EUROPEAN JOURNAL OF ENTOMOLOGY
ISSN (online): 1802-8829
http://www.eje.cz

Eur. J. Entomol. **122**: 308–322, 2025
doi: 10.14411/eje.2025.035

ORIGINAL ARTICLE

Nature conservation and insect decline in Central Europe: Loss of Lepidoptera in key protected sites is accompanied by substantial land cover changes

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Key words. Biodiversity conservation, land use, land cover, canopy openness, butterflies and moths, land abandonment, succession, homogenization

Abstract. The insect biodiversity crisis affects diverse cultural landscapes as well as natural and semi-natural habitats. Accordingly, the effectiveness of protected areas in conserving insect communities needs to be evaluated. We employed photo-interpretation of aerial photographs from the past (1938–1947) and present (2014–2019) to analyse changes in natural habitats with diverse canopy cover in seven long-term protected areas (jointly called 'reserves') in the Czech Republic, Central Europe, and evaluated potential links between these changes and butterfly and moth (Lepidoptera) declines. We observed a marked decrease in habitat heterogeneity, largely due to the expansion of closed-canopy forests at the expense of semi-open habitats (e.g. forest steppes, open woodlands) and open grasslands. An analysis of faunistic records of 162 species of butterflies and 160 species of macro-moths before and after 2000 showed that, on average, the reserves have experienced losses of 26% of butterfly species and 19% of moth species. Trait-based analyses suggested that the losses were associated with particular life-history traits. Non-generalist butterflies with a short period of seasonal flight activity, and moths associated with grasslands and with non-feeding adults, had a greater probability of going missing (meaning potentially locally extinct) in the reserves. These findings suggest that conservation efforts should prioritise active management that aims to restore habitat heterogeneity in order to mitigate the ongoing trend of insect decline.

INTRODUCTION

European nature is experiencing a significant decline in insect biodiversity (Van Dyck et al., 2009; Hallmann et al., 2017, 2020; Seibold et al., 2019). The decline concerns the loss of species, their abundances, and even biomass, and impacts open habitats like grasslands as well as forests (Seibold et al., 2019). Insects are of crucial importance for ecosystem functioning and agricultural production due to their role in decomposition and nutrient cycling, food webs, pollination and pest control (Smith et al., 2015; Ameixa et al., 2018; Powney et al., 2019; Samways et al., 2020; van der Sluijs, 2020). Human induced habitat alterations are among the principal causes of substantial changes in insect diversity worldwide (Goulson et al., 2015; Sánchez-Bayo & Wyckhuys, 2019; Jactel et al., 2020; Wagner et al., 2021; Chowdhury et al., 2023; Rumohr et al., 2023).

In the last 200 years, the European landscape has undergone significant changes that have affected natural or semi-natural habitats. These changes were associated with two different processes: first, the transition from traditional silvicultural and agricultural practices towards organised forestry or intensive agriculture management (Bürgi, 1999; Bignal & McCracken, 2000; Tscharntke et al., 2005; Müllerová et al., 2014; Buckley, 2020), and second, the abandonment of formerly used land (Beilin et al., 2014; Queiroz et al., 2014; Otero et al., 2015; Ustaoglu & Collier, 2018).

Former European woodlands were characterized by a mixture of diverse habitats, closed-canopy forest stands, as well as semi-open or open woodlands. These habitats formed as a result of traditional management practices such as wood-pasturing, in which grazing animals maintained a sparse vegetation structure of woods, or coppicing

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and pollarding, techniques involving short-rotation cutting of forest patches or trees and their subsequent regrowth, creating dynamic systems of open and shady successional stages within forests (Rackham, 2003; Kirby & Watkins, 2015; Weiss et al., 2021). These conditions allowed for the persistence of both shade-tolerant and light-demanding woodland associated organisms. In open landscapes, agro-pastoral land-use systems were characterised by a mixture of small field crops, meadows and pastures (usually used interchangeably between years), sometimes divided by pollard trees or fruit trees at boundaries between properties. Significant habitat alterations started to occur with the onset of organised forestry and agricultural revolution around 200 years ago and escalated after the Second World War (Bignal & McCracken, 2000; Müllerová et al., 2014). Simple coppices were transformed into coppice-with-standards woods and later to high forest stands, new forests were planted on formerly open land, and grazing in forests was largely restricted (Bürgi, 1999; Savill, 2015; Buckley, 2020). Open-grown trees from former pastures were often removed to create more productive pastures. In many places the area of fields and meadows increased at the expense of small scale mosaics (Eichhorn et al., 2006; Plieninger & Bieling, 2013; Šálek et al., 2021), and fertilisers and insecticides became widely used in agriculture adding to the unification of open habitats (Wesche et al., 2012; Payne et al., 2017; Habel et al., 2019, 2022a; Roth et al., 2021a).

Another significant driver of landscape changes in Europe has been the abandonment of formerly managed land (Sirami et al., 2010; Beilin et al., 2014; Hallmann et al., 2017; Miklín et al., 2018) usually associated with the migration of country folk to cities. Due to succession, grasslands on former extensive meadows or pastures have been subsequently replaced by shrublands and eventually by woodlands and the landscape has become less heterogeneous (Debussche et al., 1999; Prévosto et al., 2011; Marull et al., 2015). Land abandonment is now recognised as a major threat to European diversity along with the above mentioned agricultural intensification (Renwick et al., 2013; Queiroz et al., 2014).

To counterbalance the effects of human activities on biodiversity in cultural landscapes, protected areas have been established all over the world. In Europe, however, due to the cessation of human activities in many protected areas, their formerly diversified habitats resulting from former practices often succumb to forest encroachment in a very similar way to abandoned land (Janík et al., 2024) and their woodland habitats become denser and homogeneous due to absence of natural disturbance factors (fires, large herbivores) (Cholewińska et al., 2020). Regarding insects, the effects of these trends tend to be overlooked. In fact, many protected areas have been designated primarily for plants and vertebrates rather than the effective protection of insect communities (Chowdhury et al., 2023). In this context, the effectiveness of protected areas in conserving insect biodiversity needs to be evaluated (Chowdhury et al., 2023).

Lepidoptera, i.e. butterflies and moths, represent an important model group in ecology because they are species rich and vary greatly in their life-history traits, behavioral characteristics, host plant associations, and dispersal abilities (Dennis et al., 2003; Bartonova et al., 2014; Potocký et al., 2018; Coulthard et al., 2019). European butterflies are mostly associated with open and semi-open habitats, and due to their relatively easy identification, they have become a prominent taxon in ecological research and insect monitoring programmes. Moths, on the other hand, comprise most of Lepidoptera diversity and they constitute a significant part of insect diversity in forests, besides other habitats. Many species of Lepidoptera use multiple habitat types or microhabitats to obtain necessary resources for their full life cycle (Freese et al., 2006; Krämer et al., 2012; Liivamägi et al., 2014; Scherer & Fartmann, 2022). The group is known to be sensitive to habitat heterogeneity at local as well as landscape scale (Schneider & Fry, 2001; Söderström et al., 2001; Jeanneret et al., 2003; Krauss et al., 2003; Novotný et al., 2015; Roth et al., 2021a; Uhl et al., 2021, 2023; Habel et al., 2024). Land abandonment and simplification in habitat heterogeneity influence micro-climatic conditions as well as floral resources available for Lepidoptera. The study of temporal habitat changes in protected areas in relation to changes in communities of butterflies and moths can thus bring important information on the biological nature of the on-going ecological processes and eventually help to define future strategies in insect conservation (Habel et al., 2024).

The aim of this study is to examine associations between habitat changes and losses of butterflies and moths in several protected areas in Bohemia and Moravia (Czech Republic). We selected seven nationally important areas for biodiversity conservation on the basis that they have been the focus of nature conservation for a long time, having been protected since the 1930s or 1950s. Additionally, they host rich and diverse Lepidoptera communities with well-known historical and current composition because they were frequented by insect collectors and entomologists over the last centuries and have been subject to standardised and intensive Lepidoptera surveys for the last two decades. Specifically we aim to (i) evaluate changes in vegetation structure between past (ca. 80 years ago) and present using several categories of canopy cover ranging from open land to closed-canopy forests, (ii) compare, based on the canopy cover categories, indices of habitat heterogeneity in the studied reserves between past and present, (iii) evaluate numbers of species recorded in the reserves in past and present and missing or new species, and finally (iv) test whether the probabilities of species of butterflies and moths going missing (potentially locally extinct) are associated with particular life-history traits.

MATERIAL AND METHODS

Study areas

We analysed temporal changes of natural habitats and lepidopteran fauna in seven protected areas of different status (hereafter jointly referred to as 'reserves') in Central Bohemia and South Moravia, Czech Republic. The reserves included the most important butterfly and moth habitats in the country, they were: (1) Koda national nature reserve, (2) Karlštejn national nature re-

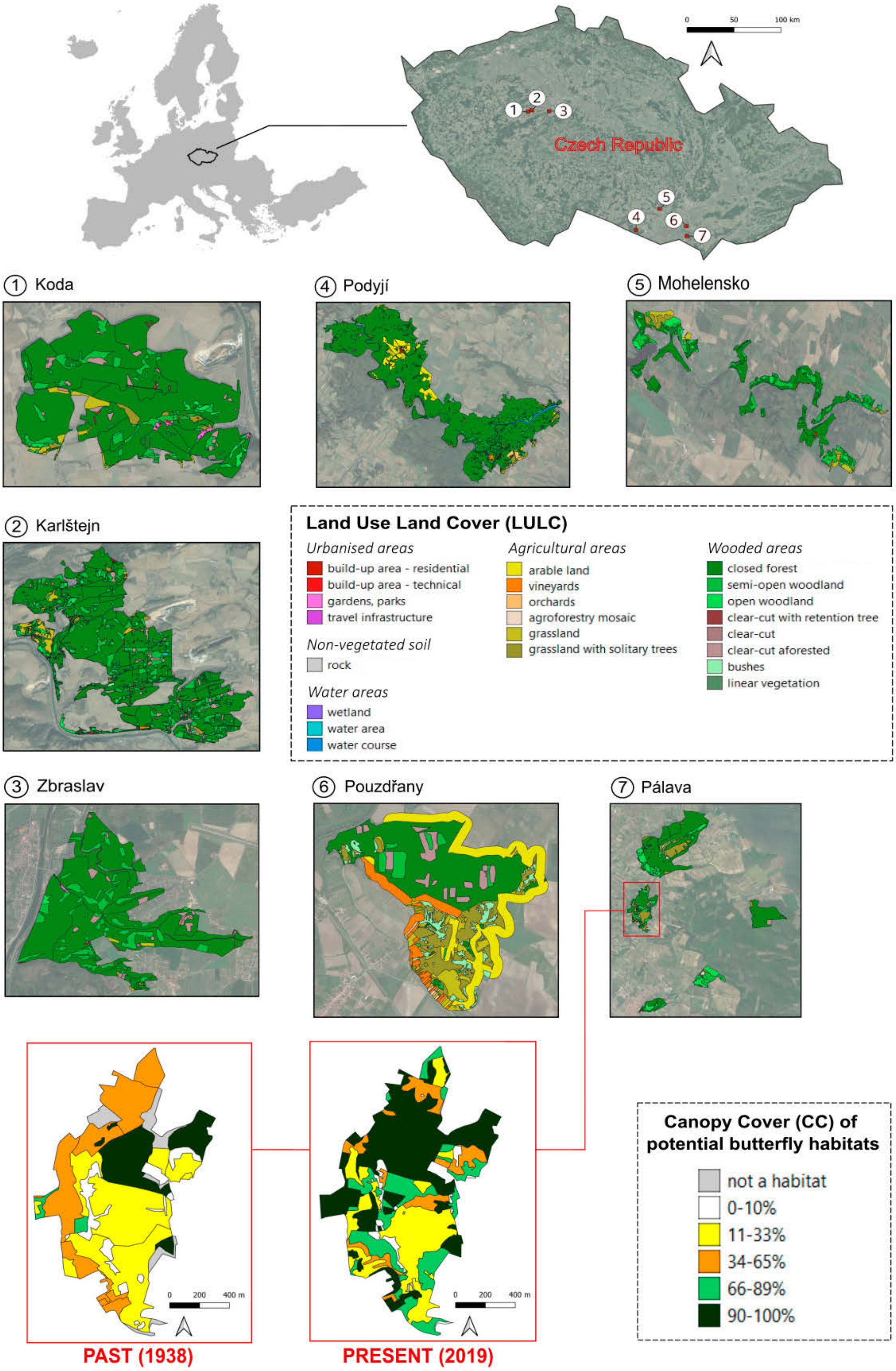

Fig. 1. Location of the studied protected areas ('reserves') in Bohemia (reserves 1, 2, and 3) and Moravia (the rest) and the representation of current land use/land cover categories (LULC; original 22 categories). For each reserve, the original LULC categories were translated into five categories of canopy cover (bottom insets, see also Table S2 for details), and the change in canopy cover between past and present was later evaluated.

serve, (3) Šance (Zbraslav) nature reserve, (4) Podyjí National Park, (5) Mohelenská hadcová step national nature reserve and several small neighbouring reserves (together referred to as 'Mohelensko'), (6) Pouzdřanská step – Kolby national nature monument (referred to as 'Pouzdřany'), and (7) Pálava Protected Landscape Area (Fig. 1). The area of each reserve consisted of several vegetation types with different structure and levels of canopy openness, such as open semi-natural meadows or steppes, scrub, open woodlands, or closed-canopy forests (see Table S1 in Supplementary Material for the description of the reserves). These reserves represent areas known for their biological value, locally considered hotspots among naturalists and conservationists for many decades. The reserves are also known for representative records of butterflies and moths from past and present thanks to being within easy reach of larger cities like Prague or Brno.

Landscape data

We evaluated changes in the amount and heterogeneity of different habitats in the reserves between past and present states. We used two sets of aerial photographs for each reserve: (i) *past state* – historical aerial photographs from 1938 to 1947 (from 1938 for Koda, Karlštejn, Podyjí, Pálava, and Pouzdřany, from 1946 for Zbraslav, and from 1947 for Mohelensko; earlier maps were not available for the latter two) and (ii) *present state* – recent photographs from 2014 (Podyjí, Mohelensko, Pouzdřany) or 2019 (the remaining reserves). The historical scanned aerial photographs in 1200 DPI resolution were obtained from the Military Geographic and Hydrometeorologic Office in Dobruška and transformed into a national coordinate system (S-JTSK) with ground resolution of 0.5 m. Using visual photo-interpretation with high precision and minimal spatial generalization we created a land use/land cover (LULC) geodatabase at 1:5000 scale of vectorization. The LULC classification comprised 22 categories (following Miklín & Smolková, 2011) (Fig. 1). From this geodatabase, we identified 14 LULC categories that can serve as habitats for butterflies and moths and associated them with five categories of canopy cover according to tree density and canopy structure. The canopy cover categories were: (1) 0–10% cover (e.g. grasslands, rocks or bare land), (2) 11–33% cover (grasslands with scattered trees), (3) 34–65% cover (open woodlands), (4) 66–89% cover (semi-open woodlands), and (5) 90–100% cover (closed-canopy forests) (Table S2). Fields (arable land) and vineyards were not defined as potential habitats for butterflies and moths because they are often subject to intensive use of insecticides in the present. Although some vineyards with integrated environment-friendly practices can potentially act as habitats for butterflies (Hluchý et al., 2007), the assessment of current as well as past practices based on aerial images is not possible. Photo-interpretation was performed by two experienced persons (J. Miklín, G. Percel) who calibrated their approach together to distinguish among the categories and avoid subjective bias. We did not use automated photo-interpretation due to differences in quality of the underlying photographs, particularly between historical and present images, which required manual assessements.

Records of butterflies and moths

We used data on records of day-flying butterflies and burnet moths (Rhopalocera and Zygaenidae; jointly as 'butterflies') and macro-moths from the Czech Butterflies and Moths Recording database (Institute of Entomology, BC CAS) and the national Species Occurrence Database (NDOP; Nature Conservation Agency of the Czech Republic) to create lists of species recorded in the areas of each reserve until 2000 (inclusive) and after 2000 (from 2001 to 2023). The Czech Butterflies and Moths Recording database contains dated and localized records of species observations extracted from historical sources and updated regularly by the national monitoring programme; these data were cross-checked and complemented with records from the Species Occurrence Database to ensure that we have current data on species occurrences. The records of species until 2000 were considered past records, the records after 2000 as recent records. The year 2000 was selected as a threshold because from that time, standardised and intensive lepidopterological inventories have been conducted in the reserves, and we may thus assume that the species not recorded after 2000 were absent from the local communities. Irregular and less intense sampling up to 2000 gives a good picture of species present in the communities during the 20th century, while at the same time providing little clue about the time of disappearance of particular species. We assessed occurrences of species in each studied reserve: species recorded both in past and present were marked as having 'stable' occurrence in particular reserve, species recorded in past but not in present were marked as 'missing' (they may also be locally extinct species), and species not recorded in the past, but recorded in the present, were marked as 'new' to the reserve. We then evaluated numbers of missing, stable and new species for each reserve.

We further extracted data on life-history traits of all recorded species from the list of traits for central-European butterflies (Bartonova et al., 2014; Suchácková Bartoňová et al., 2024) and macro-moths (Potocký et al., 2018) (see Table S3 in Supplementary Material). The lists of traits include diverse morphological, behavioural, or physiological characteristics of species, as well as 'habitat affinity traits' which describe the affinity of species to particular habitat type defined as a combination of vegetation type and habitat microclimate, e.g. mesophilic grasslands, mesophilic shrublands, mesophilic woodlands, xerothermophilic grasslands (steppe), ubiquists, etc. The traits served to help analyse whether the losses of species from local communities in reserves were associated with particular life-history traits, i.e. whether the missing species comprised diverse ecological strategies or whether they shared specific ecological traits signifying non-random extinctions. The burnet moths (Zygaenidae) were omitted from the analysis of butterfly life-history traits because the trait information was not available.

Data analysis

Evaluation of habitat amount and heterogeneity

For each reserve, we evaluated the changes in the total area and relative proportions of habitats defined by the canopy cover categories between the past and present state. We also assessed the degree of heterogeneity in habitats for each reserve and the changes in patch complexity and landscape texture. For this purpose, we computed two metrics at the landscape level (i.e. considering all canopy cover categories) – *edge density* and *contagion index* (McGarigal et al., 2023). The calculations were done using rasterized maps of canopy cover categories (patch classes) for each reserve. The edge density metric describes the proportion of borders between patches of different classes (i. e. different canopy cover categories) in the landscape (reserve); it ranges from 0 to infinity with greater values of edge density signifying more borders between different habitats. The contagion index describes the aggregation of patches of the same habitat in the landscape; it ranges from 0 to 100 with greater values signifying greater aggregation of habitats of the same class and thus lower patchiness in the landscape. We further described specific patterns in gain and loss of different canopy cover categories between periods by calculating two metrics at class levels (i.e. considering each canopy cover category independently) – *mean patch size* and *patch density* (McGarigal et al., 2023). Mean patch size may have an ecological significance since most species have minimum area requirements to meet their life-history demands. Patch density represents an availability of a particular habitat in the landscape disregarding its size. In order to quantify habitat changes in the reserves between past and present, we calculated the rate of change in mean patch size and patch density as a Δ value based on the equation: $\Delta \text{ value} = [(M_{pres} - M_{past}) / M_{past}] \times 100$, where M_{pres} is the value of the metric in the present and M_{past} is the value of the metric in the past. We then described four different patterns in habitat change based on the combination of the increase or decrease in mean patch size and patch density, these patterns were, specifically: (i) *expansion* – both mean patch size and patch density increase, signifying that the habitat patches become more common in the landscape and they are greater in size; (ii) *consolidation* – increase in mean patch size but decrease in patch density, signifying a change towards fewer patches of the habitat but with larger sizes; (iii) *disintegration* – decrease in mean patch size but increase in patch density, signifying a change towards more patches of the habitat but with smaller sizes; and (iv) *rarefaction* – both mean patch size and patch density decrease, signifying that the habitat becomes rarer in the landscape. See Fig. S1 in Supplementary Material for visual representation of the habitat change patterns. All metrics were computed using the ‘landscapemetrics’ package (Hesselbarth et al., 2019) in R 4.4.1 (R Core Team, 2024).

Loss of butterflies and moths

To analyse potential associations between life-history traits and losses of butterfly and moth species in the reserves, we performed two types of analyses: generalized linear models with binomial (Bernoulli) distribution and recursive partitioning (calculated through conditional inference trees). To analyse whether some life-history traits increase the probability of species going missing, we marked species classified as missing as 1 and species with stable occurrence as 0, and fitted generalized linear models with binomial distribution (*logit* link) with status (missing = 1, stable = 0) as a response variable and life-history traits as explanatory variables (see Table S3 for details on traits used). We selected traits with significant effects on the species status by forward selection procedure. All the available life-history traits were analysed in one model, but separately for butterflies and moths. We then performed a complementary analysis using conditional inference trees (recursive partitioning) (Hothorn et al., 2006) which account for conditional nonlinear hierarchical relationships and treat categorical, ordinal and quantitative data simultaneously. In each split of the tree, all species traits were tested and the trait that best discriminated between missing and stable species was selected. The significance of the variables used for the discrimination was tested by Monte Carlo permutation tests with 999 permutations. We only tested which life-history traits may be associated with ‘missing’ species status; we did not analyse the associations of life-history traits for species marked as ‘new’ due to low recorded numbers (see Results). The statistical analyses were performed in R 4.4.1 (R Core Team, 2024).

RESULTS

Changes in habitat amount and heterogeneity

In all reserves, closed-canopy forests (i.e. habitats with 90–100% canopy cover) markedly increased between past and present. Conversely, habitats with intermediate canopy cover between 11 and 89% (i.e. grasslands with scattered trees or shrubs, open and semi-open woodlands) experienced general declines in variable proportions depending on the reserve, except for Mohelensko, where areas of open and semi-open woodlands slightly increased. Finally, the area of habitats with 0–10% canopy cover (e.g. grasslands) showed variable changes: a decrease in Mohelensko, Podyjí, and Pouzdřany, but an increase in Koda, Zbraslav, and Pálava (Fig. 2).

Regarding heterogeneity metrics computed at the landscape level, the comparison between past and present revealed a substantial decrease in edge density (i.e. lower density of borders between patches of different canopy cover categories in the present compared to the past) in four reserves; in two reserves, Karlštejn and Pálava, the edge density increased but only negligibly. Only in Pouzdřany did edge density increase substantially (Table 1), but this was associated with the major loss of open woodlands (canopy cover category 3: 34–65%), which dominated the reserve in the past (Fig. 2). In all reserves, we revealed an increase in contagion index, i.e. higher aggregation of patches belonging to the same canopy cover category, thus lower patchiness of habitats in present than past.

The detailed evaluation of the processes behind the temporal changes of each canopy cover category revealed that the spread of habitats with 90–100% canopy cover (closed-canopy forests) in reserves happened mostly through consolidation, i.e. increase in patch size but decrease in patch density that typically occurs when formerly separated patches join together and form larger ones, or, in two reserves, through expansion when patches increase in size and new patches form (Table 2; see also Fig. S2 for the comparison of past and present distribution of habitats). The habitats with 11–33% and 34–65% canopy cover (grasslands with scattered trees and open woodlands) were the most diminished, their losses often happened through rarefaction, i.e. they became rare in the reserves due to both decrease in patch size and density, otherwise the loss of habitats were caused by disintegration, which typically occurs when formerly larger patches split and become separated. Concerning habitats with 0–10% canopy cover (open grasslands), different trends were observed in

Table 1. Comparison of habitat heterogeneity landscape metrics – edge density and contagion index – for each reserve in past and present. The edge density metric describes the proportion of borders between patches of different habitat classes (i.e. different canopy cover categories) in the landscape (reserve); it ranges from 0 to infinity with greater values of edge density signifying more borders between different habitats. The contagion index describes the aggregation of patches of the same habitat in the landscape; it ranges from 0 to 100 with greater values signifying greater aggregation of habitats of the same class and thus lower patchines in the landscape. See McGarigal et al. (2023) for a detailed description of the metrics. Higher values from the two periods are marked with bold print.

Reserve	Edge density		Contagion index	
	Past	Present	Past	Present
Koda	**131.6**	102.7	56.2	**72.2**
Karlštejn	141.7	**143.4**	55.7	**63.5**
Zbraslav	**116.7**	91.1	63.8	**76.8**
Podyjí	**134.5**	63.0	51.1	**79.9**
Mohelensko	**200.3**	149.5	42.6	**52.8**
Pouzdřany	159.7	**186.3**	46.5	**50.0**
Pálava	101.4	**101.6**	47.0	**57.8**

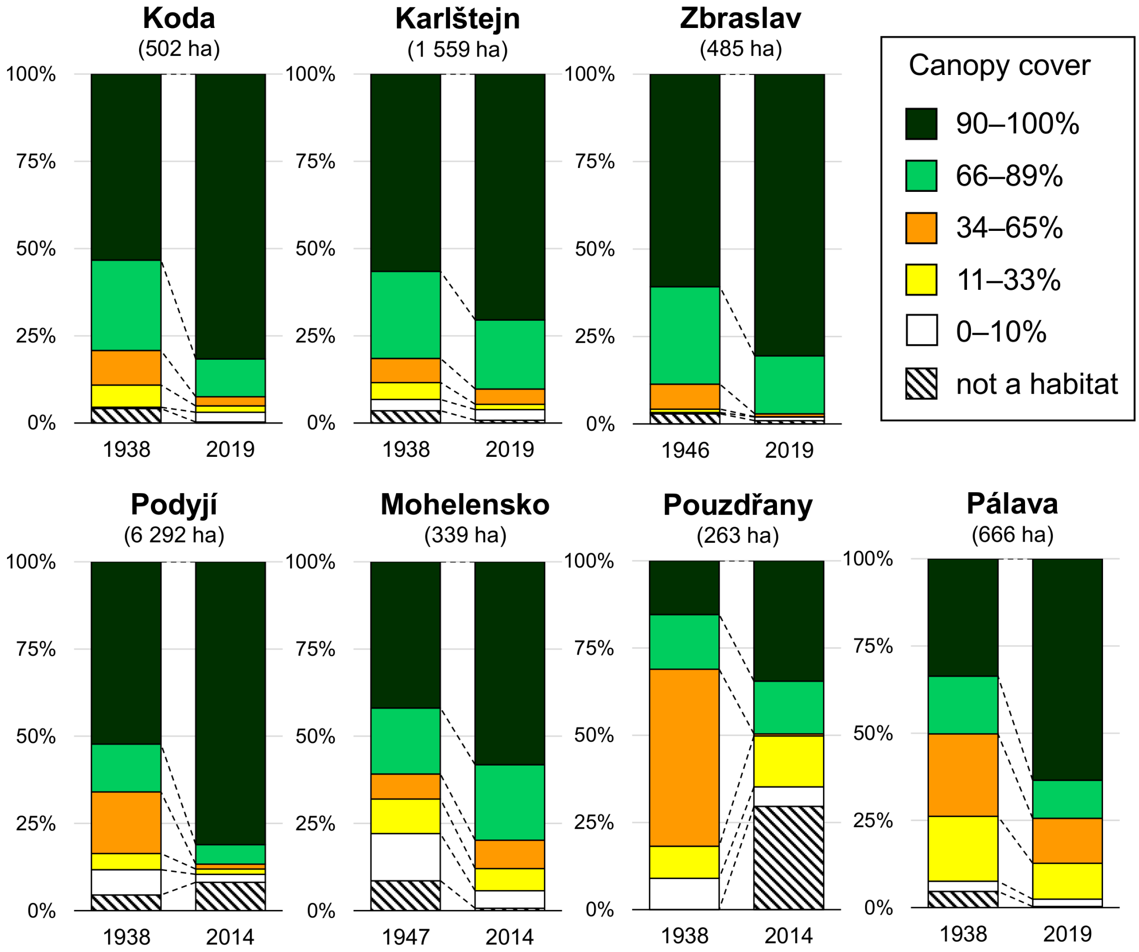

Fig. 2. Percentages of area covered by habitats with different canopy cover categories for each studied reserve in past (1938, 1946, or 1947) and in present (2014 or 2019) based on land use/land cover categories created from vectorisation of historical and recent aerial photographs. Gains or losses in the area of particular categories in each reserve are given in Table S4.

reserves, see Table 2. Overall, the trends in Mohelensko were visibly different from other reserves as all habitats changed through consolidation, i.e. formation of fewer but larger patches (Table 2).

Changes in species numbers

We analysed faunistic records of 162 species of butterflies (Rhopalocera and Zygaenidae) and 160 species of macro-moths. The comparison of the periods before and after the year 2000 showed that on average the reserves experienced a loss of 26% of butterfly species (min. 15, max. 48 species; net differences of missing minus new species) and 19% of moth species (min. 6, max. 41 species) (Fig. 3; Table 3). If new species were recorded in the reserves, there were only one or two species (Table 3). The full list of species can be found in Table S5.

Associations between missing species and their life-history traits

Using generalized linear models with binomial distribution and recursive partitioning (conditional inference trees) we revealed that in most cases the losses of species were associated with particular life-history traits (Table 4, Fig. S3). The sets of significant life-history traits predicting losses of species from local communities were variable but with some general similarities.

In butterflies, species with shorter flight period length (*FlghtPerLen*), higher fertility (*Fertility*) or non ubiquists (*Hubiquitous*) had a greater probability of going missing from most reserves. Besides this, some responses were specific for particular reserves. In Koda, species associated with xeric (steppic) grasslands (*Hxerothermophilic1*) had a greater probability of disappearing. In Karlštejn, less mobile (sedentary) species (*Mobility*) were more prone to disappear. In Zbraslav, species associated with ephemerals and small herbaceous plants were more prone to disappear than species associated with large herbaceous plants, grasses and trees (*HostPlantForm*, Table S6), on the other hand, species associated with mesophilic grasslands were less prone to disappear. In Mohelensko, hydrophilic species were more prone to go missing. In Pouzdřany, species with narrow trophic range were more likely to disappear (*Feeding*).

In moths, the models generally showed that species associated with mesic woodlands (*Hmesophilous3*) and mesic shrublands (*Hmesophilous2*), or species associated with woodlands in general (*Hab3D*) were less liable to go missing in reserves. Additionally, species with non-feed-

Table 2. Comparison of past and present values of mean patch size and patch density metrics for all habitats defined by their canopy cover categories calculated based on rasterized land use/land cover data for each reserve. *Δ values* give a rate of change in the metric value against the past state, positive for the increase in the metric value, negative for the decrease in the metric value. *Category pattern* gives one of four possible outcomes based on a combination of increase/decrease in patch density and increase/decrease in mean patch size (Fig. S1), specifically: expansion = increase in both metrics; consolidation = increase in mean patch size but decrease in patch density; disintegration = decrease in mean patch size but increase in patch density; rarefaction = decrease in both metrics. Superscripts given in the *Category pattern* column signify specific situations of the pattern: 1 = disintegration of the habitat despite an increase in total area of the habitat (Fig. 2); 2 = consolidation of the habitat despite a decrease in total area of the habitat (Fig. 2).

Reserve	Canopy cover category	Mean patch size			Patch density			Category pattern
		Past	Present	Δ value	Past	Present	Δ value	
Koda	(1) 0–10 %	0.2	0.3	52	1.9	9.0	381	Expansion
	(2) 11–33 %	2.1	0.6	–72	3.1	3.0	–4	Rarefaction
	(3) 34–65 %	1.5	0.4	–75	6.7	6.8	2	Disintegration
	(4) 66–89 %	4.0	0.8	–80	6.7	13.4	101	Disintegration
	(5) 90–100 %	14.1	58.4	315	4.0	1.4	–65	Consolidation
Karlštejn	(1) 0–10 %	0.7	0.5	–29	4.7	6.1	31	Disintegration
	(2) 11–33 %	0.9	0.3	–67	5.6	5.2	–7	Rarefaction
	(3) 34–65 %	1.8	0.5	–74	4.0	9.4	137	Disintegration
	(4) 66–89 %	2.1	1.1	–47	12.6	18.4	46	Disintegration
	(5) 90–100 %	14.2	22.9	61	4.1	3.1	–25	Consolidation
Zbraslav	(1) 0–10 %	0.5	0.3	–35	0.6	3.1	390	Disintegration[1]
	(2) 11–33 %	0.4	0.4	–5	2.5	0.2	–92	Rarefaction
	(3) 34–65 %	1.4	0.3	–80	5.3	2.9	–45	Rarefaction
	(4) 66–89 %	3.1	1.4	–55	9.3	11.9	27	Disintegration
	(5) 90–100 %	14.0	195.8	1294	4.5	0.4	–91	Consolidation
Podyjí	(1) 0–10 %	1.0	0.5	–46	7.7	4.6	–40	Rarefaction
	(2) 11–33 %	6.6	3.3	–50	0.7	0.5	–31	Rarefaction
	(3) 34–65 %	5.4	1.3	–75	3.4	1.1	–67	Rarefaction
	(4) 66–89 %	2.2	0.9	–59	6.4	6.7	4	Disintegration
	(5) 90–100 %	23.8	100.0	320	2.3	0.9	–62	Consolidation
Mohelensko	(1) 0–10 %	0.8	1.0	19	17.4	5.1	–71	Consolidation[2]
	(2) 11–33 %	0.7	0.8	15	15.2	7.7	–49	Consolidation[2]
	(3) 34–65 %	0.6	1.1	75	12.9	7.7	–40	Consolidation
	(4) 66–89 %	0.7	1.0	43	30.3	22.3	–26	Consolidation
	(5) 90–100 %	2.6	3.7	44	17.7	15.8	–11	Consolidation
Pouzdřany	(1) 0–10 %	1.2	0.6	–55	7.2	14.1	94	Disintegration
	(2) 11–33 %	1.1	1.0	–14	8.0	21.1	164	Disintegration[1]
	(3) 34–65 %	11.1	0.1	–99	4.6	5.4	18	Disintegration
	(4) 66–89 %	5.2	0.5	–90	3.0	40.1	1215	Disintegration
	(5) 90–100 %	4.0	5.7	41	3.8	8.7	127	Expansion
Pálava	(1) 0–10 %	0.8	0.5	–43	3.6	4.4	21	Disintegration
	(2) 11–33 %	9.5	3.4	–64	2.0	3.0	47	Disintegration
	(3) 34–65 %	6.6	2.4	–64	3.8	5.4	43	Disintegration
	(4) 66–89 %	4.6	1.4	–70	3.8	7.8	107	Disintegration
	(5) 90–100 %	9.7	15.7	61	3.6	4.1	12	Expansion

ing adults (*AdultFeed*) were more prone to go missing in most reserves. Specific responses were found for particular reserves. In Koda, species associated with wooded wetlands (*Hhygrophilous2*) were more likely to disappear. In Karlštejn, species with hairy larvae (*LarvHairy*) were more prone to disappear. In Mohelensko and Pálava, species with fewer generations per year (*Voltinism*) and species with diurnal activity (*DiurnAct*) had a greater probability of going missing. In Mohelensko, species with a small trophic range were also more prone to go missing. In Pálava, additionally, species associated with shrubs were more prone to

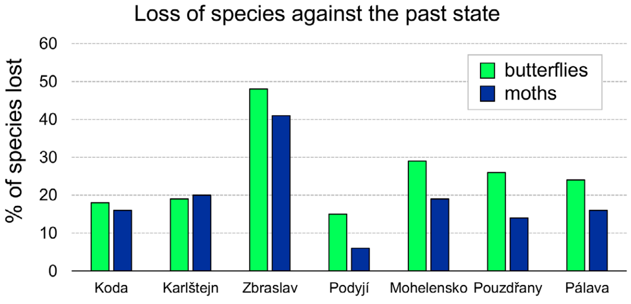

Fig. 3. Percentage losses of species of butterflies and moths in each studied reserve when total records of species from the period 2001–2023 are compared against the total records until 2000. The original numbers of missing and new species are given in Table 3.

Table 3. Numbers of species classified as *missing* according to their occurrences in the reserves between past and present state (i.e. species recorded until 2000 but not afterwards), *stable* (species recorded both until 2000 and afterwards), and *new* (species not recorded until 2000 but recorded afterwards).

Reserve	Butterflies			Moths		
	missing	stable	new	missing	stable	new
Koda	22	92	1	23	111	1
Karlštejn	24	94	1	27	109	0
Zbraslav	47	50	0	45	66	0
Podyjí	22	114	1	10	130	2
Mohelensko	43	103	0	27	110	1
Pouzdřany	31	87	0	16	82	2
Pálava	38	111	2	23	124	0

Table 4. Summary of the generalized linear models with binomial (Bernoulli) distribution testing the effect of life-history traits of butterflies and moths on the probability that the species would go *missing* in the particular reserve (occurrence status used as the response variable with 1 = missing from reserve, 0 = stable population). Numbers in parentheses in *Reserve* column give the number of species analysed in the particular model. Asterisks signify that other variables than those significant in GLM models (given in *Variable* column) were selected by recursive partitioning (see Fig. S3 of the Supplementary Material). *Effect* column shows whether the effect of the variable was positive (the higher the value, the greater the probability of going missing) (in bold) or negative (the lower the value, the greater the probability of going missing); for 'specific' patterns in host plant form see Table S6. The variables with lower *P* value, between 0.01 and 0.05, are given in italics. *Recursive part.* column informs whether the variable was selected as significant by the complementary recursive partitioning method (Fig. S3). The life-history traits were taken from the lists of Bartonova et al. (2014), Sucháčková Bartoňová (2024), and Potocký et al. (2018).

Group	Reserve	Variable	Test statistics	Effect	Recursive part.
Butterflies	Koda (99)	FlghtPerLen	$\chi^2_{(1)} = 9.47, P = 0.0019$	negative	—
		Hxerothermophilic1	$\chi^2_{(1)} = 9.56, P = 0.002$	**positive**	selected
		Fertility	*$\chi^2_{(1)} = 4.75, P = 0.0293$*	***positive***	—
	Karlštejn (103) *	FlghtPerLen	$\chi^2_{(1)} = 14.2, P = 0.0002$	negative	—
		Fertility	$\chi^2_{(1)} = 9.11, P = 0.0025$	**positive**	—
		Mobility	$\chi^2_{(1)} = 7.80, P = 0.0052$	negative	—
	Zbraslav (94)	Hubiquitous	$\chi^2_{(1)} = 29.25, P < 0.0001$	negative	—
		HostPlantForm	$\chi^2_{(3)} = 13.28, P = 0.004$	*specific*	—
		FlghtPerLen	$\chi^2_{(1)} = 10.14, P = 0.0014$	negative	selected
		Fertility	$\chi^2_{(1)} = 6.98, P = 0.0082$	**positive**	—
		Hmesophilic1 (x)	*$\chi^2_{(1)} = 5.98, P = 0.0145$*	*negative*	—
	Podyjí (118)	Hubiquitous	$\chi^2_{(1)} = 7.77, P = 0.0053$	negative	—
	Mohelensko (128) *	Hubiquitous	$\chi^2_{(1)} = 14.26, P = 0.0002$	negative	—
		Hhydrophilic	*$\chi^2_{(1)} = 5.77, P = 0.0163$*	***positive***	selected
	Pouzdřany (104)	Hubiquitous	$\chi^2_{(1)} = 11.18, P = 0.0008$	negative	—
		Feeding	*$\chi^2_{(1)} = 4.14, P = 0.042$*	*negative*	—
		Fertility	*$\chi^2_{(1)} = 5.25, P = 0.022$*	***positive***	—
		FlghtPerLen	*$\chi^2_{(1)} = 5.3, P = 0.021$*	*negative*	—
	Pálava (129)	Hubiquitous	$\chi^2_{(1)} = 12.31, P = 0.0004$	negative	—
		Fertility	*$\chi^2_{(1)} = 6.28, P = 0.012$*	***positive***	—
Moths	Koda (134)	*Hmesophilous2*	*$\chi^2_{(1)} = 6.2, P = 0.013$*	*negative*	—
		Hmesophilous3	$\chi^2_{(1)} = 7.86, P = 0.0051$	negative	—
		AdultFeed	$\chi^2_{(1)} = 7.38, P = 0.0066$	negative	—
		Hhygrophilous2	*$\chi^2_{(1)} = 4.41, P = 0.035$*	***positive***	—
	Karlštejn (136)	Hmesophilous3	$\chi^2_{(1)} = 11.56, P = 0.0006$	negative	—
		AdultFeed	$\chi^2_{(1)} = 9.73, P = 0.002$	negative	—
		Hmesophilous2	$\chi^2_{(1)} = 9.94, P = 0.0016$	negative	—
		LarvHairy	*$\chi^2_{(1)} = 5.31, P = 0.021$*	***positive***	selected
	Zbraslav (111)	Hab3D	$\chi^2_{(1)} = 18.55, P < 0.0001$	negative	selected
		AdultFeed	$\chi^2_{(1)} = 10.99, P = 0.0009$	negative	selected
		Hhygrophilous2	$\chi^2_{(1)} = 8.61, P = 0.0033$	**positive**	—
		HabHum	$\chi^2_{(1)} = 7.45, P = 0.0085$	negative	selected
	Podyjí (139)	nothing significant	—	—	—
	Mohelensko (137)	Voltinism	$\chi^2_{(1)} = 15.03, P = 0.0001$	negative	—
		Hab3D	$\chi^2_{(1)} = 10.07, P = 0.0015$	negative	selected
		AdultFeed	*$\chi^2_{(1)} = 5.75, P = 0.016$*	*negative*	—
		DiurnAct	$\chi^2_{(1)} = 10.15, P = 0.0014$	**positive**	—
		TropRange	*$\chi^2_{(1)} = 4.06, P = 0.044$*	*negative*	—
	Pouzdřany (97)	Hmesophilous2	$\chi^2_{(1)} = 11.51, P = 0.0007$	negative	selected
		AdultFeed	$\chi^2_{(1)} = 7.03, P = 0.008$	negative	—
	Pálava (146)	Voltinism	$\chi^2_{(1)} = 11.27, P = 0.0008$	negative	—
		HostPlantForm	*$\chi^2_{(4)} = 11.12, P = 0.025$*	*specific*	—
		DiurnAct	$\chi^2_{(1)} = 7.44, P = 0.0064$	**positive**	—

disappear in comparison with those associated with trees or lichens and fungi or with grasses (*HostPlantForm*, Table S6). In Pouzdřany, species associated with mesic shrublands (*Hmesophilous2*) were more prone to disappear. In Podyjí, no life-history traits proved to be significant.

DISCUSSION

We revealed general trends in the loss of open woodlands and semi-open habitats, together with the spread of closed-canopy forests in different protected areas that are considered biodiversity hotspots and are nationally recognised as key areas for Lepidoptera diversity. We found that the losses of open woodlands were predominantly associated with the decrease in their patch size, through disintegration of larger patches or rarefaction of such habitats within the reserves. This can negatively affect metapopulations of organisms associated with open woodland habitats by limiting the area of single patches below the area required by species to maintain their minimum viable population sizes (Schtickzelle et al., 2005; Dapporto & Dennis, 2013; Brown & Crone, 2016; Lange et al., 2025). In the case of rarefaction the patches are less represented in the landscape making it potentially more difficult for the associated organisms to colonise them. Furthermore, the general loss in heterogeneity of different habitats within most reserves could have adverse effects on species that require the proximity of different habitat types at the local scale (Liivamägi et al., 2014).

We revealed that all reserves experienced substantial losses of butterflies and moths. With respect to the original, historical communities in the studied reserves, one quarter of butterfly species and one fifth of moth species have been lost, on average. Such losses are striking, but within the range of declines reported from other European regions. Warren et al. (2021) reported extinctions of 8% of butterfly species in the United Kingdom, 20% of butterfly species in the Netherlands, and 29% of butterfly species in Flanders. Habel et al. (2024) reported losses of 33% and 50% of butterfly species in two locations in Austria in the last 80 years. In moths, reports on species declines are rarer. Valtonen et al. (2017) found 3% decline per decade in Hungary and Burner et al. (2021) reported 8% decline per decade in Norway. At the same time, significant declines in abundances, biomass or occurrences of moths have been observed in many regions (Conrad et al., 2006; Groenendijk & Ellis, 2011; Fox et al., 2014; Bell et al., 2020; Roth et al., 2021b; Blumgart et al., 2022). Our data suggest that even in protected areas the losses of insect species can be substantial even though the total area of natural habitats did not decrease in most of our studied reserves. The decrease in total area of natural habitats only happened in Podyjí and Pouzdřany where former agroforestry mosaics (small fields with trees) were replaced by larger fields without trees or vineyards under intensive management regimes.

Our analysis further revealed that the life-history traits of the species affected the probability of losses. These indices suggest that the conservation effort must prioritise active management interventions of habitat structure in order to mitigate species declines. The observed results can be caused by various phenomena, some associated with locally specific conditions, while larger-scale landscape trends can substantially interact with these effects.

Habitat changes in the reserves and their associations with species losses

In terms of ecological requirements, European butterflies and moths represent two relatively different groups. The majority of butterflies are associated with open habitats, grasslands, scrub or bushes. If some species are associated with woodlands then they usually require open or semi-open habitat structure (Bartonova et al., 2014). Only a very few species frequently occur in closed-canopy forests. On the contrary, in European macromoths, a considerable part of the fauna are associated with woodlands with dense vegetation, whereas open habitats host distinct communities (Pavlikova & Konvicka, 2012; Sebek et al., 2015; Potocký et al., 2018; Weiss et al., 2021; Uhl et al., 2023). For both groups, our results suggest that habitat changes dominated by the spread of closed-canopy forests have caused gradual shifts in species composition in the reserves.

In butterflies, the species marked as ubiquists (generalists) never went missing in the reserves (see Table S5). This can be simply explained by the fact that generalists often share traits like high mobility, large distribution range, low population density, polyvoltinism (several generations per year), and a long flight period (Barbaro & Van Halder 2009; Öckinger et al., 2010; Börschig et al., 2013; Bartonova et al., 2014). Indeed, the species marked as ubiquists had, on average, higher values for mobility, voltinism, as well as for flight period length and lower values for population density than the rest of the species (mean values for *Mobility*: 6.3 vs. 3.6, *Voltinism*: 2.6 vs. 1.4, *FlghtPerLen*: 7.5 vs. 3.6, and *Density*: 3.0 vs. 3.8 for ubiquists and the rest of the species, respectively). Such traits make it easier for those species to overcome local changes in habitat quality, in particular the isolation of open or semi-open habitat patches induced by the rarefaction/disintegration processes observed in most reserves. In four studied reserves, species with long flight periods, a typical trait of generalists, were less likely to disappear, which is in line with this assumption. It needs to be noted that the category of 'ubiquists' in our data counts only 19 common and widespread species, whereas the rest of the species pool counts another 122 species (excluding burnet moths) with very diverse life histories between them. Yet, our results are in line with the observations of losses among specialists and relative predominance of generalists in European butterfly communities (Stefanescu et al., 2009; Dapporto & Dennis, 2013; Pöyry et al., 2017; Habel et al., 2016, 2019, 2022a, 2024).

In five out of seven reserves, species with higher fertility were more prone to disappear. This seems surprising and it is difficult to link this trait to the habitat changes directly. However, high fertility among European butterflies is often associated with other trait characters, like narrow diet breadth, univoltinism, low density populations or larger bodysize (Bartonova et al., 2014). Thus, fertility could have acted as a supplemental variable for combinations of some of these traits. Fertile univoltine species with narrow trophic range or specific area requirements, like *Argynnis niobe*, *Euphydryas aurinia*, *Melitaea cinxia*, *Boloria selene*, or species of the *Phengaris* genus, have often gone missing in different reserves. Local disappearance of the suitable open or semi-open habitats, which took place in the reserves, could have affected the survival of these demanding species, even though their dispersal capabilities can be relatively good (Konvickova et al., 2023). Aside from this, the informativeness of the *Fertility* trait itself can also suffer from potential bias as the trait has not been properly recorded for all species yet (Sucháčková Bartoňová et al., 2014).

In moths, the results showed that species associated with grasslands had a greater probability of going missing from the communities in comparison with forest-associated species or shrubland specialists (Table 4). This seems like a clear link to the decrease in area and proportion of semi-open habitats, which consist of shrubs or trees together with grasslands. However, the loss of grassland species may be also associated with the change in quality of the grasslands themselves. Losses of moth species associated with low nitrogen and dry grasslands have been reported in other studies (Fox et al., 2014; Valtonen et al., 2017). Mangels et al. (2017) described shifts towards generalist life-history traits among grassland moths at several sites in Germany, with communities in frequently mown and fertilized meadows being dominated by ubiquists. In two of the reserves we studied, Koda and Zbraslav, the area of open grasslands (0–10% canopy cover category) increased between past and present, and yet grassland specialists were more prone to disappear from the communities. So, the cause may have been the transition from traditional grassland management, such as grazing and low-intensity rotational mowing regimes, to abandonment or modern intensive mowing, which potentially led to changes in turf quality, especially to increased turf density, homogenisation of vegetation height, and loss of nectar-bearing plant species (Bubová et al., 2015; Lange-Kabitz et al., 2021). To some extent, external causes, like increased atmospheric deposition of nitrogen, could have affected the grassland communities (see below). In this respect, grassland moths face similar threats as xeric butterfly specialists.

In several reserves, moth species with feeding adults were less likely to disappear from the communities (the negative effect of *AdultFeed* in Table 4). Adult feeding is associated with higher habitat quality demands so this contrasts with the change in grassland communities, but also with the presumed decline of nectar resources in European temperate forests in the last 40 years (De Schuyter et al., 2024). This decline in forest nectar resources is attributed primarily to changes in light availability (De Schuyter et al., 2024) and should therefore also affect forest-dwelling moths. Our data, however, do not allow us to estimate local nectar resources in the studied habitats, and thus more targeted research would be necessary to reveal the cause of this pattern.

Other associations between the probability of disappearance and life-history traits were often locally specific. In three reserves, analyses showed an increased probability of loss for hydrophilic species, in the case of butterflies in Mohelensko and moths in Koda and Zbraslav. Lepidopteran wetland specialists have experienced population declines in many other parts of Europe (van Swaay et al., 2006; Weking et al., 2013). This is largely associated with the drainage of former wetlands, bogs, mires and swamps, which has been happening for more than a century (Habel et al., 2022a; Toman et al., 2023). In many sites, former wetlands have been replaced by woodlands due to afforestation or succession (Toman et al., 2023). The decline of wetland species was not universal across the studied reserves, primarily due to the fact that most reserves represent steppic biotopes. In Zbraslav, species associated with ephemeral and small herbaceous plants were more prone to disappear, suggesting a lack of early-successional habitats in the reserve. Potentially, this can be also connected with the presumed change in the quality of grasslands dominated by grasses; in a similar pattern grass-dependent moths in Pálava had the lowest probability of disappearing (above; Table S6). In Pálava, moths associated with shrubs had a greater probability of disappearing. Unfortunately, it is not possible to deduce a direct link between the change in habitat structure and the trait as our classification of canopy cover categories is too coarse to allow for differentiation between shrubs and young trees.

In Podyjí, the loss of butterflies and moths was the lowest and there was no significant effect of traits on moth disappearance. Podyjí was the largest protected area studied (6 292 ha compared to the mean area of 636 ha for other reserves) and, despite the substantial decrease in open and semi-open habitats in the reserve, the residual areas may still be enough large to accomodate species with diverse life-history traits. At the same time, data for this reserve specifically, may be slightly biased by the fact that the area covered by the current protected area was part of the Iron Curtain border zone, the depopulated boundary that separated former Eastern Bloc countries from Western European countries in the past, so many parts of the area were inaccessible for naturalists until the 1990s.

Influence of large scale trends

Although local environmental conditions in the reserves played an important role in the observed changes of lepidopteran communities, the diversity and distribution of species in a given area are also largely determined by landscape or regional processes. The cessation of traditional management practices, like extensive grazing and mowing as well as coppicing or wood pasture, happened in most parts of the continent, not only in the designated protected areas. Modern agricultural development has led to a simplification of field configuration and decrease in hedgerow or ecotone density which has often led to biotic homogenisations in butterfly and moth communities (Ekroos et al., 2010; Novotný et al., 2015; Habel et al., 2016, 2022b). The Czech Republic, as a former Eastern Bloc country, has one of the largest mean land unit sizes in Europe (Šálek et al., 2021); the average management parcel increased almost 50 times in the last 80 years (Slancarova et al., 2014), which had a direct negative effect on the biodiversity of butterflies (Konvicka et al., 2016). Slancarova et al. (2014) observed a negative effect of surrounding homogeneous landscape structure on butterflies in grassland reserves, with species exploiting multiple types of patches or rare biotopes being especially threatened by such structure. These changes in landscape structure happened in all parts of the country and could have affected all our studied reserves. Moreover, the increased influx of nitrogen into ecosystems due to the common use of fertilisers or due to atmospheric deposition is a common factor influencing the quality of grassland and forest habitats all over Europe, and thus also affects lepidopteran communities (WallisDeVries & van Swaay, 2006; Fox et al., 2014; Klop et al., 2015; Pöyry et al., 2017; Roth et al., 2021a; Wagner et al., 2021). A study from southern Germany analysed records of butterflies and burnet moths from the last 200 years and revealed severe declines in species associated with habitats poor in soil nutrients (Habel et al., 2016). Therefore, even if protected areas were spared from intensive agricultural managements or silvicultural changes and serve as refuges, the disappearances of some species could be associated with overall changes in their meta-populations at larger, even continental, scales. Thus, the disappearances of some species from reserves may have happened as a result of paying off the extinction debt that emerged due to a disruption of communication among local populations in the past, even though potential habitats could still be present locally (Schtickzelle et al., 2005).

Furthermore, our results may have been affected by differences between regions. First, the Bohemian reserves are located relatively close to each other, and we found similar patterns of life-history response in the three Bohemian reserves (Koda, Karlštejn, Zbraslav). This is partly caused by a high overlap of species that have disappeared from the reserves, especially in case of moths (Table S7). In the Moravian reserves (Podyjí, Mohelensko, Pouzdřany, Pálava), the response was a bit more varied and the overlap of missing species was, in general, smaller (except for Pálava and Mohelensko; see Table S7). Second, the regions have a slightly dissimilar species pool. Bohemia is colder and lacks some species, like the woodland grayling (*Hipparchia fagi*), or the false grayling (*Arethusana arethusa*). Moravia has warmer Pannonic-like climate which can buffer the potential population fluctuations of many xerophilous species and some species have larger and stable populations in Moravia in comparison to Bohemia, like the dryad (*Minois dryas*), or the clouded apollo (*Parnassius mnemosyne*) (extinct in Bohemia since the 1990s).

Climate change could have been another potential driver behind the loss of some species in our study. In Europe, climate change is characterised by milder winters and drier summers. Such changes have allowed some thermophilous species to spread northward, while at the same time some hydrophilic or cold-adapted species, including mountain specialists, abandon parts of their former range or go extinct locally (Parmesan et al., 1999; Wilson et al., 2005; Franco et al., 2006; Warren et al., 2021). Climate change can negatively affect some sensitive species through the increased occurrence of droughts (Oliver et al., 2015) or it can disrupt develoment through prolonged periods of warmer conditions (Van Dyck et al., 2015; Macgregor et al., 2019). For instance, in Britain, univoltine species of Lepidoptera were found to have been negatively affected by early emergence in warmer years (Macgregor et al., 2019). In our study, we found that univoltine species of moths were more prone to go missing in two reserves (Pálava and Mohelensko), but it was not a universal pattern across all reserves. Similarly, hydrophilic species of butterflies were more prone to disappear in only one reserve, and hydrophilic species of moths in two reserves. Besides climate change, however, these losses could potentially be caused by the general loss of wetlands in the past due to drainage (see the section above). We are thus unable to make generalisations about the effects of climate change on the species losses in our study as it seems impossible to separate its effect from the observed habitat alterations.

CONCLUSIONS

Our data indicate that over a period of around 80 years, the protected areas we studied in low and middle elevations have undergone substantial homogenisation of habitats due to the spread and dominance of closed-canopy forests, the disappearance of open woodland habitats, and the presumed change in the quality of grasslands. As a result, biodiversity of Lepidoptera has declined substantially between the past and present. Although large-scale effects (regional or continental) can be partly responsible for the observed patterns, the current state of butterfly and moth diversity in reserves is largely a result of changes in management practices applied locally. Cessation of traditional practices like pasturing and coppicing are among the main causes of the decrease in habitat heterogeneity. The situation is especially critical as the reserves represent national hotspots of Lepidoptera diversity. Conservation efforts must therefore prioritise active management interventions into habitat structure in order to effectively mitigate the trends in declines of insect biodiversity (Warren et al. 2021). Guidelines for the good management of European butterflies already exist and include the maintenance of active traditional pastoral systems, such as livestock grazing or hay cutting, diversified (rotational) mowing regimes and mosaics of different vegetation types, and active woodland management (coppicing or regular thinning) (Cizek et al. 2012, van Swaay et al., 2012; Fartmann et al., 2013; Bubová et al., 2015; Dolek et al., 2018). This active approach would also promote diversity in moths, but regarding woodland management the rotation periods of coppicing must be long enough, ca. 30–40 years, to create higher vertical heterogeneity of forests and allow for the existence of shady forest patches as well as patches of earlier forest successional stages that are rich in nectar resources (Broome et al., 2011; Weiss et al., 2021; Roth et al., 2021b; Heidrich et al., 2023; Piccini et al., 2024). Butterflies and moths served as model groups in our study, but the aforementioned measures have the potential to support communities of many other insect groups in protected areas. In some of the studied reserves, notably in Mohelensko, Pálava, or Podyjí, initiatives for the restoration of traditional mowing, pasture, and coppicing have already taken place. Data show that these initiatives have promoted biodiversity in plants and spiders (Hamřík et al., 2023; Šipoš et al., 2025), and butterflies and moths could also potentially benefit. Although the interventions were mainly local, the continuation and extension of such practices could safeguard contemporary Lepidoptera and potentially lead to more diverse communities in the future.

ACKNOWLEDGEMENTS. The study was supported by the project "Application of traditional knowledge to halt biodiversity loss in woodlands" (TO01000132) financed by the Norway Grants 2014–2021 and Technology Agency of the Czech Republic. The authors were further supported by the Institute of Entomology, BC CAS (60077344). The authors would like to thank three anonymous reviewers who provided helpful comments on the earlier version of the manuscript.

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Received February 25, 2025; revised and accepted October 4, 2025
Published online November 12, 2025

Online Supplement S1 (http://www.eje.cz/2025/035/S01.pdf):

Table S1. Description of the studied protected areas (reserves).
Table S2. Classification of original land use/land cover (LULC) categories into five categories of canopy cover.
Table S3. Description of life-history traits used for the recorded butterflies and moths.
Table S4. Gains and losses in area of all canopy cover categories for each reserve.
Table S5. List of species and their occurrences in reserves.
Table S6. Host plant form trait details.
Table S7. Shared losses of butterfly and moth species for each pair of reserves.
Fig. S1. Visual representation of habitat change patterns.
Fig. S2. Maps of reserves with canopy cover categories in past and in present.
Fig. S3. Recursive partitioning results.
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