European grasslands (WallisDeVries & Van Swaay, 2009).

The decline in butterfly diversity and abundance in Europe during the last decades exceeds those of plants and many other animal taxa (Thomas, 2005). Across Europe, long-term monitoring shows that typical grassland butterflies have declined by around one third since 1990 reflecting sustained pressures from agricultural intensification, land-use change, nutrient enrichment and climate change (Parmesan, 2006; van Swaay & Warren, 2006; Warren et al., 2021). Habitat specialists, xerothermophilic species and host plant specialists are particularly affected (Eskildsen et al., 2015). Atmospheric nitrogen deposition, in interaction with abandonment and succession, further accelerates vegetation closure, alters host plant quality, and leads to cooler near-ground microclimates, reducing habitat suitability for open-landscape butterflies (Feest et al., 2014; Roth et al., 2021).

Among European grassland types, natural steppe grasslands represent particularly valuable refugia. These dry, nutrient-poor habitats host highly specialized, xerothermophilic butterfly assemblages (Guariento et al., 2022; van Swaay, 2002; WallisDeVries & Van Swaay, 2009). In Austria, the Pannonian sandy steppes are of exceptional biogeographic importance, providing habitat for species at the western edge of their distribution ranges (Warren et al., 2021; Wiesbauer, 1997). The sandy steppes in the Marchfeld region of Lower Austria are the last remnants of a once

extensive dune landscape formed during the last ice age and at the beginning of the postglacial period. Large quantities of alluvial sand were exposed and spread across the landscape. The “Sandberge Oberweiden” represent the westernmost extension of the east European sand steppes (Wiesbauer, 2002a, 1997). At the end of the 18th century efforts were undertaken to stabilize the dunes and prevent them from encroaching into the surrounding agricultural fields (Wiesbauer, 2002b).

Currently, the Pannonian sand steppes are among the most threatened habitats in Austria. They are priority habitats according to the Fauna-Flora-Habitat Directive and therefore under special protection (Essl et al., 2004). Despite the special protection of those habitats, ongoing succession and eutrophication have led to the progressive loss of characteristic species of these open and sparsely vegetated areas (Wiesbauer, 1997). The nature reserve “Sandberge Oberweiden” is one of the last refuges for several plant and animal species adapted to sandy soil in Austria (Rabitsch, 2002; Wiesbauer, 1997).

Since the late 19th century, the study area has been regularly visited by entomologists, resulting in a rich historical dataset of insect records. The earliest butterfly record from Oberweiden dates back to 1883. The data obtained from the long history of entomological research on the site provides the opportunity to analyze changes in the butterfly community composition over an extended period.

In the present study, I analyze the butterfly and burnet moth communities of the nature reserve “Sandberge Oberweiden” and changes in species composition over more than 140 years. Recent data were collected during a survey in 2024. Historical records were compiled from ZOBODAT, the InsectIS database of the „Biologische Station Illmitz” (BSI), and relevant literature. Changes in community structure were analyzed in relation to land use changes inferred from historical maps, aerial imagery and recent orthophotos.

Specifically, following research questions were addressed:

1. Has the butterfly and burnet moth community changed over the past 140 years?
2. Have community trait compositions shifted over time?
3. Are changes in species and trait composition associated with land-use changes?

4. Does the abundance and diversity of butterfly species vary between different habitat types, and do different habitat types host distinct butterfly communities?

4. Material and methods

4.1. Study area

Fig. 1 The study site “Sandberge Oberweiden” **A** Location of the study site in Austria (insert), and its location in the Marchfeld region. The blue star represents the village “Oberweiden” located north of the study area, **B** overview of the study plots, **C** spring aspect of the study plot AW (Old meadow), **D** sandy hills (pasture) located in the north of study area.

The study was conducted at the nature reserve “Sandberge Oberweiden” (Fig. 1A, N 48° 17′ 13″, E 16° 49′ 43″), located in Lower Austria, south of the village of Oberweiden. The study area marks the westernmost extension of the East European steppe zone, comprising remnants of a formerly extensive dune landscape shaped during the last ice age and early postglacial periods (Wiesbauer, 2002a, 2002b, 1997). The core area has been protected since 1961 and was expanded by 12 hectares between 1998 and 2002 as part of an EU LIFE project (Wiesbauer, 2002b).

Currently the nature reserve covers approximately 128 hectares and is part of the Natura 2000 site "Pannonische Sanddünen." According to the European Union's Fauna-Flora-Habitat Directive (Council Directive 92/43/EEC), the area includes the priority habitat types "Pannonian sand steppes (6260*)" and "Sub-Pannonian steppic grasslands (6240*) (Schernhammer, 2023).

For the survey, the study area was divided into five different habitat types:

- **Old Meadow (AW)**: historically continuous, semi-natural grassland.
- **New Meadow (NW)**: areas added during 1998–2002 to the protected area, grassland primarily maintained through (rotational) mowing.
- **Pasture (W)**: hilly dune areas in the northern part of the site and strip reaching from south to northwest, grazed by horses since 2022.
- **Special Site Sand (SSTS)**: small patches of grassland with bare sandy ground located northeast of the former horseracing track.
- **Special Site Shrub (SSTB)**: shrubby transition area

4.2. Field work

Butterfly and burnet moth surveys were conducted by hand-netting along fixed transects on four dates between April and September 2024, following the Reduced Effort Butterfly Monitoring Scheme (BMS) as described by van Swaay et al. (2008).

In total, 59 transects were established throughout the study area. Old meadow, New meadow, and Pasture each contain 15 transects, whereas Special site Sand and Special site Shrub contain seven transects each, due to their smaller spatial extent (Fig. 2).

Each transect had a length of 50 m and was surveyed by walking along the transect at a constant speed for five minutes. Butterflies were recorded 2.5 m to the left and right, 5 m ahead and 5 m above. The surveys were mainly conducted under favorable weather conditions. During the first survey in April, temporary strong winds occurred, but sampling was still conducted

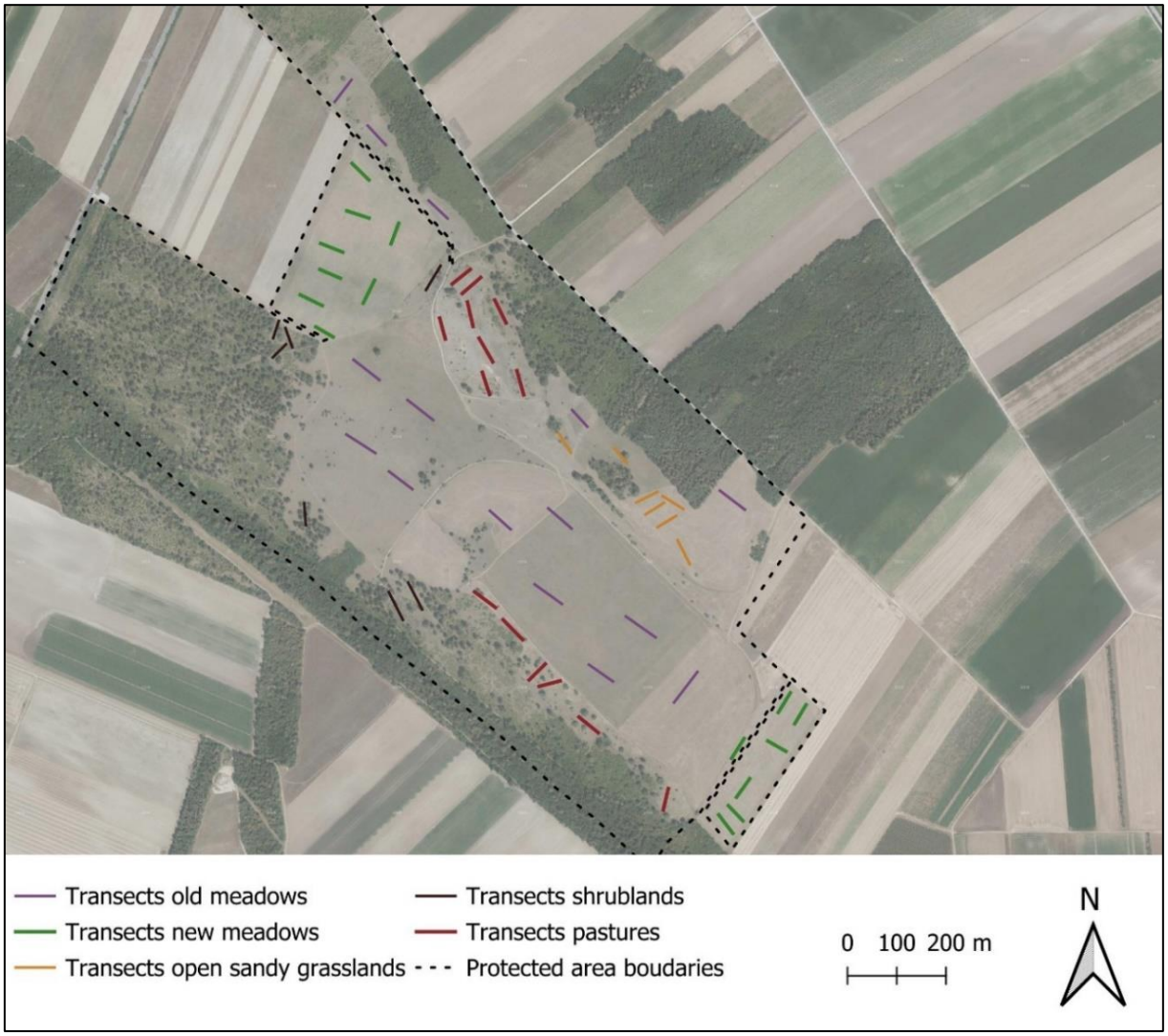

Fig. 2 Location of transects in the survey area “Sandberge Oberweiden”

Specimens were captured using a hand net and temporarily placed into tubes for later identification. Georeferencing of transect location was done using the QField application (QField Development Team, 2024). Species identification was conducted in the field using “Die Tagfalter Deutschlands und Österreichs” (Stettmer, 2022) and Lepiforum (Lepiforum, 2026).

Species-level identifications were required for inclusion in trait-based analyses. Records identified only to genus level were excluded due to the inability to assign ecological traits.

4.3. Nomenclature

Nomenclature follows the Checklist of Austrian Lepidoptera (Huemer, 2013). Where recent taxonomic changes were relevant, names were updated based on current usage in the Lepiforum database (Lepiforum, 2026).

4.4. Data Sources

Historical butterfly and burnet moth records were compiled from several sources. Data were retrieved from the ZOBODAT database (ZOBODAT, 2025) and the database of the Biological Station Illmitz (BSI). Additionally, records from Rudolf Eis were incorporated, mostly from his field surveys in 2000 (Eis, 2002). Historical data often lack precise locality information, thus all the data with locality Oberweiden was incorporated. It must be assumed that collecting activity may not have been limited to the present nature reserve but also may have included nearby locations such as the train station (Zimmermann et al., 2023). Recent survey data were collected during the field campaign in 2024 (see 3.2).

Tab. 1 Overview of decades, recorded species richness and data sources

Decade	Time Period	Species richness	Source
1883–1889	< 1930	2	Zobodat
1890–1899	< 1930	8	Zobodat
1900–1909	< 1930	15	Zobodat
1910–1919	< 1930	17	Zobodat
1920–1929	< 1930	22	Zobodat
1930–1939	1931–1966	16	Zobodat
1940–1949	1931–1966	4	Zobodat
1950–1959	1931–1966	21	Zobodat; Eis, R. (2002)

1960–1969	1931–1966	20	Zobodat; Eis, R. (2002); BSI Database
1970–1979	1967–2000	42	Zobodat; Eis, R. (2002)
1980–1989	1967–2000	16	Zobodat; Eis, R.
1990–1999	1967–2000	8	Zobodat; BSI Database
2000–2009	2001–2024	46	Zobodat; Eis, R. (2002)
2010–2019	2001–2024	10	Zobodat
2020–2024	2001–2024	52	Zobodat; Own survey

4.5. Comparability of historical and recent data

Historical data does not originate from standardized surveys and is therefore subject to potential biases. A comprehensive assessment of the lepidoptera species spectrum would require several years of intensive and systematic monitoring of the study area (Eis 2002). The most complete data derives from surveys by Rudolf Eis in 2000. Diurnal Lepidoptera have historically been collected primarily using hand nets, which remain the standard method today (e.g., Pollard, 1977). As no alternative sampling methods are documented in the available records, the use of hand nets is assumed to have remained consistent throughout the study period.

4.6. Trait data

Trait data was compiled to characterize habitat preferences, dispersal abilities, larval environment, host plant growth forms, egg laying location, basking site, phenology and voltinism. Trait assignments are based on the MAHGREB Butterfly Trait Database (Middleton-Welling et al., 2020). Additional trait information was obtained from the Red List of threatened Butterflies of Salzburg (Gros, 2023), Tagfalter und ihre Lebensräume (Schweizerischer Bund für Naturschutz, 1994) and Schmetterlinge und ihre Lebensräume (Schweizerischer Bund für Naturschutz, 1997). Abbreviations of trait categories used throughout the text and figures are provided in Appendix A.

4.7. Landscape study

Historical land-use data were obtained from georeferenced maps provided by the “Bundesamt für Eich- und Vermessungswesen” (BEV, 2026) and the

“Niederösterreichisches Geographisches Informationssystem” (NÖ GIS, 2026). The available map series covered the years 1880, 1957, 1971, 1982, 1994, 2000. The most recent orthophoto avaliable was from 2024 (basemap.at, 2026).

All spatial analyses were conducted in QGIS (QGIS Development QGIS Development Team, 2026). A buffer of 100 m was created around the study area to ensure a consistent spatial extent across all time periods, as the protected area was expanded between 1998 and 2002. This area was polygonised and classified into four land-cover categories: Agricultural field, Grassland, Open forest and shrubland, and Dense forest (Fig. 6). These categories were defined based on vegetation structure and land-cover characteristics. “Open forest and shrubland” was classified as areas with a canopy cover of less than 30%, whereas areas exceeding this threshold were assigned to “Dense forest”. “Agricultural field” comprised all arable land used for crop production. “Grassland” referred to dry grassland habitats, primarily representing sand grasslands typical of the study area. This approach was chosen to ensure that historical maps and orthophotos could be analyzed using a consistent set of land-cover categories. For the visualization of land-cover transitions, a Sankey diagram was constructed based on the years 1880, 1957, 1994 and 2024 (Fig. 7). These years were selected representative for the four main study periods (<1930, 1931-1966, 1967-2000, 2001-2024). Spatial intersections between consecutive time steps were calculated in QGIS to quantify transitions between land-cover classes.

4.8. Data analysis

All statistical analyses were conducted in R (R Core Team, 2024) using RStudio (Posit Team, 2023). Data processing and visualization were performed using *tidyverse* (Wickham, 2019) and multivariate community analyses were conducted using the *vegan* package (Oksanen et al., 2022). Figures were created using *ggplot2* (Wickham, 2019) and assembled using *patchwork* (Pedersen 2020).

To account for uneven sampling effort and ensure comparability across the study period, two complementary temporal aggregation approaches were applied depending on the analytical objective. Broad time periods (<1930, 1931–1966, 1967–2000, 2001–2024) were used for trait-based and diversity analyses, while

decadal aggregation was used for ordination analyses to preserve temporal resolution. For the period-based analyses, species occurrence data were aggregated into a period × species presence–absence matrix (Appendix A). A species was considered present within a period if at least one record was available. Temporal turnover between periods was quantified using Sørensen dissimilarity, implemented as Bray–Curtis distance on binary data (Bray & Curtis, 1957; Legendre & Gallagher, 2001).

Functional community composition was quantified using community-weighted mean (CWM) trait values, calculated as the average trait value of all species present in a period based on presence–absence data. Traits were coded in a non-mutually exclusive manner, allowing species to be assigned to multiple categories within a given trait group. For each trait group, values were normalized such that proportions summed to one. Temporal changes in trait composition were assessed using Bray–Curtis dissimilarity among CWM profiles and tested using permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) with period fitted as an ordered predictor (999 permutations). Community-level phenology and voltinism were analyzed using CWM values. Flight-period length was defined as the number of active months, and voltinism was expressed as a weighted numeric score (0.5–3 generations per year). Temporal trends for changes in community-level phenology were evaluated using linear models.

For ordination analyses, species occurrence records were aggregated into decades to retain finer temporal resolution and avoid masking gradual community changes within broader periods. The first decade spanned 1883–1889, followed by regular ten-year intervals. The most recent decade spans from 2020 to 2024 as data were only available up to 2024. Decades with fewer than 10 recorded species were excluded to reduce instability caused by sparse assemblages. Community dissimilarities among decades were calculated using binary Bray–Curtis distances. Non-metric multidimensional scaling (NMDS; Kruskal, 1964) was performed using the metaMDS function in *vegan* with two dimensions (k = 2). The ordination was used to visualize temporal trajectories in community composition.

Functional trait composition was incorporated into the ordination by calculating CWM values for each decade. Associations between trait composition and the NMDS configuration were assessed using permutation-based vector fitting (envfit; 999 permutations). P-values were adjusted using the Benjamini–Hochberg false discovery rate correction (Benjamini & Hochberg, 1995), and only significant vectors (adjusted $p < 0.05$) were plotted. Land-use composition was expressed as proportional cover per time step and used as environmental variables in the NMDS via *envfit*.

For the 2024 field survey, species richness and total abundance were calculated per transect and compared among habitat types using Kruskal–Wallis tests (Kruskal & Wallis, 1952), followed by Dunn's post-hoc tests with Benjamini–Hochberg correction. Differences in species composition among habitat types were assessed using PERMANOVA based on Jaccard distances (Anderson, 2001; Legendre & Gallagher, 2001) and homogeneity of multivariate dispersion was tested using betadisper (Anderson, 2006). Functional composition at the transect level was quantified using community-weighted mean (CWM) trait values (Lavorel et al., 2007), and differences among habitat types were evaluated using Euclidean distances and PERMANOVA (Anderson, 2001).

5. Results

5.1. Distribution and composition of species records

A total of 93 butterfly and burnet moth species were recorded in the study area across the full study time. For three species (*Carterocephalus palaemon, Jordanita globulariae, Jordanita subsolana*) no collection date could be determined, consequently these species were excluded from temporal and trait-based analyses. The dataset contains 1209 observations. The number of observations per period was uneven, with 107 (8.9%) records before 1930, 76 (6.6%) between 1931–1966, 197 (16.5%) between 1967–2000, and 762 (67.8%) between 2001–2024. Over the

whole survey period 90 species with exact date were assembled. The number of species varied over time with 41 (45.6%) species recorded before 1930, 36 (40.0%) between 1931 and 1966. 64 species (71,1%) were recorded between 1967 and 2000, and 53 (58.9%) in the most recent period (2001–2024). Temporal dynamics of the dataset are visualized in Figure 3, which shows the first and last year of observation for each species.

Since 1930, seven species have not been recorded again (*Aporia crataegi*, *Euphydryas aurinia, Melitaea athalia, Plebejus idas, Pseudophilotes vicrama, Zerynthia Polyxena*, *Zygaena brizae*), and an additional eight species disappeared since 1966 (*Fabriciana niobe*, *Hyponephele lycaon*, *Jordanita chloros, Melitaea parthenoides, Parage aegeria*, *Polyommatus daphnis, Satyrium ilicis, Speyeria aglaja)*. Only 10 species were recorded in all four time periods: *Arethusana arethusa, Callophrys rubi, Coenonympha glycerion, Cupido minimus, Lysandra coridon, Melanargia galathea, Minois dryas, Papilio machaon, Pyrgus carthami and Zygaena carniolica*. Four of these species are associated with xerotherm habitats and use bare ground or rocks for basking.

Species composition changed substantially over time. Mean pairwise Sørensen dissimilarity between periods (Sørensen = 0.49) was calculated using Bray-Curtis distance on binary presence-absence data indicating that nearly half of the species were not shared between any two time periods. The lowest turnover occurred between 1967-2000 and 2001-2024 (Sørensen = 0.28). The highest dissimilarity was observed between 1931-1966 and 2001-2024 (Sørensen = 0.64).

Metric	**Value**
Species richness per period	before 1930: **41**; 1931-1966: **36**; 1967-2000: **64**; 2001-2024: **53**
Species persisting across all periods	**10**
Species lost after 1930	**7**
Species lost after 1966	**8**
Mean pairwise Sørensen dissimilarity	**0.49**
Lowest turnover	1967-2000 vs. 2001-2024: **0.282**
Highest turnover	1931-1966 vs. 2001-2024: **0.640**

Tab. 2 Summary of species richness and Sørensen dissimilarity across the four time periods

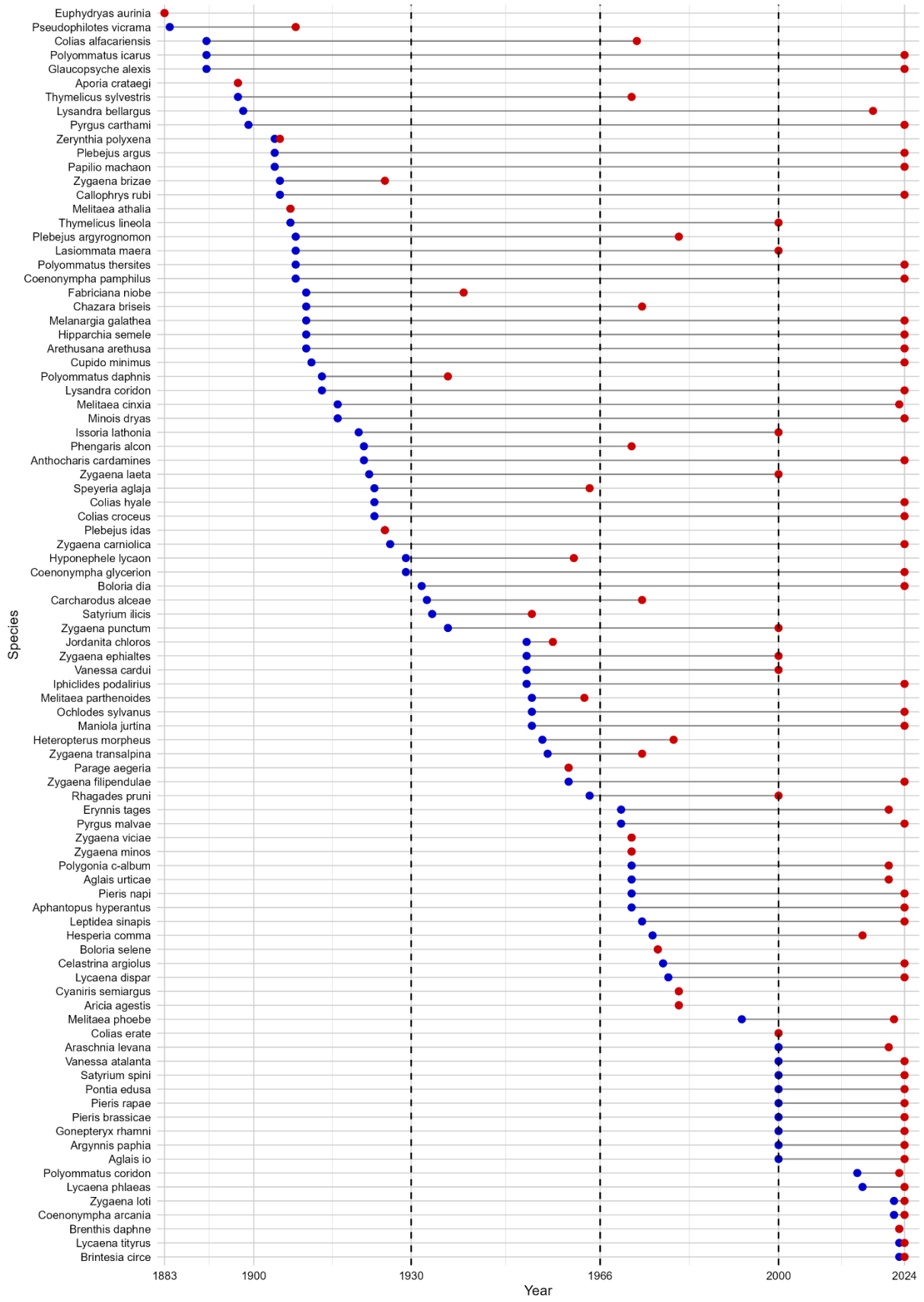

Fig. 3 Overview on year of first (blue) and last (red) observation of all recorded butterfly and burnet moth species. The dashed vertical lines delineate the four different time periods used in the analyses.

5.2. Trait-based shifts in community composition across time periods

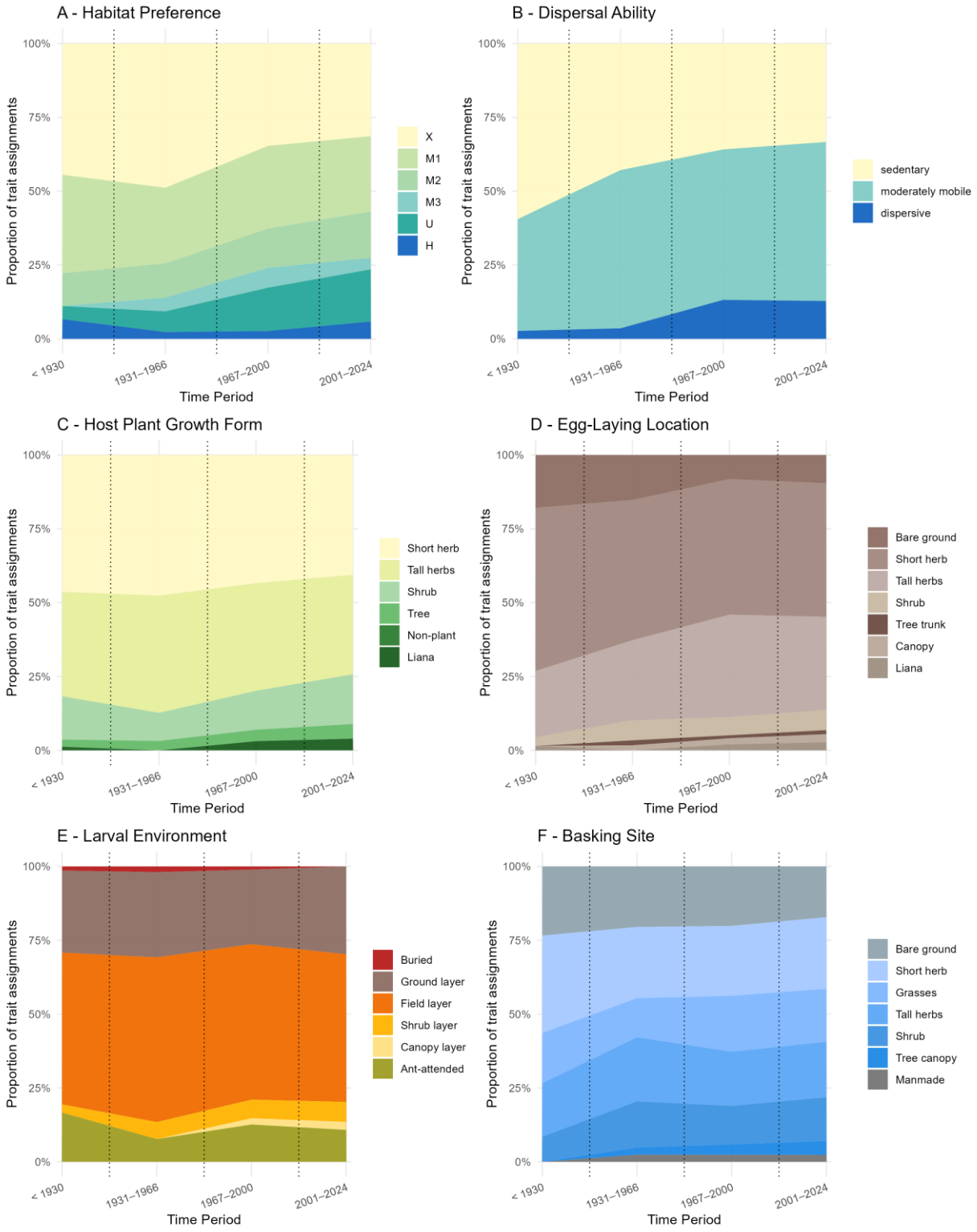

Fig. 4 A-F Changes in ecological traits of the recorded butterfly and burnet moths communities over time in the survey area. Legend: X = xerothermophilic species, M1 = Mesophilic open-land species, M2 = Mesophilic species of transitional zones between woodland and open land, M3 = Mesophilic species of light woodland structures, H = Hygrophilic species, U = Ubiquitous species.

The community-weighted trait composition (CWM) of several traits related to species ecology of butterfly and burnet moth species in the survey area changed between the four time periods (Fig. 4). A PERMANOVA on Bray–Curtis distances of period-level trait profiles, with time period treated as an ordinal variable (1 = before 1930 to 4 = 2001–2024), indicated no significant temporal trend in functional composition (pseudo-F = 3.30, R^2 = 0.62, p = 0.167).

For habitat preference, there was a long-term decline in xerothermophilic species (X), which decreased from 44.4% before 1930 and 48.8% in 1931–1966 to 33.9% in 2001–2024. At the same time, ubiquitous species (U) increased from 4.4% to 16.9%. Mesophilic groups (M1–M3) expanded moderately over time.

Dispersal ability within the communities shifted strongly over time. Sedentary species declined from 59.5% before 1930 to 38.3% in 2001–2024, while moderately mobile species increased (37.8% → 51.1%). Dispersive species also increased (2.7% → 10.6%). Together, moderately mobile and dispersive species now constitute more than 60% of the recent community assemblage.

Bare-ground basking decreased from 23.4% before 1930 to 19.1% in 2001–2024, and short-herb basking declined from 33.0% to 25.7%. In contrast, basking on shrubs and tall herbs increased (shrub: 8.5% → 13.2%; tall herbs: 18.1% → 17.8%). Tree-canopy basking, which was absent before 1930, now accounts for 4.6% of the CWM trait composition in 2001-2024.

Egg-laying location showed a similar vertical shift towards higher vegetation strata. Bare-ground oviposition declined from 17.9% before 1930 to 11.8% in 2001–2024, while shrub and tall-herb oviposition increased (shrub: 3.0% → 5.9%; tall herbs: 22.4% → 30.6%). Species laying eggs in short-herb layers declined from 55.2% to 45.9%.

For larval environment, the proportion of species with buried larvae decreased from 1.4% before 1930 to 0% in 2001–2024. Species utilizing the field layer as larval environment declined only slightly (51.4% → 50.0%), whereas species developing in the shrub layer increased markedly (2.8% → 5.8%).

Host plant growth form showed a decline in short-herb feeders (46.3% → 42.6%), while shrub-feeding species increased slightly (14.6% → 15.7%). Species utilizing

lianas as host plants increased from 1.2% to 3.5%, and tree-feeding species also became more frequent (2.4% → 4.3%).

Overall, changes in functional composition were less pronounced than the observed taxonomic turnover. Mean Bray–Curtis dissimilarity among CWM profiles among periods was 0.102. Pairwise dissimilarities ranged from 0.038 (1967–2000 vs. 2001–2024) to 0.141 (before 1930 vs. 2001–2024), with the largest functional differences occuring between the earliest and most recent period.

5.3. Changes over time in community voltinism and phenology

Community-level flight phenology showed a clear trend towards earlier and longer seasonal activity, although statistical support for directional change across the four time periods remained limited. Community-weighted mean (CWM) flight length increased from 5.49 months before 1930 to 6.54 months in 2001–2024, reflecting a broadening of the flight window at community level. The circular community peak flight month remained relatively stable.

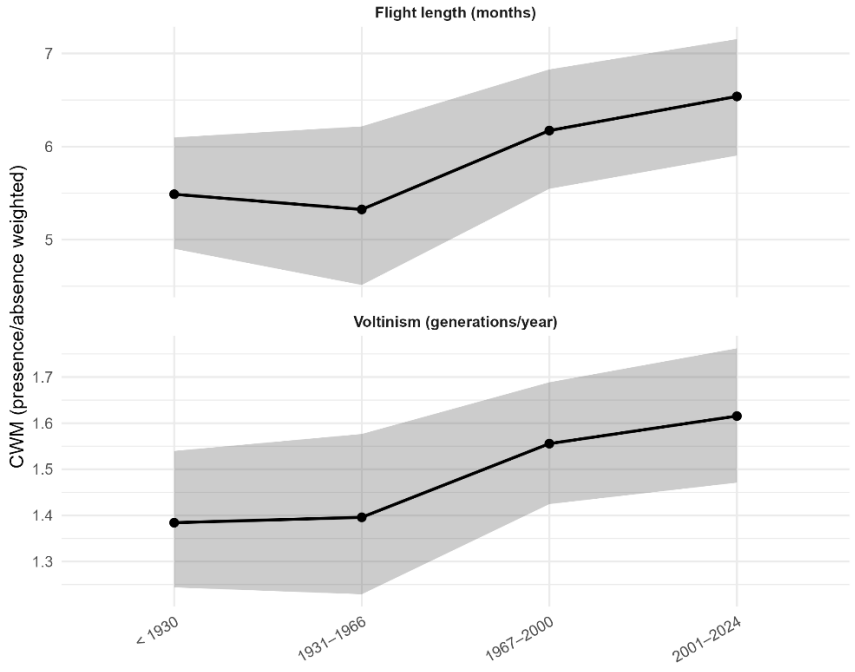

Fig. 5 Changes in community weighted means of flight length and voltinism over four time periods. To account for uncertainty around period means nonparametric bootstrap confidence intervals (5,000 resamples) were used across species present in each period.

The extension of activity at the beginning and end of the season is evident in the monthly CWM proportions, which show increasing early-spring (March–April) and

late-summer (September–October) activity in the more recent periods. Linear trend models confirmed an increasing flight period length (slope = +0.40 months per period, R^2 = 0.82), although the slope was not significant (p = 0.097).

Voltinism also showed a consistent community-level increase, from a CWM of approximately 1.38 generations before 1930 to about 1.63 in 2001–2024. The linear model detected a significant positive trend (slope = +0.085, R^2 = 0.91, p = 0.047) indicating an increasing prevalence of multi-generational species in the community.

To evaluate broader changes in seasonal activity structure, monthly CWM phenology profiles for each period were compared using Bray–Curtis dissimilarity. Functional turnover between periods was moderate (0.036–0.111), with the strongest dissimilarity occurring between 1931–1966 and 2001–2024 (0.111).

5.4. Changes in habitat composition over time

Fig. 6 Land-cover in and around the protected area (incl. a 100 m buffer) in Oberweiden in **A** 1880, **B** 1957, **C** 1994, **D** 2024

Land-cover composition changed markedly between 1880 and 2024 across the four considered categories (Agricultural field, Dense forest, Open forest and shrubland, and Grassland). In 1880, the landscape was strongly dominated by grassland, which accounted for 75.8% of the total area. Agricultural fields represented 21.1% while dense forests (1.0%) and open forests and shrublands (2.1%) covered only minor proportions.

Between 1880 and 1957, grassland decreased markedly to 46.3% while agricultural fields increased slightly to 26%. Most notably, open forest and shrubland expanded considerably from 2.1% to 11.5% largely due to transitions from grassland. Dense forest cover also increased to 16.2%.

From 1957 to 1994, land cover dynamics were characterized by a pronounced increase in forest cover. Dense forest became the dominant class, rising to 38.4%.At the same time, agricultural fields increased moderately to 29.7%, while grassland further declined to 30.1%. Open forests and shrublands decreased to 1.7%, mainly due to transition into dense forests.

Between 1994 and 2024, dense forests remained the dominant land cover type (36.5%), although its proportion slightly decreased. Grassland showed an increase to 36.1% due to the expansion of the protected area between 1998 and 2002. Open forests and shrublands increased again to 5.4%, while agricultural fields declined to 22.0%.

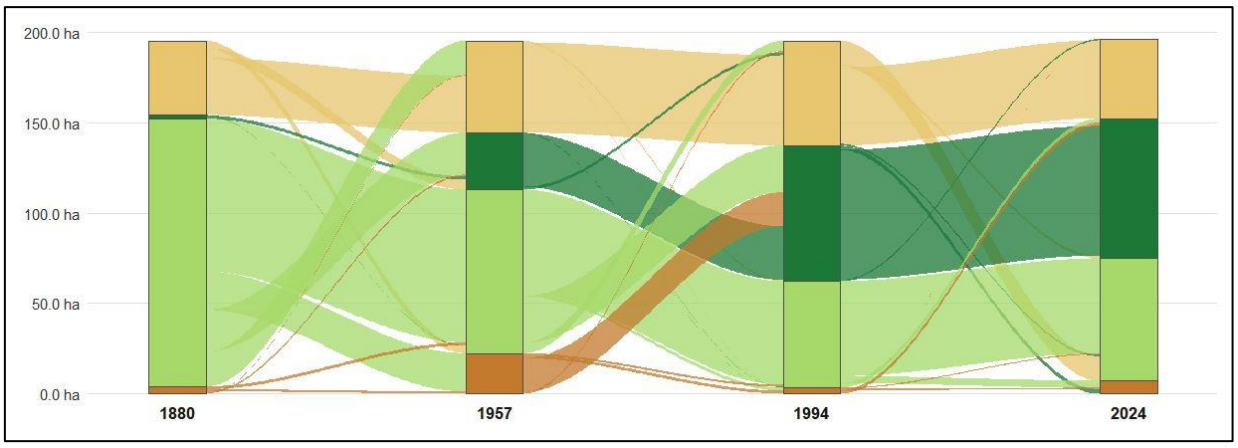

Fig. 7 Land-cover transitions between 1880, 1957, 1994, and 2024. Flows connect consecutive time periods and represent changes between land-cover classes: Agricultural field (pale brown), Dense forest (dark green), Open forest and shrubland (brown), and Grassland (pale green). Flow width is proportional to area (ha), indicating the magnitude of transitions between classes.

Tab. 3 Land-cover categories used for landscape mapping of the study area in Oberweiden based on historical maps and aerial orthophotos (1880, 1957, 1971, 1982, 1994, 2000) and recent aerial orthophotos (2024), including total area (ha) per category and year. Years highlighted in grey were used for the Sankey diagram (Fig. 7), whereas all years were included in the NMDS envfit analysis (Fig. 8).

Land-cover category	**1880**	**1957**	**1971**	**1982**	**1994**	**2000**	**2024**
Agricultural field	41,17	50,91	61,98	57,96	58,00	58,20	42,88
Dense forest	2,05	31,55	48,02	72,19	75,02	75,79	71,27
Grassland	147,94	90,39	58,66	61,10	58,85	57,84	70,47
Open forest and Shrubland	4,05	22,36	26,54	3,96	3,33	3,38	10,59
Sum	195,21	195,21	195,21	195,21	195,21	195,21	195,21

4.1. NMDS ordination of community trait composition

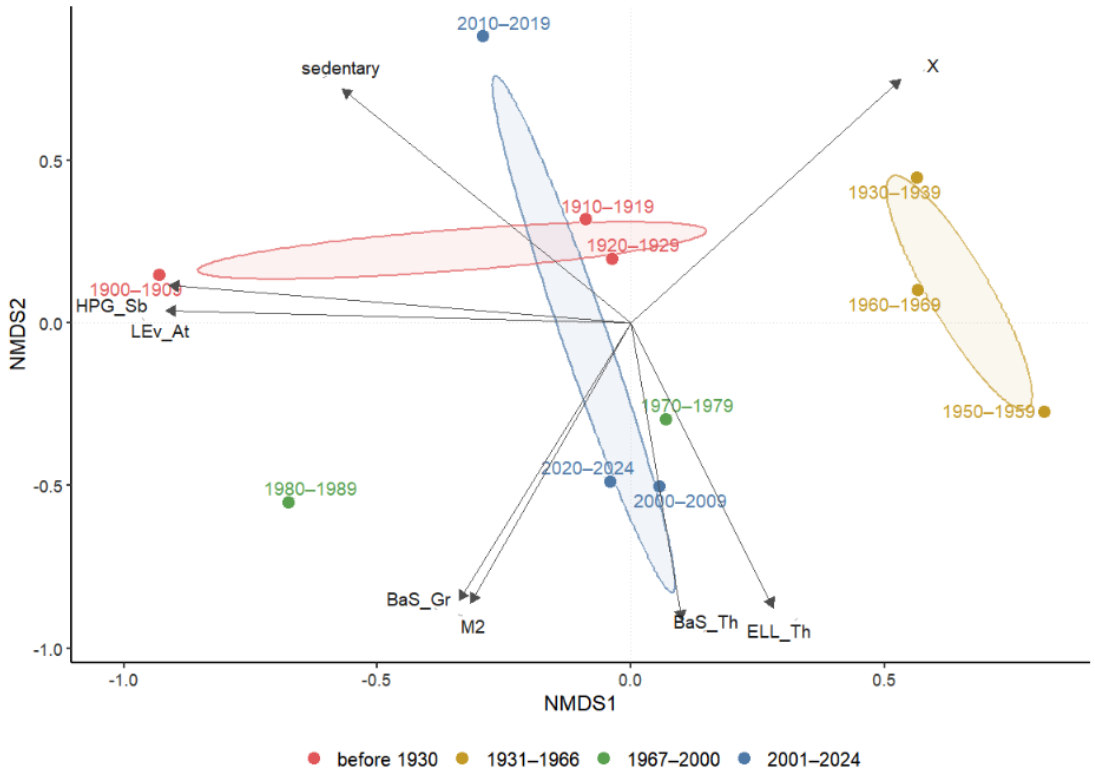

Fig. 8 NMDS of changes in butterfly community trait composition over time based on Sørensen (binary Bray–Curtis) dissimilarities of presence–absence data; arrows show BH-significant CWM trait vectors (envfit, 999 permutations). Stress = 0.129.

The NMDS ordination (stress = 0.129) revealed a gradual temporal shift in community composition across decades. Early decades (<1930) were positioned on

the negative side of NMDS1 while mid-century decades (1931–1966) were clearly separated along the positive side of NMDS1. Recent decades (2001–2024) occupied intermediate positions but were primarily distinguished along NMDS2.

Permutation-based vector fitting identified several functional traits significantly associated with the ordination after Benjamini–Hochberg correction (Tab. 4). Early decades were strongly associated with sedentary species, shrub-related traits (HPG_Sb) and ant-attended larval environments (LEv_At). In contrast, later decades were associated with traits linked to taller vegetation structures, including tall herbs (ELL_Th, BaS_Th), grasses (BaS_Gr), and mesophilic species (M2).

Land-cover variables showed no significant association with the ordination, although shrub-cover exhibited a marginal relationship (p = 0.0625, Tab. 4). This indicates that functional community change was more strongly related to trait composition than to broad land-cover categories.

Overall, the NMDS suggests a gradual but directional reorganization of the butterfly assemblage, characterized by a shift from sedentary, shrub-associated species towards more mobile, mesophilic species associated grasses (basking site) and tall herbs (basking site, egg laying location).

Tab. 4 Significant functional trait vectors fitted to the NMDS ordination (p_BH = Benjamini-Hochberg corrected p-values) and Land-cover variables.

trait	**NMDS1**	**NMDS2**	**r2**	**p**	**p_BH**
X	0,57781419	0,81616834	0,73623474	0,006	0,029
HPG_shrub_Sb	-0,99202098	0,12607292	0,73462797	0,006	0,029
ELL_tall_mature herbs_Th	0,30618765	-0,95197118	0,78152414	0,001	0,029
LEv_Attended_At	-0,99912594	0,04180143	0,79271623	0,003	0,029
BaS_grasses_Gr	-0,36942354	-0,92926113	0,80689599	0,003	0,029
BaS_tall herbs_Th	0,10881251	-0,99406229	0,80231715	0,004	0,029
sedentary	-0,62064195	0,78409411	0,68220028	0,013	0,047125
M2	-0,34450355	-0,93878502	0,66827584	0,012	0,047125
Land-cover variable	**NMDS1**	**NMDS2**	**r2**	**p**	**p_BH**
Open forest and shrubland	0,98163093	0,1907897	0,50814989	0,0625	0,25
Agricultural field	0,35179701	-0,93607631	0,36117108	0,1594	0,3188
Grassland	-0,41746097	0,90869486	0,21733306	0,3746	0,49946667
Dense forest	-0,11386926	-0,99349574	0,14654056	0,523	0,523

4.2. Current abundance and diversity of butterflies and burnet moths across habitat types

Species richness and total abundance were calculated at the transect level. For each individual transect the number of species and the total number of individuals recorded in 2024 were determined. These transect-level values were then compared among habitat types (Fig. 9, Tab. 5).

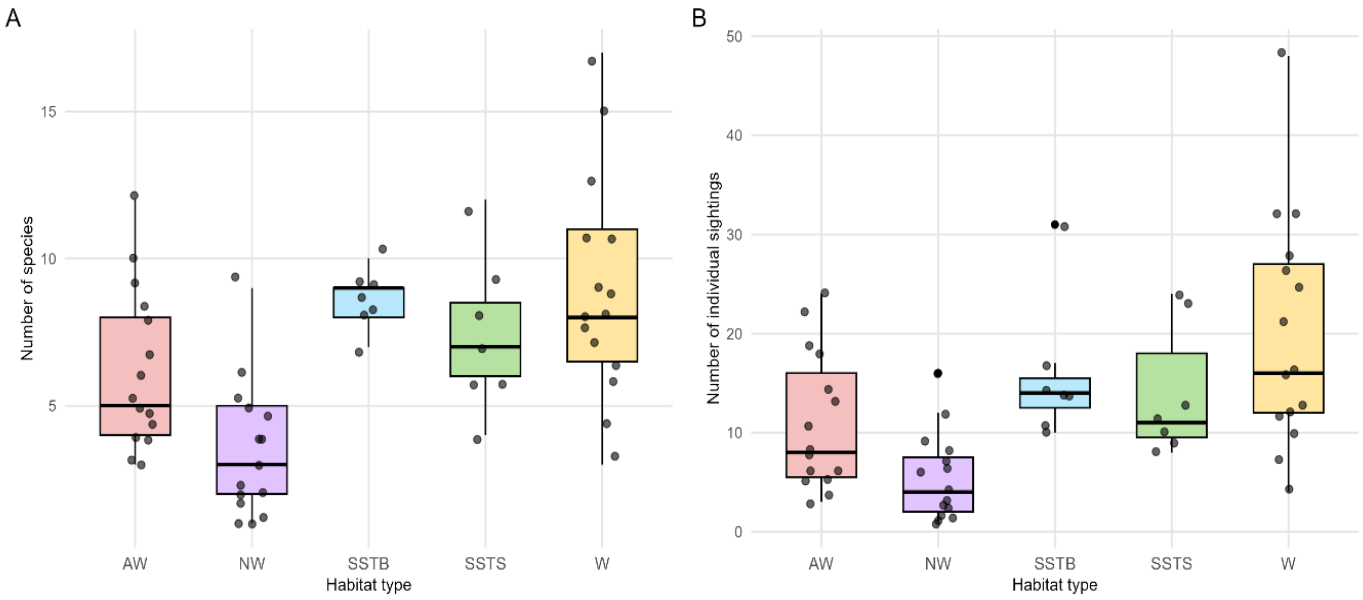

Fig. 9 Boxplots showing (A) mean butterfly species richness per transect across habitats and (B) mean individual counts per transect across habitat in 2024. Each point represents a transect (AW = old meadow (n=15), NW = new meadow (n=15), SSTB = special site shrub (n=7), SSTS = special site sand (n=7), W = pasture (n=15)).

Tab. 5 Descriptive statistics of species richness and total abundance per habitat (2024)

Habitat	n	Species richness (mean ± SD)	Richness median (min–max)	Abundance (mean ± SD)	Abundance median (min–max)
AW	15	6.20 ± 2.70	5 (3–12)	11.07 ± 6.91	8 (3–24)
NW	15	3.47 ± 2.26	3 (1–9)	5.40 ± 4.42	4 (1–16)
SSTB	7	8.57 ± 0.98	9 (7–10)	15.86 ± 7.06	14 (10–31)
SSTS	7	7.43 ± 2.57	7 (4–12)	14.00 ± 6.68	11 (8–24)
W	15	9.00 ± 3.87	8 (3–17)	20.13 ± 11.75	16 (4–48)

Mean species richness per transect differed significantly among habitat types. Pastures (W) and special site shrub (SSTB) showed the highest mean richness values, whereas new meadow (NW) had the lowest mean richness. Median values followed the same pattern. Substantial within-habitat variability was evident from the dispersion of values in the boxplots.

Kruskal–Wallis tests revealed significant differences among habitat types for both species richness ($\chi^2 = 23.0$, df = 4, $p < 0.001$) and total abundance ($\chi^2 = 23.0$, df = 4, $p < 0.001$).

Post-hoc Dunn tests with Benjamini–Hochberg correction showed that new meadow (NW) supported significantly fewer species per transect than pastures (W), special site shrub (SSTB), and special site sand (SSTS). The same pattern was observed for abundance, with NW having significantly lower numbers of individuals per transect than W, SSTB, and SSTS. No consistent significant differences were detected between AW, W, SSTB and SSTS.

These results indicate that newly established meadow habitats currently support less diverse and less abundant butterfly assemblages compared to pasture and shrub-dominated habitats.

Community composition differed significantly among habitat types; however, the significant betadisper result indicates that differences in within-habitat dispersion also contributed to this pattern.

Tab. 6 PERMANOVA results for differences in community composition among habitat types (Jaccard distance)

Factor	df	F	R^2	p
Habitat type	4	2.2436	0.1425	0.001

A betadisper analysis indicated unequal multivariate dispersion among habitats ($F_{4,54} = 7.30$, $p < 0.001$), suggesting that differences in community composition were partly influenced by variation in within-habitat heterogeneity. SSTB and W exhibited comparatively higher internal similarity.

Tab. 7 Test for homogeneity of multivariate dispersion among habitat types (betadisper)

Factor	df	F	p
Habitat type	4	7.3025	< 0.001

4.3. Differences in current community trait composition across habitat types

Functional composition, quantified as community-weighted means (CWMs) calculated at transect level, differed significantly among habitat types. The strongest functional contrasts were observed between new meadow (NW) and special site shrub (SSTB). NW supported significantly lower CWM values for habitat preference category M2 and for multiple basking-site strategies (short-herb, bare-ground, and tall-herb basking). Differences were also evident in oviposition traits, with NW showing lower representation of shrub-associated and tall-mature-herb egg-laying strategies compared to SSTB. Likewise, larval use of the shrub layer was significantly reduced in NW relative to SSTB.

Old meadows (AW) showed intermediate functional patterns but also differed significantly from SSTB in habitat preference (M2), shrub oviposition, tall-herb oviposition, and shrub layer larval development.

Additional differences were detected among other habitat combinations. SSTB showed higher representation of ant-attended larval environments compared to pasture (W), and stronger shrub-associated egg-laying location compared to both W and SSTS. SSTB also differed from SSTS in habitat preference category M2.

Multivariate analysis of CWM profiles (Euclidean distance, PERMANOVA, 999 permutations) confirmed significant overall differences in functional composition among habitat types.

Overall, basking site, egg-laying location and larval microhabitat emerged as the primary drivers of functional differentiation among habitats.

Tab. 8 Significant pairwise differences in community-weighted mean traits among habitat types (Dunn test, BH corrected)

Trait	Comparison	Higher in	p_adj
BaS_rock\bare earth_Bg	NW vs SSTB	NW	0.00481
BaS_short herb_Sh	NW vs SSTB	NW	0.00239
BaS_shrub_Sb	NW vs SSTB	SSTB	0.0226
BaS_tall herbs_Th	NW vs SSTB	SSTB	0.0144
ELL_shrub_Sb	NW vs SSTB	SSTB	0.0102
ELL_shrub_Sb	AW vs SSTB	SSTB	0.0163
ELL_shrub_Sb	SSTB vs SSTS	SSTB	0.0205
ELL_shrub_Sb	SSTB vs W	SSTB	0.0205
ELL_tall_mature herbs_Th	NW vs SSTB	SSTB	0.0128
ELL_tall_mature herbs_Th	AW vs SSTB	SSTB	0.0435
LEv_Attended_At	NW vs SSTB	NW	0.0146
LEv_Attended_At	SSTB vs W	W	0.0196
LEv_shrublayer_Sl	AW vs SSTB	SSTB	0.0292
LEv_shrublayer_Sl	NW vs SSTB	SSTB	0.0292
M2	NW vs SSTB	SSTB	0.000581
M2	AW vs SSTB	SSTB	0.00805
M2	SSTB vs SSTS	SSTB	0.0492

5. Discussion

5.1. Long-term changes in butterfly community composition and trait turnover

The results reveal pronounced long-term changes in butterfly and burnet moth species composition over the past 140 years in the protected area Oberweiden. Sørensen dissimilarity values up to 0.60 show substantial species turnover between butterfly community compositions throughout the survey time with only 10 species being present in all four time periods. This level of turnover is comparable to findings in other European long-term butterfly surveys (Van Dyck et al., 2009; Warren et al., 2021).

The community shifted from being dominated by xerothermophilic species in the earliest two periods toward assemblages increasingly characterized by moderately mobile or mobile species and ecological generalists. Although changes in functional composition were less pronounced than taxonomic turnover, NMDS ordination (Fig. 8) revealed that xerothermophilic species were strongly associated with the period spanning from 1931-1966. In parallel, traits related to vegetation structure show a transition from bare ground, sparse short-herb vegetation, and field-layer microhabitats toward taller vegetation layers. This collective pattern points to a long-term decline of sand steppe and dry grassland specialists and a progressive functional homogenization towards mobile, habitat-generalist assemblages. This pattern is consistent with regional declines in xerothermophilic butterflies across Europe due to nitrogen deposition, land-use intensification, and shrub encroachment (Wallisdevries & Swaay, 2006). Recent studies have shown that interacting effects of climate warming and anthropogenic pressures promote generalist species while specialist species decline, ultimately leading to functional homogenisation of communities (Scharnhorst et al., 2026).

Inspection of the dataset (Fig. 3, Appendix A) shows that several common generalist species (*Aglais io, Gonepteryx rhamni, Vanessa atalanta*) were absent during the first two time periods (before 1930, 1931-1966). One plausible explanation is collector bias: early entomologists often focused on rare, larger, or more attractive species (Boakes et al., 2010; Isaac & Pocock, 2015). Moreover, even common and/or highly mobile species can be missed, if collected over brief time periods

(Fattorini, 2013; Kharouba et al., 2018). An alternative explanation is that habitat conditions in the late 19th and early 20th century were so extreme that generalist species were genuinely absent. Orthoptera surveys in the Kiskunság National Park (Hungary), a still intact dune landscape with comparable ecological characteristics, revealed the complete absence of ubiquitous species. Only species adapted to the extreme habitat conditions were present (Oswald, pers. comm. 2025).

Changes in voltinism and flight phenology at community level further illustrate long-term functional restructuring of the butterfly assemblage. These findings do not indicate that individual species have shifted in voltinism and phenology over time but show trait-based community turnover. The increase in community weighted means in voltinism from approximately 1.38 generations per year before 1930 to about 1.63 in 2001-2024 indicates a higher proportion in bi- and multivoltine species in the recent community composition. Similarly, the increase in community-level flight length reflects a shift towards species that have longer activity windows, earlier seasonal onset and/or extended late summer activity. Although the community weighted analysis cannot detect within species shifts in phenology or voltinism through time, comparable responses have been documented in long term monitoring studies across Europe and North America, where butterflies have advanced their flight periods, prolonged their active seasons or increased the frequency of partial generations under climate warming (Altermatt, 2010; Diamond et al., 2011; Forister & Shapiro, 2003; Parmesan, 2006).

5.2. Impact of habitat change

Habitat variables did not show significant correlations with the NMDS ordination. In the present study, the habitat data was restricted to broad habitat categories and. Earlier phases of habitat transformations, including the conversion of open sand steppes and dune stabilization likely altered microhabitat conditions and may have led to loss of species and species turnover. Across Europe, land-use intensification, abandonment of extensive management and resulting habitat fragmentation are well-known drivers of butterfly declines, particularly in semi-natural grasslands and open dry habitats (Wallisdevries & Swaay, 2006).

Factors like mowing regime and grazing intensity were not considered when doing the field survey in 2024. Also, the available habitat data did not allow for analysis in qualitative changes of the land use management. Zimmermann et al. (2023), analyzing the same landscape for wild bee communities, similarly found that coarse habitat categories underestimated ecologically relevant changes and that unrecorded management alterations like mowing frequency and grazing intensity likely had greater impacts than broad areal habitat shifts.

Butterfly species adapted to dry grasslands and steppe habitats depend on open, heterogeneous microhabitats with warm ground-level microclimates, patchy host plant distribution and exposed soil (Guariento et al., 2022; Wenzel et al., 2006). *Chazara briseis,* a once common butterfly now very rare in eastern Austria was last recorded in 1974 in the survey area and is now restricted to two localities ("NSG Hundsheimer Berg" and "Truppenübungsplatz Großmittel"). This species is tightly restricted to patchy mosaics of its host plant (*Festuca*, *Sesleria, Molinia, Stipa*) with substantial bare ground between tussocks, illustrating how the loss of microhabitat heterogeneity can lead to local extinctions even when broader land-cover types appear unchanged (Bartonová et al., 2021; Kadlec et al., 2009).

5.3. Present-day habitat differences and conservation implications

The 2024 survey revealed pronounced differences in butterfly richness and abundance among habitat types, reflecting the strong influence of structural heterogeneity. NW exhibited the lowest species richness and individual counts. This habitat is characterized by large-scale, synchronized mowing, which leads to low structural variability, temporary loss of floral resources, and reduced availability of host plants and basking sites. Such homogenization is known to negatively affect butterfly diversity in grassland systems (Aguirre-Gutiérrez et al., 2017).

In contrast, Pasture (W) and Special Site Shrub (SSTB) supported the highest species richness and abundance. Pastures likely benefited from the introduction of horse grazing in 2022, which created a mosaic of short-grazed areas and bare ground through trampling. Bussan (2022) found that the effect of cattle grazing on individual butterfly species as well as on butterfly communities was largely positive when it included low-moderate intensity or extensive grazing. Although no pre-

grazing comparison exists for the study site in Oberweiden, the significantly higher diversity in W relative to NW suggests that low intensity grazing improved habitat conditions for a variety of butterfly and burnet moth species.

SSTB, despite representing a later successional stage with substantial shrub encroachment, also hosted high species richness. Shrub edges are known to increase microhabitat diversity by providing sheltered warm pockets, vertical structure for basking, and diverse flowering resources. This is consistent with studies showing that heterogeneous shrub–grassland ecotones can support high butterfly diversity due to fine-scale variation in microclimate (Roth et al., 2021; Wenzel et al., 2006).

Trait CWMs revealed a clear functional differentiation among habitat types, with the strongest contrasts between New Meadow (NW) and Special Site Shrub (SSTB). NW supported significantly fewer M2 species and species using shrub or tall-herb strata for basking, oviposition, and larval development. SSTB, in contrast, showed the highest representation of shrub- and tall-herb associated traits and more ant-attended larvae, indicating a structurally richer environment. Old Meadows (AW) displayed intermediate functional composition.

Taken together, the results emphasize that management promoting heterogeneous, structurally diverse grassland systems is essential for maintaining butterfly diversity in the survey area. Practices such as rotation instead of synchronized mowing and moderate grazing can improve habitat conditions. In order to restore sand dune habitat conditions, more drastic measures like topsoil removal and tree removal to reestablish exposure to wind erosion might be necessary (Cousins et al., 2015; Riksen et al., 2006; Zimmermann et al., 2023).

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7. Appendix

Appendix A Period x species matrix

Species	**< 1930**	**1931–1966**	**1967–2000**	**2001–2024**	**n_periods_present**
Aglais io	0	0	1	1	2
Aglais urticae	0	0	1	1	2
Anthocharis cardamines	1	0	1	1	3
Aphantopus hyperantus	0	0	1	1	2
Aporia crataegi	1	0	0	0	1
Araschnia levana	0	0	1	1	2
Arethusana arethusa	1	1	1	1	4
Argynnis paphia	0	0	1	1	2
Aricia agestis	0	0	1	0	1
Boloria dia	0	1	1	1	3
Boloria selene	0	0	1	0	1
Brenthis daphne	0	0	0	1	1
Brintesia circe	0	0	0	1	1
Callophrys rubi	1	1	1	1	4
Carcharodus alceae	0	1	1	0	2
Celastrina argiolus	0	0	1	1	2
Chazara briseis	1	1	1	0	3
Coenonympha arcania	0	0	0	1	1
Coenonympha glycerion	1	1	1	1	4
Coenonympha pamphilus	1	0	1	1	3
Colias alfacariensis	1	1	1	0	3
Colias croceus	1	0	0	1	2
Colias erate	0	0	1	0	1
Colias hyale	1	0	1	1	3
Cupido minimus	1	1	1	1	4
Cyaniris semiargus	0	0	1	0	1
Erynnis tages	0	0	1	1	2
Euphydryas aurinia	1	0	0	0	1
Fabriciana niobe	1	1	0	0	2
Glaucopsyche alexis	1	0	1	1	3
Gonepteryx rhamni	0	0	1	1	2
Hesperia comma	0	0	1	1	2

Heteropterus morpheus	0	1	1	0	2
Hipparchia semele	1	1	0	1	3
Hyponephele lycaon	1	1	0	0	2
Iphiclides podalirius	0	1	1	1	3
Issoria lathonia	1	1	1	0	3
Jordanita chloros	0	1	0	0	1
Lasiommata maera	1	0	1	0	2
Leptidea sinapis	0	0	1	1	2
Lycaena dispar	0	0	1	1	2
Lycaena phlaeas	0	0	0	1	1
Lycaena tityrus	0	0	0	1	1
Lysandra bellargus	1	0	0	1	2
Lysandra coridon	1	1	1	1	4
Maniola jurtina	0	1	1	1	3
Melanargia galathea	1	1	1	1	4
Melitaea athalia	1	0	0	0	1
Melitaea cinxia	1	0	0	1	2
Melitaea parthenoides	0	1	0	0	1
Melitaea phoebe	0	0	1	1	2
Minois dryas	1	1	1	1	4
Ochlodes sylvanus	0	1	1	1	3
Papilio machaon	1	1	1	1	4
Parage aegeria	0	1	0	0	1
Phengaris alcon	1	1	1	0	3
Pieris brassicae	0	0	1	1	2
Pieris napi	0	0	1	1	2
Pieris rapae	0	0	1	1	2
Plebejus argus	1	0	1	1	3
Plebejus argyrognomon	1	0	1	0	2
Plebejus idas	1	0	0	0	1
Polygonia c-album	0	0	1	1	2
Polyommatus coridon	0	0	0	1	1
Polyommatus daphnis	1	1	0	0	2
Polyommatus icarus	1	0	1	1	3
Polyommatus thersites	1	0	1	1	3
Polyygonia c-album	0	0	0	1	1
Pontia edusa	0	0	1	1	2
Pseudophilotes vicrama	1	0	0	0	1
Pyrgus carthami	1	1	1	1	4

Pyrgus malvae	0	0	1	1	2
Rhagades pruni	0	1	1	0	2
Satyrium ilicis	0	1	0	0	1
Satyrium spini	0	0	1	1	2
Speyeria aglaja	1	1	0	0	2
Thymelicus lineola	1	0	1	0	2
Thymelicus sylvestris	1	0	1	0	2
Vanessa atalanta	0	0	1	1	2
Vanessa cardui	0	1	1	0	2
Zerynthia polyxena	1	0	0	0	1
Zygaena brizae	1	0	0	0	1
Zygaena carniolica	1	1	1	1	4
Zygaena ephialtes	0	1	1	0	2
Zygaena filipendulae	0	1	1	1	3
Zygaena laeta	1	1	1	0	3
Zygaena loti	0	0	0	1	1
Zygaena minos	0	0	1	0	1
Zygaena punctum	0	1	1	0	2
Zygaena transalpina	0	1	1	0	2
Zygaena viciae	0	0	1	0	1

Appendix B Trait definitions

Trait	**Definition**
Habitat preference	
X	Xerothermophilous species; associated with dry and warm habitats
M1	Mesophilous open land species; typical of mesic open habitats (meadows, grasslands)
M2	Mesophilous ecotone species; associated mesic transitional habitats between forest and open land
M3	Mesophilous woodland species; characteristic of mesic habitats within open or lightly structured woodland
H	Hygrophilous species; associated with moist or wet habitats such as wetlands, marshes, or humid meadows
U	Ubiquitous species; Ecologically tolerant species occurring across a wide range of habitat types and environmental conditions
Dispersal ability	

sedentary	sedentary; low dispersal ability
moderately mobile	moderately mobile; medium dispersal ability
dispersive	dispersive; high dispersal ability
Hostplant growth form	
HPG_short herb_grass_Sh	Hostplant growth form short herb/grass; non-woody species having a primary stem of less than 1m
HPG_tall herb_Th	Hostplant growth form tall herb; non-woody plants having a primary stem of greater than 1m
HPG_shrub_Sb	Hostplant growth form shrub
HPG_tree_Tr	Hostplant growth form tree
HPG_non plant_Np	Hostplant growth form non plant (moss, lichen)
HPG_liana_Li	Hostplant growth form liana; climbing woody plants such as lianas
Egg laying location	
ELL_bare ground or ground artifact_ Bg	Egg laying location on bare ground or artifact; deposited directly on bare soil, stones, or other ground-level substrates rather than on vegetation
ELL_short turf_herbs_Sh	Egg laying location on short herbs; low-growing herbaceous plants
ELL_tall_mature herbs_Th	Egg laying location on tall, mature herbs; on tall, herbaceous plants
ELL_shrub_Sb	Egg laying location on shrubs; woody shrubs or within shrub-dominated vegetation layers
ELL_tree trunk_Tt	Egg laying location on tree trunks; on the bark or surface of tree trunks
ELL_canopy_Ca	Egg laying location in tree canopy; within the foliage layer of trees
ELL_liana_Li	Egg laying location on liana; on climbing woody plants such as lianas
Larval environment	
LEv_buried_Bu	Larval environment buried; larvae develop below the soil surface, feeding on underground plant structures
LEv_groundlayer_ Gl	Larval environment groundlayer; Larvae develop at or directly above the soil surface, often feeding on low vegetation, litter-associated plants, or basal plant parts
LEv_fieldlayer_Fl	Larval environment fieldlayer; Larvae develop within the herbaceous vegetation layer above the ground, feeding on non-woody plants such as herbs or grasses
LEv_shrublayer_Sl	Larval environment shrublayer; Larvae develop on woody shrubs or within shrub-dominated vegetation layers
LEv_canopy layer_Cl	Larval environment canopy layer; Larvae develop in the upper vegetation layer of trees, feeding on leaves or other parts of tree species

LEv_Attended_At	Larval environment ant attended; Larvae engage in myrmecophilous interactions with ants
Basking site	
BaS_rock\bare earth_Bg	Basking site rock/bare earth; exposed rock surfaces or bare ground
BaS_short herb_Sh	Basking site short herb; on low-growing herbaceous vegetation
BaS_grasses_Gr	Basking site grasses
BaS_tall herbs_Th	Basking site tall herbs; tall herbaceous vegetation
BaS_shrub_Sb	Basking site woody shrubs or within shrub-dominated vegetation layers
BaS_tree canopy_Tc	Basking site within canopy layer of trees