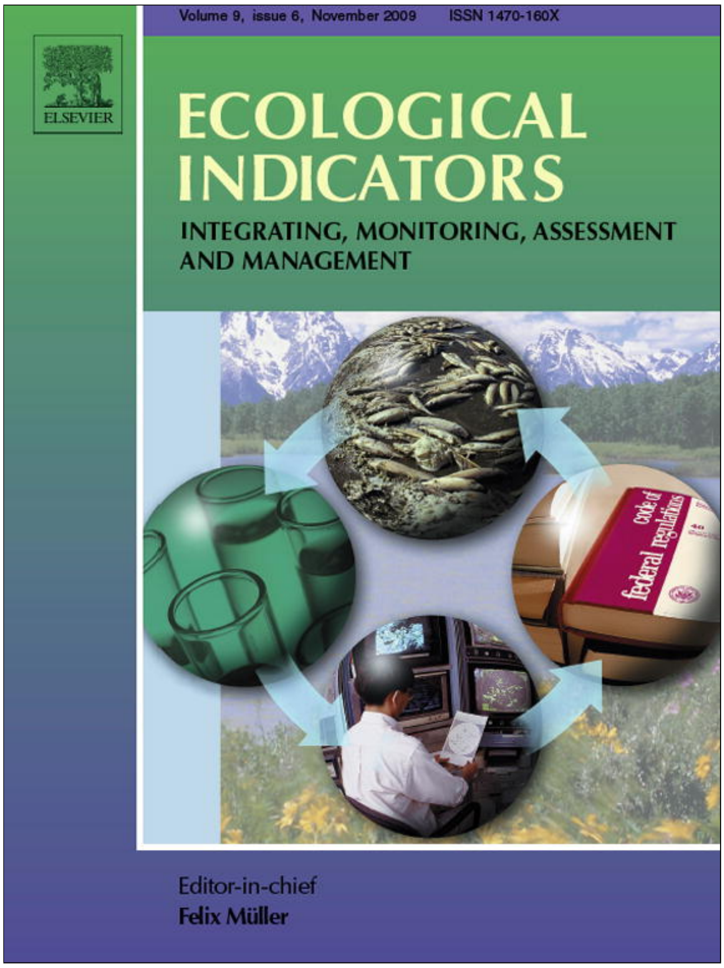
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The Large Blue butterfly, *Phengaris [Maculinea] arion*, as a conservation umbrella on a landscape scale: The case of the Czech Carpathians

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ABSTRACT

Conservation umbrellas are charismatic species, the conservation of which also conserves the high diversity of associated plants and animals. The Large Blue butterfly, *Phengaris [Maculinea] arion* (Lepidoptera, Lycaenidae), is a textbook example of a charismatic endangered invertebrate, intensively studied throughout Europe and protected by the EU Habitat Directive. While surveying *P. arion* at the westernmost outskirts of the Carpathians (Javorniky and Vsetinske Mts.), within a stronghold of the species in the Czech Republic, we asked whether occupied sites differed from unoccupied ones in the composition of vascular plants and butterfly assemblages. The occupied sites ($n = 65$) were small pastures, including abandoned ones, with S to W exposure, located on rugged terrain and displaying a high microtopographic heterogeneity; the unoccupied sites ($n = 101$) were typically mown or intensively grazed. The vegetation of occupied sites was characteristic for non-intensive submountain pasture, butterfly assemblages were species richer, contained more specialised species, and significantly higher proportion of red-listed species. *P. arion* thus may act as an umbrella for a high number of species associated with traditional land use in the study area and elsewhere. Its survival will depend on the continuation of small-scale land use varying in space and time, and can be threatened by uniformisation of management, even if practised under the guise of agri-environmental payments.

1. Introduction

Because conservation resources are limited and conservation success depends on acceptance of conservation goals by the general public, much of our efforts are focused on a few charismatic species. This finds justification in the concept of umbrella species, the conservation of which should provide for the needs of innumerable species sharing habitat requirements with the umbrellas (Simberloff, 1998). Despite its intuitive appeal, this approach remain little tested and it is often barely known if conserving charismatic umbrellas indeed helps the conservation of non-target species (Caro, 2003; Bifolchi and Lode, 2005; Rowland et al., 2006).

The Large Blue butterfly, *Phengaris arion* (Linnaeus, 1758) (Lepidoptera: Lycaenidae) is a textbook example of a charismatic invertebrate. It is famous for an intricate predatory relationship with ants (Thomas, 1995a; Als et al., 2004; Fric et al., 2007) and has been intensively studied from ecological and evolutionary points of view (e.g., Fiedler, 1998; Thomas, 2002; Pech et al., 2004; Mouquet et al., 2005; Settele et al., 2005; Pecsenye et al., 2007). The interest initiated after the then-enigmatic extinction of native British populations in late 1970s (Thomas, 1980), caused by cessation of traditional sheep grazing at their sites. Restoring that land use allowed reintroduction of the species to Britain, a remarkable success story of European insect conservation (Thomas, 1995a,b; Simcox et al., 2005; Fox et al., 2006). In the meantime, populations of the butterfly deteriorated on the European mainland as well due to habitat loss triggered by agricultural intensification or land abandonment. The butterfly is endangered all over Europe at present (van Swaay and Warren, 1999) and is protected by the EU Habitat Directive [herein HD]. As a species associated with traditional cultural landscapes, *P. arion* can be safeguarded only by preserving traditional management practices (Mouquet et al., 2005; Simcox et al., 2005).

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Here we report on patterns of landscape-scale co-occurrence of *P. arion* with plants and other butterflies of traditionally used grasslands (pastures and hay meadows) at the westernmost slopes of the Carpathian chain in the Czech Republic. We specifically ask first, which habitat features differentiate the occupied and unoccupied grasslands, and thus predict the occurrence of *P. arion*. Second, we compare the vegetation composition at occupied and unoccupied sites, and third, we compare quantitative records of co-occurring butterflies, documenting that *P. arion* grasslands indeed host higher-quality plants and butterfly assemblages.

2. Methods

Throughout the paper, butterfly (Papilionoidea + Hesperioidea) and burnet moth (Zygaenidae) nomenclature follows Lastuvka (1998) and Fric et al. (2007), vascular plants nomenclature follows Kubat et al. (2002) and listing of endangered species follows Vrabec et al. (2005).

2.1. Study system

The axis of the study area is the Becva River, separating two rather low mountain chains, the Vsetinske Mts. to the north and the Javorniky Mts. to the south (maximum altitudes 1024 and 1071 m, respectively) (Fig. 1). The bedrock is Carpathian flysch. Systematic exploitation of the region begun relatively lately in the Middle Ages. It relied on sheep grazing on pastures established by woodland clearance and gave rise to a scattered pattern of settlement, with individual households surrounded by mosaics of hay meadows, pastures, tiny arable fields, orchards, and remnant woods. The sheep-based economy has receded since the early 20th century, triggering reforestation of the mountains, so that forests now cover ca. 60% of the region. Still, remnants of the traditional land use were preserved even during the communist-era land consolidation, as the authorities tended to ignore farmers living in remote mountain valleys. At present, few people tend sheep as their main source of livelihood, but many keep a few animals as an additional source of income in small lots near their houses. The remote valleys thus represent the last Czech stronghold for many endangered plant and animal taxa, such as orchids (Pavelka and Trezner, 2001) and the *P. arion* butterfly.

This butterfly used to be widespread across the country until the mid-20th century. It has subsequently declined and currently inhabits just 12 atlas grid squares, or 1.8% of the Czech Republic total of 675 squares (Benes et al., 2002; and unpublished data). It is single-brooded, with adult flight in July in the mountains. Females lay eggs on flowers of *Thymus* spp. and *Origanum* spp. Larvae first feed on developing seeds, then fall to the ground where they are adopted by *Myrmica* ants. They then feed as predators of ant broods, overwinter in ant nests and emerge in summer of the next year (e.g., Thomas, 1995b; Mouquet et al., 2005; Sielezniew and Stankiewicz, 2008).

2.2. Data collecting and explanatory variables

In 2005, we carried out a *pilot survey* of *P. arion* colonies, systematically surveying all grasslands, except for alluvial ones, in valleys of the Becva River and its tributaries. Six participating persons covered approximately16 km^2 of grasslands during *P. arion* flight period (Fig. 1).

A *detailed study*, analysed in this paper, was carried out in 2006. During the *P. arion* flight period, between July 4 and July 28, we visited 166 individual grassland sites within a sub-area containing the highest density of *P. arion* colonies (Fig. 1). The sites comprised a wide variety of management types, from recently abandoned pastures and meadows through active pastures to improved hay meadows. Their areas ranged from 0.04 to 3.1 ha (mean: 0.46, median 0.3 ha) and they were all distinguished from other such grasslands either by barriers such as hedgerows, or by distinct land use.

Each site was visited by two persons, a botanist and lepidopterist. The lepidopterist visited each site just once, always between 9:30 and 16:30 h, CE Summer Time, and in weather suitable for butterflies (temperature at least 20 °C, none to mild wind). Duration of the visits scaled with the site area: 10 min for <0.25 ha, 20 min for 0.25–1 ha,

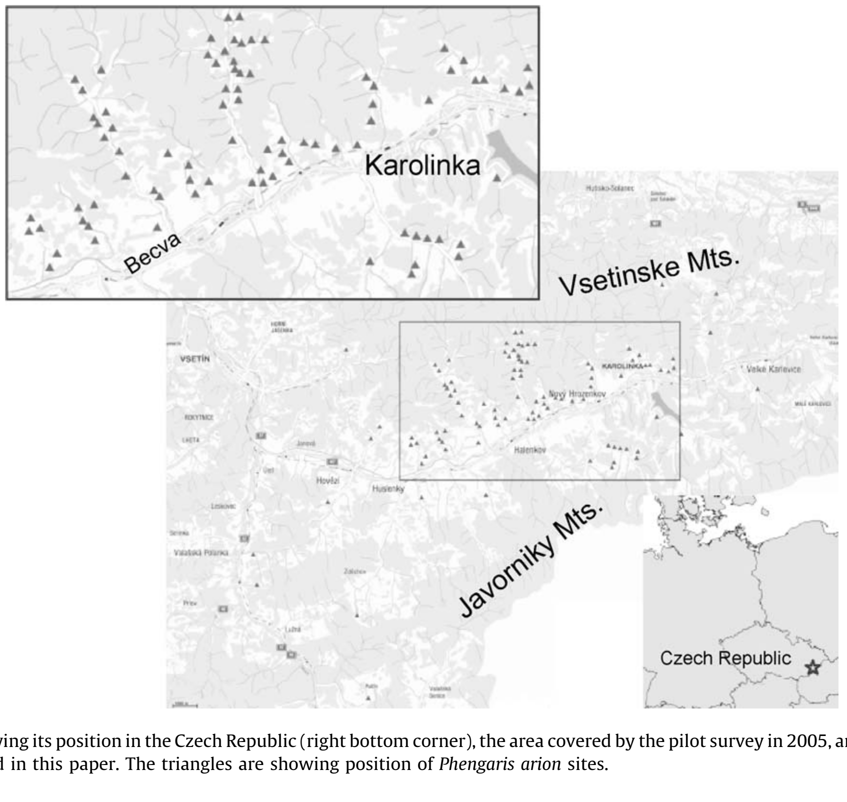

Fig. 1. Map of the study area, showing its position in the Czech Republic (right bottom corner), the area covered by the pilot survey in 2005, and the subset area selected for the detailed survey in 2006, analysed in this paper. The triangles are showing position of *Phengaris arion* sites.

30 min for >1 ha. Each site was drawn to map and systematically surveyed for butterflies by a zigzagging walk. For *P. arion* adults, exact numbers of individuals seen were recorded. All other observed species of butterflies and burnet moths were recorded using a semiquantitative abundance scale (1 individual, 2 individuals, <5, <10, <20, <100, <200, above 200 individuals). The pairs of sibling species *Colias alfacariensis*—*C. hyale*, *Leptidea sinapis*—*L. reali* and *Zygaena minos*—*Z. purpuralis* were treated as compound taxa. Additional information recorded were time of day (closest hour), wind intensity (0–3 scale), sunshine (from 1, full sun, to 3, overcast), and nectar supply (0–3 scale).

Vegetation was always sampled prior to the first cut of hay meadows. The botanist zigzagged each site, noting down all vascular plant species seen. Time spent at each site again scaled with area, but was extended by 50% compared to the time spent by butterfly recording (<0.25 ha: 20 min, 0.25–1 ha: 30 min, >1 ha: 45 min). Immediately after the zigzag walk, all species recorded were indexed by semiquantitative abundances, using the scale: 1, <1% of total cover; 2, 1–10%; 3, 10–50%; 4, >50%.

Further variables describing each patch were latitude, longitude and altitude (herein Lat., Long. and Alt.); area; the distance to the closest occupied patch; and the detailed predictors listed in Table 1. They were recorded directly in the field, except for information on management (obtained directly from land owners), area, and inclination (the latter two read from 1: 10 000 maps).

2.3. Analyses

2.3.1. Potentially confounding covariables

The composition of butterfly records depends on such circumstances as time of day, momentary nectar supply or weather (e.g., Wikström et al., 2009), and the presence of individual species depends on proximity to other occupied sites (e.g., Krauss et al., 2004; Ockinger and Smith, 2006). We statistically controlled for possible effects of these conditions by treating them as covariables describing: (i) *visit circumstances*, i.e. time of day, nectar availability and weather; (ii) *geography*, i.e. geographic coordinates including altitude; (iii) *geometry*, i.e. area and distance to the closest colony; and (iv) *combined covariables*, linear combinations selected from (i)–(iii).

2.3.2. Patch suitability

Expecting complex intercorrelation structure among predictors, we used the principal component analysis (PCA) to extract main directions of variation in the high number of variables. This was done in CANOCO v. 4.0 (Leps and Smilauer, 2003), using centering and standardisation of data.

To assess the relationships between *P. arion* and ordination results, we mapped the presence and abundance of the butterfly onto ordination diagrams. We used CanoDraw (© Petr Smilauer) that uses either generalised linear (GLM) or generalised additive (GAM) algorithms. Using logit-link for presence and log-link for abundance, we selected the most parsimonious method for each individual trial according to the Akaike information criterion.

2.3.3. Species composition of vegetation

We used redundancy analysis (RDA), a linear constrained ordination method, to relate the species composition of vegetation to *P. arion* presence and abundance. *Thymus pulegioides* and *Origanum vulgare*, host plants of the butterfly likely influencing its distribution, were set as 'supplementary species', a CANOCO option that visualises the species, but does not consider their effect in ordinations. As in the previous case, we computed raw models first, and then series of models controlled for *visit*, *geography*, *geometry*, and *combined* covariables.

2.3.4. Butterfly species richness

We used the *t*-test for independent samples and Spearman's rank correlation to compare numbers of butterfly species, *P. arion* excluded, between *P. arion* occupied and unoccupied sites. Because outcomes of such comparisons could be influenced by confounding covariables, we next constructed regression models that tested for the significance of *P. arion* presence/abundance on variation residual after inclusion of covariables to the regressions. We did so in S-plus, v. 4.0 (MathSoft, 2000), using GLMs with expected binomial (presence) and Poisson's (abundance) distribution of errors. We used backward stepwise term deletion procedures, selecting from all possible *visit*, *geography*, *geometry* and *combined* covariables, until we obtained minimal adequate models, in which all variables were significant and different one from another. We then added the variable of interest to the model and tested if the resulting model differed significantly from the model without this variable.

2.3.5. Butterfly species composition

We used RDA to relate butterflies seen per site, *P. arion* excluded, to the presence and abundance of *P. arion*. Confounding effects of *visit*, *geography*, *geometry* and *combined* covariables were again controlled for in partial ordinations. We used χ^2 test to compare the numbers of endangered species among butterflies positively and negatively associated with *P. arion*, using positive/negative species ordination scores from the presence/absence RDA.

Table 1
Site predictors, used for the PCA analyses of occupancy of individual grassland sites by the *Phengaris arion* butterfly.

Variable name	Type	Description
Character	Factor, 3 states	Hay meadow, Pasture, Wasteland
Management	Factor, 7 states	Intensively mown (>1 cuts per year), extensively mown (1 cut per year or less), improved sheep pasture, improved cattle pasture, non-improved pasture (sheep or mixed herd), abandoned (>2 seasons)[a], afforested (<5 years)
Host plant	Ranked	Abundance of host plants, ranked on 0–3 cover scale. See Section 2.2
Sward density	Ranked	1 = sparse, 2 = intermediate, 3 = dense.
Sward height	Numeric	Five randomly placed measurements scattered across the patch (always measured before mowing at hay meadows)
Sward heterogeneity	Ranked	1–3 scale, 1 being homogeneous and neat, 3 being very rough
Cover of vegetation strata	4 numeric variables	Moss, herb, shrubs, trees. In per cent of total area
Perimeter	9 numeric variables	Conifers, Deciduous, Banks with shrubs, Wasteland, Household, Grassland, Arable, Orchard, Road. In per cent of patch perimeter
Inclination	Ranked	Using the 1–5 system, in which 5 denotes southwestern, 1 denotes northeastern, and 3 denotes no inclination
Slope	Numeric	Number of level lines, read from 1: 10 000 maps

[a] In case that a grassland was abandoned for less than two seasons, we inquired owners for previous management.

Table 2
PCA analysis of predictors of the 166 grassland sites, both occupied and unoccupied by *P. arion* butterfly, and subsequent mapping of *P. arion* presence and abundance onto the PCA models. The mapping proceeded using either generalised linear models (GLM) or generalised additive models (GAM), and each situation was modelled using both linear (-L) or quadratic (-Q) response, selecting among competing models using to the Akaike information criterion.

Model	PCA of site predictors						Mapping *P. arion* onto the PCA ordination					
	Eig 1	*Eig 2*	*Eig 3*	*Eig 4*	Var. total	Var. model	Fitting of	Using	d.f.	% fit	*F*	*P*
No covariables	0.133	0.115	0.066	0.062	1.00	0.376	Presence	GLM-Q	4, 161	35.8	24.38	****
							Abundance	GLM-Q	4, 161	37.0	17.15	****
Visit covariables	0.115	0.081	0.056	0.046	0.92	0.352	Presence	GAM-Q	4, 161	10.1	5.62	**
							Abundance	GLM-L	2, 163	8.5	5.04	**
Geography covariables	0.107	0.091	0.053	0.046	0.88	0.383	Presence	GLM-Q	4, 161	34.6	22.80	****
							Abundance	GLM-Q	4, 161	37.4	17.82	****
Geometry covariables	0.119	0.094	0.058	0.048	0.97	0.340	Presence	GLM-Q	4, 161	23.8	14.63	****
							Abundance	GLM-Q	4, 161	24.2	9.17	****

F-test of GAM/GLM fit to the data.
** $P < 0.01$.
**** $P < 0.0001$.

3. Results

3.1. General

We detected 94 *P. arion* colonies during the *pilot survey* (2005), covering less than 1% of total area of grasslands in the surveyed region. During the 2006 *detailed survey*, we detected *P. arion* on 65 out of 166 sites visited (39.2%). The total number of *P. arion* records was 217. The vegetation data consisted of 128 vascular plant species (Appendix 1). In addition to *P. arion*, we recorded a further 62 butterfly and 10 burnet moth species, in, roughly, 24 000 individuals (Appendix 2). Thirteen of these species (17.8% of the species number) are red-listed in the Czech Republic.

Grasslands hosting *P. arion* colonies had mean sward height 46 cm (S.D. = 16 cm, range 10–100 cm). We observed a total of 13 egg-laying events in the two study years combined, 11 on *Thymus pulegioides* (mean height of egg placement: 12 cm, S.D. = 5.6) and two on *Origanum vulgare* (mean height 30 cm, S.D. = 7.1).

3.2. Patch suitability

The PCA of patch predictors produced a model explaining 37.6% of variation (Table 2, Fig. 2). The main gradient directed from uniformly mown meadows with dense sward, often located on flat terrains, having a low cover of *P. arion* host plants and being surrounded by arable fields or mown grasslands, towards either grazed or abandoned grasslands having S or SW inclination, heterogeneous surface, high cover of *P. arion* host plants, and a representation of woody structures along their circumference. The second ordination axis separated abandoned grasslands, often with a high sward and containing some shrubs, from actively used low-sward pastures. The partial models controlled for *visit*, *geography* and *geometry* (Table 2) all returned essentially identical patterns, although the amounts of variation explicable to predictors slightly decreased.

Mapping of *P. arion* onto the ordinations (Table 2) revealed its association with high scores at the first ordination axis, or a preference for grasslands on S to SW oriented, often steep slopes, with high sward heterogeneity, high host plants cover, and presence of some shrubs. The highest predicted values, however, pointed towards abandoned, rather than actively used pastures. They also revealed a positive influence of wind-sheltering woody structures (Fig. 2). Comparing models for presence and abundance (figures not shown) also revealed that the highest *P. arion* abundances were recorded at grasslands with high nectar and some representation of shrubs; i.e., at sites not grazed too intensively or left temporarily fallow.

3.3. Vegetation

Grasslands hosting *P. arion* differed from unoccupied ones in the species composition of vegetation (Table 3, Fig. 3). The former hosted a high representation of characteristic herbs and grasses of warm and flower-rich pastures, such as *Briza media*, *Carlina acaulis* or *Anthoxanthum odoratum*. The latter were characterised by either tall, tussocky grasses (*Dactylis glomerata*), or competitively strong nitrophilous forbs (*Arctium minus*, *Heracleum sphondylium*). These patterns applied also to tests with *P. arion* abundance, and to all tests controlled for potentially confounding covariables (Table 3).

3.4. Butterfly richness and composition

Sites with *P. arion* hosted significantly more other butterfly species (means 13.7 vs. 8.5, $t_{164} = 6.11$, $P < 0.001$) and the same applied for *P. arion* abundance (Spearman rank, $r_s = 0.21$, $t_{166} = 2.71$, $P < 0.01$). Both relationships hold even after excluding sites with <10 recorded butterfly species from the analyses (means 15.7 and 13.4, $t_{92} = 2.84$, $P < 0.01$; Spearman's $r = 0.27$, $t_{92} = 2.71$,

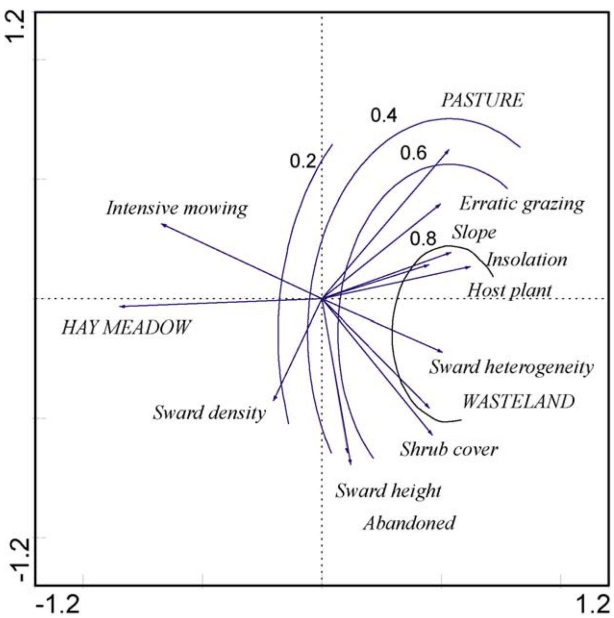

Fig. 2. PCA ordination biplot used to extract patterns from predictors of individual sites surveyed for *P. arion*: analysis not considering potentially confounding covariables. See Table 1 for the predictors and Table 2 for numeric results. The probability of *presence* of *P. arion* was subsequently mapped onto the ordination, using quadratic-level GLM, and is shown as the isolines with probability values.

Table 3
Results of RDA analyses, comparing the species composition of vegetation of sites occupied and unoccupied by the *P. arion* butterfly. Models are described as *response ~ predictor|covariable*, *Eig 1–Eig 4* denote eigenvalues of four separate ordination axis, *F* and *P* values refer to Monte-Carlo tests (999 permutations).

Model	*Eig 1*	*Eig 2*	*Eig 3*	*Eig 4*	Var. total	Var. model	*F*	*P*
~Presence	0.048	0.121	0.077	0.057	1.000	0.048	8.25	***
~Presence|visit[a]	0.018	0.077	0.062	0.050	0.912	0.020	3.23	***
~Presence|geography[b]	0.054	0.075	0.067	0.046	0.955	0.057	9.60	***
~Presence|geometry[c]	0.032	0.084	0.063	0.051	0.962	0.033	5.61	***
~Presence|combined[d]	0.012	0.072	0.051	0.038	0.841	0.014	2.19	***
~Abundance	0.033	0.101	0.069	0.054	1.000	0.033	5.54	***
~Abundance|visit[a]	0.012	0.079	0.064	0.050	0.912	0.013	2.21	**
~Abundance|geography[b]	0.035	0.088	0.068	0.048	0.955	0.037	6.08	***
~Abundance|geometry[c]	0.022	0.092	0.064	0.052	0.962	0.023	3.80	***
~Abundance|combined[d]	0.008	0.073	0.052	0.038	0.841	0.010	4.83	***

Structure of covariate models, obtained by forward-selection from potentially confounding covariates.
[a] Day + Day^2 + Hour + Wind.
[b] Long + Lat × Alt + Alt^2.
[c] Area + Distance.
[d] Long + Lat + Alt^2 + Lat × Alt + Day + Day^2 + Hour + Wind + Area + Distance.

$P < 0.01$). Table 4 documents that they sustained controlling for effects of confounding covariables.

The ordinations (Fig. 4) revealed a highly significant difference between sites with and without *P. arion*, even if controlled for potentially confounding covariables (Table 5). Multiple specialised species of warm seminatural grasslands (*Argynnis niobe*, *Zygaena angelicae*), mesic grasslands (*Lycaena hippothoe*, *Cyaniris semiargus*) and scrubland (*Satyrium accaciae*) were associated with *P. arion*, whereas widespread, ubiquitous species (e.g. *Pieris rapae*, *Aglais urticae*) displayed negative associations. Endangered butterflies were represented by thirteen, and three species among butterflies positively and negatively associated with *P. arion* ($\chi^2_{1d.f.} = 4.38$, $P = 0.036$).

4. Discussion

4.1. *P. arion* as umbrella species

On westernmost slopes of the Carpathians, *P. arion* inhabits remnants of traditional pastures, situated on warm and steep slopes and characterised by heterogeneous relief and vegetation. The occupied sites contain a high proportion of plants associated with seminatural pastures and host richer assemblages of butterflies, including threatened species, than unoccupied sites. Conserving localities of *P. arion*, mandated by the EU legislation, thus conserves both the sensitive vegetation and the species-rich butterfly assemblages of the submountain pastures.

Our sampling of co-occurring butterflies comprised just one visit per site during *P. arion* flight period. It missed spring and late-summer phenological aspects, which would be a serious limitation in lowlands, but not in the mountain region, where the flight period of *P. arion* coincides with the flight of a majority of grassland butterflies. We missed a few early-season species, such as *Anthocharis cardamines* (Linnaeus, 1758) and *Pyrgus malvae* (Linnaeus, 1758), but these species are still widespread in the Czech Republic and of little conservation concern (Benes et al., 2002), whereas the majority of late-season butterflies occurring in the region are late broods of common multivoltine species (cf. Cizek et al., 2006). Hence, our approach was sufficiently robust for comparison among the sites, and our finding that sites hosting *P. arion* hosted more valuable plant and butterfly assemblages sustained controls for this seasonal effect, as well as for other potential sources of confounding variation.

The finding that conserving *P. arion* sites conserves numerous non-target species is an important one, given that listings of endangered species and subsequent allocation of conservation resources are essentially policy decisions, affected by numerous non-biological considerations (e.g., Stinchcombe et al., 2002; Rawls and Laband, 2004). There are much more endangered species in Europe than the handful of HD protected ones (see, for butterflies, van Swaay and Warren, 1999) and the original selection of HD species preceded the availability of reliable background data for the whole continent. As a result, HD not always protects the most deserving species, which is illustrated by the HD-protected butterfly *Lycaena dispar* (Haworth, 1803), a species endangered in NW Europe but expanding and safe in Central and Eastern regions (Pullin et al., 1998; Konvicka et al., 2003). No such reservation applies for the case of Carpathian *P. arion*, which is both endangered and performing as a suitable indicator of site quality for other organisms.

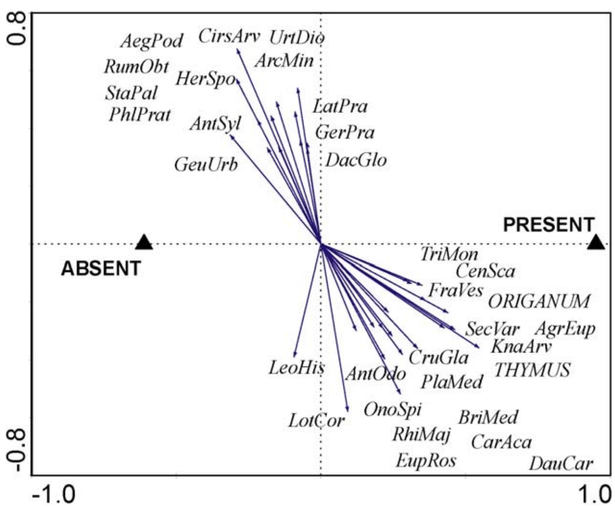

Fig. 3. RDA ordination biplot showing the differences in species composition of vegetation between sites occupied and unoccupied by *P. arion*. Only a selection of plant species with the highest fit to ordination is shown. Host plants of the butterfly, *Thymus pulegioides* and *Origanum vulgare* (*THYMUS* and *ORIGANUM* at the plot), were treated as supplementary species in the analysis and did not influence its results. Key to species names. Diagram upper sector: *AegPod—Aegopodium podagraria*; *ArcMin—Arctium minus*; *CirArv—Cirsium arvense*; *DacGlo—Dactylis glomerata*; *GeuUrb—Geum urbanum*; *GerPra—Geranium pratense*; *HerSpo—Heracleum sphondylium*; *LatPra—Lathyrus pratensis*; *AntSyl—Anthriscus sylvestris*; *PhlPrat—Phleum pratense*; *RumObt—Rumex obtusifolius*; *StaPal—Stachys palustris*. Lower sector: *AgrEup—Agrimonia eupatoria*; *AntOdo—Anthoxanthum odoratum*; *BriMed—Briza media*; *CarAca—Carlina acaulis*; *CenSca—Centaurea scabiosa*; *CruGla—Cruciata glabra*; *DauCar—Daucus carota*; *EupRos—Euphrasia rostkoviana*; *FraVes—Fragaria vesca*; *LeoHis—Leontodon hispidus*; *LotCor—Lotus corniculatus*; *KnaArv—Knautia arvensis*; *OnoSpi—Ononis spinosa*; *PlaMed—Plantago media*; *RhiMaj—Rhinanthus major*; *SecVar—Securigera varia*; *TriMon—Trifolium montanum*.

Table 4
GLM-models, used to test if sites occupied or not-occupied by *P. arion* differed in numbers of other butterfly species, after considering potentially confounding effects of *visit*, *geography* and *geometry* covariables. The covariate models were constructed via the backward elimination procedure. Separate tests based on mere *P. arion* presence and *P. arion* abundance are presented.

Model, covariates	Model internal structure	d.f.	Deviance	*AIC*	*P. arion* effect
All sites					
Null		165	5757.3	5827.1	
Visit covariables	+Day + Nectar − Wind	3, 162	4258.6	5809.9	
	+Presence	4, 161	3940.0	4184.7	$F_{(1, 161)} = 13.02^{***}$
	+Abundance	4, 161	3832.7	4070.7	$F_{(1, 161)} = 17.89^{****}$
Geography covariables	+Lat + Long + Alt^2 + Lat × Long + Long × Alt	6, 159	5176.2	5530.6	
	+Presence	7, 158	4000.2	4405.2	$F_{(1, 158)} = 46.45^{****}$
	+Abundance	7, 158	4240.9	4670.3	$F_{(1, 158)} = 34.85^{****}$
Geometry covariables	+Area + Distance + Area × Distance	3, 162	4930.1	5147.6	
	+Presence	4, 161	4378.2	4650.2	$F_{(1, 161)} = 20.29^{****}$
	+Abundance	4, 161	4480.1	4758.4	$F_{(1, 161)} = 16.17^{****}$
Combined covariables	+Day + Nectar + Sun − Wind + Alt + Long + Alt^2 + Alt × Long + Lat × Alt + Area + Distance + Area × Distance	13, 152	3513.5	4160.7	
	+Presence	14, 151	3308.8	3966.2	$F_{(1, 151)} = 9.34^{***}$
	+Abundance	14, 151	3243.4	3887.7	$F_{(1, 151)} = 12.58^{****}$
Sites with >10 species					
Null		84	1353.0	1385.2	
Visit covariables	+Day + Nectar − Wind	3, 81	1233.1	1354.9	
	+Presence	4, 80	1131.7	1273.2	$F_{(1, 80)} = 7.17^{**}$
	+Abundance	4, 80	1163.2	1308.6	$F_{(1, 80)} = 4.81^{*}$
Geography covariables	−Alt	1, 83	1302.4	1365.2	
	+Presence	2, 82	1165.3	1250.6	$F_{(1, 82)} = 9.65^{***}$
	+Abundance	2, 82	1223.4	1313.0	$F_{(1, 82)} = 5.30^{*}$
Geometry covariables	n.a.				
Combined covariables	Nectar + Lat + Long + Alt + Lat × Long + Lat × Alt + Area + Distance	8, 76	1040.3	3504.1	
	+Presence	9, 75	886.6	1123.0	$F_{(1, 76)} = 13.00^{***}$
	+Abundance	9, 75	965.4	1223.0	$F_{(1, 76)} = 5.82^{*}$

The positive association between *P. arion* and other endangered insects appears to apply outside of the study region as well. In Britain, Randle et al. (2005) investigates a possible tritrophic relationship between *Myrmica* ants hosting *P. arion*, violets (*Viola* spp.) and the endangered, violet-feeding butterfly, *Boloria euphrosyne* (Linnaeus, 1758). The ants often carry elaiosome-bearing violet seeds to their nests, the seeds tend to germinate more readily if a nest is deserted, sometimes due to depredation by *P. arion* larvae, and *B. euphrosyne* prefers violets growing on deserted anthills. The activity of *P. arion* thus indirectly supports another butterfly. Several other endangered insects prefer sites managed for *P. arion* in England (Schonrogge et al., 2002; Thomas et al., 2005) and in karstic regions at the Hungary-Slovakia border (Varga et al., 2005).

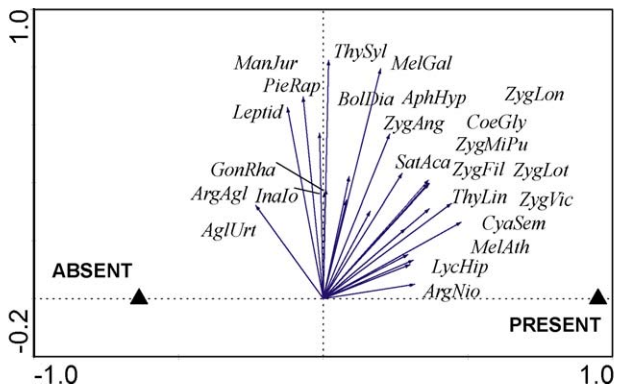

Fig. 4. RDA ordination biplot showing the differences of butterfly assemblages between grasslands occupied and unoccupied by *P. arion*. Key to species names. *AglUrt—Aglais urticae*; *AphHyp—Aphantopus hyperanthus*; *ArgAgl—Argynnis aglaja*; *ArgNio—Argynnis niobe*; *BolDia—Boloria dia*; *CyaSem—Cyaniris semiargus*; *CoeGly—Coenonympha glycerion*; *GonRha—Gonepteryx rhamni*; *Leptid—Leptidea sinapis* and *Leptidea reali*; *LycHip—Lycaena hippothoe*; *ManJur—Maniola jurtina*; *MelAth—Melitaea athalia*; *MelGal—Melanargia galathea*; *PieRap—Pieris rapae*; *SatAca—Satyrium accaciae*; *ThyLin—Thymelicus lineola*; *ThySyl—Thymelicus sylvestris*; *ZygAng—Zygaena angelicae*; *ZygFil—Z. filipendulae*; *ZygLon—Zygaena lonicerae*; *ZygLot—Zygaena loti*; *ZygMiPu—Zygaena minos* and *Zygaena purpuralis*; *ZygVic—Zygaena viciae*.

Unlike Randle et al. (2005), we cannot provide a mechanistic explanation for the high diversity of *P. arion* sites. It seems that a majority of sensitive butterflies co-occur with *P. arion* not via a direct association, but through shared requirements for diverse vegetation and microtopography. The south-facing slopes attract thermophilous species, which are increasingly threatened in intensively farmed lowlands (e.g. *Polyommatus bellargus*, *Zygaena canriolica*) (Benes et al., 2002). Some co-occurring butterflies utilise patches of barren ground, such as sheep tracks (e.g., *Spialia sertorius*) (cf. Lepidopterologen Arbeitsgruppe, 1997). Coarser vegetation at less frequently grazed or temporarily abandoned sites supports such species as *Zygaena brizae*, a thistle-feeding specialist tending to disappear from sites with too tidy management (Zarzycki and Darrowski, 1986). A mechanism similar to that supporting *Boloria euphrosyne* in Britain might apply to *Argynnis niobe*, a violet-feeding butterfly critically endangered in Central Europe (cf. Benes et al., 2002; Reinhardt et al., 2007). Our preliminary observations indicate that its females preferentially oviposit near patches of barren soil, including anthills. Patches of barren ground are also used by the critically endangered cricket *Psophus stridulus* (Linnaeus, 1758) (Spitzer, 2007).

4.2. Management needs, threats, and prospects

Besides (sheep) pasture, the decisive factor behind the suitability of grasslands for *P. arion* is site heterogeneity, or presence of heterogeneous vegetation and some shrubs. The butterfly thrives in mosaics of pastures and temporarily abandoned "wastelands", while being practically absent from uniformly managed pieces of land, regardless of whether they are grazed or mown.

Table 5
RDA analyses comparing the species composition of butterflies at sites occupied and unoccupied by the *P. arion* butterfly. See Table 3 for more details on mode description and statistical tests.

Model	*Eig 1*	*Eig 2*	*Eig 3*	*Eig 4*	Var. total	Var. model	*F*	*P*
~Presence	0.049	0.288	0.093	0.068	1.000	0.049	8.24	***
~Presence|visit[a]	0.015	0.232	0.066	0.062	0.836	0.018	2.76	*
~Presence|geography[b]	0.057	0.233	0.079	0.065	0.908	0.063	10.43	***
~Presence|geometry[c]	0.035	0.262	0.093	0.067	0.957	0.037	6.03	***
~Presence|combined[d]	0.011	0.200	0.060	0.057	0.761	0.014	2.10	*
~Abundance	0.030	0.246	0.112	0.076	1.000	0.03	5.01	***
~Abundance|visit[a]	0.019	0.229	0.066	0.059	0.836	0.023	3.54	**
~Abundance|geography[b]	0.040	0.235	0.092	0.066	0.908	0.044	7.21	***
~Abundance|geometry[c]	0.025	0.261	0.101	0.069	0.957	0.026	4.22	***
~Abundance|combined[d]	0.012	0.199	0.060	0.056	0.761	0.016	2.41	*

Structure of covariate models, obtained by forward-selection from potentially confounding covariates.
[a] Day + Day^2 + Sun + Wind.
[b] Long + Long^2 + Alt^2 + Lat × Long + Long × Alt.
[c] Distance + Area × Distance.
[d] Day + Day^2 + Hour^2 + Sun + Wind + Long + Long^2 + Lat × Long + Long × Alt.

The preference for heterogeneity is explicable on both landscape and local scale. At the former, uniform management synchronises conditions among sites, synchronising, e.g., flowering of host plants, adult emergence dates, or larval pressures on the ant colonies. Entire metapopulations then become more vulnerable to regionally acting unfavourable developments, such as harsh weather (Hanski, 1999). In contrast, management varying among sites and in time, typical for traditional farming, desynchronises the population dynamics, allowing the recolonisation of temporarily vacant but suitable patches, and hence contributes to the resiliency of the entire system. Within sites, it must be kept in mind that any active management, although beneficial in the long-term, causes both direct mortality and temporarily depletes butterfly resources, such as nectar (Morris, 2000). Heterogeneous relief, and the presence of such structures as sheltering taller plants, reduce the possible negative effects of management actions, ensuring that more vital resources occur syntopically (Dennis et al., 2003; Fred et al., 2006) and providing a wider scope of alternatives, such as microsites with slightly differing microclimates, which can be vital in the ever-changing world (Davies et al., 2006).

The sward height at Czech *P. arion* sites was taller than reported, e.g., from Britain (Thomas, 1995a), in line with the observations that in warmer regions of Europe, the microclimate suitable for *P. arion* occurs under taller vegetation (Thomas et al., 1998; Thomas and Simcox, 2005). This preference explains why many occupied sites were abandoned pastures, including former pastures freshly afforested by spruce. The suitability of such sites is of course short-lived, each such abandoned site will become unsuitable in the longer term.

Survival of the *P. arion* stronghold thus depends on continuation of fine-scaled land use, with intensity of management, or temporary absence of it, varying among sites and years. The need for management heterogeneity is shared by countless invertebrates of traditional rural landscapes (Hendrickx et al., 2007; Rundlof et al., 2008), including butterflies closely related to *P. arion* (Johst et al., 2006; Drechsler et al., 2007), and homogenous site management is increasingly recognised as a negative force affecting grassland invertebrates (Benton et al., 2003; Davies et al., 2007; Konvicka et al., 2008).

The heterogeneity is currently maintained by scattered land holding patterns, local farmers wish to maintain the traditional landscape structure (unpublished interviews). The accession of the Czech Republic to European Union, however, brought forth new pressures towards landscape homogenisation. The EU Agri-environmental payments, purportedly aiming on preserving biodiversity, motivate the farmers either to hay harvest practised uniformly for multiple years, or for grazing with invariable stocking (Konvicka et al., 2008). Additional risks include such nuisances as the ban on domestic slaughters, which certainly does not motivate for continuation of traditional pastoralism. Perhaps the gravest threat are government-provided subsidies for afforestation, which reward farmers for planting trees at the most remote, rugged sites—exactly those preferred by *P. arion*. Indeed, 10.8% of occupied sites were recently fully or partially planted by spruce, and hence will be lost in the long run. Both the general policy and detailed provisions of agricultural payments need urgent reconsideration if they are to contribute to preserving the biodiversity of rural landscapes in the Czech Carpathians, and elsewhere across Europe (e.g., Cremene et al., 2005; Schmitt and Rakosy, 2007).

5. Conclusion

A dense system of colonies of the EU-protected butterfly *P. arion* inhabits the remote valleys of the NW Carpathians in the Czech Republic. The occupied sites host richer plant and butterfly diversity, rendering the butterfly a perfect umbrella for preserving traditionally used grasslands. The whole system depends on small-scaled, heterogeneous, and time-variable land use and is threatened by the currently applied system of agricultural and afforestation subsidies, which favour uniformity over diversification.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolind.2008.12.006.

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