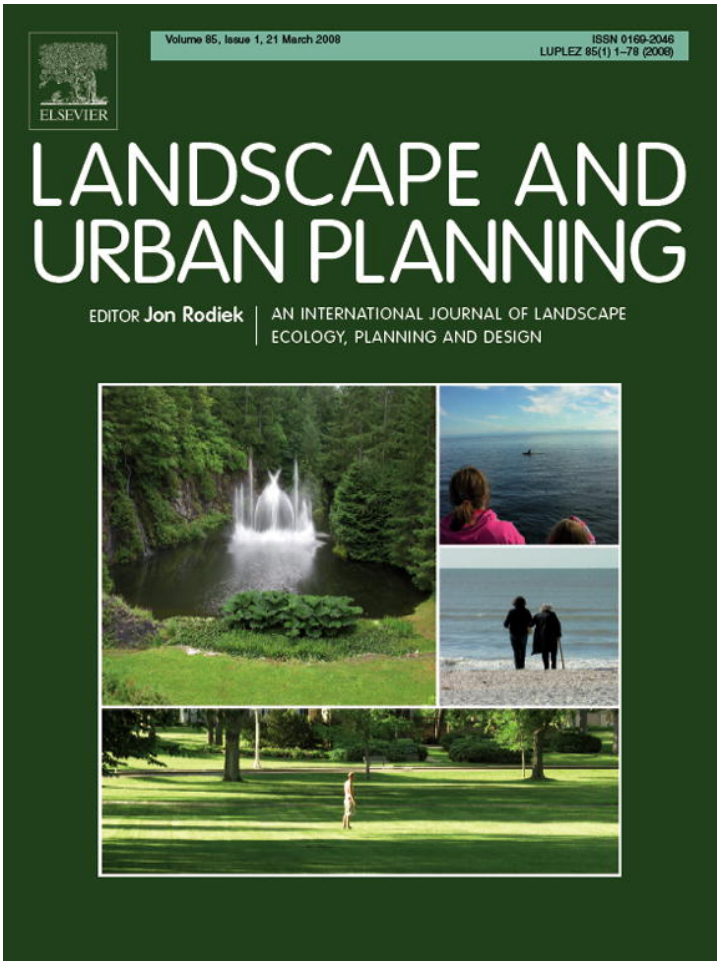
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Revisiting urban refuges: Changes of butterfly and burnet fauna in Prague reserves over three decades

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Abstract

We studied changes in the composition of butterfly and burnet fauna in 25 reserves of xeric grasslands within the city Prague, Czech Republic, based on a recent repetition of a survey conducted three decades ago. The past and recent survey detected 91 and 84 species, 12 species were lost and four were gained between the surveys. There was no significant change in mean numbers of species per reserve or in mean species incidences, even if the categories of the habitat association, mobility and body size were analysed separately. Contrary to these comparisons, ordination analyses indicated a significant shift in species composition in individual reserves. Species of short-sward xeric grasslands tended to be associated with the past survey, whereas species of taller grasslands and xeric scrub were associated with recent survey. These shifts were more prominent in large reserves with high proportion of natural (as opposed to urban) perimeter, connected with other reserves, having diverse topography and high plant and biotope richness. We interpret this by gradual successional changes which affect the reserves despite conservation management. Despite these changes, butterfly losses were lower than in comparable surveys recently conducted elsewhere in Central Europe, partly because major losses occurred long before the 1980s survey and partly owing to a high heterogeneity of the urban landscape surrounding the reserves.

Keywords: Butterfly conservation; Reserve design; Species loss; Urban ecology; Papilionoidea; Zygaenidae

1. Introduction

A purpose of establishing nature reserves is to provide safe havens for populations, species and biotic communities unable to survive in non-reserve lands. If a reserve is an isolated piece of land carved from originally much larger extent of a natural landscape, the species richness of the reserve should gradually diminish until reaching a new, lower equilibrium governed by reserve area and the spatial requirements of species present (Soule et al., 1992; Watling and Donnelly, 2006). Understanding this limitation, modern conservation hold that reserves should provide temporary refuges, where species can survive until a more hospitable management of entire landscapes is feasible (Sinclair et al., 1995; Rosenzweig, 2003; Samways, 2007).

In reality, reserves are only rarely completely isolated, because landscapes also contain habitats and resources (e.g., Blair, 1999; Dennis, 2004; Shepherd and Debinski, 2005). A notable exception might be urban reserves, surrounded by urbanised land uninhabitable for wild fauna and flora. Urban reserves might suffer faster losses of species than reserves surrounded by non-urban lands (Thompson and Jones, 1999; Er et al., 2005). Alternatively, urban areas may be spared the negative effects of intensive agriculture and forestry, because city dwellers prefer a recreation value of the land (DeStefano and DeGraaf, 2003). These societal preferences may even allow for the emergence of “new wilderness” in peripheral areas of large cities. Reserves imbedded within such landscapes thus can be relatively hospitable for plant and animal life, if compared with those located within intensively farmed rural areas (Hanski, 2005; McFrederick and LeBuhn, 2006).

There are more considerations rendering urban reserves important for global conservation efforts. Historically, cities often arose near prominent land forms, such as steep hills or

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major rivers and as a result, city locations are often species rich (Kuhn et al., 2004). The substantial parts of this original diversity could have been preserved by accidents of history, e.g., as royal parks or sacred grounds. Urban planers may set aside tracks of natural habitats for human enjoyment (Colding et al., 2006). Urban reserves are irreplaceable for conservation education of the general public (Miller and Hobbs, 2002). Their accessibility has promoted a long tradition of recording and hence a possibility to detect biodiversity changes (e.g., Chocholouskova and Pysek, 2003; Tait et al., 2005).

All these aspects apply to the reserve system of Prague, Czech Republic. It consists of 88 reserves with a total area of 2353 ha, covering a rich array of habitats from wetlands and ancient woodlands to calcareous and siliceous steppes. The reserves host remarkable biodiversity: for instance, a half of the higher plants of Czech flora occur within Prague (Sprynar and Marek, 2001). Still, their scientific potential remains weakly explored. To date, no study has compared past and present diversity of a group of organisms inhabiting the reserves, and thus, in essence, the efficiency of the reserve system.

We performed such a comparison for the model group of butterflies (Lepidoptera: Papilionoidea + Hesperioidea) and burnet moths (Zygaenidae). We built on an inventory conducted in the reserves three decades ago and compare the results with the current situation. Butterflies and burnets are severely declining across Europe (van Swaay and Warren, 1999) and Prague represents their diversity hot spot within the Czech Republic (Benes et al., 2002). Comparing the two surveys allows us to address the following questions. (i) Did species richness of the reserves decrease during the three decades? (ii) How did the changes, if any, manifest in the numbers of species per reserve and in species incidences, i.e., the numbers of reserves inhabited per species? (iii) Were some life history traits of individual species associated with particular species' gains and losses? (iv) Was there a detectable shift in species composition, in terms of identities of species inhabiting individual reserves? (v) Were the changes in species composition, if any, associated with the environmental characteristics of the reserves? By comparing these results with other regional studies of butterfly fauna in Central Europe, we also address the more general question of the relative contribution of urban reserves to conservation efforts.

2. Material and methods

2.1. Prague reserves

Prague reserves cover a wide array of biotopes of the topographically diverse and relatively warm Prazska kotlina region. Whereas woodland reserves prevail on flat plateaux to the south and east of the city, reserves of xeric grasslands prevail on the slopes of the Vltava River valley. All the reserves were established during the second half of the 20th century (the oldest one in 1964), but some enjoyed an earlier protection as attractive scenic sites. Practically all the grassland reserves were pastures in the past; they were unmanaged in the 1960s and 1970s, but after successional changes became apparent, management in form of scrub reduction, mowing and grazing was gradually introduced in the 1980s (Strejcek, 2004).

2.2. Butterfly and burnet surveys

Both butterflies and burnets are referred to as "butterflies" and the nomenclature follows Lastuvka (1998).

The *past survey* was conducted from 1984 until 1988 and subsequently published (Cila and Skyva, 1993a,b). A team of fifteen lepidopterists covered 48 reserves and 18 additional "green islets" not afforded protection. The surveys aimed to record as many species as possible, so that the visits always included all seasonal aspects and large reserves were visited more intensively than the smaller ones. However, the total number of visits varied among reserves and years. We selected 25 sites (21 reserves, four parks) for the comparison (Fig. 1). They all harboured xeric grasslands at the time of their establishment and hence represent a rather homogeneous subset of the 1980s surveyed sites which also included woodlands. A further rule for the selection of sites for the current study was to cover the entire variation of the available grasslands reserves in terms of area (mean: 22.0 ha ± 33.3 S.D., median: 7.32, range: 0.6–114.2), central/peripheral position within the city, bedrock type and isolation from other natural localities.

We carried out the *recent survey* in 2003 and 2004. We visited each reserve monthly from May to August in both years, totalling eight visits per reserve. During each visit, a recorder searched through the entire reserve, covering all the biotopes present and trying to locate as many species as possible. Approximately the

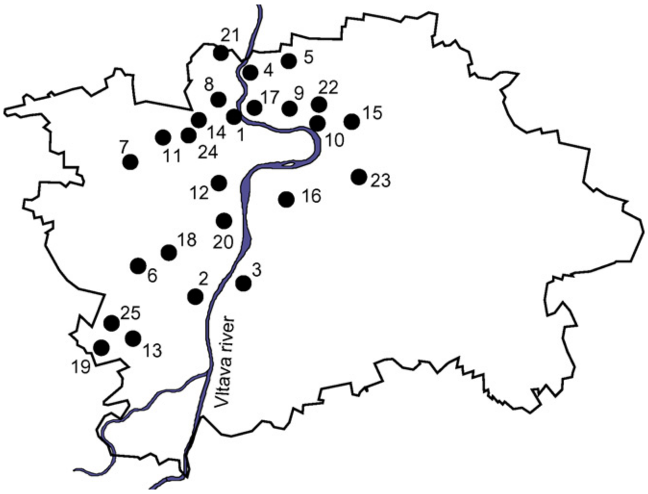

Fig. 1. Map of Prague, showing the positions of 25 reserves and parks covered by a comparison of past and present butterfly faunas. The numbers denote the following reserves: (1) Baba, 7.3 ha; (2) Barrandovske skaly, 11.6 ha; (3) Branicke skaly, 9.1 ha; (4) Bohnicke udoli, 4.6 ha; (5) Cimicke udoli, 11.2 ha; (6) Dalejsky profil, 22.8 ha; (7) Divoka Sarka, 25.4 ha; (8) Dolni Sarka, 6.2 ha, (9) Havranka, 4.2 ha; (10) Jablonka, 1.3 ha; (11) Jeneralka, 1.5 ha; (12) Lesopark na Petrine, 30.0 ha; (13) Lochkovsky profil, 39.1 ha; (14) Nad Mlynem, 4.0 ha; (15) Okrouhlik 0.6 ha; (16) Park na Karlove namesti 4.0 ha; (17) Podbabske skaly 0.8 ha; (18) Prokopske udoli, 101.5 ha; (19) Radotinske udoli, 103.3 ha; (20) Santoska – Pavi vrch, 20 ha; (21) Tiche udoli a Roztocky haj, 114.2 ha; (22) Trojska, 1.3 ha; (23) Zidovske pece, 6.2 ha; (24) Zlatnice, 3.3 ha; (25) Zmrzlik 16.4 ha.

same route was followed each time, varying in details in order to check places with seasonal concentrations of butterflies, such as patches of nectar plants. Duration of the visits scaled with reserve area (<1 ha: 30 min, <10 ha: 60 min, <100 ha: 90 min, above 100 ha: 180 min), the sequence of visits was randomised within months. The visits were limited to 10:00–16:00 (Central European summer time) and to suitable weather (over 17 °C, sunny, none to mild wind). For species pairs or groups not identifiable in field (*Colias hyale-alfacariensis*, *Plebeius idas-argyrognomon*, *Zygaena minos-purpuralis*, *Adscita* spp., *Jordanita* spp.), up to five individuals per visit were taken to the laboratory for genital preparation. *Leptidea sinapis* and *L. reali* are considered as one compound species, as the two were not distinguished in the past survey. Only presence/absence data, available for the past survey, are analysed here.

2.3. Species traits and reserve characteristics

Besides of species richness, we considered the numbers of endangered species (after Vrabec et al., 2005), species basic habitat associations (xerophilous, mesophilous and ubiquitous after Benes et al., 2002); their size, assessed as wing span and categorised as small (<40 mm), medium (40–57 mm) and large (57 mm) after Higgins and Riley (1970); and mobility (low, intermediate and highly mobile, based on merging the 1–3, 4–6 and 7–9 categories in Bink, 1992) (Appendix A). Selection of the characteristics assumes that changing conditions should cause changing representation of habitat specialists (Wenzel et al., 2006); smaller remnants of habitats should suffice for small but not for large species; and the representation of sedentary species should depend on conditions within the reserves, whereas large and mobile species may be more influenced by the broader landscape (Thomas, 2000).

External predictors of the reserves, being proved to affect their butterfly and plant species richness in the past survey (V. Jarosik and T. Kadlec, unpublished data), were used to explain changes in the butterfly fauna. These characteristics (Table 1) were chosen because large reserves support more species than small ones, while isolated reserves loose species faster than interconnected ones (area and connectivity in Table 1; Krauss et al., 2004). Altitudinal range, topographical aspect and biotope diversity were considered as measures of heterogeneity, increases of which are associated with increasing species richness (Weibull et al., 2000; Triantis et al., 2003). Plant richness was used because it directly affects the richness of plant-feeding herbivores (Hawkins and Porter, 2003). Forest cover was considered because butterflies reach the highest species richness at intermediate proportions of forest (most species avoid dense forests, but many require some woody vegetation to be present). Four variables in Table 1 describe the positions of reserves with respect to urban or natural biotopes at their perimeters (urban/natural distance/perimeter), and three additional ones describe the management of the reserves (grazing, mowing and scrub clearance).

The predictors were extracted from a monograph by Kubikova et al. (2005), supplemented by inspection of topographic maps, aerial photographs, "reserve management files" of the Conservation Authority Prague, and observations in the field. Plant richness and habitat diversity data originated from Sprynar

Table 1
Characteristics of 25 Prague reserves, used in ordination analyses of changes of butterfly faunas during the last 30 years

Variable	Description	Situation in mid-1980s			Situation in 2005		
		Mean	Minimum	Maximum	Mean	Minimum	Maximum
Area	Numeric (ha)	22.0	0.6	114.2			
Connectivity	Ranked variable: 1 – isolated; 2 – in cluster; 3 – adjoining other reserve						
Aspect	Ranked: 1 – north to north-east; 2 – plain; 3 – south-east and west; 4 – south and south-west; 5 –all aspects present						
Plant richness[a]	Numeric; number of vascular plant species	318.8	139	696			
Biotope diversity[a]	Numeric; number of plant communities	7.9	1	25			
Altitudinal range	Numeric; the difference between the minimum and maximum altitude (m)	60.2	15	110			
Natural distance	Numeric; min. distance to the closest habitat similar to that protected in the reserve (m)	238.8	0	1000	238.8	0	1000
Urban distance	Numeric; min. distance to built-up area (m)	184.8	0	1250	65	0	500
Natural perimeter	Numeric; length of perimeter formed by other than built-up area (m)	1800.8	0	5300	1786.2	0	5655
Urban perimeter	Numeric; length of perimeter formed by built-up area (m)	606.6	0	2360	621.2	35	2460
Forest cover	Numeric; proportion of woody cover of the total reserve area (%)	0.54	0	1	0.55	0	1
Grazing	Ranked variable; percentage of area managed by grazing: 1 – grazing not applied, 4 – more than half of the reserve grazed						
Mowing	Ranked variable, coded as above						
Scrub clearance	Ranked variable, coded as above						

For numeric characteristics, their means and ranges are given.

[a] From Sprynar and Marek (2001), based on mid-1990s surveys, i.e., between the past and recent butterfly surveys.

and Marek (2001). Variables characterising position of reserves with respect to urban/natural biotopes and reserve management were recorded separately for the earlier and recent survey.

Records of vagrant species with erratic occurrence and those of hardly detectable species with arboreal habit may bias comparisons of past and present faunas (Dennis et al., 2006). This was of particular concern, because numbers of visits to individual reserves varied in the past survey, and also because the past survey spanned many years, which increased the chances of recording occasional vagrants. To mitigate this, we repeated all analyses with exclusion of *Aporia crataegi*, *Pieris brassicae*, *Pontia daplidice*, *Colias crocea*, *C. hyale*, *Vanessa cardui*, *V. atalanta*, *Inachis io*, *Aglais urticae*, *Issoria lathonia* (vagrant), *Apatura ilia*, *A. iris*, *Thecla betulae*, *Satyrium w-album* (arboreal), and *Nymphalis antiopa*, *N. polychloros* (both); we refer to them as vagrant/arboreal species.

2.4. Analyses

Changes in the species richness (losses versus gains) across all reserves were compared using the exact binomial test. Changes in the relative representations of endangered species, and species belonging to the biotope association, body size and mobility categories were compared using χ^2-tests. Cochran's Q-tests were used to assess the increases or declines in the numbers of reserves occupied by individual species. Wilcoxon's matched pair tests were used to compare the species incidences (= how many reserves were occupied by an average species) and the numbers of species per reserve; these tests were conducted for the total species numbers, the numbers of endangered species, and the numbers of species in the habitat association, mobility and body size categories.

Changes in species composition were analysed using ordination techniques. To visualise major trends structuring past and recent faunas, we used detrended correspondence analysis (DCA), an indirect technique that ordinates samples according to the species composition (Ter Braak and Smilauer, 1998). Past and present surveys entered the analysis as separate samples. To test for the statistical significance of the changes, we used a constrained version of DCA, the detrended canonical correspondence analysis (DCCA), with the (categorical) predictor being "survey" (past versus recent). We tested for the significance of the ordination via the Monte Carlo test, using a split-plot design reflecting the temporal structure of the data (reserves forming not-permuted whole plots, surveys permuted as time series).

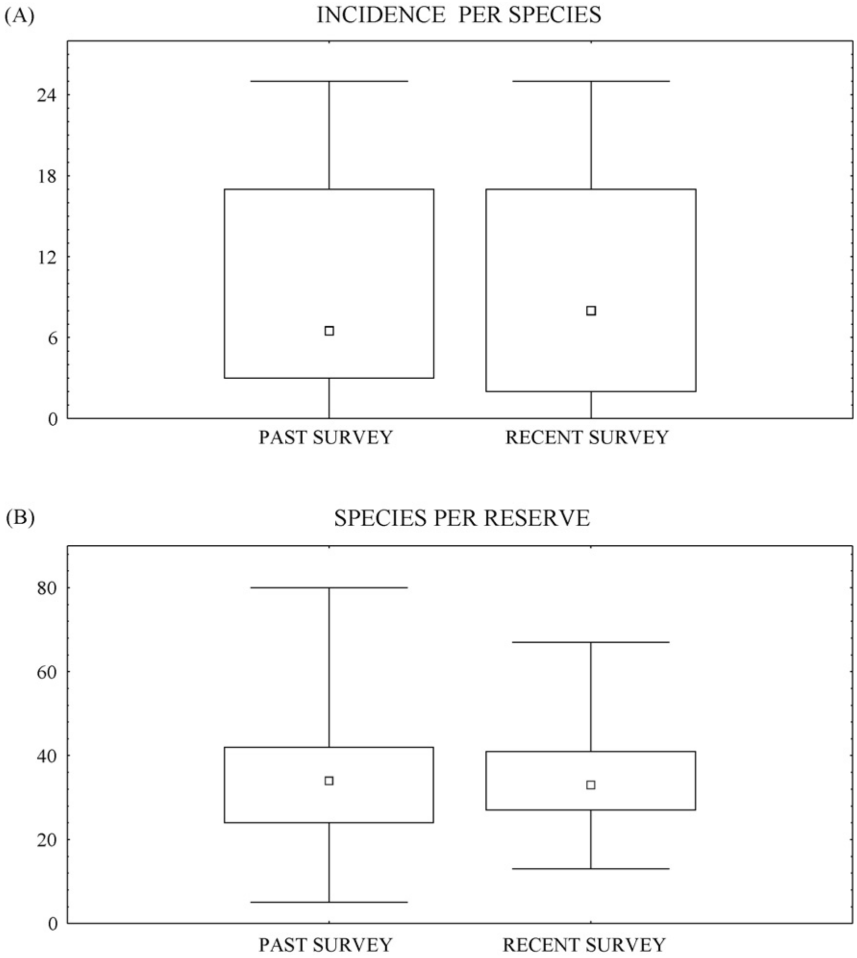

Fig. 2. Comparison of the incidences (numbers of reserves occupied per species) (A) and the species richness (B) of butterflies and burnets in 25 xeric grassland reserves in the city of Prague, as found by past (mid-1980s) and recent (2003–2004) surveys. Plots for all species, showing median, quartiles and range.

We then asked how did the characteristics of the reserves contribute to the changes. If y was a change in species composition between the two surveys, s was the categorical variable denoting survey, and x was a variable characterising the reserves, then the significant interaction $x \times s$ suggests an effect of x on temporal change in species composition. We tested for the interactions by first constructing, for each variable from Table 1 (x_i), a DCCA model containing x_i, s, and the interaction ($y \sim x_i + s + x_i \times s$) and second, by holding the effects of x_i and s constant (setting them as covariables) and assessing the significance of the independent contribution of $x_i \times s$. The permutation design was as above.

3. Results

The past survey detected 91 species, the recent survey 84 species. Together, the surveys detected 96 species, or 59% of the Czech butterfly and burnet fauna (Appendix A). Twelve species (12.5%) were lost and four (4.2%) were gained in the recent survey. The loses included one migrant (*Colias crocea*), five mesophilous (*Lasiommata maera*, *Boloria selene*, *Cyaniris semiargus*, *Nymphalis polychloros*, *N. antiopa*), and six xerophilous (*Pyrgus armoricanus*, *Cupido argiades*, *Plebeius idas*, *Polyommatus dorylas*, *Chazara briseis*, *Zygaena purpuralis*) species. The gains included one vagrant (*Aporia crataegi*), two mesophilous (*Brenthis ino*, *Argynnis aglaja*) and one xerophilous (*Zygaena laeta*) species. The losses prevailed over the gains (binomial test, $n = 96$, $z = -2.47$, $p = 0.013$); even after the exclusion of vagrant/arboreal species ($n = 80$, $z = -2.60$, $p = 0.009$).

The two surveys did not differ in the proportions of endangered species (22 past versus 21 recent: $\chi^2_{1\text{df}} = 0.02$, $p = 0.90$), ubiquitous, mesophilous and xerophilous species (18, 44 and 43 versus 17, 39, 38: $\chi^2_{2\text{df}} = 0.03$, $p = 0.99$), sedentary, mobile and migratory species (37, 48 and 7 versus 33, 44 and 7: $\chi^2_{2\text{df}} = 0.04$, $p = 0.98$), or small, medium and large species (57, 25 and 12 versus 52, 23, 9: $\chi^2_{2\text{df}} = 0.18$, $p = 0.91$). According to the Cochran Q-tests, nine species occupied significantly more reserves in the past survey and eleven species in the recent survey (see Appendix A for test results). The subsequent comparisons with binomial distributions showed that the numbers of decreasing and increasing species did not differ ($n = 96$, $z = 0.70$, $p = 0.48$); the same applied after the exclusion of vagrant/arboreal species ($n = 80$, $z = -1.11$, $p = 0.10$).

No differences between the surveys were found in species incidences and in numbers of species per reserve (Fig. 2A), even if split according to the biotope or life history categories. Interestingly, the numbers of species per reserve decreased their ranges and moved towards median values in the recent survey (Fig. 2B).

Despite all the negative results, the ordinations pointed to changes in species composition. In the DCA, the changes did not manifest at the first ordination axis (eigenvalue: 0.181, 13.9% of explained variation) but at the second axis (0.088, 6.7%). The two surveys formed two loose but clearly visible groups (Fig. 3), apparent even after excluding vagrant/arboreal species (first axis: 0.189, 15.3%; second axis: 0.089, 6.7%). As showed by the DCCA, the change was statistically significant (Fig. 4). Inspection of the ordination diagrams shows, besides of the obvious association of species recorded only in one of the surveys with that survey, that (i) species associated with woodlands or scrub (e.g., *Limenitis camilla*, *Pararge aegeria*, *Satyrium acaciae*) pointed towards the recent survey; (ii) specialists of xeric grasslands tended to point towards the past survey (e.g., *Pseudophilotes vicrama*), although there were some exceptions (e.g., *Scolitantides orion*).

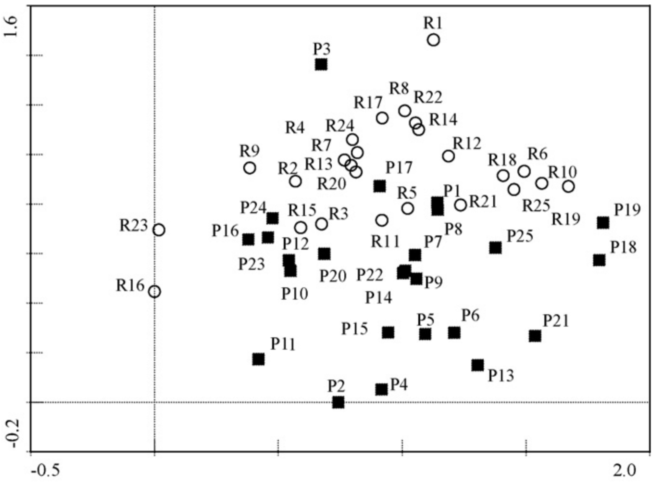

Fig. 3. Indirect (DCA) ordination of 25 Prague xeric grasslands reserves according to their past (1980s: P) and recent (2004–2005: R) butterfly faunas. The numbering of reserves corresponds with the numbers in Fig. 1.

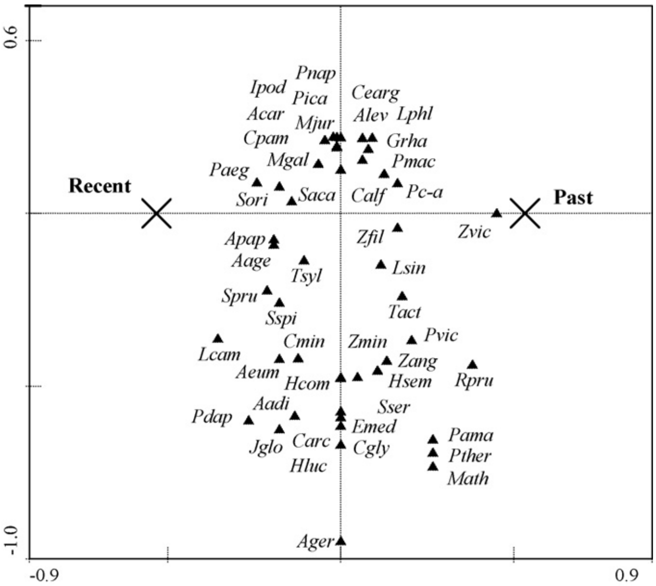

Fig. 4. Direct ordination (DCCA with symmetric scaling, detrended by 4th-level polynomials) of butterflies in 25 Prague xeric grasslands reserves, in which past (1980s) and recent (2004–2005) butterfly species compositions entered as two separate samples, and "survey" entered as a categorical explanatory variable. The plot depicts an ordination after exclusion of vagrant/arboreal species. Eigenvalue of first canonical axis: 0.06, F(999 Monte-Carlo permutations) = 2.41, $p < 0.001$. If all species entered the ordination, the results were: eigenvalue: 0.07, $F = 2.54$, $p < 0.001$. Abbreviations of the species names are given in Appendix A.

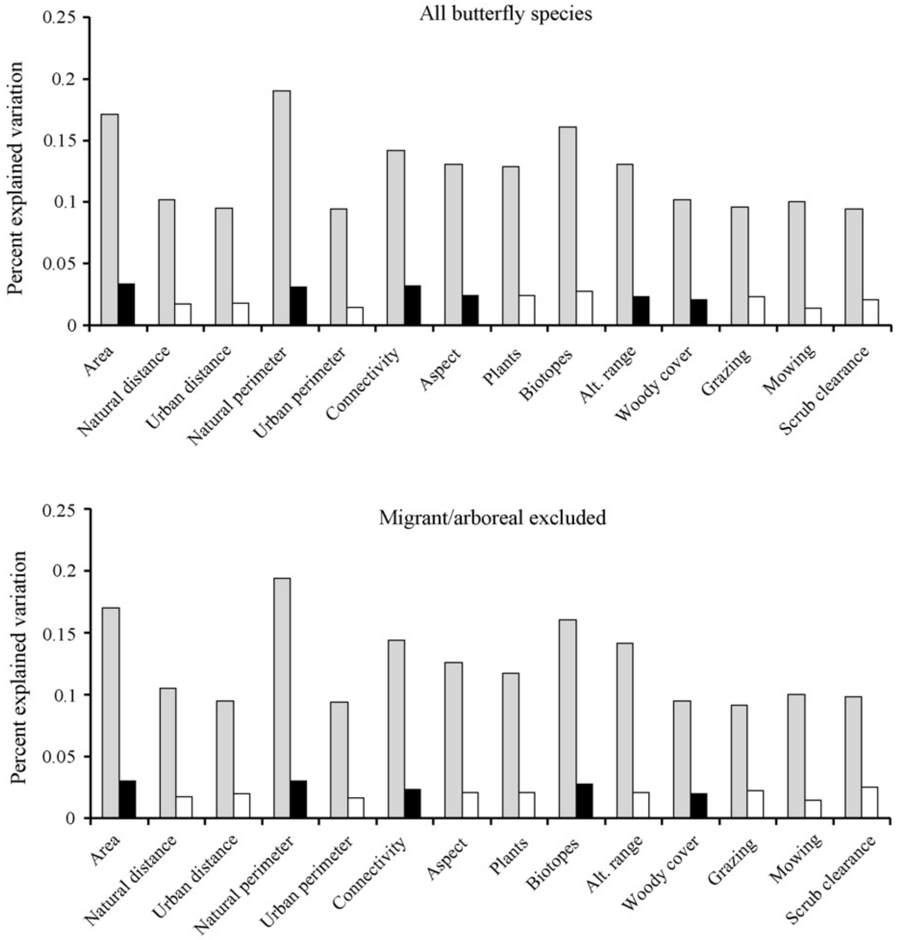

Fig. 5. Results of DCCA ordinations relating changes of butterfly fauna of 25 Prague reserves to external characteristics of the reserves. The (taller) grey bars show percentage variation explained by an external variable + survey (past vs. recent) + the variable × survey interaction. The shorter bars show variation attributable solely to the interaction, obtained by holding the effect of survey and the external variable in question constant. Black bars show tests statistically significant at $p < 0.05$ level, white bars show non-significant tests (Monte-Carlo, 999 permutations).

All models jointly considering a characteristic of the reserve (x_i), the time of the survey (s) and the interaction of survey with the variable in question appeared statistically significant (Fig. 5). After holding the effects of x_i and s constant, the effects of reserve characteristics on the temporal changes were significant for six (all species) or five (vagrant/arboreal excluded) reserve characteristics. Inspecting the effects showed that (i) woodland/scrubland species became associated with larger reserves in the recent survey; (ii) natural perimeter increased the representation of grassland species in the past, and of woodland/scrubland species recently; the same pattern applied for increasing values of (iii) connectivity; (iv) aspect; and (v) plant and (vi) biotope richness (Fig. 6).

4. Discussion

The reserves of xeric grasslands within the Prague metropolitan area lost about ten per cent of butterfly species during the last three decades and the losses prevailed over new gains. Still, no changes were detected in the representation of species belonging to habitat association or life history categories, incidences of species per reserves, or per reserve species richness. Detected changes concerned narrowing the range of species richness per reserves and shifts in the species composition of reserve faunas. The representation of species associated with woodland and scrub has increased, especially so in large reserves surrounded by natural habitats and rich in plant species and biotopes.

The absence of patterns with regard to habitat categories, body size or mobility implies that these categories were too coarse to account for the actual changes in reserve faunas. Any such categorisation necessarily simplifies the diversity of species' life histories (Shreeve et al., 2001; Dennis et al., 2004). Blind reliance on such categories, without applying species-based ordination analyses, would not disclose any changes in the composition of reserve faunas. Although categorisations of species' traits will always represent a useful tool for exploring the natural world, such tools should be used with extreme caution in conservation monitoring and policy. Also, the categorisation widely used in Europe, such as that by Bink (1992), are based on the situation in NW Europe, whereas species may differ in their ecology across their ranges. This was also the reason why we used only the simplest categories, likely to be robust against regional variation.

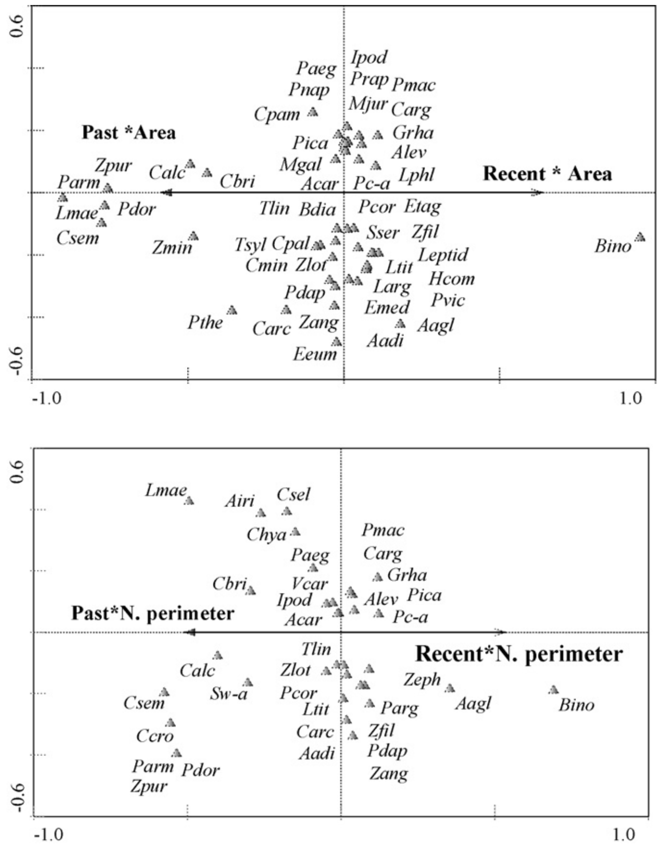

Fig. 6. Examples of DCCA ordinations testing the effect of external variable × survey interaction on the composition of butterfly fauna of 25 Prague reserves. (a) Area × survey, ordination with all butterflies. (b) Natural perimeter × survey, ordination with all butterflies. Abbreviations of the species names are given in Appendix A.

4.1. Gains and losses

Three of the four newly added species prefer other biotopes than xeric grasslands and two of them (*Aporia crataegi* and *Brenthis ino*) are currently expanding their ranges in Central Europe (Fric et al., 2000; Zimmermann et al., 2005). Some losses also affected mesophilous species of woodlands or humid grasslands, and might be associated with currently warming climate (Konvicka et al., 2003). *Zygaena laeta*, the only xerophilous specialist newly gained for the reserves, prefers late-successional stages of xeric grasslands and is recently expanding in the Czech Republic (Lastuvka and Marek, 2002).

The loss of xeric grassland specialists deserves particular attention, because negative effects of warming climate are unlikely for thermophilous species, such as *P. armoricanus*, *P. dorylas*, *P. idas* and *C. briseis*. All the lost species depend on warm short-turf grasslands (e.g., Dolek and Geyer, 2002; Ockinger, 2006). The most plausible interpretation of their losses is a successional overgrown of the sites, causing habitat loss or reduction in quality. The ordinations indicated that conditions that should normally increase reserve quality, such as large area, natural perimeter, heterogeneous relief and high plant and biotope diversity (Pysek et al., 2002), promoted the occurrence of short-turf specialists in the past but scrubland/woodland specialists in present. This points to an ongoing "mesophilisation" of the reserves, occurring despite efforts to maintain the xeric grasslands by active management. The significant (survey) × (area) interaction supports this interpretation. Battling successional changes by labour-intensive methods (e.g., scrub clearance) is easier in small than in large reserves and hence, successional changes should be more prominent in larger reserves.

Perhaps the most spectacular loss is that of *C. briseis*. This species used to be common in the Prague region in a past (Moucha and Prochazka, 1962). It requires large areas of short-turf grasslands (Johannesen et al., 1997), a habitat that still exists in the reserves, but probably has decreased in extent below a threshold necessary to sustain this relatively large butterfly. A parallel development is under way across whole temperate Europe (e.g., Buszko, 1997; Cremene et al., 2005).

Several species sharing with *C. briseis* the requirements for short-turf grasslands but still persisting in the reserves illustrates species-specificity of the responses. Prague still represent the Czech stronghold for two such species, *Hipparchia semele* and *Pseudophilotes vicrama* (cf. Benes et al., 2002). However, they both displayed an association with the past in the ordinations and may become threatened in a near future, if the mesophilisation trends continue. In contrast, *Scolitantides orion*, a threatened inhabitant of rocky biotopes (cf. van Swaay and Warren, 1999), pointed towards the recent survey. This butterfly successfully colonises such sites as stony walls (Höttinger and Timpe, 2002), which may explain its favourable status.

4.2. Efficiency of the reserve system

Despite all the losses, the situation in Prague reserves seems to be *better* than in cases of several recent butterfly re-inventories in Central Europe. Wenzel et al. (2006) detected losses of over one third of species from grassland reserves in the valley of river Mosel, Germany, over three decades. The losses mainly affected specialists demanding large areas of habitat and occurring in high population densities. Similarly high losses occurred, e.g., in the Düsseldorf area and the Dübener Heide, Germany (Grosser, 2002; Lenz and Schulten, 2005), or Opava and Moravian Karst regions of the Czech Republic (Benes and Kuras, 1998; Lastuvka and Marek, 2002). Prague reserves are thus remarkably efficient in preserving butterflies.

This may be interpreted in two ways. First, archival data (e.g., Sterneck, 1929) documents that many losses had occurred long before the period when Cila and Skyva (1993a) conducted their survey. They mainly affected species that are declining across the entire region of Central Europe (e.g., *Colias myrmidone*, *Polyommatus damon*, cf. van Swaay and Warren, 1999). What deserves to be explained are the relatively low losses during last 30 years. It is tempting to attribute the low losses to peculiar (sub)urban conditions. A majority of the studied reserves are situated in a suburban perimeter that has escaped the modern homogenisation of rural landscapes. They are surrounded by mosaics of gardens, parks, undeveloped barrens and post-industrial brownfields, plus a dense fabric of linear habitats along roads and railways. Landscape heterogeneity positively affects butterfly richness (Balmer and Erhardt, 2000; Weibull et al., 2000; Bergman et al., 2004), brownfields attract species requiring early-successional conditions (Benes et al., 2003; Eyre et al., 2004) and linear structures increase the connectivity (Saarinen et al., 2005; Valtonen et al., 2007). There are other studies documenting that outer urban perimeters may host more species than "undisturbed" non-urban lands (e.g., Ruszczyk and De Araujo, 1992; Blair and Launer, 1997; Hardy and Dennis, 1999).

These considerations highlight the conservation potential of urban reserves. On the other hand, the case of *C. briseis* illustrates a limitation when it comes to species requiring large extents of habitat. Another limitation stems from slow and subtle habitat changes, such as the mesophilisation detected here. Whereas the latter limitation may be amenable by targeted management, battling the former requires a reconciliation of conservation and other uses of non-reserve lands in urban regions. The conservation management of urban green areas, such as gardens and parks offers many opportunities (Gaston et al., 2005a,b; Angold et al., 2006), but to be effective, it should aim on providing resources for priority species occurring in urban reserves. For species of xeric grasslands, green areas outside of reserves should include rocky structures, sparse scrub, fallow, and even patches of sparsely vegetated barrens. Such features would, besides contributing to preserving biodiversity, enrich the visual appearance of urban green areas, which now often consist of planted trees alternating with intensively mown lawns.

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Appendix A

List of butterfly and burnet species found in 25 Prague xeric grassland reserves. P indicates species found during the past (1980s) but not recent survey, R stands for species detected during the recent survey (2004–2005) only, whereas B stands for species detected during both surveys.

Abreviation: abbreviations as used in ordination diagrams.
Threatened (yes/no): status in the Czech Republic according to Vrabec et al. (2005)
Biotope: basic biotope association categories M – mesophilous, X – xerophilous, U – ubiquitous
Body size: S – small, M – middle, L – large
Mobility: L – low, I – intermediate, H – high
Lost/gained: denotes species present in the past but not present in recent survey (L), and species not present in the past but present in recent survey (G)
Cochran's *Q*: results of single-species tests of incidence changes; "D" stands for significant ($p < 0.05$) decrease, "I" for significant increase.

Species	Abbreviation	Threatened	Biotope	Body size	Mobility	Baba	Barrandovske skaly	Bohnicke udoli	Divoka Sarka	Dolni Sarka	Havranka	Lesopark na Petrine	Prokopske udoli	Radotinske udoli	Santoska - Pavi vrch	Tiche udoli a Roztocky haj	Zlatnice	Branicke skaly	Cimicke udoli	Dalejsky profil	Jablonka	Jeneralka	Lochkovsky profil	Nad mlynem	Okrouhlik	Park na Karlove namesti	Podbabske skaly	Trojska	Zizkov Zidovske pece	Zmrzlik	Lost/gained	Cochran's Q	Past / recnt no. of inhabited reserves
Rhagades pruni	*Rpru*	no	X	S	I								P	B		B			P	P				P								**D**	6/2
Adscita globulariae	*Aglo*	no	X	S	I									R		P														R			1/2
A. geryon	*Ager*	yes	X	S	I									B																			1/1
A. statices	*Asta*	no	X	S	I		P						P			B			P				B										5/2
Zygaena purpuralis	*Zpru*	no	X	S	I								P																		**L**		1/0
Z. minos	*Zmin*	no	X	S	I						R			P		P							R										2/2
Z. loti	*Zlot*	no	X	S	I	B			R	B	B		B	B		P	R	P	B	B		B	R	R	R		B	R		B			11/16
Z. carniolica	*Zcar*	yes	X	S	I	P							P	R		P		R	P			R	B					P		B			7/5
Z. viciae	*Zvic*	no	M	S	I					P			P	P	B			P	P	P			P	P	P			P		P		**D**	12/1
Z. filipendulae	*Zfil*	no	M	S	I	P				P	P		B	B	R	B	P	B	P	B	P	B	R	B	P		P	B		B			17/11
Z. angelicae	*Zang*	no	X	S	I	P				P			P	B						R								R		P			5/3
Z. ephialtes	*Zeph*	no	M	S	I	B				P			B	B	P	B			P	R	R		R		B			P		P			10/8
Z. laeta	*Zlae*	yes	X	S	I	R																									**G**		0/1
Erynnis tages	*Etag*	no	X	S	I	B	P	R	B	B	B		B	B		B		P	B	B	R	B	B	B	B		P	B		B			18/17
Carchadorus alceae	*Calc*	yes	X	S	I	R					R		P			P					R							R	R				2/5
Spialia sertorius	*Sser*	yes	X	S	S						P		B	B		B				B			R							P			6/5
Pyrgus malvae	*Pmal*	no	M	S	S	P	P	R	P	B	P		B	B		B	R	P	B	B	P	B	B	R	B		P	B		B			18/14
P. armoricanus	*Parm*	yes	X	S	S								P																		**L**		1/0
P. carthami	*Pcar*	yes	X	S	S	R		R	P				B	B		R		P		B			B				R	P					7/8
Carterocephalus palaemon	*Cpal*	no	M	S	S	R			P	P	B		P	B		B	P		R	R				R			B			B			9/9
Thymelicus sylvestris	*Tsyl*	no	M	S	S	B			B	B	R		P	B		B				R	R	R	B					B		R			8/12
T. lineolus	*Tlin*	no	M	S	I	B			B	B	B	R	B	B	R	B		R	R	R	B	R	R	R	B		B	B		B		**I**	12/20
T. acteon	*Tact*	yes	X	S	S	P	P				P		B	B		P		P		R			R		P								8/4
Hesperia comma	*Hcom*	yes	X	S	I								B	B		B				R			B					P		B			6/6
Ochlodes venatus	*Oven*	no	M	S	H	B	R		B	B	B		B	B	B	B	R		B	B	R	R	B	R	R		B	R		B			13/20
Papilio machaon	*Pmac*	no	M	L	I	P	P	R	B		P	P	B	B	P	B		P	B	B			B	R	P	P		P	P			**D**	17/9
Iphiclides podalirius	*Ipod*	yes	X	L	I	B	B	R	B	R	B	B	B	B	B	B	B	B	B	B	R	R	B	B	B	B	B	B	B	B			21/25
Leptidea sp.	*Leptid*	no	M	M	H	P	R		P	P	P		B	B		B	P		P	B		B	B	B						B			14/9
Aporia crataegi	*Acra*	yes	X	L	H				R																						**G**		0/1
Pieris brassicae	*Pbra*	no	U	L	I	B		R	B	B	B	B	B	B	B	B	B	B	B	R	B	P	B	B	P	P	B	B	P	B			22/20
P. rapae	*Prap*	no	U	M	I	B	R	R	B	B	B	B	B	B	B	B	B	B	B	B	B	B	R	B	B	B	B	B	B	B			22/25
P. napi	*Pnap*	no	U	M	I	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B			25/25
Pontia edusa	*Pedu*	no	U	M	H	R		R	R			R	B	P	R	R		R		R			R	R				R				**I**	2/12
Anthocharis cardamines	*Acar*	no	M	M	I	B	B	R	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B			24/25
Colias hyale	*Chya*	no	U	M	I		P		R		P	P	P	P		P		B	P	P			P			P			P			**D**	12/2
C. alfacariensis	*Calf*	no	X	M	I	B		R	B	B	B	B	B	B	P	B	B		R	R	P	B	R	B	P	P	R	B	P	B			18/18
C. crocea	*Ccro*	no	U	M	H								P	P																	**L**		2/0
Gonepteryx rhamni	*Grha*	no	M	M	I	P	R	R	B	P	B	P	B	B	B	B	R	R	P	B	P		B	R	P	B	B	P	P	P			19/15
Apatura iris	*Airi*	no	M	L	I				B					P		P																	3/1
A. ilia	*Aili*	no	M	L	S		R		P			P	P	B		P	R			R				R					P				6/5
L. camilla	*Lcam*	yes	M	M	S						R		R	B			R			R												**I**	1/5
Nymphalis polychloros	*Npol*	no	M	L	I								P	P		P									P						**L**	**D**	4/0
N. antiopa	*Nant*	no	M	L	I							P	P	P		P									P						**L**	**D**	5/0
Inachis io	*Inio*	no	U	M	I	B	B	R	B	B	P	B	B	B	B	B	B	R	P	B	B	B	B	B	B	B	B	B	B	B			23/23
Vanessa atalanta	*Vata*	no	U	M	H	B	R	R	R	R	B	B	B	B	R	B	R	R	B	R	R			R	P	P	B	P	P	R			12/19
V. cardui	*Vcar*	no	U	M	H	B	R	R	B	B	B	B	B	B	B	B	R	B	B	B	R	R	B	R	B	B	R	B	B	R			17/25
Aglais urticae	*Aurt*	no	U	M	I	B	B	B	B	B	B	B	B	B	B	B	P	B	B	B	B	B	B	P	P	B	B	B	B	B			25/22
Polygonia c-album	*Pc-a*	no	X	M	I	P	B	R	B	B	B	P	B	B		B	B		B	R	P	P	B	P	P	P	P	P	P	B		**D**	21/13
Araschnia levana	*Alev*	no	X	S	I	P	P	R	B	B	B	B	B	B	P	B	P	P	B	B	B	B	P	B	B	B	P	P	B	B		**D**	24/17
Argynnis paphia	*Apap*	no	X	L	I	R	R	R	B	R	R		B	B		B	R	R		R			B	B		P				R		**I**	7/15
Argynnis aglaja	*Aagl*	no	X	M	S								R							R			R							R	**G**	**I**	0/4
Argynnis adippe	*Aadi*	yes	X	L	S					R			B	B									R							B			3/5
Issoria lathonia	*Ilat*	no	U	M	H	B			R	P	B	B	B	B	R	B		R	B	R	R	R	B	B		P	P	R	P	R			13/17
Clossiana selene	*Csel*	no	M	M	S						P					P							P								**L**		3/0
C. dia	*Cdia*	no	M	S	I	B		R	R	B	B		B	B		B	R		B	B		R	P	R	P		R	B		B			12/16
Brenthis ino	*Bino*	no	M	M	S									R																	**G**		0/1
Mellicta athalia	*Math*	no	M	S	S								P	B						P													3/1
Melanargia galathea	*Mgal*	no	M	M	S	B	R	R	B	B	B	B	B	B	B	B	R	R	B	B	R	R	B		R	P	B	B	P	B			18/23
Hipparchia semele	*Hsem*	yes	X	L	S				P				B	B		P				R			B	P									6/4
Chazara briseis	*Cbri*	yes	X	L	S								P	P		P		P					P								**L**	**D**	5/0
Erebia medusa	*Emed*	no	M	M	S								B	B						B			B							B			5/5
Maniola jurtina	*Mjur*	no	U	M	I	B	B	B	B	B	B	B	B	B	B	B	R	B	B	B	B	R	B	B	B	P	B	B	B	B			23/24
Aphantopus hyperanthus	*Ahyp*	no	M	M	S	B	B	P	B	B	B	P	B	B	B	B	R	B	B	B		R	B	R	P	P	B	P	P	B			21/18
Coenonympha pamphilus	*Cpam*	no	U	S	S	B	B	R	B	B	B	B	B	B	B	B	R	B	B	B	B	B	B	B	B	P	B	B	B	B			23/24
C. arcania	*Carc*	no	X	S	S								P	B		P				R			R							B			4/4

C. glycerion	*Cgly*	no	M	S	S								P	B					R														2/2
Pararge aegeria	*Paeg*	no	M	M	I	R	B	R	R	R	B	R	B	B	R	B	R	R	R	R			P		R							**I**	6/16
Lasiommata megera	*Lmeg*	no	U	M	I	B	B	R	B	B	B	R	B	B	B	B		B	B	B	P	R	B	B	P		B	B		B			19/20
L. maera	*Lmae*	no	M	M	S											P															**L**		1/0
Hamearis lucina	*Hluc*	yes	M	S	S									B		P							B							R			3/3
Thecla betulae	*Tbet*	no	M	S	S								B	P	P												P			R			4/2
Quercusia quercus	*Qque*	no	M	S	S			P		P	P		B	B	P	B	R		B		B		P		B	R		P	R				9/12
Satyrium pruni	*Spru*	no	M	S	S				R	P			B	P	R	R				R			R					R					3/7
S. w-album	*Sw-a*	yes	M	S	S								P			P			R											R			2/2
S. spini	*Sspi*	yes	X	S	S	B				R	R		B	B		P		R					R				R					**I**	4/8
S. acaciae	*Saca*	yes	X	S	S	B	R	R	R	B	B		B	B	B	B		R	P	R	R	R	R	B			B	B		R		**I**	11/19
Callophrys rubi	*Crub*	no	M	S	I	B		P		R			P	B									R										4/4
Lycaena phlaeas	*Lphl*	no	U	S	I	B	B	R	B	P	B	B	B	B	P	B		P	B	B	B	B	P	B	B	B	P	B	P	P			23/18
L. tityrus	*Ltit*	no	M	S	I	B			P	P	B		P	R		B			B		R	B	P	R	P		P	P		R			12/19
Cupido minimus	*Cmin*	no	X	S	S	R					R		B	B						B			B	R						B			5/8
Cupido argiades	*Cuarg*	no	X	S	I																	P									**L**		1/0
Celastrina argiolus	*Cearg*	no	M	S	I	P	B	R	B	P	B	P	B	P	B	B	R	P	B	R	R	P	B		B	B		P	B	B			19/16
Pseudophilotes vicrama	*Pvic*	yes	X	S	S	P			P				B	B		P				B		P	R	P						P			9/4
Scolitantides orion	*Sori*	yes	X	S	S	B	R	R	B	B	B		R	B	R	B	B		R	R	R		R	B			B	R				**I**	9/18
Plebejus argus	*Parg*	no	X	S	S								P			R														R			1/2
Lycaeides idas	*Lida*	yes	X	S	S									P																	**L**		1/0
L. argyrognomon	*Larg*	no	X	S	I				P	P	P		B	B		B			B		R	P		B	P		R	B		B			12/9
Aricia agestis	*Aage*	no	X	S	I	B			R	R		R	B	B		B			B	R	R		R	B			R	P		R		**I**	7/15
Eumedonia eumedon	*Eeum*	yes	M	S	S									P		R				R				R						B			2/4
Cyaniris semiargus	*Csem*	no	M	S	I									P																	**L**		1/0
Polyommatus amandus	*Pama*	no	M	S	I					P			P	B						R													3/2
P. dorylas	*Pdor*	yes	X	S	S								P	P																	**L**		2/0
P. thersites	*Pthe*	yes	X	S	S								P	P						R										P			3/1
P. coridon	*Pcor*	no	X	S	I	B		R		B	B		B	B	P	P		B	B	B	B	B	B	B			B	B		B			17/17
P. daphnis	*Pdap*	yes	X	S	S								B	B						R			R	R						R		**I**	2/6
P. icarus	*Pica*	no	U	S	I	B	B	R	B	B	B	B	B	B	B	B	B	B	R	B	B	B	B	B	B	B	B	B	B	B			23/25
Total past						**44**	**21**	**5**	**37**	**40**	**42**	**25**	**79**	**80**	**27**	**66**	**15**	**26**	**39**	**34**	**20**	**23**	**43**	**29**	**35**	**23**	**32**	**39**	**24**	**43**			
Total recent						**40**	**25**	**32**	**39**	**35**	**40**	**22**	**56**	**67**	**27**	**51**	**27**	**27**	**37**	**60**	**29**	**30**	**54**	**41**	**21**	**13**	**29**	**33**	**14**	**51**			

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