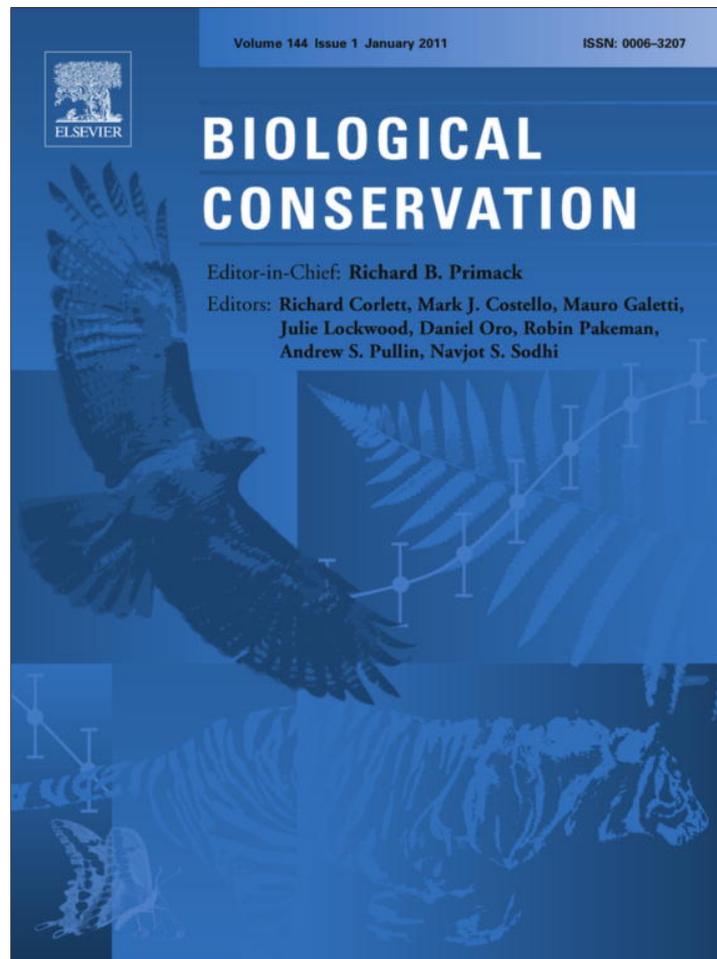


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Conservation in a city: Do the same principles apply to different taxa?

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ABSTRACT

Factors shaping overall species richness and representation of endangered species of vascular flora and butterflies were determined in 48 nature reserves in Prague, Czech Republic. Total species richness of both groups, and the presence of endangered butterflies, reflect the present status of habitats, while that of endangered plants reflects habitat composition at the time of reserve establishment. Reserve area has a much stronger effect on the species richness of sessile plants than mobile butterflies which, especially endangered species, respond more positively to heterogeneity than to area. Both species richness and endangered species peak in reserves half covered with forest, likely because they harbor species of both woodland and non-woodland habitats, and edge specialists. Solely relying on area and disregarding habitat quality, or a failure to conserve small but high quality sites, may be counterproductive for conserving endangered plant and butterfly species. To conserve diversity of plants and butterflies current management practices, often aimed at maintaining large blocks of pre-selected plant communities, should change to include maintenance of fallows, edges and transient zones.

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1. Introduction

Ongoing urbanization fundamentally alters the abiotic and biotic components of landscapes, increasing the awareness of the importance of urban landscapes for biodiversity protection of a wide range of taxa (Hamer and McDonnell, 2008; McDonald et al., 2008; Davies et al., 2009; Rees et al., 2009). Maintaining biodiversity in urbanizing landscapes has therefore become a top conservation priority (Palmer et al., 2008; Pennington et al., 2008; Filippi-Codaccioni et al., 2008; Loss et al., 2009; Vermonden et al., 2009) and management strategies are being developed to conserve urban biodiversity (Teillac-Deschamps et al., 2009; Toth et al., 2009).

Cities are generally hostile environments for wildlife, and urbanization represents a dramatic form of natural habitat destruction. In urban areas, remnants of natural habitats remain restricted to small and isolated patches, and thus fragmented populations of native plants and animals. In addition these fragmented populations face common risks associated with small population sizes, and pressures from heavily altered urban environments. These include altered water and nutrient availability, pollution,

exposure to aggressive alien species, and increased disturbance (Celesti-Gradow et al., 2006; Ricotta et al., 2009; Raupp et al., 2010). All these processes make conserving the native biodiversity in urbanized areas particularly challenging.

Yet, the biodiversity of the urban environment may even exceed that of surrounding rural landscapes, owing to heterogeneous environments (Fuchs et al., 2002; Shapiro, 2002; Zerbe et al., 2003), and location of many cities in naturally species rich areas (Kühn et al., 2004; Celesti-Gradow et al., 2006; Kadlec et al., 2008). Even if this was not so, conservation of natural remnants within cities is recently rising in prominence. Most people lives and work in cities (Miller and Hobbs, 2002) and access to natural habitats improves their quality of life and generates support for conservation (Turner et al., 2004). Low economic importance of agriculture and forestry in metropolitan areas locally releases human pressure on natural landscapes (Hanski, 2005). In the long term, biodiversity may only be saved by reconciling nature and human presence (Rosenzweig, 2003), for which cities provide a natural testing ground.

This study analyses species richness of vascular plants and butterflies in reserves in the city of Prague, Czech Republic. Prague contains spectacular natural features, rarely seen in other metropolitan areas of comparable size (496 km²), protected in 88 nature reserves (Kubíková et al., 2005). Our analyses build on systematic surveys of flora and butterflies, carried out in the late 1980s/early 1990s, which produced a unique data set of the diversity of both groups in an urban setting. The reserves are important sanctuaries

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for both groups, as Prague hosts more than half of the plant and butterfly species occurring in the Czech Republic (Špryňar and Marek, 2001; Kadlec et al., 2008).

We studied factors associated with species richness of both groups in the reserves, with special emphasis on endangered species. The main goals were: (i) to compare factors influencing the species richness of the two model groups, butterflies and plants; (ii) to explore whether the effect of urbanization on a subset of endangered species differs from that on the total species richness; and (iii) by highlighting factors that can be manipulated when establishing and/or managing reserves, to provide recommendations on how to preserve the diversity of endangered plants and butterflies.

2. Material and methods

2.1. Prague's nature reserves

Butterfly and plant data were available for 48 reserves. They are distributed relatively evenly across the metropolitan area, both in central and peripheral parts of the city between 14°13'51 and 14°43'80N and 49°56'33 and 50°12'23E. The habitats range from rocks and disused quarries, through thermophilous grasslands (usually former grazing commons) to seminatural woodlands. The largest and most spectacular reserves are deep canyons, either on calcareous or acidic substrates. In contrast, the smallest reserves protect tiny areas of grassland or rocky outcrops surrounded by a built-up area. Nineteen of the reserves (mainly rocks and disused quarries) were originally established to protect geological or palaeontological sites, and 15 to conserve rare plants; they include woodlands (typically historical hunting grounds), steppe grasslands and one wetland. None of the reserves were established for the conservation of butterflies.

2.2. The data

Plant lists originated from inventory surveys of all reserves commissioned by Prague conservation authorities and carried out by experienced botanists between mid-1980s and mid-1990s; the botanists were asked to visit the sites repeatedly and to find as many plant species as possible. The species lists were published by Špryňar and Marek (2001). We distinguished (i) number of species spontaneously occurring per reserve, excluding planted shrubs and trees (mean = 291, 117–683, total for all reserves $N = 1309$) and (ii) endangered species (mean = 5, 0–35, $N = 90$), following the red list by Kubát et al. (2002). Species classified in categories C1 (critically threatened taxa, corresponding to the IUCN category “critically endangered”) and C2 (strongly threatened taxa, corresponding to the IUCN “category endangered”; see Holub and Procházková (2000) for details) were considered as endangered.

Butterflies (*Hesperioidea*, *Papilionoidea*) and burnet moths (*Zygaenoidea*) were surveyed in a similar manner; the results were published by Číla and Skyva (1993a,b). We again distinguished (i) the total number of species (mean = 31, range 5–80; total for all reserves $N = 95$) and (ii) number of endangered species (mean = 4, 0–19, $N = 23$), the latter following Beneš and Konvička (2002) (butterflies) and Laštůvka (1993) (burnets).

Explanatory variables (Appendix A) were divided into six groups (A–F), reflecting well known determinants of species richness in insular reserves:

A. Geography: Two general determinants of species richness were included, namely (1) area (0.51–225.5 ha) and (2) isolation (three levels): isolated (>1000 m from the closest reserve), clustered (distance to closest reserve <300 m) and neighboring (administratively separate reserves adjoining one another (e.g. MacArthur

and Wilson, 1967; Whittaker et al., 2005; Chiarucci et al., 2008). (3) Reserve age since the year of establishment (15–52), as a measure of duration of its separation from presumably contiguous natural environments. (4) Aspect with five levels: north to north-east; plain; south-east and west; south and south-west; valley (all aspects present), determining solar intake of site, which is important especially for xerophilous species (Thomas, 1993). Further, two factors affecting both local topoclimate and habitat heterogeneity (Konvička et al., 2006), namely (5) altitude, i.e., the mid value between minimum and maximum altitude (199–345 m a.s.l.) and (6) altitudinal range, i.e., maximum minus minimum altitude (5–177 m). Finally, (7) railway with two levels (adjoining the reserve, or not), presumably enhancing connectivity via microclimatically hot embankments (Noordijk et al., 2009).

B. Past habitats: the proportional representation of habitat types at the time of reserve establishment. **C. Present habitats:** referring to the current state. Both are expressed as proportional representation of forest (0–0.99 and 0–1.00, respectively), arable land (0–0.31, 0–0.31), pasture (0–1.00, 0–0.88), grassland (0–0.55, 0–0.56), orchards (0–0.62, 0–0.09), wasteland (0–1.00, 0–1.00) and built-up area (0–0.09, 0–0.03).

D. Substrate: (1) soil type (eight levels: alluvial; acid; calcareous; neutral; acid and alluvial; acid and neutral; acid and calcareous; acid, neutral and calcareous), known to affect vegetation and, indirectly, insect diversity. Two indicators of the presence of nutrient-poor microclimatically hot habitats (Beneš et al., 2003; Dennis et al., 2004), one of natural origin, namely (2) bare bedrock, and the other of artificial origin, namely (3) quarry (both of two levels: present or absent).

E. Vegetation heterogeneity: used only for butterflies: (1) vascular plant species richness (117–696), which is assumed to have direct influence on insect herbivores (Hawkins and Porter, 2003). Unlike for plants when used as a response variable, planted taxa of trees and shrubs were included here. (2) Number of plant communities (1–25), defined as associations of the phytosociological classification system (Moravec, 1995), used as a correlate of habitat diversity (Schaffers et al., 2008).

F. Urbanization: (1) minimum distance to another natural habitat (0–2150 m); (2) minimum distance to built-up area (0–1250 m); (3) built-up perimeter, i.e. length of perimeter formed by built-up area (0–2550 m); (4) natural perimeter, i.e. length of perimeter formed by other than built-up area (270–6150 m).

2.3. Statistical analysis

The response variables were (i) total number of species in each reserve, called species richness of plants and butterflies and (ii) proportional representations of endangered plants and butterflies in each reserve, called endangered plants and butterflies. To ascertain the relative importance of the individual explanatory variables from all six groups of the explanatory variables (A–F), and whether the species richness and the endangered species increase or decrease over the individual explanatory variables, all the data were first analyzed by random forests (RFs) (Breiman, 2001), with the richness and proportions of endangered species across the reserves divided into values above and below median value. This enabled to apply the RFs novel “out-of-bag” method for determining variable importance, having very high classification accuracy (Appendix B). We also simultaneously utilized RFs abilities to model complex interactions among predictor variables and give robust results for small sample size (Breiman and Cutler, 2004). RFs make no distributional assumptions about the explanatory and response variables, and can handle situations in which the number of explanatory variables greatly exceeds the number of observations. RFs thus could be safely used to analyze all the 30 explanatory variables in a single, general model for the only 48 reserves. RFs

are also not affected by colinearity of the explanatory variables (Cutler et al., 2007). The ranking of explanatory variable importance by RFs thus guards against the elimination of variables which are good predictors of the response, and may be ecologically important, but which are correlated with other predictors.

The variable importance measure in RFs may be used to subjectively identify ecologically important variables for interpretation, but the method does not choose subsets of variables in the way the variable subset is selected by the traditional statistical inference methods. It is not suitable for hypothesis testing, and does not calculate parameters of the explanatory variables and their probability values. In addition, because the response variable was binary, dividing the richness and proportions of endangered species just into values above and below median value, RFs were unable to identify domed relationships, with low values of the response both at low and high value of the explanatory variable. For these reasons, the data were then analyzed with GLIM, v. 4 (Francis et al., 1994), separately for the six (A.–F.) groups of environmental variables, by the use of generalized linear models (GLMs). This enabled common analysis of related explanatory variables by traditional inference methods, keeping the number of the variables 6–10 times smaller than the number of observations (Neter et al., 1996). The explanatory variables were divided into (i) categorical variables (factors), defined by levels and (ii) continuous variables (covariates) defined by ranges. All covariates were standardized to zero mean and unit variance to achieve their comparable influence. Each GLM included all factors and covariates of a particular group, the interaction of each covariate with each level of each factor, and one-level interactions among the covariates. To test for non-linear relationships, square powers were added to the covariates. Each analysis determined the minimal adequate model (MAM), in which all explanatory variables differed from zero and from one another, and all non-significant explanatory variables were removed (Appendix C). Explained variance of the individual MAMs was expressed by r^2 , taking into account sample sizes and number of predictors (e.g. Quinn and Keough, 2002, p. 139). To test whether the models did not violate the basic assumption of the independence of errors of the observations due to spatial autocorrelation (Legendre and Fortin, 1989; Legendre, 1993; Legendre and Legendre, 1998, pp. 12–13; Dormann et al., 2007), the response variables entering the analyses and the residuals of the individual MAMs were evaluated by Moran's I correlograms (Sokal and Oden, 1978; Legendre and Legendre, 1998, pp. 714–721) in SAM 3.0 (Rangel et al., 2006) (Appendix D).

Within MAMs, significant interactions between two covariates were examined on centered variables, separately for their linear and quadratic terms, by simple slopes of the models at three specific values of the changing variable: mean, and mean plus and minus its sample standard deviation (Quinn and Keough, 2002, pp. 131–133). The effects of substrate were evaluated on angular transformed data by factorial ANOVA with disproportional and unequal sample sizes in SPSS (2004). An *a priori* hypothesis that the proportional representation of endangered butterflies is larger on calcareous soils than elsewhere (van Swaay, 2002) was tested by orthogonal contrast. MAMs for butterflies that ignored/included plant communities were compared using the Schwarz Bayesian Information Criterion (BIC) where smaller values indicated a more parsimonious model (Schwarz, 1978).

3. Results

3.1. Overall effect of explanatory variables

For plant richness, the descending ranking of explanatory variable based on random forests classification (Appendix B: Fig. A1)

Table 1 Overall significance of the total number of species (F , df , P) and of proportional representation of endangered species (χ^2 , df , P) explained by the minimal adequate models (MAMs). r^2 is the explained variance adjusted for the number of parameters. Parameters of the models and their description are in Appendix C (Table A1–A3).

Group of explanatory variables	Total number of species (species richness)						Proportional representation of endangered species						
	Plants			Butterflies			Plants			Butterflies			
	F	df	P	F	df	P	χ^2	df	P	χ^2	df	P	
A. Geography	8.10	4, 43	<0.001	7.58	3, 44	<0.001	8.69 ^a	3, 44	<0.001	0.40	66.88	3	<0.001
B. Past habitats	–	–	–	3.97	2, 45	0.03	5.04 ^a	1, 46	0.03	0.19	–	–	–
C. Present habitats	8.43	4, 43	<0.001	5.12	2, 45	0.01	–	–	–	–	33.11	6	<0.001
D. Substrate	–	–	–	–	–	–	–	–	–	–	18.57 ^b	1, 46	<0.001
E. Vegetation heterogeneity	Not analyzed	–	–	9.94	2, 45	<0.001	Not analyzed	–	–	–	52.01	4	<0.001
F. Urbanization	–	–	–	11.76	1, 46	0.001	3.46 ^a	2, 45	0.04	0.09	6.61 ^a	4, 43	<0.001

^a Rescaled and tested by F -test due to overdispersion.

^b F -test using iterative approximate estimation with type III sum of squares on angular transformed data.

indicated that reserve area was the most important factor, followed by proportion of wasteland in the past, natural perimeter of the reserve and past proportion of arable land. All the remaining variables were less than 50% as important as the area. Large reserve area and its natural perimeter supported high plant richness, while large areas of past wasteland had a negative effect. The proportion of past arable land had no direct effect but appeared useful in interactions with the other explanatory variables (Fig. A2). The ranking of variable importance for butterfly richness, and both groups of endangered species, was characterized by the dominance of a single explanatory variable. Both groups of butterflies were mostly positively affected by altitudinal range, and endangered plants were affected by soil type (Fig. A1). For endangered plants, large reserve area was also ranked as an important predictor, directly increasing their representation. However, for both groups of butterflies, area was a much less important factor, appearing nearly exclusively in interactions with other explanatory variables (Fig. A2).

Generalized linear models indicated that butterflies were significantly affected by more groups of explanatory variables than plants, and geography always accounted for most of the variance among the groups (Table 1). For species richness, the percentage of variance explained was always higher for plants (average r^2 per group: 46% for plants vs. 21% for butterflies) and the opposite was the case for endangered species (average: 23% for plants vs. 38% for butterflies). For plants, the predictors were stronger for richness than for endangered species, while for butterflies, the reverse was true (Table 1). None of the results were biased by spatial autocorrelations (Appendix D).

3.2. Geography

Comparing *plant and butterfly richness* revealed that reserve area exerted more than three times greater positive effect on overall richness of plants (standardized regression slope \pm SE of MAM: 1.50 ± 0.43 ; $F = 12.32$; $df = 1, 44$; $p = 0.001$) (Fig. 1A) than on overall richness of butterflies (0.46 ± 0.19 ; $F = 5.86$; $df = 1, 45$; $p = 0.02$). The area effect on butterflies interacted with altitudinal range (0.39 ± 0.20 ; $F = 3.67$; $df = 1, 45$; $p = 0.06$), being positive (0.52 ± 0.20 ; $F = 6.55$; $df = 1, 45$; $p = 0.01$) at large ranges (Fig. 2A), but nonsignificant (0.042 ± 0.13 ; $F = 0.10$; $df = 1, 45$; ns) at small ranges (Fig. 2B). The altitudinal range also positively affected plant richness, but only at intermediate levels of the range (square altitudinal range \pm SE in MAM: -0.60 ± 0.25 ; $F = 5.90$; $df = 1, 44$; $p = 0.02$) (Fig. 1B). Significantly more plants (the difference in MAM: $F = 6.65$; $df = 1, 44$; $p = 0.01$) occurred in clustered and neighboring than in isolated reserves, and in valley reserves ($F = 5.71$; $df = 1, 44$; $p = 0.02$) than in all others. The butterfly richness tended to be higher ($F = 1.93$; $df = 1, 44$; $p = 0.17$) in reserves adjoining a railway (Fig. 2C).

For *endangered plants*, area again exerted the strongest effect, but unlike its effect on plant richness, it interacted with reserve isolation (Fig. 1C and D): it was significant (1.00 ± 0.17 ; $F = 19.68$; $df = 1, 45$; $p < 0.001$) in neighboring (Fig. 1C) but not in isolated or clustered reserves (Fig. 1D). Clustered reserves harbored more ($F = 4.96$; $df = 1, 45$; $p = 0.03$) endangered plants than isolated and neighboring reserves.

The effect of area on *endangered butterflies* interacted with aspect; their representation rapidly decreased with increasing area

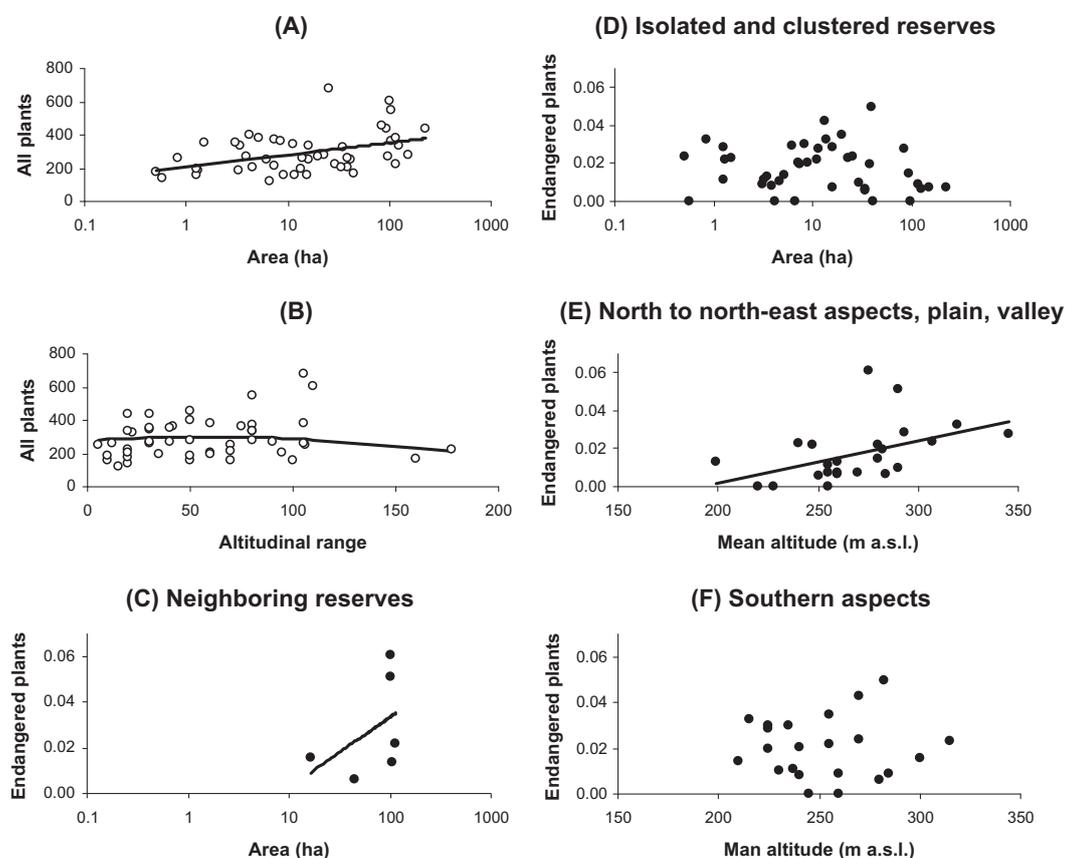


Fig. 1. The relationships between total number of plants (All plants, open circles) and proportional representation of endangered plants (endangered plants, closed circles), and the *geography* of the reserves. For easy presentation, the explanatory variables are not standardized, and the total numbers and proportions are not transformed. All plots are marginal effects, i.e. they do not include the effects of the other explanatory variables. Lines or curves suggest significant or marginally significant relationships for the parameters in the minimal adequate models (MAMs) described in the text.

of reserves facing south-east and west (-2.30 ± 0.49 ; $\chi^2 = 21.87$; $df = 1$; $p < 0.001$). This interaction appeared because of the six nature reserves having this aspect (Fig. 2D) four were very small rocky outcrops (large points in Fig. 2D) rich in endangered butterflies. Endangered butterflies also decreased with isolation, which interacted with the altitudinal range (Fig. 2E and F). For isolated and neighboring reserves, the proportion of endangered species increased (0.84 ± 0.11 ; $\chi^2 = 57.07$; $df = 1$; $p < 0.001$) with altitudinal range (Fig. 2E); this did not apply for clustered reserves (Fig. 2F).

Some of the remaining factors exerted effects exclusively on endangered plants or butterflies. Mean altitude was positively associated with endangered plants. It interacted with aspect, causing an increase in the proportion of endangered plants (0.38 ± 0.09 ; $F = 10.61$; $df = 1, 45$; $p = 0.002$) with increasing altitude in all reserves except those facing south (Fig. 2E and F). Age of reserve and the presence/absence of railway had significant effect only on butterflies. The effect of railway was not direct, but interacted

with reserve age. Endangered butterflies increased (0.23 ± 0.083 ; $\chi^2 = 7.38$; $df = 1$; $p = 0.006$) with reserve age only in those without a railway (Fig. 2G), but not in those with a railway (Fig. 2H).

3.3. Past and present habitats

The MAMs for plant richness indicated two domed effects (Fig. 3A and B) and a linear one (Fig. 3C). The domed effects were related to present forest (square term: -1.51 ± 0.47 ; $F = 10.20$, $df = 1, 44$; $p = 0.003$) (Fig. 3A) and arable land (Fig. 3B). The former was symmetrical, peaking at 50% of forest representation (Fig. 3A). The latter was right-skewed (linear term: 5.83 ± 2.01 ; $F = 8.45$; $df = 1, 44$; $p = 0.006$; square term: -0.83 ± 0.32 ; $F = 6.67$; $df = 1, 44$; $p = 0.01$), predicting the highest richness in areas covered by about 5% arable land (Fig. 3B). The linear effect indicated increasing richness with an increase in the current representation of built-up

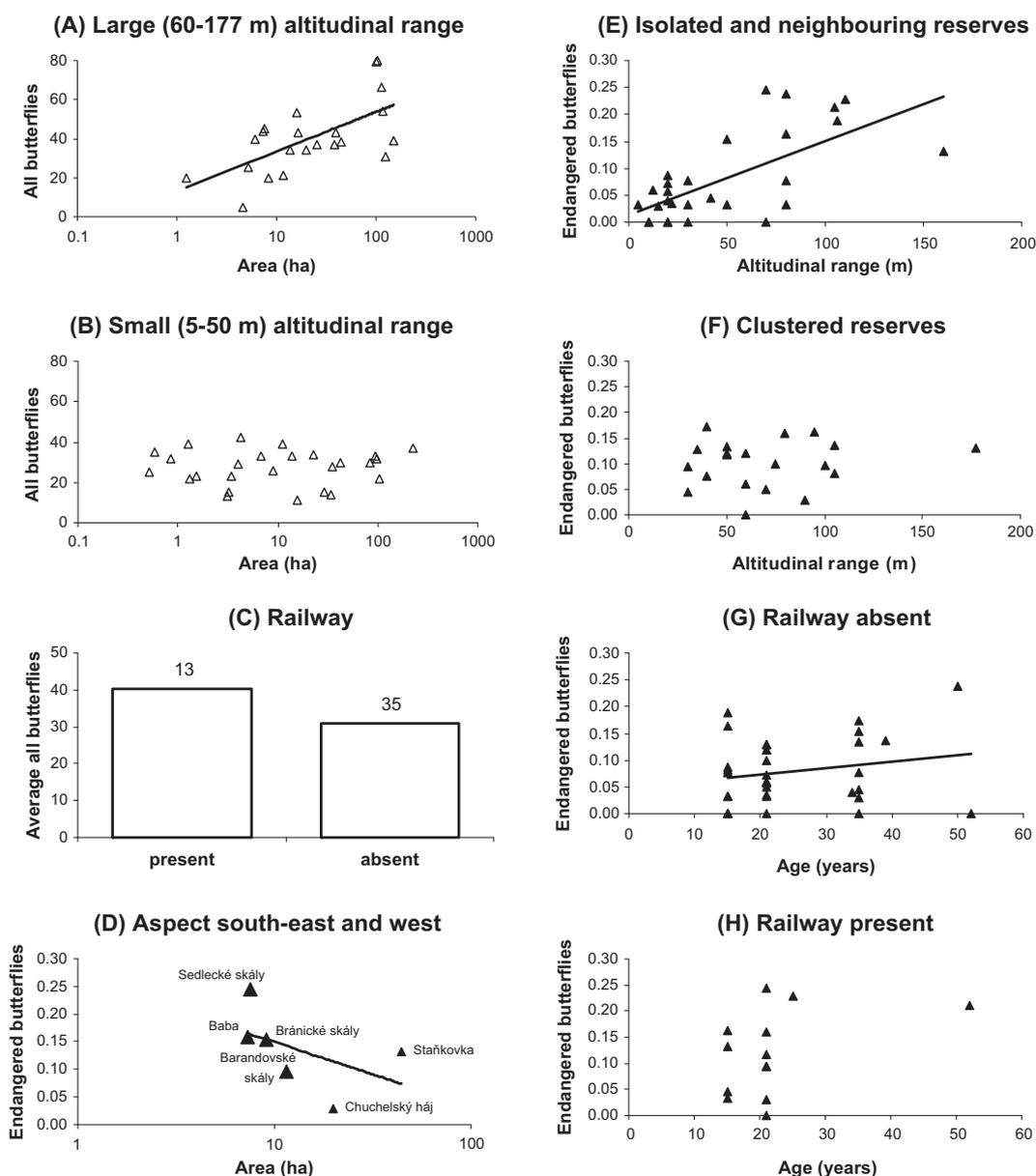


Fig. 2. The relationships between total number of butterflies (all butterflies, open triangles) and proportional representation of endangered butterflies (endangered butterflies, closed triangles), and the geography of the reserves. Figures above the bars (plot C) are sample sizes, names next to the points (plot D) indicate the reserves. Otherwise as in Fig. 1.

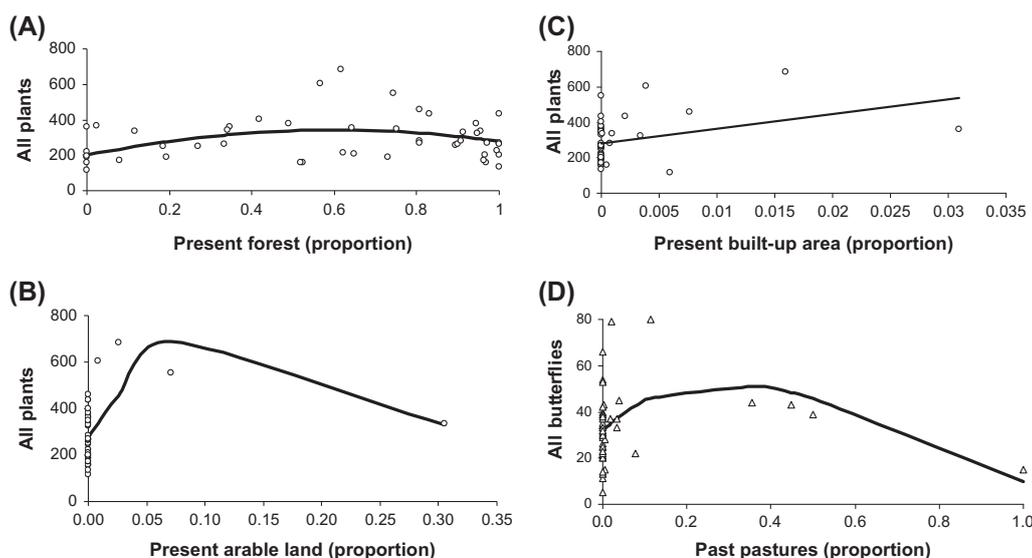


Fig. 3. The relationships between total number of plants (all plants, open circles) and total number of butterflies (all butterflies, open triangles), and *present and past habitats*. Otherwise as in Fig. 1.

areas (1.20 ± 0.40 ; $F = 9.02$; $df = 1, 44$; $p = 0.004$), which always covered less than 3.1% of reserves (Fig. 3C).

Butterfly richness responded to the effect of current area of arable land in the same way as plant richness (Fig. 3B) (linear term: 2.35 ± 0.77 ; $F = 9.32$, $df = 1, 46$; $p = 0.004$; square term: -0.35 ± 0.13 ; $F = 7.59$; $df = 1, 46$; $p = 0.008$). Otherwise, it was only affected by past pastures (Fig. 3D), the effect being domed and right-skewed (linear term: 1.37 ± 0.50 ; $F = 7.34$; $df = 1, 46$; $p = 0.009$; square term: -0.40 ± 0.14 ; $F = 7.90$; $df = 1, 46$; $p = 0.007$), predicting the highest richness in reserves that consisted of 8–50% pastures at the time of establishment (Fig. 3D).

Endangered plants and butterflies were significantly affected only by a domed proportional representation of forests. While endangered plants peaked at 50% of past forest (square term in the MAM: -0.71 ± 0.20 ; $F = 5.04$; $df = 1, 47$; $p = 0.03$), endangered butterflies peaked at 50% of current forest (square term: -0.46 ± 0.15 ; $F = 6.11$; $df = 1, 46$; $p = 0.02$).

3.4. Vegetation heterogeneity

Neither butterfly nor plant richness nor the representation of endangered plants was affected by variables related to substrate. However, presence of bare bedrock increased representation of *endangered butterflies* (Table 1).

When substrate was considered together with the variables related to plants to predict *butterfly richness*, there again was no effect of the variables related to substrate, but a significant non-linear interaction between the number of plant species and communities (0.10 ± 0.04 ; $F = 6.60$; $df = 1, 46$; $p = 0.01$). In reserves with few plant species (Fig. 4A), the relationship between butterfly richness and plant communities appeared domed (square term: -0.014 ± 0.0067 ; $F = 4.45$; $df = 1, 45$; $p = 0.04$), with the highest richness at an intermediate number of communities. In those with a large number of plant species, this relationship was non-linear but not domed (square term: 0.010 ± 0.0034 ; $F = 8.75$; $df = 1, 45$; $p = 0.005$); butterfly richness increased and accelerated with an increasing number of plant communities (Fig. 4B).

The MAM for endangered butterflies revealed significant effects of both substrate and plants, pointing to a positive effect of bare bedrock (0.97 ± 0.30 ; $\chi^2 = 12.63$; $df = 1$; $p < 0.001$) and using orthogonal contrast, a higher (0.45 ± 0.19 ; $\chi^2 = 5.15$, $df = 1$;

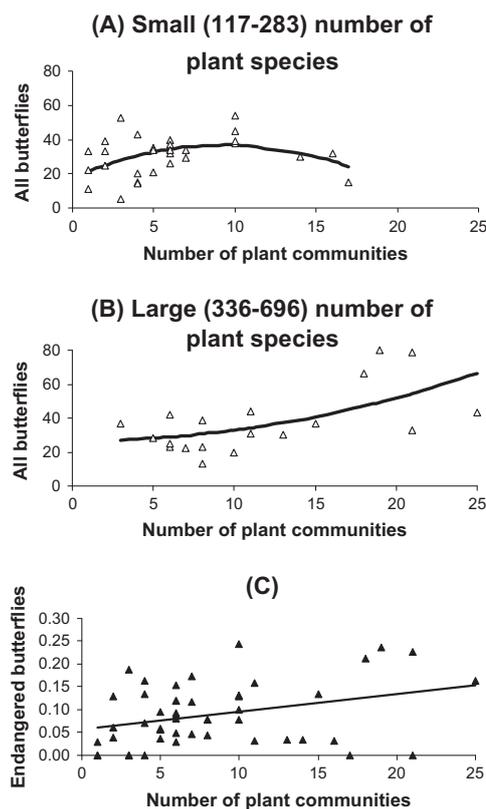


Fig. 4. The relationships between total numbers of butterflies (all butterflies, open triangles) and proportional representation of endangered butterflies (endangered butterflies, closed triangles), and the *vegetation heterogeneity*. Otherwise as in Fig. 1.

$p = 0.02$) representation of endangered butterflies on calcareous soils. As in the case of butterfly richness, endangered butterflies increased (0.29 ± 0.07 ; $\chi^2 = 17.06$; $df = 1$; $p < 0.001$) with the number of plant communities, following a linear trend (Fig. 4C). They also tended to increase (0.30 ± 0.17 ; $\chi^2 = 3.02$, $df = 1$; $p = 0.08$) in reserves containing a quarry.

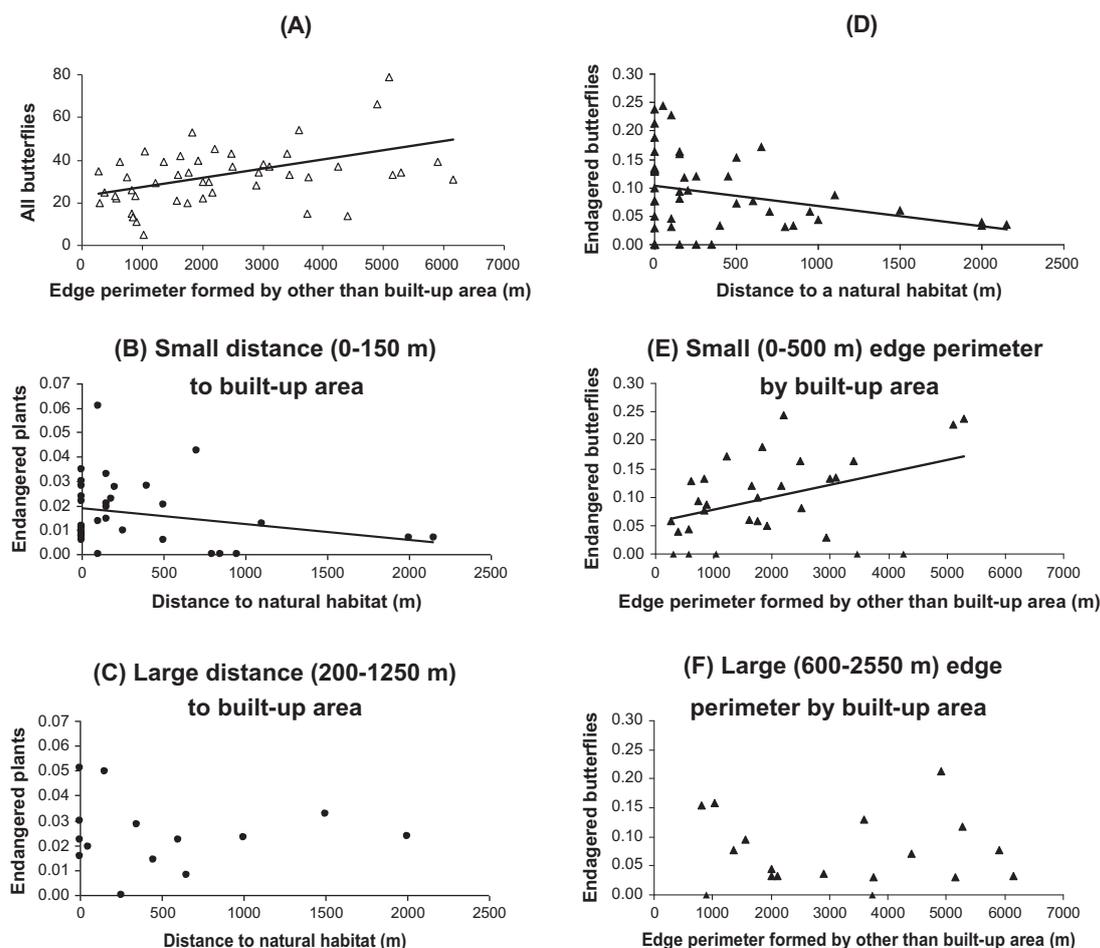


Fig. 5. The relationships between total numbers of butterflies (all butterflies, open triangles) and proportional representation of endangered plants (endangered plants, closed circles) and butterflies (Endangered butterflies, closed triangles), and urbanization. Otherwise as in Fig. 1.

3.5. Urbanization

None of the urbanization variables affected plant richness, and only the presence of natural perimeters caused a linear increase (0.59 ± 0.17 ; $F = 11.76$; $df = 1, 46$; $p = 0.001$) in butterfly richness (Fig. 5A).

More effects were found on endangered species. There was a tendency for a decrease in the representation of endangered plants with increasing distance to natural habitats. This applied only when the distance to the nearest built-up area was short (-0.022 ± 0.012 ; $F = 3.50$; $df = 1, 45$; $p = 0.07$) (Fig. 5B), disappearing when the distance was large (-0.0051 ± 0.0098 ; $F = 0.27$; $df = 1, 45$; ns) (Fig. 5C). The same trend, but independent of built-up area, holds for endangered butterflies (-0.27 ± 0.14 ; $F = 3.90$; $df = 1, 44$; $p = 0.05$) (Fig. 5D). Similarly to butterfly richness (Fig. 5A), endangered butterflies increased with natural perimeter, but only if the length of built-up perimeter was small (small: 0.0036 ± 0.000084 ; $F = 14.30$; $df = 1, 45$; $p = 0.0005$; large: 0.000013 ± 0.000098 ; $F = 0.01$; $df = 1, 45$; ns) (Fig. 5E and Fig. 5F).

4. Discussion

4.1. Comparison of plants and butterflies

For both groups, the models explained slightly more variance for the representation of endangered species ($r^2 = 0.32$) than for species richness ($r^2 = 0.28$). A plausible interpretation is that

endangered species are ecologically more homogeneous, and hence more readily fit a set of the explanatory variables. The majority of endangered species occurring in Prague are associated with xeric grasslands (Kubíková et al., 2005; Kadlec et al. 2009), whereas complete species lists include species occurring in a wide array of habitats, including ruderal and weedy species.

The effect of area on species richness was considerably weaker for butterflies than for plants. Clearly, sessile plants fill up reserve space in a more direct way, obtaining all resources from their locations, whereas butterflies may rely on resources occurring outside the reserves (Ouin et al., 2004). This is consistent with the effects of isolation (negative for plant richness, none for butterfly richness), and with the positive relation between endangered species and proximity of natural habitats, and negative relation between endangered species and proportion of built-up perimeter. There are minimal resources on built-up land (Blair and Launer, 1997; Hardy and Dennis, 1999) and presence of buildings interferes with dispersal (Ricketts, 2001; Ries and Debinski, 2001). Butterfly richness also increased in reserves adjoining railways, highlighting the importance of linear features with sunny, dry surfaces for butterfly dispersal (Munguira and Thomas, 1992; Saarinen et al., 2005).

4.2. Past vs. present habitats

Whereas plant and butterfly richness, and representation of endangered butterflies, reflect current habitats, the representation of endangered plants reflects habitat composition at the time of re-

serve establishment. This indicates conservatism in the distribution of endangered plants compared to non-endangered plants and butterflies. Endangered species include, almost by definition, species that are rare, specialized and poorly mobile, and hence slow in reacting to habitat change (Kotiaho et al., 2005). In addition, plants are more persistent than insects at individual sites owing to longevity, lower requirements for habitat area, durable diaspores and ability to survive for years without successful reproduction. Butterflies must reproduce every year, rely on sexual reproduction, and often require relatively large population sizes for reproduction (Thomas, 2005; Kadlec et al., 2010). They may depend on several resources scattered across relatively large areas (e.g. Brommer and Fred, 1999; Dennis, 2004). Therefore, endangered plants may persist in reserves long after conditions became unsuitable for viable populations, whereas endangered butterflies quickly disappear. In contrast, active dispersal allows butterflies to track changes more rapidly than endangered plants (Davies et al., 2005). As a result, butterflies reflect current habitats, while plants reflect past habitats. A corresponding situation was recently reported for plant richness of calcareous grasslands in Estonia, which reflects the area and connectivity of the habitat half a century ago, indicating a serious extinction debt (Helm et al., 2006; Hahs et al., 2009). This is similar for the changes in plant and butterfly ranges in Britain during the last few decades, where the former have not changed while the latter have declined (Thomas et al., 2004).

Patterns related to urbanization further support this distinction between plants and butterflies. Urbanization does not appear to suppress plant species richness, but diminishes the proportion of endangered plants and total butterfly richness. The lack of a decline in total plant richness is possibly due to ruderal species and aliens, which increase in urbanized areas, counteracting the loss of native species (Pyšek, 1998; Chocholoušková and Pyšek, 2003; Celesti-Grappow et al., 2006). In previous studies of nature reserves in the Czech Republic, density of human population was a significant predictor of plants introduced in the last 500 years (Pyšek et al., 2004; Chytrý et al., 2005), but not of all plants (Pyšek et al., 2002a,b). In the set of reserves analyzed in this study, alien species comprised 17.8% of the flora (range 4.7–32.3%), of which 6.0% (range 2.0–17.4%) are neophytes, introduced in the last few centuries. Most current invasive species (in terms of Richardson et al., 2000; Pyšek et al., 2004) recruit from this group (Lambdon et al., 2008). Therefore, although these values are much lower than those reported for complete floras of large cities in Europe and elsewhere (Pyšek, 1998; La Sorte et al., 2007, 2008; La Sorte and Pyšek, 2009; Ricotta et al., 2009), the effect of alien species on the patterns found was not negligible. This is possibly because most of the alien species are associated with disturbed habitats and benefit from human-induced disturbance. Czech butterflies in contrast, do not include any alien species, and only a few species tolerate ruderal conditions.

4.3. Effect of habitat heterogeneity

Several patterns relate to another determinant of species richness, namely, the heterogeneity of available habitat. In butterflies, area contributed to richness at large, but not at small altitudinal ranges. Taking the ranges as a surrogate for habitat heterogeneity, there seems to be a threshold area below which heterogeneity does not seem to have an effect. At large altitudinal ranges, butterfly richness responded to the heterogeneity rather than to the area, possibly because some of the largest reserves were homogenous woodlands, harboring only few butterflies. The interaction between isolation and altitude range also indicated that isolated and neighboring reserves host more endangered species if they had a heterogeneous relief. In clustered reserves, species may com-

pensate for lack of heterogeneity by migration among sites (cf. Dennis et al., 2003). All these observations suggest that relief (and associated habitat composition) can be more important for maintaining the biota of reserves than area alone. Solely relying on area and disregarding habitat quality, or a failure to conserve small but high quality sites like rocky outcrops, may be counterproductive for conserving endangered species.

In both groups, richness and proportions of endangered species peaked in reserves in which half consisted of forest. A mechanistic explanation is that such reserves harbor both woodland and non-woodland species, and additionally, edge specialists. In central Europe, a decline in traditional woodland management displaced many species to edges and mantles, rendering many of them critically endangered (plants: Strandberg et al., 2005; butterflies: Čížek and Konvička, 2005). In addition, some grassland butterflies use woody structures for shelter, mating or other activities (e.g. Dover et al., 1997). It is a consequence of geometry that the maximum representation of edges occurs at an intermediate forest cover.

The hump-shaped pattern of arable land predicted maximum richness in reserves with 5% arable land. This low proportion enriches the species lists with agricultural weeds, as well as butterflies feeding on crop plants (e.g. *Pieris whites*). Similarly, the increase in plant richness with a low proportion of built-up land indicates a contribution of ruderal plants. The proportions of arable or built-up land were always very low; further increase would likely result in species loss due to habitat attrition.

4.4. Butterfly's eye view: vegetation diversity

The representation of endangered butterflies increased in reserves containing bare bedrock and quarries. Early seral conditions, indicated by barren substrate, support several endangered butterflies in Europe (Beneš et al., 2003; Tropek et al., 2010). Examples from Prague's reserves include, e.g. *Chazara briseis* and *Hipparchia semele* (cf. WallisDeVries and Raemakers, 2001; Kadlec et al., 2010).

Butterfly richness peaked at an intermediate number of plant communities, but only when the communities consisted of a low number of plant species. When they consisted of a large number of plant species, with an increase in the number of plant communities, butterfly richness increased more rapidly. On the other hand, the representation of endangered butterflies always increased with an increase in the number of plant communities in a simple, linear way.

Butterflies naturally do not distinguish plant communities in terms of a phytosociological classification. Indeed, regressing butterfly richness against the number of plant species resulted in a linear increase (standardized values: total number of butterflies = 5.63 + 0.53 plant species; $F = 9.18$; $df = 1, 46$; $p = 0.004$). Therefore, it is tempting to ignore the interactions between plant communities and species (Fig. 4A and B) and rely on plant species alone. However, the model with both species and communities attains a better predictive power (r^2) and information value (BIC) (including: $r^2 = 0.28$, BIC = 18.46; ignoring: $r^2 = 0.15$, BIC = 23.41). The same applies for endangered butterflies ($r^2 = 0.46$ vs. 0.40, BIC = 21.67 vs. 26.86). The logical interpretation is that plant communities reflect habitat characteristics in a more complex way than mere species richness does, perhaps by reflecting the relative cover of vegetation layers, shade, or nectar availability.

4.5. Implications for reserve management

The inclusion of plants and butterflies, a herbivorous group with presumed links to vegetation, in the same study enables a more comprehensive view on how to select and manage reserves. However the limitation of this study is that it is descriptive. A large

number of variables, assumed to be relevant for species richness of butterflies and plants in a very diverse set of nature reserves, had to be selected *a priori*. Richness of butterflies was linked to a larger number of predictors than the richness of plants. Additionally, richness models gave consistently better fits for plants. Given that fewer factors are easier to manipulate, the lower number of predictors, combined with higher explanatory power, suggests that conserving plants might be easier than conserving butterflies. The pattern was, however, reversed for endangered species, where the explained variance was higher for butterflies.

These contradictions are attributable, first, to unthreatened and often highly mobile butterflies which are not confined to particular reserves. A situation within the reserves is unlikely to influence richness of these species, in a clear contrast to both endangered and common plants. Second, because butterflies respond to changing conditions more rapidly than plants, a part of the variance in the representation of endangered plants may be attributable to some aspects of a reserve's past not reflected by current conditions. Combining the two patterns, butterflies appear to instantly respond to a high number of factors, whereas plants exhibit slower responses, some already surviving in depressed and unviable populations.

A simple remedy for the adverse effect of urbanization on both plants and butterflies would be a denser network of larger reserves. This is impossible in a big city such as Prague, where practically all undeveloped habitats already enjoy protection. Thus, it is important to appreciate the positive effect of heterogeneity for the representation of endangered species, as well as for diversity at various scales (Weibull et al., 2000; Konvička et al., 2006). Heterogeneity, rather than area or isolation, can be manipulated by reserve management. It is often criticized that current management practices strive to maintain model examples of pre-selected vegetation types, suppressing edges and transient zones (e.g. Balmer and Erhardt, 2000; Hanski, 2005). In the long run, a failure to maintain heterogeneity nullifies the very purpose of conservation, i.e., to maintain high biodiversity and provide suitable conditions for endangered species. Our results document that future management must provide more heterogeneous conditions via maintenance of early successional stages (Beneš et al., 2003) and diversification of interventions via rotational grazing and patchy mowing (e.g. Saarinen and Jantunen, 2005). Further, the creation of transient zones among successional seres, including restoration of such traditional practices as woodland coppicing is needed. Outside reserves, maintenance of open vegetation along linear structures, such as railway tracks, may increase the functional connectivity of the reserve network (Kadlec et al., 2008; Dover and Settele, 2009). This is a big challenge for conservationists: rather than managing particular habitats according to pre-defined sets of rules, it requires a more adaptive and context-dependent approach to each site.

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Appendix A. Supplementary material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.10.002.

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