

Restoring a Butterfly Hot Spot by Large Ungulates Refaunation: The Case of the Milovice Military Training Range, Czech Republic

Martin Konvicka (✉ konva333@gmail.com)

Entomologicky ustav Akademie ved Ceske republiky <https://orcid.org/0000-0002-4339-8923>

David Ričl

Holíková 470, CZ-25401 Jílové u Prahy

Veronika Vodičková

Faculty of Sciences, University South Bohemia

Jiří Beneš

Entomologicky ustav Akademie ved Ceske republiky

Miloslav Jirků

Akademie ved Ceske republiky + Česká Krajina o.p.s., Kutná Hora

Research article

Keywords: *Bison bonasus*, *Bos taurus*, climate, *Equus caballus*, Lepidoptera conservation, life history traits, temperate grassland, trophic rewilding

Posted Date: December 11th, 2020

DOI: <https://doi.org/10.21203/rs.3.rs-122442/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License. [Read Full License](#)

Abstract

Background: Refaunation/rewilding by large ungulates represents a cost-efficient approach to managing natural biotopes and may be particularly useful for areas whose biodiversity depends on disturbance dynamics and is imperilled by successional changes. To study impacts of refaunation on invertebrates, we focused on butterflies inhabiting the former military training range Milovice, Czech Republic, refaunated since 2015 by a combination of Exmoor pony (“wild” horse), Tauros cattle (“aurochs”), and European wisent.

Methods: We compared butterfly presence-absence patterns immediately after the military use termination (early 1990s), prior to the refaunation (2009), and after it (2016–19); and abundance data gained by monitoring butterflies at refaunated and neglected plots. We used correspondence analysis for presence-absence comparison and canonical correspondence analysis for quantitative data, and related results of both ordination methods to the life history, climatic, and conservation-related traits of recorded butterflies.

Results: Following the termination of military use, several poorly mobile species inclining towards oceanic climates were lost. Newly gained species are more mobile and prefer warmer continental conditions. The numbers of butterfly species did not differ between refaunated and neglected plots, but the former hosted higher abundances. Butterflies developing on coarse grasses and shrubs inclined towards neglected plots, whereas refaunated plots supported species developing on small forbs.

Conclusion: The changes in species composition following the cessation of military use were attributable to successional change, coupled with climate-driven changes in species pool. By blocking succession, large ungulates support butterflies depending on competitively poor plants. Restoring large ungulates populations represents a great hope for conserving specialised insects, provided that settings of the projects, and locally adapted ungulate densities, do not deplete resources for species with often contrasting requirements.

Introduction

In most continents, late-Pleistocene and early Holocene human pressure extirpated, or drastically reduced, the populations of large ungulate herbivores, which reshaped the ecological dynamics of entire biomes (Corlett 2004; Johnson et al. 2009; Galetti et al. 2018). This affected nutrient cycling (e.g., Zimov et al. 1995), fire regimes (e.g., Galetti 2004; Navarro and Pereira 2012), seed dispersal and germination (Vera 2000; Doughty et al. 2012), and overall vegetation physiognomy (Feurdean et al. 2018). Subsequent activities of preindustrial agriculturalists and pastoralists resumed the role of large wild ungulates, maintaining the disturbance-succession dynamics exploited by numerous species, including invertebrates. Many enigmas and paradoxes encountered in European insects conservation – such as the affiliation of many taxa to purportedly “cultural” grasslands (Thomas 1993; van Swaay et al. 2012), ancient ways of forests use (Warren 1991; Dolek et al. 2018), frequently disturbed habitats (Rehoukova et al. 2016; Tropek et al. 2017), or finely-grained landscapes (Slamova et al. 2012; Slancarova et al. 2014) – are resolved, once the large ungulates activity is factored in. The current biodiversity has evolved in a megafaunal world (Bartonova et al. 2018; Todisco et al. 2010). Modern ecosystems are functionally incomplete, with entire trophic levels impoverished or missing, and if not actively managed, they fail to provide habitats for a sizeable portion of associated biota (Dirzo et al. 2014; Sebek et al. 2015).

The current refaunation /rewilding /naturalistic grazing movements (Seddon et al. 2014; Merckx and Pereira 2015; Svenning et al. 2016; Cromsigt et al. 2018; Garrido et al. 2019) strive to reverse the transformation of ecosystems that started in the late Pleistocene and culminated with recent land use intensification (Dirzo et al. 2014; Jirku and Dostal 2015; Henning et al. 2017; Pedersen et al. 2019). Although insect conservationists have long advocated habitat management by ungulate grazing (e.g., Öckinger et al. 2006; Cizek et al. 2013; Slancarova et al. 2014), relatively few megafauna refaunation projects have focused primarily on insect conservation or are systematically monitored for impacts on insects (van Klink et al. 2018). Each refaunation project develops within specific sociocultural constraints, rarely allowing for proper replications (cf. Root-Bernstein et al. 2018; but see Garrido et al. 2019). There is an urgent need to study refaunation effects on invertebrates, both as encouragement for others and as feedback for the wider conservation community (Jepson 2016; van Klink et al. 2018). The effects may differ from targeted conservation grazing, a well-established practice for managing habitats of some insect species (e.g., Thomas et al. 2009). Conservation grazing tends to be practiced on smaller scales, covering relatively short seasonal time windows and under constant supervision of managers (e.g., van Swaay et al. 2012; Bubova et al. 2015), whereas refaunation operates on larger scales with minimum interventions.

The initial refaunation plans for the Czech Republic (cf. Jirku and Dostal 2015) aimed at large protected areas or actively used military training ranges. It was believed that in these large and biotically rich areas, restoring populations of large ungulates would be most feasible. The first refaunation project, however, has materialised on the relatively small scale of two grazing reserves within a disused military training range, in otherwise densely populated Central Bohemia (Fig. 1). Since 2015, three once near-extirpated components of native European megafauna are roaming on grasslands formerly used for army training: the European bison or wisent (*Bison bonasus*), a species rescued from near-certain extinction (Olech 2008); the back-bred “aurochs” in its restored Tauros form, derived from several taurine breeds of domestic cattle (*Bos taurus*) (Goderie et al. 2015); and the horse (*Equus caballus*), in an ancient feral Exmoor pony breed (Baker 1993; Hovens and Rijkers 2013).

Coincidentally, the area was surveyed for butterflies immediately after the cessation of its military use (Matouš 1994), and again in the following decade, in a survey of abandoned military ranges (Cizek et al. 2013). The setting thus offers a unique opportunity to study butterfly assemblages’ responses to the abandonment of a military-used landscape, and to monitor effects of large ungulates refaunation on such assemblages. Such past-present comparison should also account for factors beyond locally operating disturbance-succession dynamics. An obvious candidate is the

changing climate, which restructures faunas on the continental scale (Warren et al. 2001; Essens et al. 2017), although warming may not necessarily improve conditions for thermally demanding species, if microclimates cool down due to eutrophication (Wallis de Vries and Van Swaay 2006). Non-climatic drivers of species' distribution shifts, such as large-scale land use changes (Aguirre-Gutierrez et al. 2016), may also play a role.

A promising approach to generalisation from single-site results focuses on life history (= functional) traits of constituent species. It links habitat properties and the species composition of assemblages via species-specific traits (Legendre et al. 1997; Carmona et al. 2016). By linking species traits to results of habitat manipulation, it may disclose the mechanisms of species responses to habitat change (Slancarova et al. 2014; Gamez-Virues et al. 2015).

Here, we first compare butterfly records, life history traits, climatic niche traits, and conservation-related attributes from the three subsequent surveys: shortly after the military use termination, shortly before the refaunation by large ungulates, and under the large ungulates' impact. For this *past-present comparison*, we hypothesised that cessation of military use was followed by losses of specialists of early-successional disturbed grounds (H1), whereas subsequent species gains should reflect the recently warming climate (H2) and ongoing changes in species' distribution extents (H3). We then analyse results of the *current monitoring* of butterfly assemblages on refaunated versus neglected plots. The whole-year grazing by wild ungulates should not decrease species richness and abundances compared to neglected plots (H4), but the assemblage should shift from species associated with competitively dominant host plants, typical for successional advanced and little disturbed vegetation, towards species associated with competitively inferior host plants typical for frequently disturbed conditions (H5). We believe that this study is innovative in considering the twin roles of management and climate factors on development of butterfly assemblages, and by utilising life history traits for understanding the situation.

Material And Methods

Study area, refaunation, and earlier butterfly surveys

The Milovice military training range (50.26N, 14.89E, altitude 200–250 m a.s.l., mean annual temperature 8–9 °C, annual precipitation 500–600 mm) (Fig. 1) was established in 1904, originally on 34.6 km². It was subsequently used by all armies that operated on Czech territory, gradually expanding its area to 40 km². The last users were the Soviets, who operated an air force base and headquarters here for the former Czechoslovakia until 1991. The natural setting is the gently rolling Středočeská Tabule Plain formed by Mesozoic carbonate-rich sandstones, siltstones, and claystones, and covered by brown soils, rendzinas, and carbonate rich sands. Woodlands dominated by *Quercus petraea*, *Pinus sylvestris*, and *Betula pendula* are interspersed by finely grained mosaics of shrublands, grasslands, and early successional vegetation that developed on former farmlands (mainly wheat, vegetables, and dairy family farms) and were utilised for training troops for over 80 years (Cizek et al. 2013).

Following the cessation of military use, parts of the open training fields were developed (golf course, amusement park, industrial zone), while three large areas were proclaimed a Site of European Community Importance (SCI) Milovice-Mladá. The Central site (local toponym: Pozorovatelná, hereinafter "C", 50.254N, 14.881E) has been partly managed by conservation grazing by fenced sheep, while the Northern (Traviny, "N", 50.278N, 14.883E) and Southern (Pod Benáteckým vrchem, "S", 50.241N, 14.886E) sites remained unmanaged, except for occasional disturbance of S by armoured vehicles practiced by military history enthusiasts and for domestic cattle grazing in a corner of N in 2014–2016. Much of all three sites had suffered succession-driven homogenisation of the once diverse vegetation mosaic by competitively dominant grasses (mainly *Calamagrostis epigejos* and *Arrhenatherum elatius*), ruderal forbs and shrubs (mainly *Crataegus*, *Prunus*, and *Rosa*).

The site S (2015–2017, 40 ha; 106 ha since 2018) has been grazed since spring 2015 by ≈ 35 Exmoor ponies (hereinafter "horse") and ≈ 20 Tauros cattle (hereinafter "aurochs"). Since spring 2016, ≈ 35 horses and ≈ 20 wisents have grazed the site N (125 ha) (Fig. 1). Both S and N are thus year-round cross-grazed by horses and big bovids (aurochs or wisent) living in naturally structured social units, i.e. mixed sex/age harems/herds. To provide variable management regimes, both temporally and permanently ungrazed plots of various sizes (units to tens of hectares) are present both within and outside the grazing reserves at any given time. The animals receive no supplementary feeding and no medication, except for strictly determined individual cases, and predators enter the sites freely (Jirku et al. 2018). The wolf, as a re-expanding apex predator, is not present yet, but its colonisation is expected. To control grazing intensity, facilitate gene-flow, and avoid social stress, two to three year-old surplus animals are transferred to similar projects in the Czech Republic and abroad.

The first targeted butterfly survey of the area was conducted immediately after the cessation of military use. Matouš (1994) published a commented list of species, treating the entire military range as a single locality. Fifteen years later, in 2009, the training fields S, C and N were surveyed in a semiquantitative manner (Čížek et al., 2013). The current monitoring of the refaunation impact, launched in spring 2016, thus represents the third survey.

Current butterfly monitoring

We set 16 rectangular plots (50 × 200 m) at both refaunated (n = 7) and neglected (n = 9) sections of N and S sites (n = 8 each) (Fig. 1). From spring 2016 onwards, one of us (DR) visited the plots five times each year (May, early June, late June, July, August) to cover seasonal aspects of butterfly assemblages. The recording followed the timed survey protocol by Kadlec et al. (2010), appropriate for heterogenous environments with temporally changing locations of butterfly resources, such as flower patches. Each visit to a plot lasted 30 min, abundances of all butterfly species present were recorded using a net when necessary and taking vouchers of species not recognisable in the field. We also recorded the closest hour, cloudiness (3-

point ordinal scale, from clear sky – 1 to overcast – 3), wind (Beaufort scale 1–4, i.e., calm to gentle breeze), and nectar supply (0 – no flowers within the plot, 1 – flowers scarce but present, 2 – flowers moderately abundant, 3 – flowers abundant). We restricted the visits to the highest butterfly activity period (10 AM – 4 PM) and to weather suitable for butterflies, randomising their sequence with respect to time of day. A single round of visits took 2–3 consecutive days.

Statistical analyses

For the *past-present comparison*, we visualised the patterns defined by species presences/absences recorded by Matouš (1994), Cizek et al. (2013) and the current monitoring, the latter collated across the four years, using correspondence analysis (CA), an unconstrained ordination appropriate for 1/0 data, in CANOCO, v. 5.0 (Ter Braak and Smilauer 2013). We computed four variants of CAs: 1) based on three “samples” defined by the three consecutive surveys; 2) differentiating records from the locations N, C, and S (possible using Cizek et al. (2013) and the current data), thus obtaining six “samples”; and 3 + 4) as in the previous two cases, but after exclusion of migrant and arboreal species.

We interpreted the CA results by three sets of the constituent species traits (Table 1, Appendix 1): (a) *life history traits*, mostly associated with feeding modes, dispersal and population structure, as compiled for Central Europe by Bartonova et al. (2014); (b) *climatic niche traits*, compiled by Schweiger et al. (2014) on the basis of species ranges in Europe and known to contribute to population trends (Essens et al. 2017); and (c) *conservation attributes* describing the distribution and Red-list status in the Czech Republic. We used the CANOCO option “explanation of species scores for functional traits”. This analysis, a multivariate version of the fourth-corner approach (Legendre et al. 1997; Dray et al. 2014), relates the species ordination scores from the CA ordination to trait values of the species, testing for strengths of the relationship using redundancy analysis (RDA), a multivariate version of linear regression (Ter Braak and Smilauer 2013). We analysed the three sets of traits separately, using the forward selection process to attain best-fitting traits combinations.

Table 1

List of life history traits, climatic niche traits and conservation-related traits used for analyses of butterfly assemblages inhabiting the former Milovice military range, currently grazed by large ungulates.

Life history traits (Bartonova et al., 2014)	Description	Character
Wing span		Numeric (mm)
Host plant form	Ephemerals – 1, larger forbs – 2, grasses and sedges – 3, trees and shrubs – 4	Ranked
Voltinism	Average number of generations, C. Europe	Numeric
Fertility	Average number of eggs per female at eclosion	Categories 1–9
Mobility	Ranked tendency to disperse	Categories 1–9
Density	Ranked average density per area of habitat	Ranked 1–9
Diet breadth	Number of plant families fed on by larvae in the Czech Republic	Numeric
Flight period length	Number of adult occurrence months (hibernation months excluded)	Numeric
Overwintering stage	Ranked, larva – 1, adult – 5	
Climatic niche traits (Schweiger et al., 2014)		
Annual temperature	Mean annual temperature	°C
Annual temperature niche breadth [NB]	SD of the above	
Continentality	Annual range in monthly temperatures	°C
Continentality NB	SD of the above	
Precipitation	Annual precipitation sum	mm
Precipitation NB	SD of the above	
Oceanity	Annual range in monthly precipitation sum	mm
Oceanity NB	SD of the above	
Winter GDD	Accumulated growing degree days [GDD] (> 5 °C), January – February	°C
Winter GDD NB	SD of the above	
Spring GDD	Accumulated GDD, January – April	°C
Spring GDD NB	SD of the above	
Early summer GDD	Accumulated GDD, January – June	°C
Early summer GDD NB	SD of the above	
Summer GDD	Accumulated GDD, January – August	°C
Summer GDD NB	SD of the above	
Water availability	Soil water content of the upper horizon (0.5 m)	No unit (0–1)
Water availability NB	SD of the above	
Conservation related traits		
Red list status	Czech Republic (1– no status, 2– near threatened, 3– vulnerable, 4– endangered, 5– critically endangered)	Ranked 1–5
Present CZ distribution	Occupied Czech Republic 10 × 10 km grid squares 2002–2014	Numeric
Past CZ distribution	Occupied Czech Republic grid squares 1951–2001	Numeric
CZ distribution trend	[1– (Present distribution/Past distribution)], details in Bartonova et al. (2014)	Numeric
Global range size	Categorized, (1 – smaller than Europe, 5 – larger than the Palaearctic)	Numeric

Life history traits (Bartonova et al., 2014)	Description	Character
European range size	Number of occupied (ca 70 × 70 km) grid squares in Europe (Schweiger et al. 2014)	Numeric

To compare numbers of butterfly species and individuals recorded during the *current monitoring*, we used 2-way analysis of variance with factors *year* (4 levels) and *management* (2 levels, refaunation vs. neglect, the latter including the plots grazed by cattle in 2016–17). Cumulative numbers of species and summed numbers of individuals across the five yearly visits were the dependent variables.

To study the current composition of butterfly assemblages, we used canonical correspondence analysis (CCA), a constrained ordination method relating the species composition of samples to external predictors and testing the relationships of species composition to predictors using the Monte Carlo test with 999 permutations, again in CANOCO. We log-transformed species abundances per plot visits, and used the downweighting rare species option. We reflected the temporal dependency in our data using a hierarchical split-plot permutation design, permuting the individual plots randomly, and the 20 subsequent visits per plot as mutually dependent cyclic shifts. We first ran separate tests for all possible nuisance covariables, i.e. *year* (both as 4-level factor and as a linear value), *site* (N vs. S), *hour* (as factor and 2nd-degree polynomial), *weather* (a combination of cloudiness and wind), *nectar* and plots *position* (forward-selected from *latitude*, *longitude*, their polynomials and interaction).

For the pivotal effect of refaunation itself, we used two different codings, aiming to answer two slightly different questions. *Refaunation* (3-level factor: *refaunation*, *cattle*, and *neglect*) aimed to disclose the effect of wild ungulates, while *ungulates* (5-level: *horse*, *aurochs*, *wisent*, *cattle*, and *neglect*) aimed to decipher effects of the three ungulate animals. We also tested for military vehicle effect (2-level factor *tanks*). We developed the models by systematically adding the covariates that had significant effects in the single-term CCAs to the *refaunation* and *ungulates* models until we reached models that significantly explained the distribution of monitored butterflies while being stringently controlled for nuisance effects.

Analogously to the *past-present comparison*, we interpreted the final CCA *current monitoring* models by species traits, relating the CCA scores to the three sets of traits and using forward selection to select the best-fitting traits combinations.

Results

Past-present comparison

The early 1990s survey of the entire military range (Matouš et al. 1994) detected 72 butterfly species (14 currently Red-listed); the interim survey of the sites N, C, S (Čížek et al. 2013) detected 51 (6 red-listed) species and the 2016–19 monitoring at the sites N and S detected 58 (7 Red-listed) species (Table 2). The numbers are comparable only with caution. The earliest survey covered all biotopes in the area, including wooded parts outside the grasslands. It recorded a higher representation of arboreal species (n = 9) than the two latter surveys (4 and 5). The two latter surveys focused on grasslands, but while the interim survey consisted of five visits in a single year, the current monitoring consisted of 20 visits in four years. Still, even after exclusion of arboreal species and migrants whose abundances vary greatly among years, the earliest survey detected more species than the latter two surveys pooled.

Table 2

List of butterfly species (nomenclature and system: Wiemers *et al.*, 2018) recorded from the former Milovice military training range during the three consecutive surveys, split into respective localities if possible, with their Czech Republic Red-list [RL] status (NT – near threatened, VU – vulnerable, EN – endangered, CR – critically endangered) following Hejda *et al.* (2017). The study of Matouš (1994) refers to the early 1990s, Čížek *et al.* (2013) to 2009, and this study to the 2016–2019 monitoring. Abbreviations are used in the ordination diagram at Figure 4.

Species	Abbreviation	RL status	Matouš (1994)	Čížek <i>et al.</i> (2013)			This study			
				Entire area	Site S	Site C	Site N	Pooled	Site S	Site N
Hesperiidae										
<i>Carcharodus alceae</i>	<i>Calc</i>	NT	+	-	-	-	-	+	+	+
<i>Erynnis tages</i>	<i>Etag</i>	-	+	+	+	+	+	+	+	+
<i>Carterocephalus palaemon</i>	<i>Cpal</i>	-	+	+	+	+	+	+	+	+
<i>Pyrgus malvae</i>	<i>Pmal</i>	-	+	+	+	+	+	+	+	+
<i>Pyrgus armoricanus</i>		EN	+	-	-	-	-	-	-	-
<i>Ochlodes sylvanus</i>	<i>Osyl</i>	-	+	+	+	+	+	+	+	+
<i>Thymelicus lineola</i>	<i>Tlin</i>	-	+	+	+	+	+	+	+	+
<i>Thymelicus sylvestris</i>	<i>Tsyl</i>	-	+	+	+	+	+	+	+	+
<i>Thymelicus acteon</i>		EN	+	-	-	-	-	-	-	-
<i>Spialia sertorius</i>	<i>Sser</i>	VU	+	+	+	+	+	+	+	+
<i>Hesperia comma</i>	<i>Hcom</i>	VU	+	-	-	-	-	+	+	+
Papilionidae										
<i>Papilio machaon</i>	<i>Pmac</i>	-	+	+	+	+	+	+	+	+
<i>Iphiclides podalirius</i>	<i>Ipod</i>	NT	-	-	-	-	-	+	+	+
Pieridae										
<i>Pieris brassicae</i>	<i>Pbra</i>	-	+	+	+	+	+	+	+	+
<i>Pieris napi</i>	<i>Pnap</i>	-	+	+	+	+	+	+	+	+
<i>Pieris rapae</i>	<i>Prap</i>	-	+	+	+	+	+	+	+	+
<i>Leptidea juvernica</i>	<i>Ljuv</i>	-	+	+	+	+	+	+	+	+
<i>Gonepteryx rhamni</i>	<i>Grha</i>	-	+	+	+	+	+	+	+	+
<i>Colias alfacariensis</i>	<i>Calf</i>	VU	+	+	+	+	+	+	+	+
<i>Colias hyale</i> ^{\$\$}	<i>Chya</i>	-		-	-	-	-			
<i>Colias crocea</i> ^{\$\$}	<i>Ccro</i>	-	+	-	-	-	-	+	+	+
<i>Anthocharis cardamines</i>	<i>Acar</i>	-	+	+	+	+	+	+	+	+
<i>Pontia edusa</i> ^{\$\$}	<i>Pedu</i>	-	+	+	+	+	+	+	+	+
Nymphalidae										
<i>Apatura iris</i> [§]	<i>Airi</i>	-	+	-	-	-	-	+	-	+
<i>Apatura ilia</i> [§]		-	+	+	-	-	-	-	-	-
<i>Aglais urticae</i>	<i>Aurt</i>	-	+	+	+	+	+	+	+	+
<i>Nymphalis antiopa</i> [§]		-	+	+	+	+	+	-	-	-
<i>Nymphalis polychloros</i> [§]		-	+	-	-	-	-	-	-	-
<i>Vanessa atalanta</i> ^{\$\$}	<i>Vata</i>	-	+	+	+	+	+	+	+	+
<i>Vanessa cardui</i> ^{\$\$}	<i>Vcar</i>	-	+	+	+	+	+	+	+	+
<i>Inachis io</i>	<i>lio</i>	-	+	+	+	+	+	+	+	+
<i>Araschnia levana</i>	<i>Alev</i>	-	+	+	+	+	+	+	+	+
<i>Polygonia c-album</i>	<i>Pc-a</i>	-	+	+	+	+	+	+	+	+

<i>Malitaea athalia</i>		NT	+	-	+	+	+	-	-	-
<i>Malitaea cinxia</i>		VU	+	-	-	-	-	-	-	-
<i>Issoria lathonia</i>	<i>llat</i>	-	+	+	+	+	+	+	+	+
<i>Argynnis aglaja</i>	<i>Aagl</i>	-	+	+	+	+	+	-	+	+
<i>Argynnis adippe</i>	<i>Aadi</i>	-	+	+	-	+	-	+	-	+
<i>Argynnis paphia</i>	<i>Apap</i>	-	+	+	+	+	+	+	+	+
<i>Boloria dia</i>	<i>Bdia</i>	-	+	+	+	+	+	+	+	+
<i>Boloria selene</i>		NT	+	-	-	-	-	-	-	-
<i>Coenonympha arcania</i>	<i>Cacr</i>	NT	+	+	+	+	+	+	+	+
<i>Coenonympha glycerion</i>	<i>Cgly</i>	-	+	+	-	-	+	+	+	+
<i>Coenonympha pamphilus</i>	<i>Cpam</i>	-	+	+	+	+	+	+	+	+
<i>Erebia medusa</i>	<i>Emed</i>	NT	+	-	-	-	-	+	+	+
<i>Erebia aethiops</i>		EN	+	-	-	-	-	-	-	-
<i>Melanargia galathea</i>	<i>Mgal</i>	-	+	+	+	+	+	+	+	+
<i>Lasiommata megera</i>	<i>Lmeg</i>	-	+	+	+	+	+	+	+	+
<i>Lasiommata maera</i>		NT	+	-	-	-	-	-	-	-
<i>Pararge aegeria</i> [§]	<i>Paeg</i>	-	+	+	-	-	-	-	+	+
<i>Maniola jurtina</i>	<i>Mjur</i>	-	+	+	+	+	+	+	+	+
<i>Hyponphele lycaon</i>		CR	+	-	-	-	-	-	-	-
<i>Aphantopus hyperanthus</i>	<i>Ahyp</i>	-	+	+	+	+	+	+	+	+
<i>Hipparchia semele</i>		CR	+	-	-	-	-	-	-	-
Lycaenidae										
<i>Thecla betulae</i>			-	+	-	-	-	-	-	-
<i>Neozephyrus quercus</i> [§]			-	+	-	-	-	-	-	-
<i>Callophrys rubi</i>	<i>Crub</i>	NT	+	+	+	+	+	+	-	+
<i>Satyrium acaciae</i>	<i>Saca</i>	-	-	-	-	-	-	-	+	+
<i>Satyrium pruni</i>	<i>Spru</i>	NT	+	-	-	-	-	+	-	+
<i>Satyrium w-album</i> [§]		NT	-	-	+	-	+	-	-	-
<i>Satyrium spini</i>	<i>Sspi</i>	VU	-	-	-	-	-	-	+	+
<i>Lycaena alciphron</i>		VU	-	-	-	+	+	-	-	-
<i>Lycaena dispar</i>	<i>Ldis</i>	-	-	-	-	-	-	+	+	+
<i>Lycaena phlaeas</i>	<i>Lphl</i>	-	+	+	+	+	+	+	+	+
<i>Lycaena tityrus</i>	<i>Ltit</i>	-	+	+	+	+	+	+	-	+
<i>Lycaena virgaureae</i>	<i>Lvir</i>	NT	+	+	+	+	+	+	+	+
<i>Celastrina argiolus</i>	<i>Carg</i>	-	+	+	+	+	+	+	+	+
<i>Cupido minimus</i>	<i>Cmin</i>	VU	+	+	-	-	+	+	+	+
<i>Aricia agestis</i>	<i>Aage</i>	-	+	+	+	+	+	+	+	+
<i>Aricia eumedon</i>		NT	+	-	-	-	-	-	-	-
<i>Plebejus argyrognomon</i>	<i>Pargy</i>	-	+	-	-	-	-	+	+	+
<i>Plebejus argus</i>	<i>Parg</i>	NT	+	+	+	+	+	+	+	+
<i>Cyaniris semiargus</i>		VU	-	-	-	+	+	-	-	-

<i>Phengaris alcon</i> *	<i>Palc</i>	EN	+	+	+	+	+	+	+	+
<i>Polyommatus bellargus</i>	<i>Pbell</i>	VU	-	-	-	-	-	-	+	+
<i>Polyommatus amandus</i>	<i>Pama</i>	NT	+	+	+	+	+	+	+	+
<i>Polyommatus icarus</i>	<i>Pica</i>	-	+	+	+	+	+	+	+	+
<i>Polyommatus coridon</i>	<i>Pcor</i>	VU	+	+	+	+	+	+	+	+
<i>Polyommatus daphnis</i>	<i>Pdap</i>	VU	+	+	+	+	+	+	+	+
<i>Polyommatus thersites</i>		VU	+	-	-	-	-	-	-	-
Total		32	71	50	47	49	51	55	55	60
Arboreal and migrants excluded		31	61	44	45	42	46	50	50	54
[§] Arboreal and ^{§§} migrant species excluded from some analyses. *The "rebel" ecological form, developing on <i>Gentiana cruciata</i> .										

The indirect CA analyses (Fig. 2) revealed differences among the three surveys in butterfly species composition (total variation = 0.22, axis 1 separating the earliest and the two subsequent surveys: 59.5%, axis 2 distinguishing the interim and the current survey: 40.5%). The pattern held if the localities N, C, S were treated separately (variation = 0.40; % subsequent axes: 45.2, 29.0). Removing 11 arboreal and vagrant species (cf. Table 2) decreased the explained variation (three samples variant: 0.25, six samples variant: 0.35) without changing the overall pattern (% successive axes: 59.9, 40.1, vs. 47.9, 31.0).

Interpreting the CA ordinations by life history traits gave results consistent across the four variants (Table 3). Species present shortly after the cessation of military use and lost subsequently tended to be less mobile. Their ranges were characterised by a broader oceanity niche, narrower continentality niche and lower mean annual temperatures (Fig. 2). Species inclining towards the current survey require higher mean annual temperatures and higher numbers of growing degree days. The species lost since the earliest survey are declining in the Czech Republic, while those gained recently display rather restricted distributions in the country (Table 3).

Table 3

Results of explaining species scores obtained from the correspondence analyses (CA) of three successive butterfly assemblages surveys (early 1990s, 2009, 2016–19) in the (former) Milovice military training range, by life history traits, climatic niche traits and conservation attributes of constituent species.

Analysis	Life history traits				Climatic niche traits				Conservation attributes			
	Ordination axes: traits correlations	% var.	Axis1 <i>F, P</i>	All axes <i>F, P</i>	Ordination axes: traits correlations	% var.	Axis1 <i>F, P</i>	All axes <i>F, P</i>	Ordination axes: traits correlations	% var.	Axis1 <i>F, P</i>	All axes <i>F, P</i>
3-level		–	–	–	+Ax1: Oceanity NB; -Ax1: Summer GDD NB +Ax2: Early summer GDD, Summer GDD -Ax2: Summer GDD NB	17.0	14.5***	5.0***	-Ax1: Distribution trend CZ; Current range CZ -Ax2: Current range CZ	17.3	19.9***	9.2***
3 level, arboreal/migrant spp. excluded	-Ax1: Mobility	2.2	2.5+	–	+Ax1: Precipitation NB -Ax1: Early summer GDD +Ax2: Continentalty NB	13.5	10.9**	4.5***	-Ax1: CZ distribution trend, CZ current range; +Ax2: CZ current range	20.8	13.4***	9.8***
6-level	-Ax1: Mobility	2.0	2.6*	–	-Ax1: Summer GDD +Ax1: Summer GDD	2.5	3.0*	–	-Ax1: CZ distribution trend, CZ current range; -Ax2: CZ current range	18.6	15.9***	12.5***
6 level, arboreal/migrant spp. excluded	-Ax1: Mobility -Ax2: Mobility	3.5	3.4*	–	-Ax1: Summer GDD +Ax2: Summer GDD	2.4	2.6*	–	-Ax1: CZ distribution trend, CZ current range; -Ax2: CZ current range	20.2	14.7***	9.5***

Three-level analyses pooled individual sites surveyed, while six-level analyses treated the grasslands sites S, C, and N separately, if allowed by the data. -/+ signs preceding the Ax1-Ax4 values indicate the direction of the correlation with respective CA axes. %var, F and P values refer to Monte Carlo tests for the significance of the relationships between trait values and CA ordination scores.

Current monitoring of refaunation effects

The 61 species currently recorded (Table 2) were observed in 25,322 individuals. The mean(\pm SD) /median/ range per plot and year, summed across the five yearly visits, were 24.6(\pm 4.88)/ 24/ 15–38 species, and 395.7(\pm 214.55)/ 343/ 99–1,057 individuals. The numbers of species per plot differed significantly among years and refaunation performed marginally better than neglect, except for 2018 with an opposite pattern, resulting into marginally significant management \times year interaction (ANOVA, year $F_{(3,56df)} = 3.72$, $P < 0.05$; management $F_{(1,56df)} = 2.88$, $P = 0.095$; interaction $F_{(3,56df)} = 2.36$, $P = 0.082$). The numbers of individuals also differed among years and were consistently higher at refaunated plots (ANOVA, year $F_{(3,56df)} = 3.11$, $P < 0.05$; management $F_{(1,56df)} = 4.93$, $P < 0.05$; interaction $F_{(3,56df)} = 1.45$, $P = 0.237$) (Fig. 3).

In the CCA analyses (Table 4), the potential nuisance covariates *nectar*, *hour*, and *weather* did not affect the composition of assemblages, implying that nectar was available rather evenly across the plots and visits, and visits were carried out under suitable weather. The strong effect of factorially coded *year* explained the highest variation of all (co)variables. It was followed by plots *position*, specifically latitude, collinear with the effect of *site*. *Tanks* as a separate predictor had no effect. For *ungulates*, the first axis, which distinguished *urochs* and *horse* from *neglect*, *cattle* and *wisent*, was

not significant. The significant second and (still canonical) third axes distinguished *neglect* and *cattle*, respectively, from other situations. *Refaunation* alone had no significant effect.

Adding *tanks* into either *ungulates* or *refaunation* models increased the models' statistical significance, suggesting that some butterflies responded to the thus created intensive disturbance. The models also dramatically improved after inclusion of *factorial year + latitude* as covariates (Table 4, Fig. 4). Apparently, the originally weak effects of the focal predictors were due to variation among years and collinearity between grazing regimes and positions of plots.

Table 4

Results of CCA analyses, comparing the 2016–19 *current monitoring* results from plots refaunated by large ungulates versus neglected plots. E1–E4 are eigenvalues of respective canonical axes, F and P values refer to results of Monte Carlo tests for the first canonical axis and all canonical axes.

Model	E1	E2	E3	E4	% variation	Axis1 F, P	All axes F, P
~nectar	0.039				1.2	4.9, ns	
~weather	0.034	0.027			1.7	4.2, ns	3.8, ns
~factorial hour	0.021	0.016	0.012	0.008	0.6	2.5, ns	1.3+
~polynomial hour	0.017	0.006			0.3	2.1, ns	1.4*
~factorial year	0.114	0.049	0.019		6.1	14.5*	7.9**
~linear year	0.045				1.4	5.6, ns	
~position (forward selected: latitude)	0.026				0.7	3.2**	
~site	0.026				0.7	3.2**	
Covariate model ¹⁾ (~factorial year +latitude)	0.114	0.054	0.020	0.019	8.0	14.5*	6.8***
~tanks	0.015				0.3	1.9, ns	
~tanks latitude +factorial year	0.007				0.1	1.0, ns	
~refaunation ²⁾	0.019	0.010			0.5	2.3, ns	1.8, ns
~refaunation latitude +factorial year	0.019	0.006			0.4	2.5**	1.7**
~refaunation +tanks	0.029	0.014	0.010		1.1	3.6, ns	2.2*
~refaunation +tanks latitude +factorial year	0.022	0.009	0.004		0.5	2.9**	1.6**
~ungulates ³⁾	0.023	0.015	0.010	0.005	0.8	2.8, ns	1.6*
~ungulates latitude +factorial year	0.020	0.009	0.006	0.003	0.3	2.5*	1.2+
~ungulates +tanks	0.035	0.015	0.015	0.010	1.4	4.2*	1.9*
~ungulates +tanks latitude +factorial year	0.023	0.010	0.009	0.004	0.4	3.0*	1.3*

†: P < 0.1, *: P < 0.05, **: P < 0.01, ***: P < 0.001

¹⁾Obtained by forward selection from all significant terms above. ²⁾3-level factor (refaunation, cattle, and neglect); ³⁾5-level factor (horse, aurochs, wisent, cattle, and neglect).

For *refaunation*, the ordination now clearly separated plots grazed by large *ungulates* from neglected plots at the first axis, and *cattle* plus *tanks* from all the other factors at the second axis. The butterflies closely associated with large ungulates were narrowly specialised herb-feeders, such as the obligatorily myrmecophilous *Phengaris alcon*, multiple other Lycaenidae (*Plebejus argus*, *Polyommatus coridon*), but also some more specialised Pieridae (*Colias alfacariensis*) and Hesperidae (*Erynnis tages*, *Pyrgus malvae*). Species associated with *neglect* were those preferring coarse grasslands (the fritillary *Boloria dia*; the Satyrinae *Melanargia galathea*, *Maniola jurtina*; the hesperids *Ochlodes venatus*, *Hesperia comma*) and shrubs (*Iphiclides podalirius*, *Coenonympha arcania*). Cattle pasture was associated with common generalists (*Pieris brassicae*, *Vanessa cardui*, *Thymelicus lineola*), but also with the nationwide vulnerable hesperid *Spialia sertorius*, which was also closely associated with *tanks*. Almost identical patterns arose in the analysis with *ungulates*: The first axis distinguished *neglect* from the three megafaunal species, the second axis distinguished *cattle* plus *tanks*, and the (still canonical) third and fourth axes separated *aurochs* from *wisent* and *cattle* from other management types, respectively (see Appendix 3 for detailed positions of all butterfly species).

Interpreting results of the CCA model ~ *refaunation + tanks* | *factorial year + latitude* by species traits returned a single significant pattern (Fig. 4), associating the first and second ordination axes with the life history trait host plant form. For a similarly structured model *ungulates + tanks* | *factorial*

year+ locality), the result was identical, although only marginally significant, and the same held for analogous models not containing covariables (Appendix 4). Species inclining towards *neglect* (first axis) but also towards *tanks* and *cattle* (second axis), tended to develop on woody plants or coarse grasses, while those inclining towards *refaunation* tended to develop on small forbs. No climatic niche or conservation-related trait performed significantly in these analyses.

Discussion

The former Milovice military training area harbours rich butterfly assemblages; the 55–60 species currently recorded per site is above average for nature reserves in the country (Slancarova et al. 2014; Bartonova et al. 2016). This richness was arguably preserved there owing to exclusion of intensive agriculture and forestry, combined with the past finely-grained disturbance-succession dynamics typical for military areas (Reif et al. 2011; Cizek et al. 2013; Busek and Reif 2017). Following the cessation of military use, several species were lost, while others were subsequently gained. The presence of aurochs, horses, and wisents increases per-plot butterfly abundances and contributes to maintaining their diversity, providing for multiple species of conservation concern, including the critically endangered obligatorily myrmecophilous *Phengaris alcon* (cf. Thomas and Settele 2014).

Changes since termination of military use

The termination of military activities was followed by the successional overgrowth of the disturbed sparsely vegetated surfaces, and gradual dominance of coarse grasses and tall forbs. We therefore expected (hypothesis H1) decrease of specialists associated with small competitively inferior forbs, which our analyses of life history traits did not support. The only life history trait responding to the past-present ordination was mobility. Poorly mobile species were associated with the past military use. Among European butterflies, high mobility is a generalist trait associated with broad trophic ranges, long flight period and other features facilitating survival in human-dominated landscapes (Dapporto and Dennis 2013; Bartonova et al. 2014; Habel et al. 2019), whereas poor mobility increases extinction risks (Birkhofer et al. 2017; Essens et al. 2017). Because mobility relates inversely to local population density (Bartonova et al. 2016), some poorly mobile species may need large habitat areas to sustain viable populations. The changes after cessation of military use probably led to shrinking habitats supply for poorly mobile specialists.

Associations of lost and gained species with climatic niche traits (H2) were more straightforward. In agreement with the warmer and drier climate in Central Europe during the last few decades (Stuhldreher and Fartmann 2018), the lost species shared broad oceanicity or precipitation niches, whereas the newly gained species require higher temperatures. Also, in agreement with H3, the locally lost species display decreasing distribution trends in the Czech Republic and elsewhere in Central and Western Europe (cf. van Swaay et al. 2010).

A combination of restricted mobility and broad oceanicity or precipitation niches applies to several locally lost and nationally threatened species (cf. Benes et al. 2002; Hejda et al. 2017): the hesperids *Pyrgus armoricanus* (currently re-expanding elsewhere in Central Europe: Benes et al. 2020; Kettermann et al. 2020) and *Thymelicus acteon* and the satyrines *Hipparchia semele*, *Hyponephele lycaon*, and *Erebia aethiops*. The latter is a sparse woodland species (Slamova et al. 2012) only loosely associated with grasslands, but its current occurrence in the area was safely excluded by concurrent targeted searches. The remaining four, all declining in Central Europe (van Swaay et al. 2010), require sparsely vegetated substrates and often colonise such landforms as disused quarries and post-industrial barrens (Bourn and Thomas 2002; Benes et al. 2003; Tropek et al. 2010; Tropek et al. 2017). Broad oceanicity tolerance certainly applies to *Hipparchia semele*, distributed from Eastern Europe to Atlantic coastal dunes (Schirmel and Fartmann 2014), but also to *Hyponephele lycaon* and *Pyrgus armoricanus*, whose distribution follows maritime climates far north to southern Fennoscandia (Fourcade et al. 2017; Mikkola 1979). The species newly gained during the last two decades include *Iphiclides podalirius*, *Satyrium acaciae*, *S. spini*, *Lycaena dispar*, and *Polyommatus bellargus*, all currently (re)expanding in Central Europe. The first three are associated with shrubs (Benes et al. 2002), and the fourth with tall ruderal forbs (Strausz et al. 2012), hence they might have profited from concurrent effects of successional abandonment. Only the fifth, gained as late as 2018, develops on *Securigera varia* (L) host plants growing at sparsely vegetated surfaces (Benes et al. 2003), which apparently profits from the ungulates' grazing. The gains and losses thus reflect the interacting forces of climate and land use change (Reif et al. 2008; Thomas et al. 2015).

Refaunation by large ungulates

Large ungulates did not demonstrably change per plot species richness while increasing butterfly abundances, only partly supporting our hypothesis H4. At the same time, refaunation affected the local assemblages' composition. It favoured species developing on small forbs over those developing on large forbs, grasses or shrubs, supporting our hypothesis H5.

As in other studies (cf. Hennig et al. 2017; Cromsigt et al. 2018b; Zielke et al. 2019), the immediate effects of year-round ungulates' presence included reduction of tall coarse grasses, slowing down scrub growth due to browsing and bark peeling, reduction of grass blooming by feeding on grass inflorescences, and exposing barren ground around tracks and wallows. As in experiments with feral horses (Garrido et al. 2019), some richly blooming forbs, including species that rarely bloomed in the years preceding the refaunation (unpublished data), became notably more abundant. The differences in butterfly assemblages composition between refaunated and neglected plots became apparent only after statistical control for the effect of years and to monitored plots position. Still, species benefitting from refaunation included the iconic *Phengaris alcon f. rebeli*, whose host plant, the poorly competitive (cf. Petanidou et al. 1995; Habel et al. 2007) and chemically protected (Popovic et al. 2019) perennial *Gentiana cruciata* (cf. Petanidou et al. 1995), boomed shortly after the establishment of grazing. This obligatorily myrmecophilous butterfly is likely host plant limited, because its females prefer oviposition on plants overtopping surrounding vegetation (Meyer-Hozak 2000; Habel et al. 2016; Vilbas et al. 2016).

The simplest explanation of the higher butterfly numbers at refaunated plots, attraction to increased nectar, is unlikely, as covariable *nectar* had no effect in ordinations. A tempting explanation is the smaller size of the forbs-feeding specialists, related to higher local population densities and lower mobility (cf. Bartonova et al. 2014). In any case, it is intriguing that many plant groups avoided by horses (e.g., Rosaceae, Fabaceae, Polygonaceae, Orobanchaceae: Chodkiewicz 2020), once the dominant grazers of West-Palaeartic grasslands, are frequent in the larval diet of European butterflies. Possible coevolutionary relationships between mammalian megafauna and herbivorous insects, and their conservation implications, deserve further investigation.

The patterns revealed by ordinations relating species composition to refaunation were admittedly less convincing than in studies comparing starkly contrasting habitats, such as close woodlands vs. clearings (cf. Benes et al. 2006; Sebek et al. 2015). It appears that the refaunated and neglected plots were interconnected by individual movements. The distances among study plots were within the routine movement abilities of most butterflies (Fric et al. 2010; Stevens and Bagueette 2010; Vodickova et al. 2019), although this may not apply for the least mobile species (Korosi et al. 2008). Also, the small-scale vegetation mosaic at the study sites (Jirku et al. 2020; Fig. 1) could blur potential effects to species community structures. It is likely that individual butterflies located some of their vital resources at both grazed and ungrazed sections of the area, in line with the resource-based understanding of (animal) habitats (Dennis et al. 2006; Turlure et al. 2019).

The setting of our study did not allow distinguishing between the effects of horses and big bovids, as both pastures contained combinations of these ungulates. The literature on refaunation in temperate (e.g., Vera 2000; Zielke et al. 2020) and northern boreal (Macias-Fauria et al. 2020) regions agrees that these two ungulate groups supplement each other in effects on vegetation, as well as seasonal and diurnal habitat use. Additionally, both horses and bovids acted as dominant grazers in late Quaternary European ecosystems, and both were present in traditional rural landscapes.

The mechanical disturbance by armoured vehicles (factor *tanks*) exhibited no separate effect, seemingly countering the claims (e.g. Heneberg et al. 2016) that it provides disturbed conditions beneficial for some insects. Presence of *tanks*, however, increased the explanatory power of models containing ungulates or refaunation effects (Table 4), suggesting a complementarity with large grazers for some butterfly species. This might be the case of *Spialia sertorius*, a skipper closely associated with *tanks* in ordination diagrams and developing on *Sanguisorba minor*, a competitively inferior forb preferring sparsely vegetated surfaces (cf. Gros 2002). It is tempting to postulate that on military lands, and in the current Milovice reserves, the heavy vehicles supplement yet another lost component of the megaherbivore fauna of interglacial Europe, proboscideans (van Kolfschoten 2000).

The effect of domestic cattle, grazed at two plots for two years of the project, was orthogonal to the ordination gradient distinguishing refaunation and neglect. The cattle were grazed with high stocking and supplementary feeding during the vegetation season and were not grazed in winter. Such grazing style suppresses forbs and fails to suppress coarse grasses. Grazing by domestic breeds in more biodiversity-friendly ways is possible (Enri et al. 2017; Henning et al. 2017; Hall and Bunce 2019), but this was not the case in our system.

While being demonstrably positive for butterflies associated with poorly competitive forbs, the refaunation did not detectably imperil species associated with coarse grasses or shrubs. In this respect, the Milovice situation differs from some projects with documented negative outcomes for insect assemblages (cf. Lorimer and Driessen 2014; van Klink and WallisDeVries 2018). It seems beneficial that contrary to some refaunation sites amidst urbanised landscapes (Lorimer and Driessen 2014), our study system is situated in a diverse rural setting, including ungrazed/neglected plots, which provide conditions contrasting with the grazed sites. This habitat diversity likely allows for resource compensation/supplementation by the butterflies (Quin et al. 2004), enabling coexistence of species requiring different disturbance levels (Bergman et al. 2018). The current grazing pressure ≈ 0.5 grazers*ha⁻¹ does not deplete the sites of larval host plants or nectar. There is a potential long-term risk, as the whole operation is funded from the EU Agri-environmental scheme "grazing", which requires maintaining stable grazing intensity. Flexibility may be necessary, as grazing levels appropriate for restoring overgrown sites may become too high once species-rich dry grasslands develop, as well as if accelerating climate change will decrease rainfall levels during the vegetation period.

Conclusion

We demonstrated that abandonment and successional changes of a former military area restructured the rich local butterfly fauna, and that refaunation of parts of the area by megafaunal grazers contributes to maintaining high butterfly abundances and species richness. Analysing traits of the constituent butterfly species revealed that the post-abandonment changes, spanning across two decades, affected butterfly assemblages via different mechanisms than does the current megaherbivores activity. The post-abandonment changes led to losses of some poorly mobile species and gains of some regionally expanding species, presumably rather good dispersers. The changes also had a climatic component, consistent with ongoing climatic warming. The megaherbivores affect butterfly assemblages by transforming vegetation, and hence supporting species developing on small forbs on the expense of large forbs, coarse grasses and woody plants feeders. Local heterogeneity of conditions, and existence of ungrazed sections in the vicinity of the grazed ones, ensure that species from the other group are not locally imperilled. Given that many of the species lost since abandonment of the area by the military were poor dispersers, reintroductions of some of the lost species, whose habitats the ungulates have restored, is a logical next step.

Unresolved questions include differences among ungulate species in affecting butterfly larval and adult resources, possible legacies of coevolution between temperate butterflies and ungulates, and future development of the butterfly assemblages. The latter question is tractable by sustained monitoring, whereas the former two can be approached by expansion of studies similar to ours to sites varying in composition of both butterfly

assemblages and ungulate species. This ambitious programme is increasingly feasible, as the refaunation movement expands and the number of potential study systems rapidly increases. In the Czech Republic alone, progeny of the Milovice ungulate herds currently roam at an additional seven sites, offering rich opportunities for future research.

Abbreviations

CA – correspondence analysis. CCA – canonical correspondence analysis

Declarations

Ethics approval and consent to participate:

Any handling of the butterflies fully conformed to valid legal provisions of the Czech Republic. The welfare of vertebrate animals was not affected by this study.

Consent to publish:

Not applicable.

Availability of data and materials:

All the primary data are included to this manuscript as electronic appendices.

Competing interests:

We declare no competing interests, financial or otherwise.

Funding:

EU Operational Programme Environment (CZ.1.02/6.2.00/13.21986, CZ.7.02/6.2.00/15.29686), and the Central Bohemia regional government (S-2140/OŽP/2014, S-3815/OŽP/2015, S-15873/OŽP/2016, S-2325/OŽP/2018, S-8570/OŽP/2018) – preparing and running the refaunation project, funding the monitoring in the field. Technology Agency of the Czech Republic (TB020MZP045, SS01010526) and Czech Academy of Sciences (RVO 60077344) – analysing the data and preparing the manuscript.

Authors' contributions:

M. Konvicka (MK), V. Vodickova (VV), and M. Jirku (MJ) planned and designed the study. J. Benes (JB) analysed the historical records and contributed current knowledge on butterfly species distribution. David Rícl (DR) performed the current butterfly monitoring, JB checked vouchers of difficult species. MJ contributed background details about the refaunation project. MK, VV, and MJ analysed the current monitoring data and jointly wrote the manuscript. All authors have read and approved the manuscript.

Acknowledgements:

We thank the nature-loving public and the brave people of Milovice, Benátky nad Jizerou, and Lipník, for supporting their wonderful project. Our friends and colleagues A. Bartoňová-Sucháčková, L. Čížek, D. Dostál, and M. Šálek were indispensable in various stages of the work.

References

1. Aguirre-Gutierrez J, Kissling WD, Carvalheiro LG, WallisDeVries MF, Franzen M, Biesmeijer JC (2016) Functional traits help to explain half-century long shifts in pollinator distributions. *Sci Rep* 6: 24451
2. Altermatt F (2010) Tell me what you eat and I'll tell you when you fly: diet can predict phenological changes in response to climate change. *Ecol Lett*, 13: 1475–1484
3. Baker S (1993) *Survival of the Fittest – A natural history of the Exmoor Pony*. Exmoor Books, Dulverton, Somerset, 249 pp
4. Bartonova A, Benes J, Faltynek-Fric Z, Chobot K, Konvicka M (2016) How universal are reserve design rules? A test using butterflies and their life history traits. *Ecography* 39: 456–464

5. Bartonova A, Benes J, Konvicka M (2014) Generalist-specialist continuum and life history traits of Central European butterflies (Lepidoptera) - are we missing a part of the picture? *Eur J Entomol* 111: 543–553
6. Bartonova A, Konvicka M, Korb S, Kramp K, Schmitt T, Fric ZF (2018) Range dynamics of Palaearctic steppe species under glacial cycles: the phylogeography of *Proterebia afra* (Lepidoptera: Nymphalidae: Satyrinae). *Biol J. Linn Soc* 125: 867–884
7. Benes J, Kepka P, Konvicka M (2003) Limestone quarries as refuges for European xerophilous butterflies. *Conserv Biol* 17: 1058–1069
8. Benes J, Konvicka M, Dvorak J, Fric Z, Havelda Z, Pavlicko A, Vrabec V, Weidenhoffer Z (2002) Butterflies of the Czech Republic: Distribution and conservation (in Czech, extended English summaries). SOM, Prague, 857 pp
9. Benes J, Cizek O, Dovala J, Konvicka M (2006) Intensive game keeping, coppicing and butterflies: The story of Milovicky Wood, Czech Republic. *Forest Ecol Manag*, 237: 353–365
10. Benes J, Ruzicka J, Spitzer L (2020) Recent expansion of Oberthür's Grizzled Skipper (*Pyrgus armoricanus* [Oberthür, 1910]) (Hesperiidae, Lepidoptera) in the Czech Republic. *Acta Carp Occ* 10:74–85 (in Czech, English summary)
11. Birkhofer K, Gossner MM, Diekötter T, Drees C, Ferlian O, Maraun M, Scheu S, Weisser WW, Wolters V, Wurst S, Zaitsev AS, Smith HG (2017) Land-use type and intensity differentially filter traits in above- and below-ground arthropod communities. *J Anim Ecol* 86: 511–520
12. Bourn NAD, Thomas JA (2002) The challenge of conserving grassland insects at the margins of their range in Europe. *Biol Conserv* 104: 285–292
13. Bubova T, Vrabec V, Kulma M, Nowicki P (2015) Land management impacts on European butterflies of conservation concern: a review. *J Insect Conserv* 19: 805–821
14. Busek O, Reif J (2017) The potential of military training areas for bird conservation in a central European landscape. *Acta Oecol* 84: 34–40
15. Carmona CP, de Bello F, Mason NWH, Leps J (2016) Traits Without Borders: Integrating Functional Diversity Across Scales. *Trends Ecol Evol* 31: 382–394
16. Dennis RLH, Shreeve TG, Van Dyck H (2006) Habitats and resources: The need for a resource-based definition to conserve butterflies. *Biodivers Conserv* 6: 1943–1966
17. Bergman KO, Daniel-Ferreira J, Milberg P, Ockinger E, Westerberg L (2018) Butterflies in Swedish grasslands benefit from forest and respond to landscape composition at different spatial scales. *Landscape Ecol* 33: 2189–2204
18. Chodkiewicz A (2020) Advantages and disadvantages of Polish primitive horse grazing on valuable nature areas - A review. *Global Ecol Conserv* 21: e00879
19. Cizek L, Fric Z, Konvicka M (2006) Host plant defences and voltinism in European butterflies. *Ecol Entomol* 31: 337–344
20. Cizek O, Vrba P, Benes J, Hrazsky Z, Koptik J, Kucera T, Marhoul P, Zamecnik J, Konvicka M (2013) Conservation Potential of Abandoned Military Areas Matches That of Established Reserves: Plants and Butterflies in the Czech Republic. *PLoS ONE*, 8: e53124
21. Cromsigt JPGM, te Beest M, Kerley GIH, Landman M, le Roux E, Smith FA (2018a) Trophic rewilding as a climate change mitigation strategy? *Phil Trans R Soc B Biol*, 373(S1): e20170440
22. Cromsigt JPGM, Kemp YJM, Rodriguez E, Kivit H (2018b) Rewilding Europe's large grazer community: how functionally diverse are the diets of European bison, cattle, and horses? *Restor Ecol* 26: 891–899
23. Dapporto L, Dennis RLH (2013) The generalist-specialist continuum: Testing predictions for distribution and trends in British butterflies. *Biol Conserv* 157: 229–236
24. Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B (2014) Defaunation in the Anthropocene. *Science* 345: 401–406
25. Dolek M, Kőrösi Á, Freese-Hager A (2018) Successful maintenance of Lepidoptera by government-funded management of coppiced forests. *J Nat Conserv* 43: 7–84
26. Doughty CE, Wolf A, Morueta-Holme N, Jorgensen PM, Sandel B, Violle C, Boyle B, Kraft NJB, Peet RK, Enquist BJ (2016) Megafauna extinction, tree species range reduction, and carbon storage in Amazonian forests. *Ecography* 39: 194–203
27. Dray S, Choler P, Doledec S, Peres-Neto PR, Thuiller W, Pavoine S, ter Braak CJF (2014) Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95: 14–21
28. Enri SR, Probo M, Farruggia A, Lanore L, Blanchetete A, Dumont B (2017) A biodiversity-friendly rotational grazing system enhancing flower-visiting insect assemblages while maintaining animal and grassland productivity. *Agr Ecosyst Envir* 241: 1–10
29. Essens T, van Langevelde F, Vos RA, Van Swaay CAM, WallisDeVries MF (2017) Ecological determinants of butterfly vulnerability across the European continent. *J Insect Conserv* 21: 439–450
30. Feurdean A, Ruprecht E, Molnár Z, Hutchinson SM, Hickler T (2018) Biodiversity-rich European grasslands: Ancient, forgotten ecosystems. *Biol Conserv* 228: 224–232
31. Fourcade Y, Ranius T, Ockinger E (2017) Temperature drives abundance fluctuations, but spatial dynamics is constrained by landscape configuration: Implications for climate-driven range shift in a butterfly. *J Anim Ecol* 86: 1339–1351
32. Fric Z, Hula V, Klimova M, Zimmermann K, Konvicka M (2010) Dispersal of four fritillary butterflies within identical landscape. *Ecol Res* 25: 543–552
33. Galetti M (2004) Parks of the Pleistocene: recreating the Cerrado and the Pantanal with megafauna. *Nature Conserv* 2: 93–100

34. Galetti M, Moleon M, Jordano P, Pires MM, Guimaraes PR, Pape T, Nichols E, Hansen D, Olesen JM, Munk M, de Mattos JS, Schweiger AH, Owen-Smith N, Johnson CN, Marquis RJ, Svenning JC (2018) Ecological and evolutionary legacy of megafauna extinctions. *Biol Rev* 93: 845–862
35. Gamez-Virues S, Perovic DJ, Gossner MM, Borsching C, Bluthgen N, de Jong H, Simons NK, Klein AM, Krauss J, Maier G, Scherber C, Steckel J, Rothenwohrer C, Steffan-Dewenter I, Weiner CN, Weisser W, Werner M, Tschamtker T, Westphal C (2015) Landscape simplification filters species traits and drives biotic homogenization. *Nat Commun* 6: 8568
36. Garrido P, Marell A, Ockinger E, Skarin A, Jansson A, Thulin CG (2019) Experimental rewilding enhances grassland functional composition and pollinator habitat use. *J Appl Ecol* 56: 946–955
37. Goderie R, Lenstra JA, Upadhyay M, Crooijmans R, Linnartz L (2015) Aurochs genetics, a cornerstone of European biodiversity. *Rewilding Europe*, https://rewildingEurope.com/app/uploads/2016/01/Aurochs-genetics_summary_final.pdf
38. Gros P (2002) Interessante Tagfalterfunde (Lepidoptera: Rhopalocera) aus dem Bundesland Salzburg (Oesterreich). Erster Teil: Hesperidae und Pieridae. *Beitr Entomofaunistik*, 3: 7–15
39. Gutierrez D, Thomas CD, Leon-Cortes JL (1999) Dispersal, distribution, patch network and metapopulation dynamics of the dingy skipper butterfly (*Erynnis tages*). *Oecologia* 121: 506–517
40. Habel JC, Schmitt T, Hardtle W, Lutkepohl M, Assman T (2007) Dynamics in a butterfly–plant–ant system: influence of habitat characteristics on turnover rates of the endangered lycaenid *Maculinea alcon*. *Ecol Entomol* 32: 536–543
41. Habel JC, Teucher M, Ulrich W, Bauer M, Rödder D (2016) Drones for butterfly conservation: larval habitat assessment with an unmanned aerial vehicle. *Landscape Ecol* 31: 2385–2395
42. Habel JC, Trusch R, Schmitt T, Ochse M, Ulrich W (2019) Long-term large-scale decline in relative abundances of butterfly and burnet moth species across south-western Germany. *Sci Rep* 9, 14921
43. Hall SJG, Bunce RGH (2019) The use of cattle *Bos taurus* for restoring and maintaining holarctic landscapes: Conclusions from a long-term study (1946–2017) in northern England. *Ecol Evol* 9: 5859–5869
44. Hejda R, Farkac J, Chobot K (eds.) (2017) Red List of Threatened species of the Czech Republic. Invertebrates. *Priroda*, Praha 36: 1–612
45. Heneberg P, Bogusch P, Rezac M (2016) Off-road motorcycle circuits support long-term persistence of bees and wasps (Hymenoptera: Aculeata) of open landscape at newly formed refugia within otherwise afforested temperate landscape. *Ecol Eng* 93: 187–198.
46. Henning K, Lorenz A, von Oheimb G, Hardtle W, Tischew S (2017) Year-round cattle and horse grazing supports the restoration of abandoned, dry sandy grassland and heathland communities by suppressing *Calamagrostis epigejos* and enhancing species richness. *J Nature Conserv* 40: 120–130.
47. Hovens HJPM, Rijkers TAJM (2013) On the origins of the Exmoor pony: did the wild horse survive in Britain? *Lutra* 56: 129–136
48. Jepson P (2016) A rewilding agenda for Europe: creating a network of experimental reserves. *Ecography* 39: 117–124
49. Jirku D, Hais M, Jirku M (2020) Osud vojenských prostorů: krajiny protékající mezi prsty [The Fate of Military Areas: Landscapes that Seep through Your Fingers]. *Živa* 2020: 265–267
50. Jirku M, Dostal D (2015) Alternativní management ekosystémů: Metodika zavedení chovu býložravých savců jako alternativního managementu vybraných lokalit. [Alternative ecosystems management: Guidelines for refaunation by large ungulate herbivores as alternative management of selected localities]. Report for the Czech Ministry of Environment, Online [https://www.mzp.cz/C1257458002F0DC7/cz/zavedeni_chovu_bylozravych_savcu_metodika/\\$FILE/OZCHP-TACR_Metodika_2015_Prirozena%20pastva_opr-20160324.pdf](https://www.mzp.cz/C1257458002F0DC7/cz/zavedeni_chovu_bylozravych_savcu_metodika/$FILE/OZCHP-TACR_Metodika_2015_Prirozena%20pastva_opr-20160324.pdf)
51. Jirku M, Dostal D, Robovsky J, Salek M (2018) Reproduction of the golden jackal (*Canis aureus*) outside current resident breeding populations in Europe: evidence from the Czech Republic. *Mammalia* 82: 592–595
52. Johnson CN (2009) Ecological consequences of Late Quaternary extinctions of megafauna. *Proc R Soc B Biol* 276: 2509–2519
53. Kadlec T, Tropek R, Konvička M (2012) Timed surveys and transect walks as comparable methods for monitoring butterflies in small plots. *J Insect Conserv* 16, 275–280
54. Kettermann M, Münsch T, Stuhldreher G, Fartmann T (2020) Manche mögen's heiß – aktuelle Ausbreitung von *Pyrgus armoricanus* (Oberthür, 1910) im Diemeltal (Ostwestfalen/Nordhessen) und in Deutschland als Folge von Hitzesommern. *Nachr Entomol Ver Apollo NF* 40: 209–214
55. Korosi A, Orvosy N, Batary P, Kover S, Peregovits L (2008) Restricted within-habitat movement and time-constrained egg laying of female *Maculinea rebeli* butterflies. *Oecologia* 156: 455–464
56. Legendre P, Galzin R, HarmelinVivien ML (1997) Relating behavior to habitat: Solutions to the fourth-corner problem. *Ecology* 78: 547–562
57. Lorimer J, Driessen C (2014) Wild experiments at the Oostvaardersplassen: rethinking environmentalism in the Anthropocene. *T I Brit Geogr*, 39: 169–181
58. Macek J, Lastuvka Z, Benes J, Traxler L (2015) Motýli a housenky Střední Evropy IV. Denní motýli. *Academia*, Praha.
59. Macias-Fauria M, Jepson P, Zimov N, Malhi Y (2020) Pleistocene Arctic megafaunal ecological engineering as a natural climate solution? *Phil Trans R Soc B Biol* 375: article 20190122
60. Matouš J (1994) Motýli bývalého VVP Mladá. *Prác Muz Kolín Přírod* 1: 97–126

61. Merckx T, Pereira HM (2015) Reshaping agri-environmental subsidies: From marginal farming to large-scale rewilding. *Basic Appl Ecol* 16: 95–103
62. Meyer-Hozak C (2000) Population biology of *Maculinea rebeli* (Lepidoptera: Lycaenidae) on the chalk grasslands of Eastern Westphalia (Germany) and implications for conservation. *J Insect Conserv* 4: 63–72
63. Mikkola K (1979) Vanishing and declining species of Finnish Lepidoptera. *Notul Entomol* 59: 1–9
64. Navarro LM, Pereira HM (2012) Rewilding abandoned landscapes in Europe. *Ecosystems* 15: 900–912
65. Öckinger E, Eriksson AK, Smith HG (2006) Effects of grassland abandonment, restoration and management on butterflies and vascular plants. *Biol Conserv* 133: 291–300
66. Olech W, IUCN SSC Bison Specialist Group (2008) “Bison bonasus”. The IUCN Red List of Threatened Species: e.T2814A9484719. Retrieved 11 January 2018
67. Quin A, Aviron S, Dover J, Burel F (2004) Complementation/supplementation of resources for butterflies in agricultural landscapes. *Agr Ecosyst Environ* 103: 473–479
68. Pedersen PBM, Olsen JB, Sandel B, Svenning JC (2019) Wild Steps in a semi-wild setting? Habitat selection and behavior of European bison reintroduced to an enclosure in an anthropogenic landscape. *PLOS One* 14, e0198308
69. Petanidou T, Dennijs JCM, Oostermeijer JGB (1995) Pollination ecology and constraints on seed set of the rare perennial *Gentiana cruciata* L. in the Netherlands. *Acta Bot Neerl* 44: 55–74
70. Popovic Z, Krstic-Milosevic D, Stefanovic M, Matic R, Vidakovic V, Bojovic S (2019) Chemical and Morphological Inter- and Intrapopulation Variability in Natural Populations of *Gentiana pneumonanthe* L. *Chem Biodivers* 16: e1800509
71. Rehounkova K, Cizek L, Rehounek J, Sebelikova L, Tropek R, Lencova K, Marhoul P, Bogusch P, Maca J (2016) Additional disturbances as a beneficial tool for restoration of post-mining sites: a multi-taxa approach. *Environ Sci Pollut R* 23: 13745–13753
72. Reif J, Storch D, Vorisek P, Stastny K, Bejcek V (2008) Bird-habitat associations predict population trends in central European forest and farmland birds. *Biodivers Conserv* 17: 3307–3319
73. Reif J, Marhoul P, Cizek O, Konvicka M (2011) Abandoned military training sites are an overlooked refuge for at-risk open habitat bird species. *Biodivers Conserv* 20: 3645–3662
74. Root-Bernstein M, Gooden J, Boyes A (2018) Rewilding in practice: Projects and policy. *Geoforum* 97: 292–304
75. Schirmel J, Fartmann T (2014) Coastal heathland succession influences butterfly community composition and threatens endangered butterfly species. *J Insect Conserv* 18: 111–120
76. Schweiger O, Harpke A, Wiemers M, Settele J (2014) CLIMBER: climatic niche characteristics of the butterflies in Europe. *ZooKeys* 367: 65–84
77. Sebek P, Bace R, Bartos M, Benes J, Chlumska Z, Dolezal J, Dvorsky M, Kovar J, Machac O, Mikatova B, Perlik M, Platek M, Polakova S, Skorpik M, Stejskal R, Svoboda M, Trnka F, Vlasin M, Zapletal M, Cizek L (2015) Does a minimal intervention approach threaten the biodiversity of protected areas? A multi-taxa short-term response to intervention in temperate oak-dominated forests. *Forest Ecol Manag* 358: 80–89
78. Seddon PJ, Griffiths CJ, Soorae PS, Armstrong DP (2014) Reversing defaunation: Restoring species in a changing world. *Science* 345: 406–412
79. Slancarova J, Benes J, Kristynek M, Kepka P, Konvicka M (2014) Does the surrounding landscape heterogeneity affect the butterflies of insular grassland reserves? A contrast between composition and configuration. *J Insect Conserv* 18: 1–12
80. Stevens VM, Baguette M (2010) A meta-analysis of dispersal in butterflies. *Biol Rev* 85: 625–642
81. Strausz M, Fiedler K, Franzen M, Wiemers M (2012) Habitat and host plant use of the Large Copper Butterfly *Lycaena dispar* in an urban environment. *J Insect Conserv* 16: 709–721
82. Stuhldreher G, Fartmann T (2018) Threatened grassland butterflies as indicators of microclimatic niches along an elevational gradient - Implications for conservation in times of climate change. *Ecol Indic* 94: 83–98
83. Svenning JC, Pedersen PBM, Donlan CJ, Ejrnaes R, Faurby S, Galetti M, Hansen DM, Sandel B, Sandom CJ, Terborgh JW, Vera FWM (2016) Science for a wilder Anthropocene: Synthesis and future directions for trophic rewilding research. *Proc Nat Acad Sc USA* 113: 898–906
84. Ter Braak CJF, Šmilauer P (2012) CANOCO reference manual and user's guide: software for ordination, version 5.0. Microcomputer Power, Ithaca, USA.
85. Thomas JA (1993) Holocene climate changes and warm man-man refugia may explain why a 6th of British butterflies possess unnatural early successional habitats. *Ecography* 16: 278–284
86. Thomas JA, Settele J (2014) Evolutionary biology - Butterfly mimics of ants. *Nature* 432: 283–284
87. Thomas JA, Simcox DJ, Clarke RT (2009) Successful Conservation of a Threatened *Maculinea* Butterfly. *Science* 325: 80–83
88. Thomas JA, Edwards M, Simcox DJ, Powney GD, August TA, Isaac NJB (2015) Recent trends in UK insects that inhabit early successional stages of ecosystems. *Biol J Linn Soc* 115: 636–646
89. Todisco V, Gratton P, Cesaroni D, Sbordoni V (2010) Phylogeography of *Parnassius apollo*: hints on taxonomy and conservation of a vulnerable glacial butterfly invader. *Biol J Linn Soc* 101: 169–183

90. Tropek R, Kadlec T, Karesova P, Spitzer L, Kocarek P, Malenovsky I, Banar P, Tuf IH, Hejda M, Konvicka M (2010) Spontaneous succession in limestone quarries as an effective restoration tool for endangered arthropods and plants. *J Appl Ecol* 47: 139–147
91. Tropek R, Cizek O, Kadlec T, Klecka J (2017) Habitat use of *Hipparchia semele* (Lepidoptera) in its artificial stronghold: necessity of the resource-based habitat view in restoration of disturbed sites. *Pol J Ecol* 65: 385–399
92. Turlure C, Schtickzelle N, Dubois Q, Bague M, Dennis RLH, Van Dyck H (2019) Suitability and transferability of the resource-based habitat concept: A test with an assemblage of butterflies. *Front Ecol Evol* 7: 127
93. van Klink R, Wallis de Vries MF (2018) Risks and opportunities of trophic rewilding for arthropod communities. *Phil Trans R Soc B Biol* 373(S1): e20170441
94. van Kolschoten T (2000) The Eemian mammal fauna of central Europe. *Neth J Geosci* 79: 269–281
95. Van Swaay C, Cuttelod A, Collins S, Maes D, López Munguira M, Šašić M, Settele J, Verovnik R, Verstrael T, Warren M, Wiemers M, Wynhof I (2010) European Red List of Butterflies. Publications Office of the European Union, Luxembourg.
96. van Swaay, C., Collins, S., Dusej, G., Maes, D., Munguira, M.L., Rakosy, L., Ryrholm, N., Sasic, M., Settele, J. & Thomas, J.A. (2012) Dos and Don'ts for butterflies of the Habitats Directive of the European Union. *Nat Conserv - Bulgaria*, 1, 73–153
97. Vera FWM (2000) Grazing ecology and forest history. CAB International, Wallingford.
98. Vilbas M, Esperk T, Edovald T, Kaasik A, Teder T (2016) Oviposition site selection of the Alcon blue butterfly at the northern range margin. *J Insect Conserv* 20: 1059–1067
99. Wallis de Vries MF, Van Swaay CAM (2006) Global warming and excess nitrogen may induce butterfly decline by microclimatic cooling. *Global Change Biol* 12: 1620–1626
100. Warren MS (1991) The successful conservation of an endangered species, the Heath fritillary butterfly *Mellicta athalia* in Britain. *Biol Conserv* 55: 37–56
101. Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414: 65–69
102. Wiemers M, Balletto E, Dinca V, Fric ZF, Lamas G, Lukhtanov V, Munguira ML, van Swaay CAM, Vila R, Vliegenthart A, Wahlberg N, Verovnik R (2018) An updated checklist of the European Butterflies (Lepidoptera, Papilionoidea). *Zookeys* 811: 9–45
103. Zielke L, Wrage-Monnig N, Muller J, Neumann C (2019) Implications of Spatial Habitat Diversity on Diet Selection of European Bison and Przewalski's Horses in a Rewilding Area. *Diversity (Basel)* 11: Article 63
104. Zimov SA, Chuprynin VI, Oreshko AP, Chapin FS, Reynolds JF, Chapin MC (1995) Steppe-tundra transition – A herbivore-driven biome shift at the end of Pleistocene. *American Naturalist* 146: 765–794

Figures

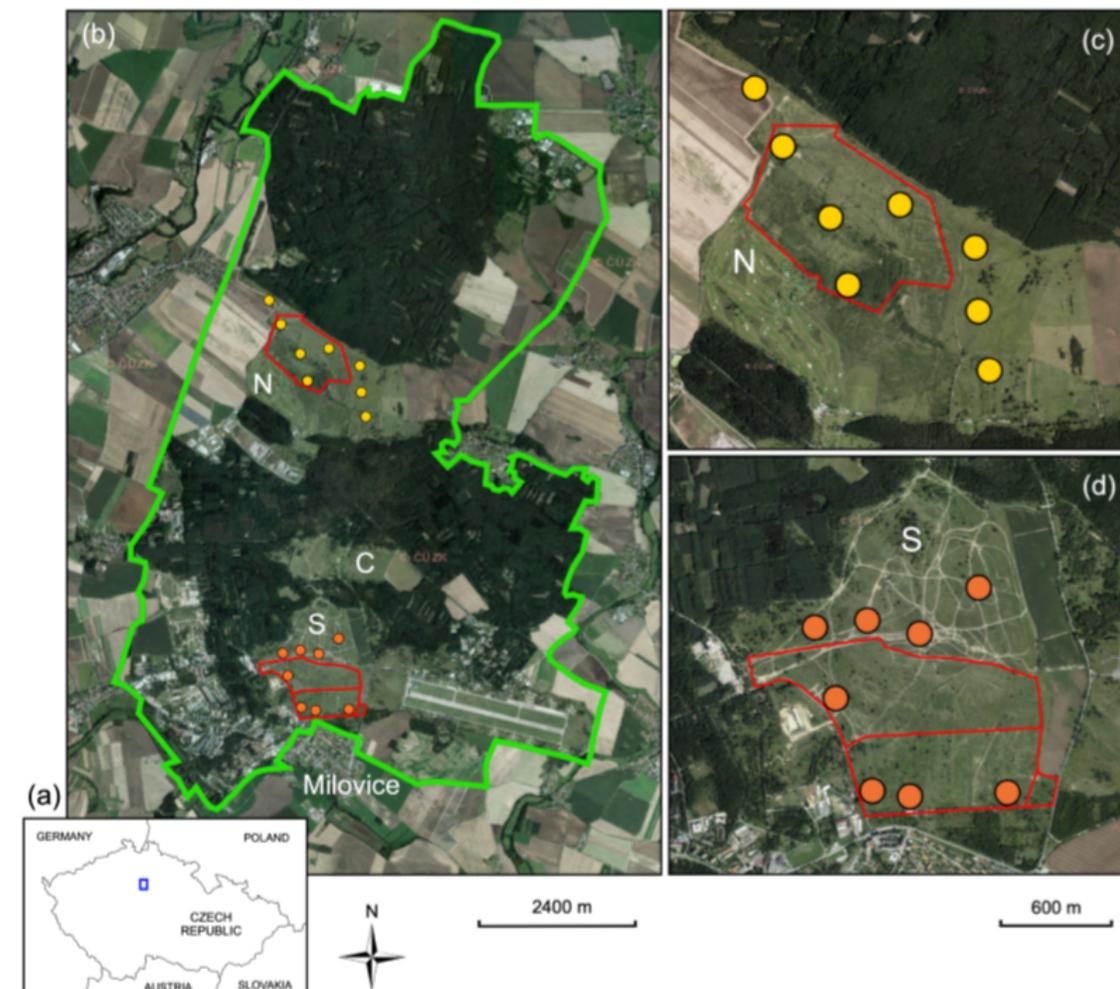


Figure 1

Former Milovice military training range. (a) The position of the range within the Czech Republic. (b) Aerial view of the area with the military range borders (green line), positions of the grasslands N, C, S, and borders of the two grazing reserves (red lines). (c, d) More detailed view at the 16 monitored plots within grasslands S and N. The background aerial photo is from mapy.seznam.cz, © Seznam.cz, a.s. Used according to general license agreement.

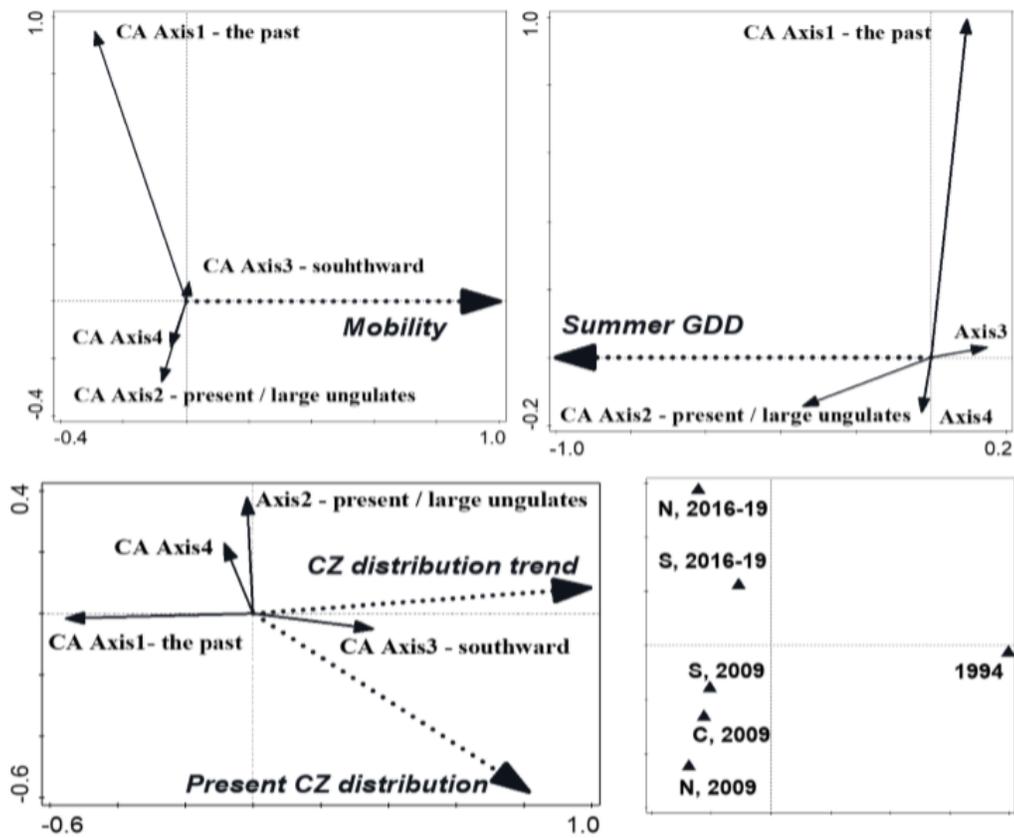


Figure 2

Interpreting three subsequent butterfly surveys of the Milovice military range by species traits. Results of CA analysis of presence/absence data obtained from the Milovice military training range (six-level analysis, arboreal and migrant species excluded, cf. Table 3) interpreted by life history traits (top left), climatic niche traits (top right) and conservation attributes (bottom left) of constituent species. Positions of the three surveys, based on CA ordination of recorded butterflies, in bottom right.

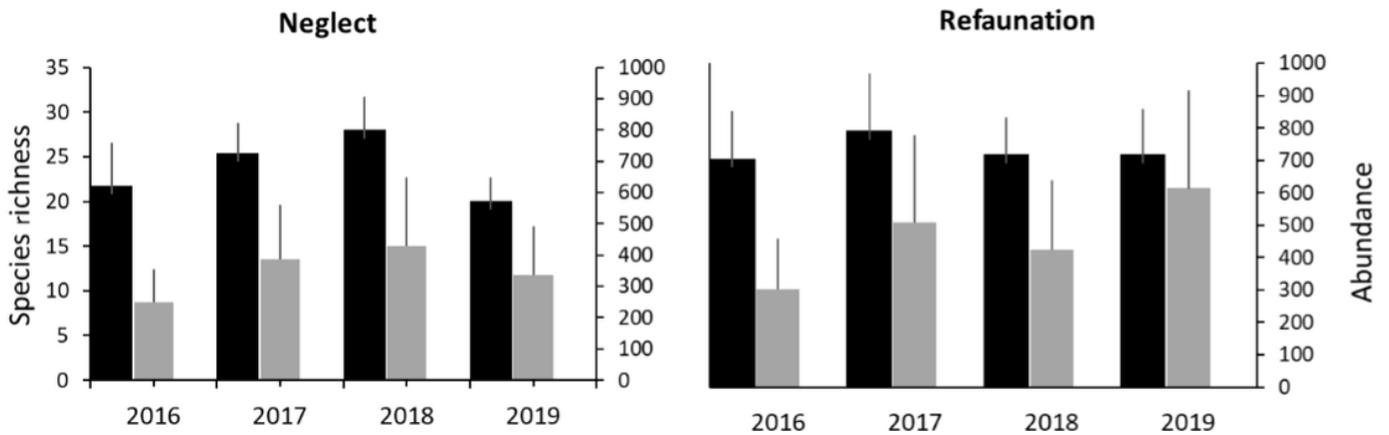


Figure 3

Butterfly species richness and abundance of neglected and refaunated plots. Numbers of butterfly species (black bars) and individuals (grey bars) recorded in the former Milovice military training range, with respect to management of the plots. Means \pm SD recorded per the plot and year are shown.

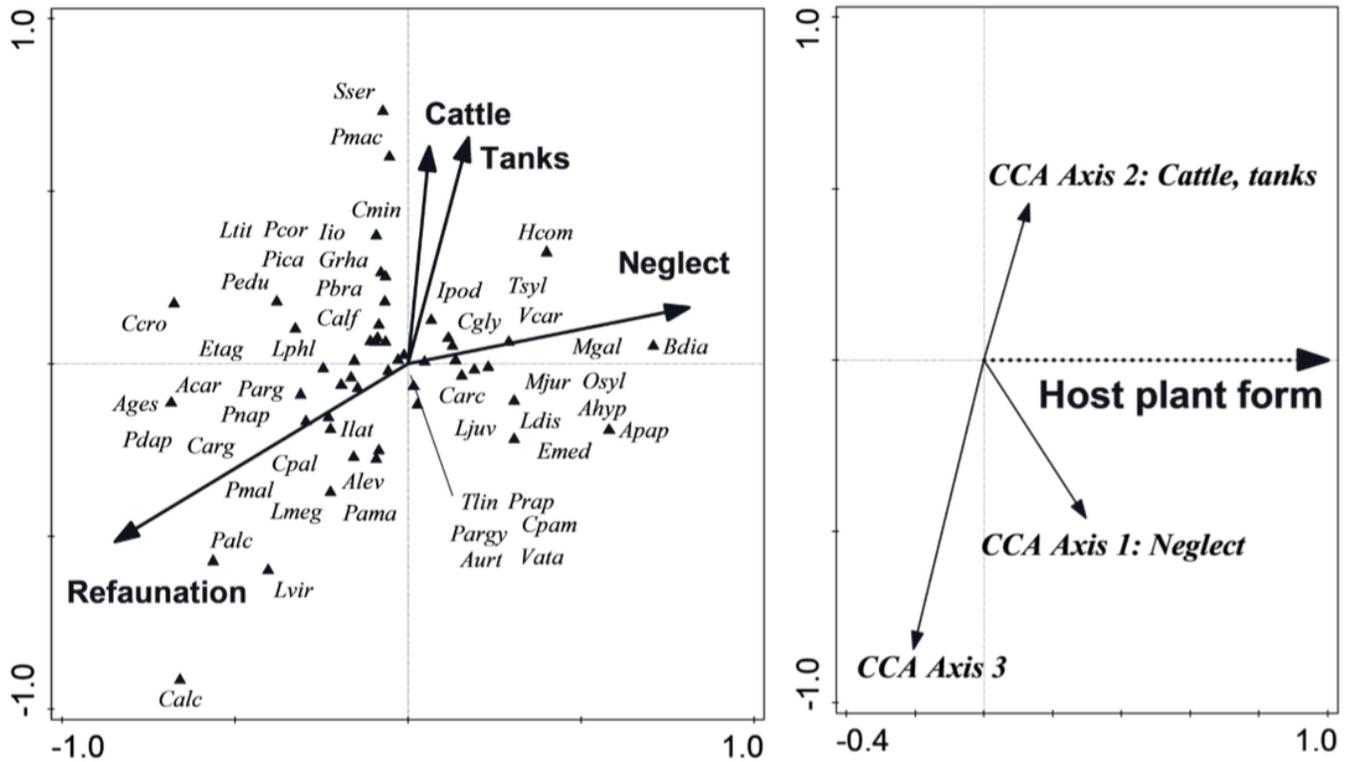


Figure 4

Ordination analysis of large ungulates refaunation effects on butterfly assemblages. Left: CCA biplot relating the current (2016–19) butterfly species composition at monitored plots in the Milovice former military training area to refaunation; model after inclusion of covariables (\sim refaunation +tanks | factorial year +latitude; see Table 4 for the CCA model parameters). Right: RDA biplot relating ordination scores of the model to the butterfly species life history traits. In this model, Host plant form was the only trait selected by a forward selection (eigenvalue 0.049, adjusted explained variation 3.3%, Monte Carlo test $F = 3.0$, $P = 0.039$).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Appendix1.xlsx](#)
- [Appendix2.xlsx](#)
- [Appendix3.xlsx](#)
- [Appendix4.xlsx](#)